Peter M. Kappeler
David P. Watts *Editors*

Long-Term Field Studies of Primates

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In memoriam Toshisada Nishida (1941–2011)

Preface

This edited volume features a collection of essays discussing the virtues and challenges of conducting long-term field projects on wild primate populations in Madagascar, the Americas, Asia, and Africa. All of these projects have been ongoing for a significant portion of the respective species' life cycle; some of them already cover multiple generations. Taken together, the contributions to this volume represent all major primate radiations and therefore provide a representative sample of taxon-specific opportunities and challenges of this type of research. Still, not all important long-term studies could be included in this volume, with the absence of specific chapters on nocturnal primates perhaps the most important omission. In contrast, some taxa, such as sifakas, capuchin monkeys, and chimpanzees, are covered in more than one chapter. In each case, the comparison revealed striking differences between study sites and populations, emphasizing the perhaps not so obvious fact that single long-term studies are apparently not sufficient to document the full range of species-typical life history adaptations and variation in social systems.

Continuous observations of habituated and individually recognizable primates originated with Imanishi's project on Japanese macaques in the late 1940s. Some of the projects described in this volume originated in the 1960s. Gombe, Amboseli, Berenty, Caratinga, Koshima, and Ketambe are names familiar to all primatologists today because these projects have contributed unique insights into the natural histories and life histories of wild primates. Such long-term studies are especially necessary in primatology, because primates have slower life histories than most other terrestrial mammals. In many cases, several decades are necessary to document the timing of important life history milestones, and in most cases this is not even sufficient to garner large enough samples to analyze the adaptive basis of life history variation. Variability in key social parameters and documentation of behavioral development provide additional justification for a long-term approach. Moreover, rare but important events, such as predation, infanticide, or dispersal, also necessitate continuous observation for many years to obtain samples large enough for satisfactory empirical analyses. Finally, most long-term primate field studies today have positive effects on local conservation efforts; this alone is enough to justify their continuation in the view of many primatologists.

The authors of the chapters on specific projects covered in this volume were asked to summarize results and insights that were only possible because of the long-term nature of their studies and thereby to provide concrete examples for the scientific necessity and benefits of this kind of research. Because long-term projects of this kind also face numerous practical problems and challenges, especially with respect to data management and continuous funding, we also asked all authors to furnish summaries of the history and logistics of their projects, which we hope will be valuable for historians of our discipline and for colleagues initiating new projects, respectively. Because this volume presents the first collective summary of unique datasets from several influential long-term primate field studies along with new research results, we hope that it will interest not just primatologists, but also anthropologists interested in the value of comparative research on nonhuman primates for understanding human evolution and the behavior of modern humans and behavioral ecologists involved in long-term projects on other vertebrates. If examples included in this volume can provide arguments and examples that convince academic administrations and funding agencies of both the scientific value and the conservation importance of such field projects, it would have achieved another important purpose.

Göttingen and New Haven
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Part I
Introduction

Chapter 1
The Values and Challenges of Long-Term Field Studies

Peter M. Kappeler, Carel P. van Schaik, and David P. Watts

Abstract In this chapter, we review some of the benefits and challenges of long-term primate field studies. We define long-term studies as those that cover a significant part of the study species' life cycle; in reality, many studies have already extended over multiple generations. We first provide a brief overview of the historical beginnings of modern primate field studies, most of which lay in the 1950s and early 1960s. Next, we identify a number of biological constraints and scientific questions that necessitate and justify a long-term approach to studying wild primate populations. Most research questions in this context are related to fitness determinants and outcomes and can be broadly classified as addressing either aspects of behavior, life history and demography, or the possible interactions among them. Positive side effects of long-term field projects on the conservation of the study site or the study species have recently become additional important reasons for the continuation of these projects. Studying individually known primates over years and decades also poses some unique challenges, however, especially with respect to data management and funding. We close this chapter by summarizing some of the unique insights about primate social systems and life history only made possible by the long-term nature of the studies, focusing on the chapters making up the remainder of this volume.

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1.1 Introduction

No matter whether you travel to the swamp forests of Indonesia or the bizarre spiny forests of Madagascar, whether you visit an East African savanna or a remote rainforest on a small tributary of the Amazon, you may run into a primatologist studying one of the local primate species in their remaining natural habitats. In all likelihood, you will find this fictive colleague of ours to be part of a team composed of local and foreign researchers, field assistants, and students working out of some more or less primitive research camp or field station. Moreover, the project is likely to have a history of several years or even decades. You may ask yourself why anybody would want to travel to the end of the world, leaving all the amenities of modern civilization behind for months or even years, only to follow a group of primates from dusk to dawn in habitats full of parasites, predators, or even rebels. In this chapter, we summarize some of the scientific reasons that motivate an increasing number of primatologists to initiate or contribute to field studies that extend well over the duration of an average PhD project, i.e., the values of long-term field studies.

Primatologists were not the first to study individually known vertebrates over significant parts of their life cycles or even over several generations (see Clutton-Brock 2012), but we focus here on those projects that have aimed at unraveling the natural and life histories of our closest biological relatives. As always, it is useful to begin with a short historical review to put current activities in perspective. We will then discuss theoretical reasons requiring or justifying a long-term approach to studying primate behavior and ecology, and we touch upon some problems and challenges unique to this type of research. We close by highlighting some insights that could only be obtained from long-term research.

1.2 A Brief History of Early Primate Field Studies

The study of the behavior of animals in their natural habitat had to wait a long time to acquire some scientific respectability. During most of the nineteenth century, fieldwork consisted of collecting for taxonomic study or comparative anatomy, and no serious biologist came up with the idea to study the behavior of wild primates. The main reason was that science was something one did in the lab, not in the field: observing spontaneously behaving animals outside strictly controlled laboratory conditions was considered utterly unscientific (e.g., Skinner 1938). The success of Darwin's natural-history-based theory of evolution did little to change this. Even psychology, the study of behavioral mechanisms, largely developed as a laboratory-based science, mainly because of the rigorous control this allowed.

Only in the early twentieth century did a few eccentric Central European and British naturalists take to the field and begin to study bird behavior, thus paving the way for the ethologists, led by Konrad Lorenz and Niko Tinbergen, who built the scientific study of behavior from the ground up during the 1930s, using a mix of observations (often from blinds) and field experimentation. More or less simultaneously, and independently, in the USA, Robert Yerkes (1876–1956) at Yale University motivated some of his students to conduct the first field studies of wild primate populations. Among them, Henry Nissen conducted the first systematic study of feeding and social behavior of wild chimpanzees (*Pan troglodytes*) over 9 weeks in French Guinea (Nissen 1931). Clarence Ray Carpenter clearly stands out in retrospect for his pioneering field studies of mantled howler monkeys (*Alouatta palliata*; Carpenter 1934), white-handed gibbons (*Hylobates lar;* Carpenter 1940), and rhesus monkeys (*Macaca mulatta;* Carpenter 1942).

The history and tradition of modern field studies was established on December 3, 1948, when Kinji Imanishi, a most remarkable person and influential scientist (Matsuzawa and McGrew 2008), and two of his students (Jun'ichiro Itani and Shunzo Kawamura) went to Koshima Island to study wild Japanese macaques (*Macaca fuscata*). They established a new style of studying wild primates based on habituation (facilitated by provisioning), individual identification, and long-term observations that still provides the methodological standard for most primatological fieldwork. In the following 7 years, Imanishi and his students exported this new and successful method to 19 other populations of Japanese macaques, most of which are still being studied today. In 1958, Imanishi and Itani also embarked on an expedition to Central Africa, paving the ground for Japanese-led field studies of chimpanzees at Mahale in 1965 (Nishida 1968; Nakamura and Nishida 2012) and bonobos (*Pan paniscus*) in the Congo basin (Furuichi et al. 2012).

During the 1950s, several more primate field studies were initiated, some of which continue until today. North American primatologists whose backgrounds were in anthropology (notably Sherwood Washburn) were particularly active in this respect, but zoological and ethological influences were also important there and in Europe. Irven DeVore, one of Washburn's students, began studying savanna baboons (*Papio cynocephalus*) in Amboseli and other East African sites in the late 1950s (Washburn and DeVore 1961). At about the same time, Phyllis Jay, another Washburn student, initiated a study of Hanuman langurs (*Semnopithecus entellus*) in India (Jay 1962), and Charles Southwick started research on wild rhesus monkeys (*Macaca mulatta*) at another Indian site (Southwick and Siddiqi 1965). George Schaller (1963) conducted the first detailed field study of mountain gorillas in 1959–1960; this research provided the basis for his PhD in Zoology at the University of Wisconsin. European primatologists went to the field in the late 1950s to study hamadryas baboons in Ethiopia (*Papio hamadryas*: Kummer and Kurt 1963), chimpanzees in the Congo (Kortlandt 1962), and lemurs in Madagascar (Petter 1962) in their natural habitats. By 1960, technological advances had made tropical field sites both more accessible and medically safer for researchers from temperate zone countries. Jane Goodall began her field study of chimpanzees at what was then Gombe Stream Game Reserve in 1960 (Goodall 1963). In 1962, Vernon and Frances Reynolds spent 9 months studying chimpanzees in Budongo Forest, Uganda (Reynolds and Reynolds 1965); Vernon Reynolds resumed this project in 1990 (Reynolds 2005), and it continues until today.

The field projects initiated in the 1950s employed more systematic methodologies than earlier studies. Also, they usually studied relatively small social groups to facilitate identification of individuals, something considered necessary for proper understanding of social dynamics. Stuart Altmann (1962) pioneered systematic study of larger groups in his research on rhesus macaques on Cayo Santiago in the early 1960s; individual recognition was possible because each monkey was distinctively marked. By now, researchers standing on the shoulders of these early pioneers have studied at least one representative of virtually every primate genus in the wild.

In sum, the current tradition of long-term field studies of known and well-habituated individuals, with its focus on observation more than on experiment, arose from the combination of the Japanese zoologists' emphasis on individual recognition and the anthropologist's penchant for patient long-term observation. Next, we turn to the reasons that motivated these early studies and contrast them with current ones.

1.3 Why Long-Term Field Studies of Primates Are Needed

The early field studies of primates were primarily motivated by the insight that comparative studies of primate behavior can inform the study of human evolution (Washburn 1951; Hooton 1954; Crook and Gartlan 1966). Later, developing interest in the social lives and ecological adaptations of wild primates *per se* contributed to the characterization of broad patterns of adaptive variation (Eisenberg et al. 1972; Clutton-Brock and Harvey 1977). For both of these purposes, it was generally assumed that a field study lasting a few months would be sufficient to identify all species-typical behaviors (Strum and Fedigan 2000). Accordingly, none of these early studies were designed as long-term projects; in fact, most were just long enough to allow data collection for a PhD project. The fact that today, we have dozens of field projects that have been ongoing for a decade or more is motivated by several specific scientific reasons as well as by conservation concerns that have only explicitly emerged since the early 1980s.

The scientific need and justification for long-term field studies can be separated into aspects related to the study of social behavior and life history, respectively. The fact that primates live longer than other mammals of similar body size (Allman et al. 1993) provides a practical justification for research in both of these domains. Whereas mouse lemurs (*Microcebus* spp.) and other small-bodied strepsirrhines may typically live only a year or two, their average longevity exceeds that of other similarly sized small mammals (Austad and Fischer 1992), and some individuals survive until age 10 (Kappeler et al. unpublished data). Other larger primates that are still small in absolute terms, such as Verreaux's sifakas (*Propithecus verreauxi*), can live up to 30 years in the wild (Richard et al. 2002). Orangutans (*Pongo* spp.) and other great apes are so long-lived that their average life expectancy exceeds the duration of most academic careers (Wich et al. 2004). Additionally, long-term data on life history variation that is independent of body size can provide important insights into adaptive strategies, as Cords (2012) nicely illustrates with her comparative analysis of guenon life histories.

We must emphasize that the adaptive significance of social behavior and life history cannot be assessed with captive populations. The only way to identify the selective agents maintaining particular traits is to study primates in their natural habitats. Moreover, captivity also can induce changes in many aspects of life histories. Primates mature more rapidly and grow larger in captivity because of the abundance of food, absence of predators, and protection from immunological and other stressors (Austad and Fischer 1992; Smith and Jungers 1997; see also Künzel et al. 2003), and may also get older in captivity for these reasons (e.g., Picq 1992). Thus, field data are necessary to obtain more realistic measures of the behavioral tactics and the timing of life history events as they occur in the ecological context under which they evolved.

1.3.1 Long-Term Studies and Behavior

Long lives generate many interesting questions about primate social behavior, several of which we briefly consider below. Most of these have general importance because they are directly linked to fitness determinants (Clutton-Brock and Sheldon 2010a), and they relate both to phenomena that play out over long periods and to events that are rare but important.

Individual behavioral development provides obvious examples in the first category. Infancy and juvenility, where much social and individual learning takes place (Rapaport and Brown 2008; see also Thornton and Clutton-Brock 2011), extends over several years in most primate species (Jaeggi et al. 2010). Perhaps unsurprisingly, only a few studies of behavioral ontogeny have been conducted on wild primates (e.g., Pereira 1988; Altmann 1998; Watts and Pusey 1993; van Noordwijk and van Schaik 2005). Study of development is all the more important because events early in life can have lasting consequences (Clutton-Brock and Sheldon 2010a) that can only be understood if we have the full behavioral histories of individuals. Similarly, many behavioral patterns and individual tactics, such as coalition formation or rank challenges, can only be interpreted in the context of known social group histories. More interestingly, some of these consequences may only become apparent in older individuals (Suomi 1997) and can only be tracked in long-term studies.

Second, short-term studies often yield significant correlations between variables relevant to fitness but leave open the question of whether these actually consistently lead to differences in lifetime fitness. A classic example concerns dominance in those species in which females and/or males typically form dominance hierarchies. Rank is generally positively correlated with instantaneous measures of reproductive success in many taxa, including many primates. However, we need to know how well instantaneous measures predict lifetime reproductive success. Also, some influences on reproductive success are characterized by time lags. In Assamese macaques (*M. assamensis*), for example, male coalitions affect reproductive success only years later (Schülke et al. 2010). Indeed, identifying the determinants of lifetime reproductive success requires that we record the changes in social position and social strategies (the career trajectory; van Noordwijk and van Schaik 2001) of both males and females over their lifetimes (Alberts 2012; Pusey 2012). This is a prerequisite for illuminating the adaptive function of different social strategies. Long-term data on dispersal, mating behavior, paternity success, and morphology of a remarkably large sample of male sifakas at Beza Mahafaly (Sussman et al. 2012) are noteworthy in this regard. For example, they show that while annual fertility rates have the strongest influence on male lifetime reproductive success, lifespan also has an important effect, something that is probably true for many primates. Thus, the questions about possible trade-offs between instantaneous and lifetime reproductive success and the resulting optimum career profile can only be addressed by long-term studies.

Third, many primate species show remarkable behavioral variation, all the way down to the group level, where local traditions and conventions form and new behavior patterns spread within and between groups (Whiten and van Schaik 2007; Nakamura and Nishida 2012). Most of the work on such variation has consisted of cross-sectional mappings of its occurrence (e.g. Whiten et al. 1999), but better insight into its origins and possible adaptive value requires detailed research on transmission and possible fitness payoffs. Japanese macaques have provided several well-studied examples of the origin and spread of novel behaviors over the decades (Kawai 1963; Leca et al. 2010). Long-term studies of white-faced capuchins (*Cebus capucinus*) have also provided remarkable examples of the temporal dynamics of the origin, spread, and extinction of novel behaviors within a population (Perry et al. 2012). These comparative data can inform the study of similar processes during human evolution.

Fourth, long-term studies provide unique opportunities to study systematic interactions between primates and their habitats. Changes in demography and habitat may provide elegant, semi-experimental tests of socio-ecological models. For instance, resource access and defendability play central roles in theoretical models of socio-ecology. Territoriality is one expected outcome when resources are potentially defendable against neighboring social units, but not all primates defend territories. Variation in whether they do along with variation in territory or home-range size and location in response to long-term demographic and ecological variation (e.g., Jolly 2012; Yamagiwa et al. 2012) can therefore provide valuable data for tests of socio-ecological predictions. In addition, only long-term data provide the information needed to understand the interactions among neighboring groups or communities (Wilson 2012; Watts 2012). Feeding ecology and socio-ecology should also respond to changes in population density, but little is known of such effects. For instance, the density of mountain gorillas at Karisoke has more than doubled over the past 30 years, and investigating the consequences is bound to improve our understanding of gorilla socio-ecology (Grüter and Robbins in preparation).

Fifth, primates are renowned for their social complexity. Kinship, permanent association of males and females from overlapping generations, and sex-specific reproductive strategies generate complex social networks in different behavioral domains (Sueur et al. 2011). One main goal of socio-ecology is to identify the patterns and dynamics of these networks and the proximate behavioral mechanisms mediating them. Achieving this goal requires long-term monitoring of dyadic relationships, ideally in multiple groups. A distinct major goal of socio-ecology is the identification of the fitness consequences of different social tactics. Because the fitness of long-lived vertebrates is best estimated by estimating lifetime reproductive success, and because social relationships can affect longevity (Silk et al. 2010), achieving this goal requires documentation of individual life histories and complete reproductive careers.

Finally, the fitness of individual primates can be severely affected by rare but important events. Formal assessment of the relative importance of such events requires long-term study of multiple individuals or groups to yield large enough sample sizes. Predation and some forms of conspecific aggression, notably infanticide, compromise individual survival, which is one determinant of fitness. We have compelling reasons to think that behavioral adaptations to mitigate the potential consequences of these attacks exist, but data with which to test functional hypotheses necessarily accumulate slowly (Janson et al. 2012). Moreover, population differences in predation rates may elicit differences in life-history traits, social organization, and mating tactics, as indicated by a comparison between different sifaka populations (Kappeler and Fichtel 2012). Another compelling example comes from research on chimpanzees in the Taï Forest, Côte d'Ivoire, where lethal intergroup aggression was first seen only after 23 years of study (Boesch et al. 2008). Lethal aggression is more common in other chimpanzee populations (Mitani et al. 2010), and its documentation at Taï helps to generate a more nuanced discussion of its functions and especially of how variation in ecology and associated variation in social strategies should lead to variation in its frequency (Boesch et al. 2008).

Long-lived species may also face rare ecological crises, for example prolonged drought or cyclones, that provide opportunities to study the effects of these events on individual behavior and the limits on behavioral flexibility under natural condition (e.g., Sussman et al. 2012). Habitats may change over time too, both due to climate change and to successional processes. Long-term primate field studies have often kept detailed and systematic long-term records of habitat composition and productivity and on climate that are invaluable for addressing questions about behavioral and demographic variation (e.g., Wright et al. 2012). For example, Bronikowski and Altmann (1996) used 10 years of data on behavior, ecology, rainfall, and temperature to document plasticity in the foraging behavior of Amboseli baboons and to show that responses to environmental variation differed among social groups in ways that led to differences in predation risk. Such differences among groups in single populations are probably widespread among primates (*ibid.*), but confirming their existence depends on comparably extensive data sets.

1.3.2 Long-Term Studies and Life Histories

Time is the crucial variable in studying primate life histories. Understanding species-typical life histories is important because they express the evolutionary integration of adaptations involving the resolution of trade-offs for particular combinations of social, ecological, and demographic variables (Stearns 2000). Life histories therefore provide particularly deep insights into evolutionary processes and mechanisms (Clutton-Brock and Sheldon 2010a). Below, we discuss some concrete examples.

First, the description of key life-history parameters provides the basis for the comparative analysis of life-history strategies and vital population statistics (Alberts and Altmann 2003). The collection of reliable data on these variables is time-consuming. Following individuals of known ages until the age of first reproduction, for example, may require up to 15 years (Wich et al. 2004). Subsequent interbirth intervals may also play out over several years. Moreover, for animals with such long lifetimes, even 30 or 40 years might be insufficient to document maximal lifespan with a sample large enough to allow the calculation of reliable descriptive statistics. Enough long-term demographic data now exist for a few species to allow investigation of senescence in the wild (Bronikowski et al. 2002, 2011), but serious research on this topic is just beginning.

Second, life-history schedules can be adapted to extreme climatic fluctuations or catastrophes, such as cyclones, droughts, El Nino effects, or, more recently, global warming (e.g., Pavelka et al. 2007; Wright 2007; Dunham et al. 2010; Sussman et al. 2012; Wright et al. 2012). If solid baseline data exist, such natural experiments can contribute to better understanding of causal relationships in life-history evolution, the identification of trade-offs, and the limits of phenotypic plasticity. Because most of the independent variables in the natural experiments are rare and unpredictable, long-term monitoring is essential.

Third, because of the effects of individual life histories on demography, local population densities fluctuate over the years. Population density can influence the behavior of individuals, such as their dispersal strategies, but also group-level phenomena, such as territoriality, and a long-term approach allows studies of behavioral plasticity in response to changes in population density (Strier and Mendes 2012). Monitoring population size over years also constitutes a crucial prerequisite for conservation planning and action. The remarkable stability of many primate populations, relative to those of the other taxa, may reflect the slowness of primate life histories because of its buffering effects on fluctuations in survival rates (Morris et al. 2011).

Fourth, the size and composition of individual social units can fluctuate, especially in group-living species. In some species, groups have short life cycles tied directly to changes in male membership (Steenbeek et al. 2000; Koenig et al. 2012). Similarly, pair-living species may exhibit long-term fluctuations in the number of adult males and females (Reichard et al. 2012). Identifying how new groups form, whether maturing males are tolerated in their natal groups, and whether males immigrate or instead take over groups is vital for full understanding of socioecology. These factors depend on individual dispersal decisions, which are often sex-, context-, and condition-dependent (e.g., Janson et al. 2012). Infrequent events such as dispersals are easy to miss, especially if multiple social units are being studied, and demographic data may become biased if dispersal cannot be distinguished from mortality, leading to spurious conclusions. Again, years of observation of known individuals are required to identify rules and regularities in the sum of independent dispersal events and maturation schedules. Fedigan and Jack (2012) provide an excellent example. In their chapter, they note that they needed many years of data to determine mean age at natal dispersal for male white-faced capuchins and to confirm that males disperse throughout their lives and that females are not exclusively philopatric. Thus, long-term studies of demography and population dynamics can provide crucial context to interpret the social structure and organization of a species.

Fifth, slow life histories also generate constraints that necessitate a long-term approach. Genetic analyses, in particular, depend on access to suitable sample sizes. Given enough patience and luck, such analyses have enabled studies of fundamental topics in behavioral ecology, such as kin-based altruism, reproductive skew, and inbreeding avoidance (see e.g., Alberts and Altmann 2012).

1.4 Possible Drawbacks of Long-Term Studies

A long-term field study in practice always requires that the subjects are fully habituated. While this has made it possible to collect the important information specified above, this standard technique of primate fieldwork has possible drawbacks.

One is that we could impair the health of our subjects. The habituation process is likely to be stressful to the animals because wild animals almost universally see humans as predators. Indeed, some recent results indicate that unhabituated orangutans show a stress response during the habituation process, but this ends once they are habituated (Williamson and Feistner 2011; see also Marty et al. unpublished data). More insidiously, nonhuman primates and humans are vulnerable to many of the same diseases, and researchers and local field assistants can unwittingly infect their study subjects. This likelihood is especially high for species phylogenetically close to humans, notably the great apes, and evidence exists for transmission of serious diseases to great apes via close contact with humans (Köndgen et al. 2008). Fortunately, careful precautions, such as inoculations and wearing facemasks, can prevent transmission, and the protection that long-term research presence affords against other threats can outweigh the risk of disease transmission.

Another unintended consequence is more subtle. The presence of humans tends to discourage the activity of some classes of predators, in particular felids. Likewise, habituated groups meeting unhabituated ones tend to gain access to potentially contested resources in overlap areas. Both effects of habituation may lead to an increase of the size of the habituated group or community. Habituating neighboring groups solves the second problem, but there is no easy solution to the first.

1.5 Unique Problems and Future Challenges to Long-Term Studies

Studying wild primates continuously for several years or decades poses some other problems that apply less forcibly, if at all, to shorter studies or surveys. First, long-term research requires reliable individual identification. In some species, this is facilitated by variation in visual traits on which human observers can focus; sexual dimorphism, sexual dichromatism, variable sexual swellings, scars of healed wounds, and age-related changes in phenotypic traits can also be useful. In some species, capture and individual marking is possible (e.g., Wright et al. 2012; Kappeler and Fichtel 2012).

Second, long-term studies face several unique logistical challenges. If animals are not individually marked, individual recognition needs to be assured across generations of students and field assistants, and interobserver reliability requires particular attention to achieve uniform methodology across seasons and years (see e.g., Perry et al. 2012). One way to guarantee long-term accuracy of recognition is to reanalyze genetic samples of individuals, especially if individuals undergo dramatic changes in appearance. Among orangutans, for instance, it may be difficult to recognize individually known unflanged males once they have become flanged. Genetic analysis confirmed that one particular male had remained unflanged for two decades (Utami et al. 2002); this observation would have been doubted in the absence of genetic analysis. Most contributors to this volume discuss the practical aspects of providing suitable working, living, and laboratory facilities required for successful field research over months or years at a time. The chapters by Koenig et al. (2012) and by Perry et al. (2012) also provide particularly useful information about logistical and methodological prerequisites and standards for setting up and operating long-term primate field projects, as does a comprehensive guide edited by Setchell and Curtis (2011).

Third, behavioral and demographic data accumulate quickly, and specific strategies and policies for data management and storage are required. The data problem should not be underestimated because resources to create these databases and to enter and edit the accumulating data are rarely available, but the productivity of many projects, measured as papers produced per year, is a positive function of project duration (Clutton-Brock and Sheldon 2010a). This economy of scale can justify the needed investment in such large, long-term endeavors.

Finally, and perhaps most seriously, long-term studies extend past the typical grant duration of most funding agencies, which creates several problems. First, all the good scientific reasons for studying wild primates listed above cannot generate tangible results with a typical funding period of 3 or so years, and grant proposals are necessarily handicapped because they cannot promise results on the underlying big questions in behavioral ecology. Second, if the chain of grants on which the infrastructure of the project depends is interrupted only once, the project is fundamentally jeopardized (see Koenig et al. 2012 for a sad example). Thus, an increasing awareness of the benefits and risks of long-term field projects is required to eventually also change the available funding mechanisms (Clutton-Brock and Sheldon 2010b). Third, it is difficult to find grant support for data management and analysis, an essential but less popular part of the fieldwork production cycle. Only long-term institutional support and commitment may provide a viable solution to all these problems in the long run (see e.g., Kappeler and Fichtel 2012).

1.6 Unintended Benefits from Long-Term Studies

Apart from the numerous scientific virtues discussed above, the main unexpected benefit of long-term study sites concerns their positive impact on conservation. In most regions where wild primates live, protected areas are not necessarily safe from exploitation or conversion. Recent work has quantified what many fieldworkers have maintained for decades, namely that areas with ongoing long-term field projects suffer less habitat disturbance than other protected areas and have higher wildlife densities (Wrangham and Ross 2008; Campbell et al. 2011). This is because resident researchers report transgressions to the authorities and they employ local people who would lose their livelihoods if the projects were to fold due to loss of habitat or animals; it is also because risk of discovery can discourage transgressors from entering areas where the probability of direct encounters with researchers or local assistants is high.

Other positive impacts are economic. Long-term projects tend to become major employers in the surrounding areas because by their very nature, they are usually located in regions with virtually no opportunities for employment or cash incomes outside of limited cash cropping or dangerous (and often illegal) extractive activities, such as logging or collection of non-timber forest products. In several cases, the name recognition created by media coverage of the research has led to increased ecotourism at the same sites or in nearby areas that, despite its attendant problems, has increased local employment and lifted those lucky enough to be steadily employed out of poverty (see e.g., Jolly 2012). In addition, several field assistants have gone on to become local politicians or government officials based on the insights gained from contact with outsiders and the educational opportunities brought by employment in long-term projects.

Finally, another impact of long-term field studies is that many students, especially but not exclusively from the host countries, get involved. In some countries, such opportunities would hardly be available without the foreign-funded projects. The impact of such training opportunities is difficult to measure but almost certainly highly positive. Unlike many collecting or recording studies, primate fieldwork involves long-term stays at a single site. Long-term exposure to a particular area tends to produce intensive familiarity and therefore love and respect for the area and its biota; it also allows participants to witness the changes in and around the area and thus to appreciate conservation problems much better. Long-term residence at a field site also inevitably leads to intense contact with local people, far more than any traveler could experience. This engenders realistic appreciation of local attitudes toward conservation and of the problems (usually related to economic security and access to information) that can impede conservation even when attitudes are positive in principle. Not surprisingly, many of the most determined and effective tropical conservationists, whether from host countries or western countries, received their initial training by participating in long-term primate field studies.

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Part II
Madagascar

Chapter 2
Berenty Reserve, Madagascar: A Long Time in a Small Space

Alison Jolly

Abstract Berenty Reserve is a privately owned reserve established in 1936. At 200 ha, it holds the largest remaining gallery forest on the Mandrare River. Scientists of many nationalities have studied there: research follows their diverse interests rather than being coordinated overall. One finding which emerged from long-term monitoring concerns the importance of both within- and between-troop competition for female *Lemur catta* and their inheritance of territory in the female line, at least in this islanded population. This may play a role in the maintenance of female dominance over males. Another aspect of long-term study is the changes brought by introduced species, including *Leucaena leucocephala*, a favored, but toxic, forage tree. The growth of leucaena stands paralleled population growth of the *L. catta* troops with access to these stands, although highly affected females lost fur and had low infant survival; eradication produced a local population crash. Introduced *Eulemur rufus x collaris* have grown from about 16 individuals in 1975–1980 to almost 600 in 2009. They are taking over the central gallery forest. *L. catta* troops maintain their original sleeping areas in the gallery forest but increasingly forage on the periphery, recreating the niche separation described for *Lemur* and *Eulemur* in natural sympatry. Overall, Berenty Reserve is drying out, with closed-canopy gallery forest giving way to more open scrub. Research on Berenty's lemurs is thus the study of evolved adaptations confronted with a changing environment.

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2.1 Introduction

Berenty Estate was founded in 1936 by the de Heaulme family in consultation with local Tandroy clans. It lies beside the Mandrare River in southern Madagascar at about S 25°00′E 46°18′. The estate comprises 6,000 ha: sisal fields, pasture, a tourist complex, and 1,000 ha of forest established as nature reserves long before conservation became fashionable, just because the forest was too beautiful to cut down. The largest reserve parcel, often just called Berenty Reserve, is 200 ha. It is continuous with about 400 further hectares of gallery and spiny forest. Berenty Reserve and the 100 ha Bealoka Reserve, which is also on Berenty Estate, are the two largest of only four remaining blocks of gallery forest on the Mandrare river below the steep tributaries of the headwaters. This is one of the most threatened forest types of Madagascar.

Lemur research at Berenty began with my arrival in 1963. Since then the de Heaulmes have welcomed scientists of all nationalities. There have been long gaps between studies, and many different projects and teams. Research follows individual interests and possibilities rather than being coordinated overall. This article focuses on two aspects of long-term interest: *Lemur catta* social behavior and the influence of introduced species on *L. catta* behavior and ecology. It also provides a bibliography to follow up other aspects of research at Berenty.

Much of what is ecologically interesting about Berenty relates to the fact that it is so small. This forest fragment serves as a scale model of large wilderness reserves. Of the various threats to a small reserve, much of the early theoretical literature focused on inbreeding depression, or on variation in reproductive success either stochastically or due to fluctuating weather, or else on edge effects (Soulé and Wilcox 1980; Frankel and Soulé 1981). At Berenty it has been the accidental or deliberate introduction of exotic species that has most profoundly changed the ecology of this limited space. Especially important have been brown lemurs, *Eulemur rufus x collaris*, and the nutritious but toxic tree *Leucaena leucocephala*. Lemur research at Berenty thus involves the study both of long-evolved species norms of behavior, and of how these adapt in the face of environmental challenges new to these species' history.

The wider importance of Berenty will be scarcely considered here. Berenty Estate is a kaleidoscope of human cultures. Local Tandroy people, traditional warrior-pastoralists, are now agriculturalists who submit to rules on forest use in return for employment that buffers them against the region's recurrent famines. Tourists (*Homo sapiens garbagedispersiensis*) provide income which ensures the reserve's support and survival. Most of the tourist personnel are multilingual Tanosy people from neighboring Fort Dauphin. The scientists themselves function like a clan or tribe: distinct from but dependent on the others. Berenty is the most televised spot in Madagascar. Nearly every foreign film features its parading ringtails and dancing Verreaux's sifaka. This may in fact be its most important contribution, as a show window for Madagascar. In 1992–1994, Helen Crowley became the first manager of the forest reserves, funded by the Wildlife Trust and by the de Heaulmes. Subsequent managers were Hajarimanitra Rambeloarivony and Sahoby Marin Raharison. The forest is now managed by Claire de Heaulme Foulon and her husband Didier Foulon (Jolly 2004, 2010).

2.2 Habitat Zones and Fauna

For a general description of Berenty Reserve see Jolly et al. (2006a Fig. 2.1). There is also a fundamental study by Sheila O'Connor and Mark Pigeon comparing Berenty and the 100 ha Bealoka Reserve. Bealoka was still grazed by goats and zebu until 1985, which gave it a much more open understory. Its one ringtail troop used the whole of the 100 ha forest, moving round from season to season with no identifiable core area – most unlike the defended, stable territories of Berenty. O'Connor went on to a career with WWF rather than publishing research, but her thesis remains a baseline for many Berenty ecological studies (O'Connor 1987).

The natural habitat zones of Berenty grade from rich alluvial Gallery forest through transitional Scrub to Spiny forest (Figs. 2.2 and 2.3). The Front zone has many introduced trees which supplement natural lemur diet (Fig. 2.4). These four zones form the 100-ha study area are called Malaza. The Ankoba zone is 70-year-old secondary forest, combining natural and introduced trees for the highest lemur population densities. There is a fivefold difference in ringtailed lemur density from about 500/km^2 in Front and Ankoba to about 100/km^2 in the Spiny zone (Jolly 1966a; Budnitz and Dainis 1975; Budnitz 1978; Mertl-Millhollen et al. 1979; Blumenfeld-Jones et al. 2006; Jolly et al. 2006a; Razafindramanana et al. 2008).

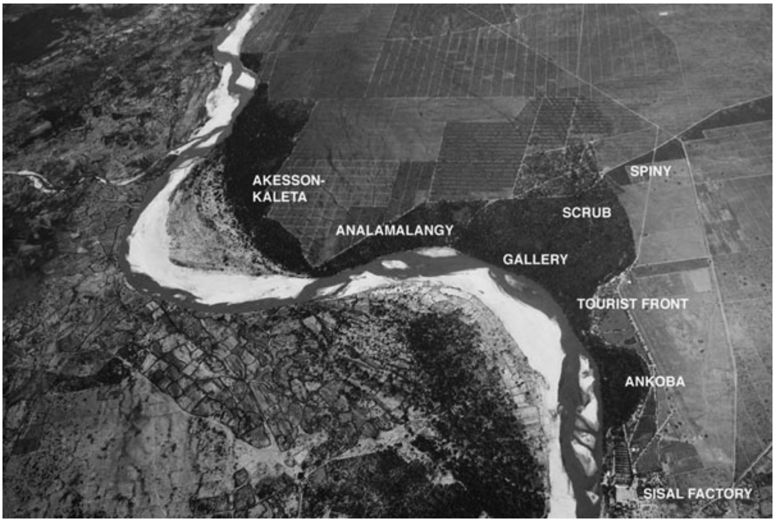

Fig. 2.1 Air photo of Berenty Reserve from the north, with habitat zones. Courtesy Barry Ferguson and the Libanona Ecoly Centre. From Jolly et al. (2006a)

Fig. 2.2 Gallery forest. Giant tamarind trees traditionally provide half the ringtails' feeding time, as well as highways and sleeping sites, though they are now largely occupied by brown lemurs. Photo © Cyril Ruoso

Fig. 2.3 Spiny forest. Verreaux's sifaka and ringtails can live without free water, gaining their food from leaves and stems. Photo © Cyril Ruoso

Southern Madagascar's climate alternates hot wet summers, with temperatures at or above 40°C at mid-day, and cold dry winters, when temperatures fall below 10°C at night. Rainfall varies erratically from 300 to 900 cm if calculated in years beginning Oct 1, which group all of the summer wet season together (Fig. 2.5). Even this masks some of the variation, as in 1991–1992, when two-thirds of the season's rain fell during a 3-day storm in January. El Niño years usually mean drought for the south of Madagascar as for southern Africa, but some El Niño years are exceptionally wet. In 1997 a violent windstorm damaged many canopy trees. Lemurs and other species are adapted to survive recurrent catastrophic years

Fig. 2.4 Front zone. Berenty's non-human primates are used to ignoring tourists. Photo © A. Jolly

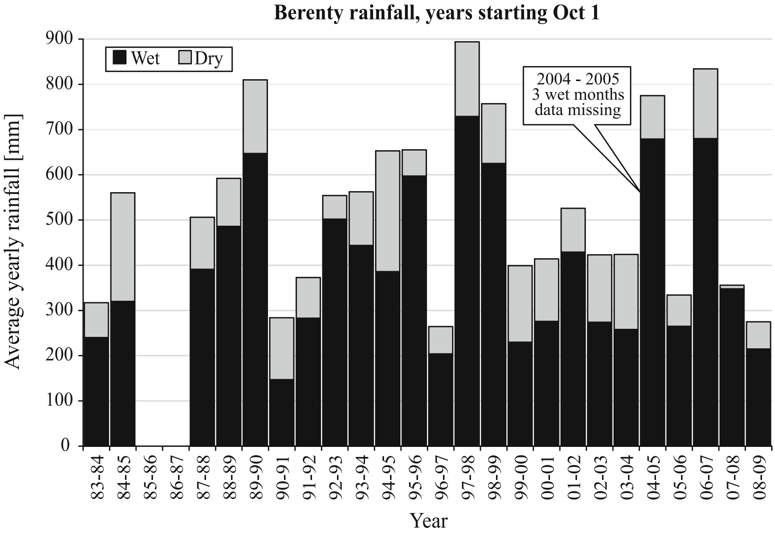

Fig. 2.5 Yearly rainfall at Berenty, which can vary threefold between years. Years begin Oct. 1, which keeps the rainy season as one block (data thanks to K. Blumenfeld-Jones, S. O'Connor, C. and A. Rakotomalala)

(Gould et al. 1999; Wright 1999; Rasamimanana et al. 2000; Richard et al. 2002; Jolly et al. 2006b).

Ringtailed lemurs (*L. catta*) numbered about 450 animals in the Malaza-Ankoba zones in 2009. The ecology of the different zones varies dramatically, with almost no overlap between plant species eaten by any lemurs in the Gallery and Spiny zones. Ringtailed lemurs rely more on leaves in the natural habitats than in the Front and Ankoba zones, since a higher proportion of fruit is available in the modified zones. Niche separation between ringtails and Verreaux's sifaka (*Propithecus verreauxi*) is clear, with the sifaka eating more leaves and flowers, and better able to detoxify secondary compounds, though the ringtails also have high tannin tolerance. Ringtails eat little prey: seasonal locusts, acacia army caterpillars, and the occasional chameleon. (Niche separation between ringtails and brown lemurs will be considered below, with the influence of introduced species; Rasamimanana and Rafidinarivo 1993; Pitts 1995; Oda 1996b; Rasamimanana 1999; Simmen et al. 1999, 2003a, b, 2005, 2006a, b, 2010; Rasamimanana et al. 2000, 2006; Rasamimanana and Anjaranantenaina 2008).

Berenty's five other lemur species each have populations of several hundred animals. Most research on Verreaux's sifaka has been done by Alison Richard and her colleagues at Beza Mahafaly (Sussman et al. 2011) further enlarged by the Kappeler team at Kirindy (Kappeler and Fichtel 2011). Sifaka research at Berenty has recently been revived by Norscia, Palagi, Simmen, Rasamimanana, and Fichtel with their colleagues and students. A strong male bias appeared in the 2006 Norscia–Palagi census: 62% of 206 animals counted were male. As Richard originally suggested, the varying sifaka sex ratios seen at Berenty may reflect greater stress on sifaka females during hard years. However, different methods so far give very different total numbers, from 206 in Malaza and Ankoba to Rasamimanana's census of 230 in Malaza alone (Richard 1978; Oda 1998; Charrier et al. 2007; Fichtel 2008; Norscia and Palagi 2008; Palagi et al. 2008; Norscia et al. 2009; Fichtel and Kappeler 2011; Rasamimanana personal communication).

Lepilemurs (*Lepilemur leucopus*) and mouse lemurs (*Microcebus murinus*, *Microcebus griseorufus*) have not been fully censused. It remains a puzzle how small-bodied lepilemurs survive the cold nights of winter on a diet of mature leaves (Charles-Dominique and Hladik 1971; Russell 1977). Grey mouse lemurs eat fruit and insects. Grey-and-red mouse lemurs (only recently identified as a separate species: Rasoloarison et al. 2000) are largely gummivorous during the dry season food shortages, with a complex pattern of sleeping associations (Génin 2001, 2007, 2008, 2010, in press; Génin et al. 2010). Hybrid brown lemurs (*Eulemur rufus x E. collaris*) were introduced in 1975, and will be discussed under the changing influence of exotic species (Sect. 2.4).

Berenty holds southern Madagascar's largest colony of the Madagascar giant fruit bat (*Pteropus rufus*). This colony seems to be diminishing from several thousand in 2000 to 927 in a census of 2006 to only 100 in a 2009 census. However, there are wide seasonal variations in numbers (Long 2002; Razafindramanana personal communication). Other mammals include Commerson's leaf-nosed bat *Hipposideros commersoni*, the rufus trident bat *Triaenops rufus*, *Miniopterus majori*, *Miniopterus manavi*, and the Malagasy mouse-eared bat *Myotis goudoti* (Fish 2010), as well as the spiny tenrec *Setifer setosus*, the large tenrec *Tenrec ecaudatus*, and the shrew-like tenrec *Microgale* spp., and the Madagascar tree-rat *Eliurus myoxinus*. There is an all-too flourishing population of *Rattus rattus*, the scourge of Malagasy small mammals (Crowley 1995; Goodman 1995). The forest is too small to hold *Cryptoprocta ferox*, the fossa, and there are no reports of the feral species of wildcat, but domestic dogs and cats, and possibly the Indian civet (*Viverricula indica*) take their place as potential lemur predators.

Fifty-two species of resident birds have been recorded out of a total of 99 species seen, of which 41% are endemic to Madagascar (Goodman et al. 1997). The genetics of the two male color morphs of the Madagascar paradise flycatcher (*Terpsiphone mutata*) have been studied in the Bealoka parcel of gallery forest (Mulder et al. 2002). Crested coua (*Coua cristata*) calls, especially alarm calls, are remarkably similar to ringtail vocalizations (McGeorge 1978a, b). Lemur predators include the harrier hawk (*Polyboroides radiatus*), the Madagascar buzzard (*Buteo madagascariensis*), and the black kite (*Milvus migrans*) (Crowley 1995; Karpanty and Goodman 1999).

Parasitism and disease are a neglected part of the ringtail story, with few published veterinary studies. The most obvious parasites are red ticks which cluster round the eyes of debilitated animals (Takahata et al. 1998; Koyama et al. 2008).

Two constants at Berenty shape much of ringtailed lemur ranging behavior: the prevalence of tamarind trees, and the year-round availability of water. *Tamarindus indica* are the dominant tree of the gallery forest. About 50% of gallery forest ringtailed lemur feeding time is on tamarind fruit pulp or leaves through all seasons. Population density largely mirrors the availability of tamarind trees, and in seasons where there is a dearth in the usual range, troops may make long excursions to fruiting trees (Rasamimanana and Rafidinarivo 1993; Mertl-Millhollen et al. 2003, 2004, 2006; Blumenfeld-Jones et al. 2006; Koyama et al. 2006; Soma 2006). This means that there are fixed points of great importance to ranging patterns, and these major food sources persist over many generations of lemurs. This is less true in the spiny forest, where not only is there less food overall, but the important food trees are smaller and more numerous in a given home range.

The Mandrare River dries up only in September–October of the worst drought years (historically about once every 10 years), and even then a few stagnant puddles remain near the bank. Gallery forest ringtails prefer to descend to the river in places where there are overhanging trees and shrubs that provide cover from aerial predators: again fixed points of great value. In the Scrub and Spiny zones water is obtained from the leaves of succulent plants. These may be in limited stands of the vine *Xerocysios* or introduced *Opuntia*, also points of value which may be worth defending, which influence daily ranging and inter-troop competition (Budnitz 1978).

2.3 Ringtailed Lemur Social Behavior

My early work focused on behavior of ringtailed lemurs, especially their near-absolute female dominance, their highly compressed mating season, and the fact that their social complexity seemed to far outweigh their interest in manipulating objects (Jolly 1966a, b, 1967). The long-term studies which followed have hugely enriched our knowledge, but not actually solved my initial questions.

2.3.1 Communication

Ringtailed lemur troops are multi-male and multi-female, ranging in size from 3 to 34 non-infants. They are highly social, with a wide range of vocal, visual, tactile, and scent communication. Vocal signals include the adult male howl or song, contact calls ranging from a soft mew to a loud meow (often given in chorus) locomotor and alarm calls (Oda 1996a). Like vervet monkeys, they use different calls toward different predators: clicks and mobbing toward snakes, yap chorus toward ground predators, and screams toward hawks, often followed by movement upward or downward as appropriate. Scent marking still has subtleties that we do not appreciate, but is done along with stereotyped posturing. A handstand during genital marking by either sex puts the mark at the height of other lemurs' noses. Male spur marking is done with side-to-side jerking of the upper body; male stink-fighting with anointing and waving the tail (Jolly 1966a; Mertl-Millhollen 2007). Urine-marking with raised tail and a "bottom-drag" along a substrate, differs from normal urination (Palagi et al. 2005a; Palagi and Norscia 2009). The scents and vocalizations are individually identifiable (Mertl 1977; Palagi and Dapporto 2006) but also are responded to between troops and even, in the case of alarm calls, between ringtails and sifaka (Oda 1996a, 1998, 1999, 2001; Oda and Masataka 1996). Mertl-Millhollen and Palagi independently conclude that females are more attentive to female marks (especially as inter-troop territorial communication), and males to both males and females (especially for mating opportunities). Mertl-Millhollen first identified the scent-marked ring of territorial boundary well within home range boundaries for both ringtails and Verreaux's sifaka in the gallery forest. The ring of intensive marking is a "battle zone" where troops confront others of their own species. (Mertl 1977; Mertl-Millhollen 1979, 1986, 1988, 2000a, b, 2004, 2006; Mertl-Millhollen et al. 1979). Visual attention, like olfactory attention, is largely directed within members of each sex, except during the brief mating season (Lane and Bard 2007, 2008).

2.3.2 Female Affiliation and Aggression

The core of each troop is a female matriline. Subgroups (cliques) reflect kinship, mainly mothers with adult daughters. Time spent in affiliative cuddling and grooming greatly outweighs time spent in aggressive behavior but aggression plays a large part in troop life (Nakamichi and Koyama 1997, 2000; Nakamichi et al. 1997; Sussman et al. 2003; Sussman and Garber 2004). Female dominance rank is highly contested and reversals may be violent (Koyama et al. 2001, 2005). The alpha female has a special role in vigilance and defense toward other troops. If she does not defend personally, her henchwomen, usually a daughter, takes a lead role (Gould 1996). An alpha female may have a relaxed style of dominance with little friction within the troop, but some are actively "spiteful," chasing subordinates and males from feeding sites even if the dominant does not feed there herself (Dubovick 1998). One may suppose that this behavior eventually pays off for the dominant in reproductive success, by imposing greater costs on her within-troop rivals. In the short term, it clearly costs the alpha energy in the chase and in lost feeding time for herself. If the observer knows enough of the troop history, the differences in alphas' style may sometimes be attributed to outside causes: for instance, if the alpha herself is an immigrant who has fought her way in from another troop, or if there is challenge from a rising sister or cousin, or if the pressure from successful adjacent troops is compressing troop range and thus exacerbating within-troop rivalries.

Larger troops, on average, have lower reproductive success, though optimal group size is smaller in the sparser areas of the reserve, and there are complex tradeoffs between group size and seasonality (Jolly et al. 2002; Pride 2003, 2005b; Pride et al. 2006). In the highest-density area of the reserve, the highest number of surviving infants was found among mid-ranked females in middle-sized and large groups with 4–9 adult females. Smaller groups with only 2–3 adult females had fewer surviving infants (Koyama et al. 2001, 2002, 2005). The somewhat lower success among the highest ranked females in large groups seems like an anomaly, but the variation in aggressivity and cortisol levels between different females, and the pressures of high-density territoriality, may need analysis on an individual by individual basis (Cavigelli et al. 2003; Pride 2003, 2005a, b).

Long-term, when a troop grows too large or when a grandmother dies or is deposed, the troop splits. A group fission involves active targeting by the dominant clique of a subordinate clique, their most distant cousins. Subordinates, once forced out, can fight to establish new territory by subdividing the original home range, or taking neighbor troops' ranges. The evicted group may remain nomadic through others' home ranges for up to 2 years before claiming discrete home range of its own with active defense of a part of this range as a territory. In 23 observed cases, the subordinate daughter troop remained in ranges adjacent to the dominants which had driven them out (Koechlin 1972; Koyama 1991; Hood and Jolly 1995; Koyama et al. 2002; Takahata et al. 2005; Ichino 2006; Ichino and Koyama 2006; Jolly et al. 2006b).

The alpha female often gives a soft call which alerts the troop that it is time to move, and nearly always leads the troop in progressions of over 30 m. A few anecdotal reports of alpha females leading troops on excursions well outside their normal range raise the suggestion whether the memory of old female lemurs is also a resource for their troops (Dolins and Jolly 2007; Miles and Rambeloarivony 2008).

Elsewhere, I argued that within-troop competition between female ringtails evolved within the constraints of a territorial system where it may be easier to evict your cousins than to expand a home range into areas used by neighbors. Frequency of encounters between troops varies with population density: Front troops may meet five or more times per day, in the Gallery forest only once per day, and in the Scrub in the 1990s only twice a week – though these figures have changed with recent population shifts. However, when troops do meet, they are equally likely to be aggressive whether at high or low densities – and much depends on the individual troop histories which neighbors are treated as the worst threats (Jolly et al. 1993, 2006b; Takahata et al. 2006). Pride showed that even in a case where owners were gaining less food per individual than raiders, the owners continued to actively defend their territory, suggesting that long-term ownership might be worth short-term loss (Pride et al. 2006). Scent marking not only indicates the territory boundaries, but serves as a long-term tradition to maintain those boundaries (Mertl-Millhollen 2000b, 2006).

One of the earliest Berenty studies was conducted by Peter Klopfer. He observed that my 1963 study troop was still in the same area in 1969, with many of the same territorial boundaries (Klopfer and Jolly 1970). Mertl-Millhollen brought order to all studies up to 1975, again noting that troops remained in the same ranges (Mertl-Millhollen et al. 1979). We now know that the ranges of subdivided troops at Berenty remain adjacent to each other, such that female descendents of the first known troops still occupy the same parts of the forest after 40 years (Jolly and Pride 1999; Jolly et al. 2006b).

2.3.3 Males, Infants, and Juveniles

Male transfer between ringtail troops during the birth season was first recorded at Berenty (Jones 1983). It has been much more extensively studied in the tagged population at Beza Mahafaly, as has male behavior (Sussman et al. 2011). Males thus choose new troops 6 months prior to actual mating. Females are only receptive for a few hours of 1 day, though the few that do not conceive may cycle again a month later. Within a troop, all females reach oestrus in a 2-week period, though there is “asynchrony within synchrony,” such that no two are receptive on the same day. The troop’s dominant male sometime, but far from always, has mating priority. Males, including extra-troop individuals, may vie in violent “jump-fights,” which often lead to canine slashes to head or body. Oddly, the female retains absolute mate choice: if she does not like the current winner of a jump-fight she remains in the open, inviting other challengers – and she may mate with several males in succession. In short, behaviorally it seems that males gain little advantage from their year-round dominance contests, their jump-fights, and from their attempts to mate-guard (including copulatory plugs which can be removed by the next male). Actual male reproductive success at Berenty is now under active investigation (Ichino personal communication).

Infants are born in September–October, with most births within about 3 weeks. Births are generally at night or during siesta hours (Okamoto 1998; Takahata et al. 2001). Infants are precocial for lemurs, transferring to the mother’s back at about 2 weeks, and are weaned in about February–March at the peak of the wet season (Gould 1990). Infants grow rapidly during in the wet season, and cease to grow in the following dry season, even under constant conditions in captivity (Pereira 1993b). Wild females normally give birth for the first time at age 3 or 4, though in captivity they give birth at 2 years. Twins are rare in the wild, common in the better-nourished conditions of captivity. Males have little to do with raising infants, but a mother's close kin may carry her infant or even let it suckle (Gould 1992; Koyama 1992; Koyama et al. 2006). Infanticide happens, though very rarely. In the few cases seen, some perpetrators were extra-troop or immigrant males, but others were females suppressing the reproduction of a subordinate (Hood 1994; Jolly et al. 2000; Ichino 2005). A quarter to a half of infants die in the first year, many during very early lactation when the mother is losing body condition at the end of the dry season (Jolly et al. 2002; Koyama et al. 2002). The mother stays with her fallen infant, or starts to follow the troop and returns as long as it can cry, but she eventually leaves it to rejoin the troop. Lemurs, unlike monkeys, do not have hands that can support a dead infant, though the mother may return to the corpse or site some hours later. The high mortality rate does not reflect maternal indifference (Nakamichi et al. 1996). What it does reflect is the extreme variability of yearly climate, such that infants die but the vast majority of females survive (Jolly et al. 2002, 2006b).

One major difference between ringtailed lemurs and anthropoid primates is in rough-and-tumble play. In most primates including humans, males have more physical contact play than females. In ringtails the sexes spend equal time in rough contact play. Juveniles of both sexes also have occasional serious wrestling bouts which lead to dominance decisions (Gould 1990; Pereira 1993a).

2.3.4 Female Dominance over Males

This is not the place for a full review of theories and studies relating to the evolution and maintenance of lemur female dominance over males. That will largely concern the differences between lemur species' intensity or expression of female dominance, first pointed out by Pereira and Kappeler (Pereira et al. 1990; Pereira and Kappeler 1997). Three lines of study at Berenty contribute to this still unsolved question.

First, it is clear that ringtailed lemur females can be highly aggressive, both within and between troops, as well as toward males. Pereira argues (and I agree) that this involves motivation to gain power per se (Pereira 2006). The adaptive advantages of such motivation are a different question. Lewis argues for "leverage" or "power" as an evolutionary correlate of female dominance (Lewis 2002). In species which are ecologically constrained to have slight or no sexual dimorphism, and where the male–female ratio is equal (or even irrelevant), females may be able to exert their leverage of mate choice over males, achieving behavioral dominance. Lewis' evolutionary reasoning may or may not apply to all the lemur species which show female dominance. The motivational aspect similarly does not apply to all species – in particular, female Verreaux's sifaka, which Lewis studied, have full female dominance but show very rare aggression within a troop, unlike the power-hungry ringtails.

A different line of argument suggested that lemur females as a whole have exceptional need for food, either physiologically or because of the highly erratic Malagasy climate (Jolly 1984; Dewar and Wallis 1999; Wright 1999; Richard et al. 2000, 2002; Dewar and Richard 2007). However, time and locomotion assessment of male and female Berenty ringtails showed that the two sexes actually consume similar amounts of protein and calories, though males' diet is more fibrous, and that the two sexes also expend similar amounts of energy (Rasamimanana and Rafidinarivo 1993; Rasamimanana 1999; Rasamimanana et al. 2006). A double-labeled water study of oxygen consumption during March (after lactation and before the mating season) also showed similar energy budgets between males and females of both ringtailed and brown lemurs (Simmen et al. 2010). It may be that seasonal changes and erratic year-to-year climate still impose extra costs on the females, since they fatten up very markedly during the rainy season in preparation for gestation during the dry season (Simmen et al. 2010), but this is also true of the males in preparation for energy expenditure during mating. Seasonality of breeding in relation to seasonality of food supply will be a part of the story, as first suggested by Hrdy, but female need is not a simple explanation for female dominance (Hrdy 1981; Pride 2005a).

The third argument is so far in need of much more evidence. Jolly et al. (2006b) suggested that inheritance of material property in the female line can increase the variance in female reproductive fitness over that of males. Males start over again in each generation with variance reflecting only their genes, their luck, and their bodily prowess. Female ringtails at Berenty inherit territory which must be defended in each generation, but which is hard to reclaim once lost. This territorial stability may be an artifact of Berenty's high density, though the aggression shown between troops at all densities, and the rough-and-tumble play of young females suggests that female competitive behavior is an evolutionary norm for ringtails. However, proving the importance of maternal inheritance of property needs mathematical rigor and actual data on males' reproductive variance as well as females', as well as further data on troop range, territoriality, and territorial inheritance in other species and at sites outside Berenty. Interestingly, E.O. Wilson now argues that the evolutionary origins of social insect society should be traced to defense of a nest or nest site, a rare and heritable resource. In Hymenoptera, with maternal inheritance, this arguably involves an extraordinary form of female dominance, while in Isoptera both the resident reproductives and the worker cast are male and female (Hölldobler and Wilson 2009; Nowak et al. 2010)

2.3.5 Complexity of Social Relations

The other interest of the very early studies was the comparison between lemur social relations and those of anthropoids. I believed that the simple composition of multi-male, multi-female troops would favor social intelligence (Jolly 1966b). I did point out that tripartite reactions in which one animal would threaten another while ensuring support from a third had not been seen in the lemurs (Kummer 1967). Since then, it seems that ringtailed lemur interactions are much more black and white than in many anthropoids – either affiliative or aggressive between any two animals, with minimal ambiguity, and no reconciliation after quarrels (Kappeler 1993). Reconciliation has recently been asserted for sifaka, ringtails and brown lemurs, using different measurements (Palagi et al. 2001, 2005b, 2008). More obvious in the field is the careful geometry of a troop, where distance between animals is a very good measure of affiliation or aggression, and arguably involves awareness of multiple individuals, not just dyads (Nakamichi et al. 1997). Complexity of social relations would be worth revisiting by someone very familiar with behavior of both monkeys and prosimians.

2.4 The Changing Ecology of Introduced Species

2.4.1 Nurse Trees and Food Trees

The concentration of fruit trees with different phenologies from the highly seasonal native forest is one of the main reasons for high lemur density in the Front zone (Rasamimanana and Rafidinarivo 1993). Introduced tree species from which lemurs obtain food and those that serve as forest nurse trees represent benign interventions, though they are far from natural. *Pithecellobium dulcii*, the "monkeypod" or "ape's earring" tree is a nurse tree, has promoted the regeneration of the Ankoba zone with its high density of all lemur species. Prickly pear, *Opuntia*, is found at the periphery, and is now spreading along the river bank. Too much would be disastrous, but it serves as an important water source for lemurs in both the Front and Scrub zones.

2.4.2 Cissus quadrangularis

Cissus, the "veldt grape" or "Devil's backbone," is a euphorb imported to Madagascar from India or Africa either as an ornamental, or for its curative qualities on broken bones and other ailments. In Berenty it is a smothering vine that blankets whole trees or sections of forest. Management campaigns have cleared sections of forest by hand, but it re-grows from tiny dropped fragments, so this is an endless process. There is nothing good to be said about *Cissus* in a forest reserve.

2.4.3 Leucaena leucocephala

Stands of leucaena were planted in or just before 1990, in the bottleneck between Ankoba and Malaza and also at the northern tip of Ankoba. They were an experiment, to see if they could provide extra fodder for cattle and ostriches. The rise in ringtail population in the Front zone tracked the growth of this fast-growing tree. Demography was studied by the Koyama team during this period of rapid population expansion. Unfortunately, leucaena contains mimosine, a non-protein amino acid that blocks cell division. Some troops became so dependent on leucaena that they ate it for 40–50% of their feeding time during dry season months. This produced “Bald Lemur Syndrome,” or rather, naked lemur syndrome in which the loss of fur from body and tail mimicked chemotherapy (Fig. 2.6). Adults mostly recovered full pelage when the diet changed with the onset of rains. Embryos seemed to be buffered against the leucaena effect. The birth rate of highly affected females was not lower, but survival of infants with no fur to cling to, and of juveniles weaned onto the toxic tree fell markedly by the end of the leucaena period in 2006–2007. Nearly all of these trees have now been removed. However, the loss of a major foodstuff has also increased adult mortality in the Japanese study troops, which are concentrated at the bottleneck (Jolly 1980, 2009a, b; Crawford et al. 2006, 2008; Soma 2006, in press; Soma et al. 2008; Berg et al. 2009; Ichino et al. in press).

2.4.4 *Brown Lemurs*

By far the largest influence on ringtails has been the introduction of brown lemurs. About eight orphaned pet *E. rufus* from the Menabe in western Madagascar, escaped to the forest during a 1975 cyclone. About eight more *E. collaris* from the Fort Dauphin region were deliberately released in the years up to 1985. These two species have different chromosome numbers, and should not be able to breed, but no one told the lemurs. They are direct and dominant competitors with the

Fig. 2.6 Bald lemur. Photo © Wiebke Berg

ringtails for habitat and food, although their social structure is quite different, as is their cathemeral activity. The hybrid population of Malaza and Ankoba numbered 596 in 2009, compared to 462 ringtails (Figs. 2.6 and 2.7). The brown population grew exponentially from their introduction until a peak of 653 in 2007 (Fig. 2.7). At that point, scientists persuaded the management to stop providing water in artificial basins in the forest. This might have finally limited the brown lemur population in space, if not in numbers, since they do not spend much time in the sunny scrub zone. Ringtailed lemur troops have largely abandoned the rich gallery forest to the brown lemurs. Although they maintain a foothold, and sleep in their old ranges, much of the daytime foraging is now concentrated on the reserve's periphery. However, their numbers have not fallen (Pinkus et al. 2006; Tanaka 2007; Razafindramanana et al. 2008; Donati et al. 2009; Norscia and Palagi 2011; Palagi and Norscia 2011; Rasamimanana et al. in press).

It is still not clear whether brown and ringtailed lemurs will continue to co-exist stably. They have re-created the classic ecological niche separation described by Sussman (1974), with browns in the central shade, feeding on the gallery forest trees once favored by ringtails, and ringtails in the peripheral sun with a diet increasingly based on plants of scrub and spiny forest. There is no clear sign that the two species are over-browsing their habitat. However, one needs perhaps another 5 years to be sure of this conclusion (Fig. 2.8).

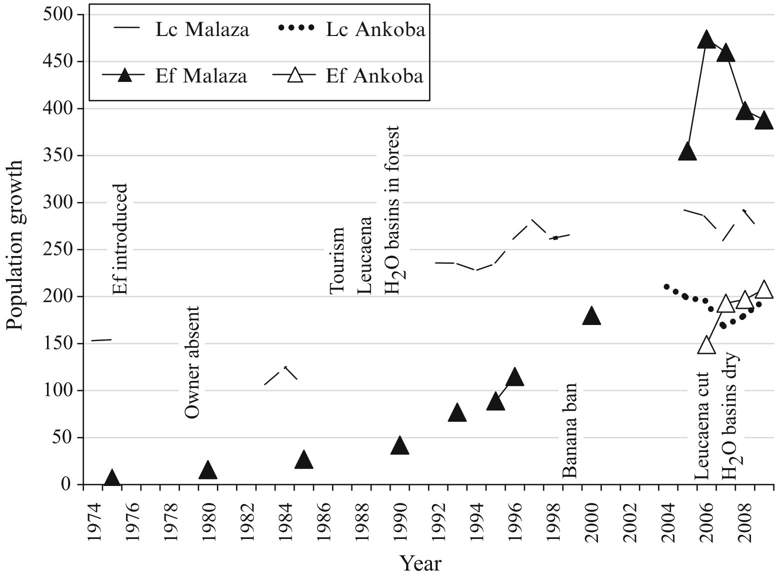

Fig. 2.7 Population growth of ringtailed and brown lemurs (Razafindramanana, Pinkus, O'Connor, Dainis, Jolly)

Fig. 2.8 Hybrid brown lemurs at Berenty. The male has the crest and eyebrows of *Eulemur rufus*, the full beard of *E. collaris*. The female has the grey head of *E. collaris* and the frontal stripe of *E. rufus*. Photo © Cyril Ruoso

2.5 The Future

Berenty is drying out. The loss of tamarind trees and closed canopy forest is clear over the decades (Blumenfeld-Jones et al. 2006; Ichino 2007). It is not clear why. One reason may be natural succession within the gallery forest. If the reserve were not so bounded there might be re-growth in other places. Another likely cause is the lowering of the water table. The Mandrare River suffers from deforestation in the headwaters, and loss of grass cover lower down; flood crests which used to pass in days now pass in hours.

Add to this the effects of climate change. Berenty has suffered repeated droughts in this decade. El Niño years commonly bring drought, and they seem to be growing commoner. All global climate models predict a greater intensity of cyclones. These can sometimes bring needed rain to the south, but a mis-timed cyclone ruins the years' crops. Madagascar lies on the intertropical convergence, in the latitudes most vulnerable to climate change. All types of native forest are much better buffered against extremes than are the annual crops, but progressive drying out could eventually destroy the forest.

Berenty Estate is also vulnerable to social change and unrest. Its reserve system has survived for 70 years. This is due to the care of the de Heaulme family, and to the fact that local people have had salaries that allied their interests with the estate. Any reserve's survival depends on the good will and enthusiasm of particular people, and on an enabling economy. When the reserve is as small as Berenty, the people are few, and outside income comes only from sisal and tourism.

Subsistence farming is at the mercy of the weather. The weather itself is at the mercy of southern deforestation and the northern greed for carbon (Koyama 2009).

Berenty has provided much, though certainly not all of our understanding of the behavior of ringtailed and other southern lemurs – especially the interplay of within- and between-troop aggression in a female-dominant species. It has served as a base for ecological research, but an ecologist at Berenty cannot simply produce a picture of the "environment of ecological adaptation" – it takes all the running a scientist can do to keep up with the changes brought by introduced species and climate fluctuations in such a small space.

The very things that make Berenty interesting, though – lemur social interactions in a region of maximum population density, and the constantly changing ecological background – also make it vulnerable. Its survival is by no means guaranteed, in the face of physical or social changes to come.

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Chapter 3
Beza Mahafaly Special Reserve: Long-Term Research on Lemurs in Southwestern Madagascar

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Michelle L. Sauther, Diane K. Brockman, Lisa Gould,
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Abstract The Beza Mahafaly Project in southwestern Madagascar was founded in 1975. It was established as a collaborative effort among the University of Madagascar (now University of Antananarivo), Washington University, Yale University, and the local communities for long-term training and research, biodiversity

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conservation, and socioeconomic development. Beza Mahafaly consists of two noncontiguous forest parcels separated by 10 km that became a protected area (Réserve Spéciale) in 1986: an 80-ha gallery forest and a 520-ha xerophytic spiny forest. The region has a diversity of habitats and a very diverse and highly endemic flora and fauna, including four species of lemurs found in or near the reserve. The ringtailed lemur (*Lemur catta*) and Verreaux's sifaka (*Propithecus verreauxi*) have been the subject of our long-term research. In this chapter we highlight some of the results of this research. Our multidisciplinary studies illustrate the feasibility of collecting long-term data on careers of individual animals and of obtaining large samples on numerous animals, across numerous social groups, in relatively isolated breeding populations. Thus, we can provide insights into many of the demographic, socioecological, anthropogenic, and epidemiological factors that shape the local ringtailed lemur and sifaka population. Here we summarize how ringtailed lemur demographic structure is affected by climatic perturbations (drought); how aspects of general health (parasite loads and dental health) are directly related to habitat, dietary, and anthropogenic factors; how tight birth seasonality in sifaka can elicit stress responses in males associated with increased male aggression, group takeovers, and infanticide risk; how life history schedules are related to evolutionary responses to extreme climatic fluctuations; and how directional selection among sifaka males leads to longer, stronger legs, but not to increase in male body mass relative to females.

3.1 The Beza Mahafaly Reserve

3.1.1 History of the Reserve

In the mid-1970s, R.W. Sussman received a phone call from Edward Steele of the Defenders of Wildlife (DOW) asking: "What can we do to save Madagascar's wildlife?" Steele (1975) had recently returned from Madagascar and had fallen in love with the country. Sussman, along with Alison Richard, then at Yale University, and Guy Ramanantsoa, then the Head of the Forestry Department of the School of Agronomy at the University of Madagascar (Ecole Supérieure des Sciences Agronomiques, ESSA/Forêts), had been discussing establishing a unique type of reserve in Madagascar. They envisaged a protected area for long-term research on biodiversity and conservation, but also to be used as a training and research center and springboard for socioeconomic development for local villagers.

Sussman explained this vision to Steele, who set up a meeting of DOW board members with Richard and Sussman. The board was impressed with the proposal. However, DOW worked mainly on litigation within the United States. Therefore, Richard Pough, a board member also on the Board of Directors of World Wildlife Fund, volunteered to present our ideas to WWF, which agreed to fund the project. In 1975, Ramanantsoa, with his collaborator the late Pothin Rakotomanga, set out to survey southwestern Madagascar, looking for a relatively accessible, undisturbed area with a representative faunal and floristic diversity. Another criterion was that local villagers agree to the project. He met the President of the Firaisana (Commune) of Beavoha, who proposed Anala Sakamena (forest bordering the Sakamena river) as this site. The site was named "Beza Mahafaly" in recognition of the commune President, who came from the village Beza Mahafaly, 8 km from the Reserve.

Local villagers were conscious of the vital importance of preserving this habitat and were enthusiastic about the project. In July 1978, the advisory committee of the local community agreed to grant two noncontiguous parcels of forest to the School of Agronomy. Thus, ESSA/Forêts began collaborative work with local communities, Yale and Washington Universities, as well as other national and international partners, to establish the Beza Mahafaly Reserve. Between 1978 and 1985, with funding mainly from WWF, reserve boundaries were demarcated, basic facilities were constructed, local guards were recruited and trained, and a field ecology school was developed for students from ESSA/Forêts.

On June 4, 1986, Beza Mahafaly was inaugurated as a Réserve Spéciale (Beza Mahafaly Special Reserve; BMSR) by government decree No. 86–168. Biodiversity research, especially on lemurs, had already begun and has continued to this day. Integration of conservation and development in villages surrounding the reserve, an integral component of the plan since the project's conception, continued, with increasing support from WWF and the U.S. Agency for International Development (USAID). In a coordinated effort with the local people, including their input and requests for assistance, community projects were begun to improve the production and marketing of crops (irrigation projects and road construction), education (construction of a local school), and health (water well construction). Students and faculty from ESSA/Forêts with local residents played an important role in the development of these activities, in partnership with Yale and Washington University.

In 1989, WWF took over management of the reserve, and in November 1995, ESSA/Forêts became the principal administrator. Research, training, and education programs as well as local development projects have continued to flourish. The site has hosted a multidisciplinary field course for fifth-year ESSA/Forêts students since 1986 (Ratsirarson 2003). Since 1994, additional support has been received from a large number of sources (see Acknowledgments).

In 2005, the management of the Reserve was transferred to Madagascar National Parks (MNP), like all protected areas in Madagascar. The School of Agronomy became the principal partner in research and training. ESSA's activities address the Reserve's management and development plan needs, and research specifically follows the annual work plan agreed by both parties (ESSA and MNP). The main objectives of the reserve continue to be long-term biodiversity monitoring and research on community ecology and conservation biology, long-term research on the lemur populations, education at the local, national, and international level and integrated research in the social and natural sciences with the goal of improving the lives of local communities while conserving the biodiversity in surrounding habitats. The main specific goals of our long-term lemur research are to provide a better understanding of behavioral ecology, demography, population genetics, reproductive biology, health status, and mating and life history strategies. Success at achieving these goals depends on, and results from, the connection between research and local development.

3.1.2 Physical Description of the Reserve

The reserve is located in southern Madagascar, 35 km to the northeast of the town of Betioky-Sud at 23°41′60″S and 44°32′20″E. Southern Madagascar is characterized by a long dry season and short wet season. During a non-drought, non-cyclone year, annual rainfall is about 700 mm, of which 600 mm falls during the austral summer between November and March. The Sakamena River is dry during the long dry season. Annual daily maximum temperatures average 25°C. Averages for wet season are high ambient temperatures (32°C), and daily maxima reach 46°C. Temperatures during the coolest months (July–August) usually range between 20°C and 30°C during the day, but can fall to 2°C at night (Sussman and Rakotozafy 1994; Ratsirarson 2003).

The reserve consists of two noncontiguous parcels separated by 10 km (Fig. 3.1). Parcel 1 is characterized by a gallery forest dominated by *Tamarindus indica*. It covers 80 ha of fenced and protected forest located on the banks of the Sakamena River, and is relatively flat with a slightly elevated plateau starting at the banks of the river (Fig. 3.2). The gallery forest is divided by marked transects whose paths intersect to form squares of 100 × 100 m. This parcel has been enclosed by barbed wire fence since 1979. Before this it was exposed to cattle and goats and used by the local people for various resources, as is the surrounding forest currently. Parcel 1 is surrounded by similar but unprotected and somewhat degraded gallery forest on the north and south. To the east is the Sakamena River and to the west is contiguous dry forest. The parcel is bounded on the south by the dirt road that runs from Betioky to the reserve and on to the small village of Analafaly 2 km east. The campsite and reception center is just south of the road. The infrastructure includes two wooden houses, a museum, an office building, a large open gazebo for courses and meetings, camping space, as well as solar energy and a water well.

Parcel 2 is a 520-ha area of xerophytic forest dominated by species adapted for the long dry season (Ratsirarson 2003, 2008). This parcel is often referred to as spiny forest. Between the two noncontiguous parcels, the vegetation transitional between the gallery and the xerophytic habitats is more degraded than the reserve, because it is used for grazing and for the collection of various forest products for food, medicines, building, etc.

3.1.3 Flora of Beza Mahafaly

The forest represented in Parcel 1 is western Malagasy dry deciduous forest (White 1983). It has an average of 369 trees of $\geq$2.5 cm DBH/1,000 m^2 (Sussman and

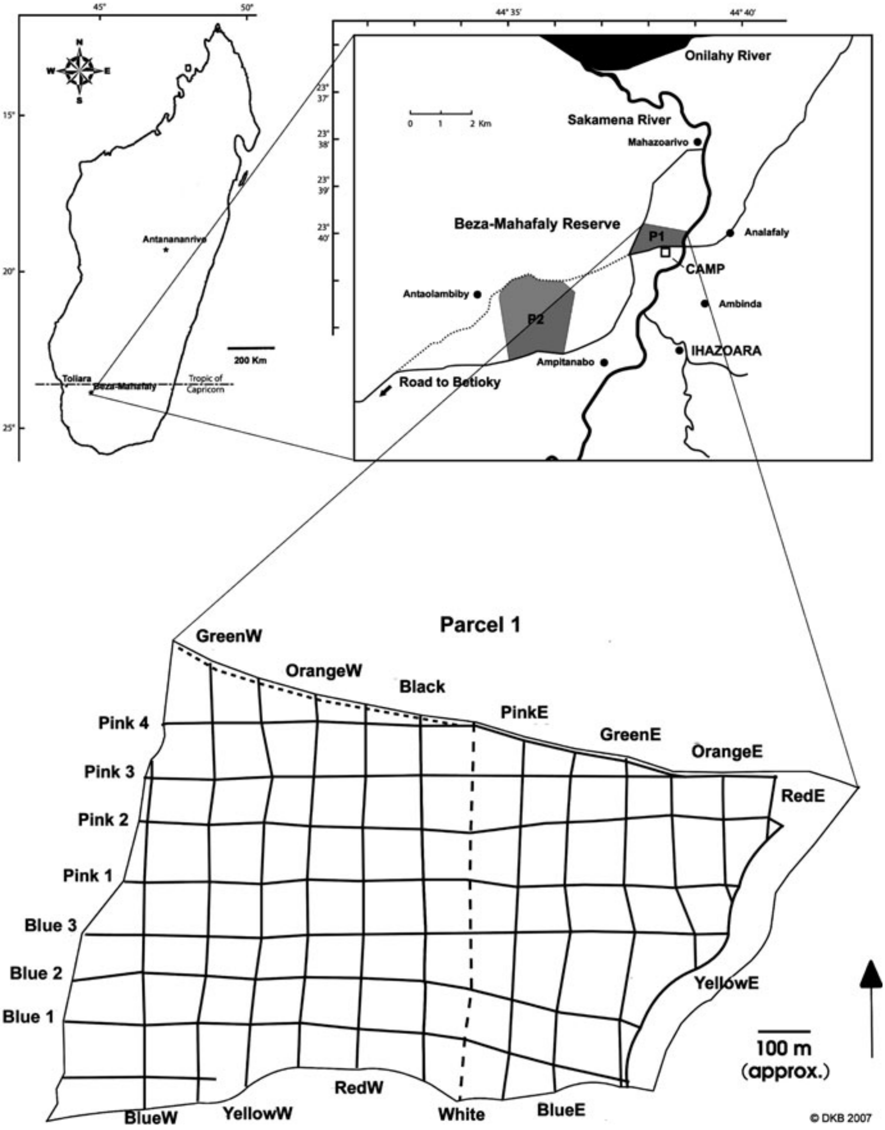

Fig. 3.1 Map of the Beza Mahafaly Special Reserve showing both parcels and marked path system in Parcel # 1 (provided by D. Brockman)

Rakotozafy 1994), which is typical of dry forests in Africa and the Neotropics (Gentry 1993). A soil moisture gradient exists, with soils becoming dryer farther from the river. Overall tree density does not decline with distance from the river, but the density of larger trees does; a uniformly closed upper canopy occurs on wet soil, but this grades into denser bush on dryer soil, where distinctions between the

Fig. 3.2 Aerial photograph of Parcel # 1 to the right of the dry Sakamena River. Photo taken from Northeast of the reserve

canopy strata are obscured and forest gradually passes into thicket. Tree height and diameter decrease progressively with increasing distance from the river (Ratsirarson 2003). On wet soils, the upper strata form a closed canopy, mostly uniform in height (15–20 m). Members of the upper stratum are species whose trunks generally exceed 25 cm DBH and may attain 50 cm or more, especially on wet soils. However, the average height of trees in Parcel 1 is 6.33 m, with an average diameter of 7.93 cm (Ratsirarson et al. 2001). *T. indica* is the dominant tree species. Other common canopy species are *Acacia rovumae*, *Euphorbia tirucalli*, and *Salvadora augustifolia*. In general, those species found in both microhabitats are not distributed equally between them. Five of the most common species are found mainly on wet soils and eight mainly on dry. Parcel 2 contains desert-like vegetation dominated by *Alluaudia procera*, *Cedrelopsis grevei*, *Commiphora* spp., and *Euphorbia* spp. (Ratsirarson 2003, 2008). Average height of trees is 4.5 m, with an average diameter of 6.5 cm (Ratsirarson et al. 2001). This forest has been the subject of fewer studies than the gallery forest.

Twelve permanent transects, each 1,000 m × 10 m, have been set inside and outside the two parcels to continuously monitor the density and distribution of plant species. All trees of ≥ 3 cm diameters were identified, tagged and their diameter as well as height measured. Overall, the flora of BMSR contains approximately 120 species and 49 families (Ratsirarson 2003). However, half the families are represented by a sole species. Euphorbiaceae and Mimosaceae are the most species-rich. A local reference herbarium and the Beza Mahafaly Osteological Collection are currently housed at the onsite Museum.

3.1.4 Fauna of Beza Mahafaly

There are four species of lemur at BMSR, two of them diurnal (Verreaux's sifaka, *Propithecus verreauxi*, and ringtailed lemurs, *Lemur catta*), and two nocturnal species (the white-footed sportive lemur, *Lepilemur leucopus*, and the grey-and-red mouse lemur, *Microcebus griseorufus*). We initially thought there were more species of *Microcebus*. However, recent genetic analysis revealed only one species with three color morphs (Heckman et al. 2006).

Three introduced carnivores (the domestic dog, *Canis lupus familiaris*, the small Indian civet, *Viverricula indica*, and the invasive wildcat, *Felis silvestris*) occur in the reserve (Brockman et al. 2008). The wildcat is semi-arboreal and distinguished from domestic cats by its large, pronounced ear lobes (Ratsirarson et al. 2001), brown and gray tabby pattern, larger size, and substantial sexual dimorphism (Brockman et al. 2008). Ratsirarson et al. (2001) saw an adult *Felis* carrying an infant ringtailed lemur in its mouth. The one endemic carnivore, the fossa, *Cryptoprocta ferox*, had not been directly observed in the reserve since 1993 (Brockman et al. 2008), but a camera trap image of a fossa moving through the reserve in 2008 and other recent observations confirm that it still exists in the area (Sauther et al. unpublished data). For a list of other mammalian species found in the Reserve, see Ratsirarson et al. (2001), Ratsirarson (2003), and Sussman and Ratsirarson (2006).

One hundred and two species of birds representing 43 families have been observed at Beza Mahafaly. Over half of the families are represented by only one species (Ratsirarson et al. 2001). The Reserve is home to at least 15 species of snakes, 17 species of lizards, one species of tortoise and fresh water turtle, and one species of crocodile; there are three species of amphibians. There also is a notable diversity of insects (Ratsirarson 2003).

3.1.5 Collection and Management of Long-Term Data

The long-term research focuses especially on the socioecology, population demography, life history, reproductive biology, mating behavior, socioendocrinology, feeding and nutritional ecology, population genetics, and health status of the diurnal lemurs (Fig. 3.3a, b). It also includes work on the conservation biology of other elements of the fauna and of the flora, monitoring of plant phenology, and research on the socioeconomics of the human population in relation to economic stability, development, and conservation. We maintain the education and training component of the reserve locally, regionally, and internationally. Each component of the project requires different strategies for data collection and management.

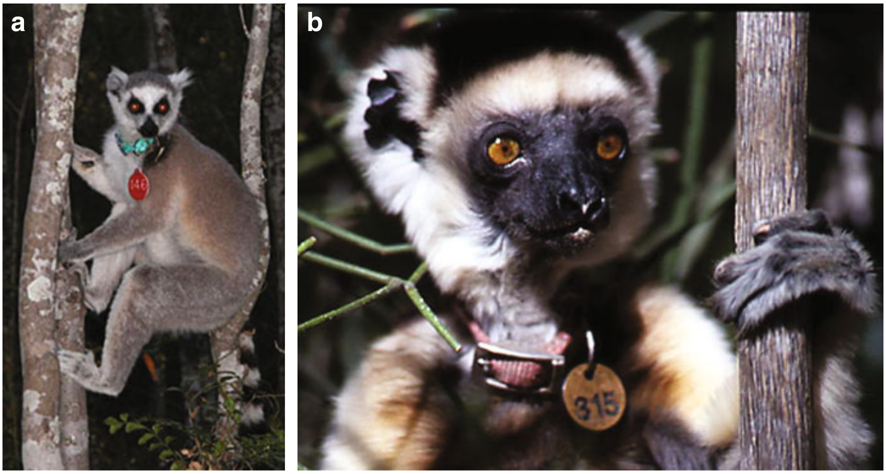

Fig. 3.3 (**a**) Collared ringtailed lemur (*Lemur catta*; photo © M. Sauther); (**b**) collared Verreauxi's sifaka (*Propithecus verreauxi*; photo © D. Brockman)

3.1.6 Future Plans for the Reserve

Beza Mahafaly Reserve was included among the sites of implementation of President Ravalomanana's "Durban vision" declared in 2003, where he set the goal of extending Madagascar's protected areas from 1.7 to 6 million ha, which is 10% of the national territory. BMSR's surface area was to increase from 500 to 4,600 ha. The two Parcels would be united into one protected zone, which would ensure better conservation of the region. Zones for controlled human utilization have been established around the protected zone in response to the needs of neighboring communities. Use of resources for commercial purposes is prohibited. However, strictly controlled harvesting of ligneous and non-ligneous products (honey, medicinal plants, wood for building, pastureland) is allowed. The right to utilize paths and trails located outside the protected zone is granted to inhabitants and livestock.

3.2 Socioecology of the Diurnal Lemurs

Two vital aspects of long-term data collection and management of socioecological information are: (1) Permanent identification of individual animals and regular censusing of these populations to document life history parameters and facilitate recensusing. Most adult ringtailed lemurs, all adult sifaka, and ~90% of all sifaka at least 1 year old are tranquilized and given color-coded collars or other marks that allow individual recognition and facilitate repeated censuses. Collection of these baseline data allows accumulation of data on known individuals and groups on topics including diet and nutrition, general and dental health status, and stress responses to demographic perturbations both inside and outside the reserve (Sussman and Ratsirarson 2006). (2) Obtaining baseline data on the flora within and surrounding the reserve. Using vegetation analysis and satellite images from BMSR as a baseline, we have estimated characteristics of vegetation cover and ringtailed lemur population density throughout this species' entire geographical range (Sussman et al. 2003, 2006). The relationship of population structure to habitat thus can be measured, as can changes over time under various conditions.

In the following, we provide some specific strategies for data collection and management in relationship to ringtailed lemur and sifaka socioecology. For more detailed information on phenological monitoring and vegetation analysis, see Sussman and Rakotozafy (1994) and Ratsirarson (2003, 2008). We also have collected data on the socioeconomy of the human population surrounding the Reserve (see Ratsirarson et al. 2001), but will not discuss these.

3.2.1 Collection and Management of Long-Term Data for Individual Identification and Population Censuses of Ringtailed Lemurs

Between June 1987 and February 1988, nine groups of *L. catta* were censused, 85 of the 88 adults in the groups were given collars for individual identification, and monitoring of the groups was initiated (Sussman 1991). This included all groups that ranged mainly in the 80-ha fenced portion of Parcel 1 and one group adjacent to it. In November, the groups were recensused and 155 individuals were identified, including infants and juveniles. Collaring of three of the groups was renewed between 2001 and 2004 (Gould et al. 2003, 2005). As of 2008, 218 individuals in nine groups had been collared; this represented virtually all of the approximately 225 individuals in the study area, which in 2003 was expanded to include 9 km^2 of fragmented forest south and west of the reserve (Cuozzo and Sauther 2006; Sauther et al. 2006). Beginning in May 2003, captured animals also received a subcutaneous microchip (PIT tag). The size and composition of these groups is monitored monthly, with new individuals captured and collared yearly (Sauther et al. 2006). Census data and data on individual identification have been computerized since 2003. Mean group size is 11.5 individuals, with a range of 3–21. Home ranges of 8–9 groups have a mean area of 25 ha and overlap extensively.

While animals are tranquilized, researchers collect systematic data on body mass, reproductive state, general physical condition, internal body temperature, ectoparasites, and dental condition. Body measurements, hair samples, and dental casts also are collected. Beginning in 2003, blood samples have been collected for white blood cell counts and measurement of packed cell volumes. Hair and blood samples also allow disease screening, isotope studies, and extraction of DNA for analyses of kinship and genealogical reconstruction. Data are recorded into the project's database on Excel. Initially, age grades were established through a combination of body weights, canine eruption patterns, general tooth wear, nipple length for females, and presence or absence of testes in males (Sauther et al. 2002). Since 2003, actual ages are known for most animals.

3.2.2 Collection and Management of Sifaka Long-Term Data

The ecology, life history, social behavior, reproductive biology, and population genetics of the sifaka population at BMSR have been studied continuously by Richard and colleagues since 1984, focusing on populations residing in, and adjacent to, Parcel 1. From 1984 to 2009, 718 individuals residing in 50–55 social groups have been captured, measured, and marked. The sifaka study population currently comprises ~280 marked and habituated individuals residing in 38 core social groups. Mean group size is 5–6 individuals, with a range of 2–16. The 38 social groups have 4–6 ha, overlapping home ranges within the boundaries of Parcel 1 (Richard et al. 1991, 2002; Lawler et al. 2009).

Individuals are immobilized using Telazol delivered from a Telinject blowgun dart (Richard et al. 2002). During the subsequent ~90-min processing period, individuals are marked and data similar to those on ringtailed lemurs are collected (see above). Data are recorded on individual capture sheets. At the end of the annual capture season, data sheets are copied and sent to Marion Schwartz, BMSR Sifaka Database Manager, who enters the capture, census, and morphological data into the sifaka database. During processing, each individual is given an identification collar and individuals are also ear-notched using a binary system that duplicates the tag number. Captures of unmarked juveniles born the previous year and of new immigrants typically occur during the austral July–August birth season, but birth season captures do not include likely pregnant females and those with dependent young. Initially, individuals were assigned to 1 of 5 age classes based on tooth wear, with the age classes calibrated from recaptures of individuals of known age (Richard et al. 1991). Today, the exact ages of most animals are known because they were born into the population.

Censuses were carried out annually between 1984 and 1991 and have been done at monthly intervals since, yielding an unparalleled computerized dataset. Also, life history data (age at first reproduction, fertility, longevity, etc.) derived from the Sifaka Database have been incorporated into the Primate Life History Database starting in 2007 (PLHD, Strier et al. 2010; http://demo.plhdb.org) to facilitate comparative analyses of species-specific mortality and fertility schedules in seven primate taxa and to test specific hypotheses about life history evolution (e.g. Morris et al. 2011).

3.3 Research Highlights

3.3.1 Ringtailed Lemurs

3.3.1.1 Demography and Life Histories

Long-term census data allowed us to determine who survived during a 2-year drought in 1991–1992, which deaths could be directly attributed to the drought, and how the population recovered (Gould et al. 1999, 2003). During this period, approximately half of the adult females died and 80% of the infants died in the second year of the drought. The population declined considerably up to 1994, 2 years after the drought ended. However, by 1997 it was recovering well. Annual reproduction, early sexual maturity, high birth rates, and dietary adaptability likely contributed to the population recovery.

Tracking which males disperse into which groups every year from the beginning of the project has contributed greatly to the analysis of patterns of male affiliative behavior (Sussman 1992; Gould 1997a,b) and has allowed us to assess migration status and to understand the strategies that males of different ages use to disperse successfully between groups (Gould 2006). Furthermore, the hormonal correlates of mating and post-mating behavior in adult males were investigated (Gould et al. 2005; Gould and Ziegler 2007). By knowing relative ages and which groups the older males had resided in over the previous years, Gould has determined how male tenure and the number of males in a group affect physiological stress levels, and how rank, tenure, and age affect testosterone levels and rates of aggression.

For example, results obtained from mating and post-mating seasons were compared to test Wingfield et al.'s (1990) "challenge hypothesis,", which predicts a strong positive relationship between male testosterone levels and investment in male–male competition for access to receptive females during the breeding season. Fecal testosterone (fT) levels and rates of intermale aggression were significantly higher during mating season compared to the post-mating period. Mean fT levels and aggression rates were higher in the first half of the mating season compared with the second half. The number of males in a group affected rates of intermale agonism, but not mean fT levels. The highest-ranking males exhibited higher mean fT levels than did lower-ranking males, and young males exhibited lower fT levels than prime-aged and old males. In the post-mating period, mean male fT levels did not differ between groups, nor were there rank or age effects. Thus, although male testosterone levels rose in relation to mating and heightened male–male aggression, fT levels fell to baseline breeding levels shortly after the early mating period, and to baseline non-breeding levels immediately after mating season had ended, offsetting the high cost of maintaining both high testosterone and high levels of male–male aggression in the early breeding period.

3.3.1.2 Effects of Habitat Fragmentation on Ringtailed Lemur Biology and Ecology

In 2003, Sauther and Cuozzo established the Beza Mahafaly Lemur Biology Project. This synergistic research program involves collaborative ties with zoos, toxicologists, virologists, and veterinarians and uses a broad perspective and a wide range of interdisciplinary approaches to study the effects of environmental change (both natural and human-induced) on lemur biology.

Health and disease ecology. Long-term monitoring of health parameters among ringtailed lemurs has allowed us to establish baseline health data and then to perform yearly assessments of how the lemurs are affected by ongoing environmental change and human disturbance. For example, Rainwater (2009) examined lemur blood for signs of environmental toxins and documented exposure of ringtailed lemurs at BMSR to multiple organochlorine pesticides and metals. The large number of captures has also allowed us to document a range of morphological variants within a natural population, including female virilization, microtia, and dental variants such as supernumerary teeth, maxillary incisor agenesis, and severe malocclusion. Such data are important for understanding natural variation in wild populations and provide a critical first step for assessing whether habitat change is creating abnormal patterns (Sauther and Cuozzo 2008).

Data on ringtailed lemurs show that habitat disturbance can have important effects on health in wild primates. For example, more degraded habitats are linked to lower body weights, reduced body fat, a higher incidence of tooth damage, and smaller body size (Sauther et al. 2006). Female dominance and residence patterns add complexity because males and females experience different pressures that result in differences in health and trauma (Sauther et al. 2006). For example, as males migrate from their natal groups, they often enter groups in which they lack established social relationships. The result can be reduced allogrooming, which can lead to serious health issues, including a higher incidence of parasite infestation, skin lesions, and hair loss (Sauther et al. 2006).

Long-term parasitological monitoring of the diurnal lemur species (Loudon et al. 2006; Loudon 2009) is revealing how socioecological variation interacts with anthropogenic change to affect the types and prevalence of parasites in each, and indicates that local domestic animals such as dogs and cattle may be transmitting parasites. Sifaka and ringtailed lemurs live in both intact and altered habitats, but ringtailed lemurs exhibit more nematodes and protistan parasites. Differences in each primate's parasite profile appear to be linked to host behavior and the ecological distribution of parasites. Ringtailed lemurs spend much more time on the ground than the sifaka and terrestrial substrate use provides greater opportunities for soil-transmitted parasites to acquire hosts. Ringtailed lemurs using the anthropogenically disturbed forests surrounding the reserve also harbor novel parasites that they may be acquiring via coprophagy or via physical contact.

Dental ecology. One of the most important health findings resulting from long-term research on ringtailed lemurs at BMSR is that severe tooth wear and loss is common. Sauther et al. (2002) initiated a systematic study of this phenomenon, which had been noted upon the initial examination of ringtailed lemurs in 1987/1988. Since then, they have documented exceptionally high frequencies of severe wear and antemortem tooth loss (greater than 20% of the population), largely due to processing the mechanically challenging fruit of the tamarind tree (*Tamarindus indica*), the dominant food and the essential fallback resource of ringtailed lemurs (Sauther and Cuozzo 2009). Severe tooth wear and tooth loss is more common in areas of degraded habitat, and, in some cases, is linked to exploitation of introduced foods (Sauther and Cuozzo 2009).

The ringtailed lemurs respond to decreases in food processing ability due to tooth loss and dental wear by changing their activity patterns and feeding behavior. For example, individuals who have lost teeth spend more time feeding and foraging throughout the day than individuals who are not dentally impaired, and in particular they forage more during early afternoon when other lemurs are resting. They also spend more time licking tamarind fruit to soften it before ingestion (Cuozzo and Sauther 2004, 2006; Millette et al. 2009).

Isotope ecology. Assessing stable isotope values has proven fruitful for understanding the ecology and habitat of living and fossil primates (e.g, Sponheimer et al. 2009). More specifically, stable isotopes have often been used to reconstruct the ecology of Madagascar's now-extinct "giant" lemurs (e.g., Crowley et al. 2011). Until recently, isotopic analyses of extinct lemur ecology have not been based on data from living lemur populations. Our comparative data from the BMSR ringtailed lemur population as well as from other sites are now providing points of comparison for interpreting the ecology of Madagascar's extinct lemurs. For example, Loudon et al. (2007) found that C_{13} and N_{13} signatures of ringtailed lemurs with poor dental health differ from other members of the population, possibly reflecting dietary changes resulting from severe wear and tooth loss, and that the C_{13} and N_{13} signatures of immigrant males differ from those in their original troops and resemble more closely those in their new groups, which exploit different resources. Also, comparisons between the ringtailed lemurs at two sites (Beza Mahafaly and Tsimanampesotse) reveal habitat-related differences in isotopic signatures. These data also have implications for the conservation biology of extant lemur species and as a tool for understanding changing environments in Madagascar.

3.3.2 Verreaux's Sifaka

3.3.2.1 Sifaka Behavioral Endocrinology

Brockman and colleagues have used a combination of endocrine data (derived from analysis of fecal steroids) and behavioral data to examine the impact of physical and social environments on reproduction and mating, social strategies, male life history, and demography in Verreaux's sifaka (Brockman 1994, 1999; Brockman and Whitten 1996; Brockman et al. 1998, 2001, 2009).

Brockman found that females have flexible mating strategies and that both sexes exercise mate choice, with the opportunity to do so enhanced by estrous synchrony within groups. She also documented intense androgen-mediated mating competition in both sexes; coercive mating tactics by males; and situation-dependent receptivity in which anovulatory females mate with immigrant males regardless of season (Brockman 1994, 1999; Brockman and Whitten 1996; Brockman et al. 1998).

Beginning in 1998, Brockman et al. (2001) used longitudinal data from individually marked sifaka to document age-specific patterns of male dispersal. They showed that males exhibit marked hormonal responses to socially disruptive events during the birth season, including substantially elevated fT concentrations in alpha males residing in unstable groups, in males making aggressive attempts to immigrate into neighboring groups, and in resident males evicting subordinates.

Previous studies examining fecal glucocorticoid (*fGC*) interactions with behavior in male sifaka at BMSR showed that high fGC levels are not a predictable cost of high rank during the birth season, and that elevated fGC concentrations coincide with specific behavioral traits and social contexts, including social instability (Brockman et al. 2001) and the aggressive eviction of subordinates by resident alpha males (Brockman et al. 1998). Using data on 124 males in 55 groups collected over several seasons, Brockman et al. (2009) found that fGC levels in males were unrelated to age, residence, group stability, or rank, but were substantially higher in males residing in groups containing infants than in those without infants. Also, annual variation in male fGC levels paralleled annual changes in infant birth rates (Brockman et al. 2009). These findings support the proposition that anticipation of relatively predictable future events, such as the birth of infants, can elicit GC responses. The entire birth season is probably a stressor, especially when births coincide with uncontrollable events such as increased intergroup male transfers and infanticides (ibid.). Of the five groups targeted for aggressive male transfers during this study, four suffered takeovers and three of those groups contained one or more infants which disappeared the following day or were mortally wounded by immigrant males. This research is the first to show that in seasonal plural breeding species, elevated fGC in males reflects specific events related to reproduction rather than states or social context during the birth season. These data provide new insights into the role of endocrine mechanisms in mediating male strategies to cope with natural sources of stress in wild lemur populations.

3.3.2.2 Sifaka Life History, Demography, and Population Genetics

Life history and demography. The combination of life history, demographic, phenotypic, and genetic datasets on the sifaka population provides powerful means to test major hypotheses in life history theory, to determine patterns of selection and adaptation, and to measure fitness. For example, Richard et al. (2000) documented how body mass influences female fertility by repeatedly capturing individual females and measuring changes in body mass over time, then combining this information with rainfall and other ecological data and data on reproduction. Male and female sifaka show seasonal fluctuations in body mass, which also is lower during drought years. When the primary productivity of the forest is low, body mass is particularly low. Females who were heavier during the previous mating season were significantly more likely than lighter females to give birth in the following birth season. Richard et al. (2000) showed specifically that (1) females lose more mass than males on a seasonal basis, (2) fertility is linked to body mass, and (3) gestation and lactation are uncorrelated with periods of high body mass. These findings suggest that sifaka females follow a strategy akin to "capital breeding," in which animals store energy for reproduction rather than immediately converting it into reproduction – that is, by decoupling energy acquisition and reproduction by storing energy to be used at a later, more adaptively advantageous time period (but see Brockman and van Schaik (2005) for a reassessment of this view).

Richard et al. (2002) also documented age-specific patterns of fertility, mortality, and dispersal. They showed that female sifaka reproduce later and live longer, in relation to body size, than females of any other primate species. The life history strategy associated with delayed reproduction and extended longevity is known as bet-hedging, where animals are selected to slow down the pace of reproduction and growth to mitigate the negative effects of stochastic fluctuations in the environment that influence animal livelihoods. Because climate determines food availability, Richard et al. (2002) argued that particular rainfall patterns in Madagascar were the main drivers of the life history schedules of Malagasy fauna, which (especially those of mammals) are characterized by extreme "fastness" or "slowness" as evolutionary responses to climatic fluctuations.

Subsequently, Dewar and Richard (2007) provided additional evidence that patterns of rainfall on Madagascar show uniquely high intra- and inter-annual variability compared to locales outside of Madagascar. The influence of rainfall on sifaka demography was modeled explicitly by Lawler et al. (2009). They showed that demographic parameters such as survival, reproductive value, and expected life span were depressed when annual rainfall was below 300 mm. Furthermore, a decrease in mean annual rainfall or an increase in the variance in annual rainfall resulted in negative population growth rates. These studies concur in finding that climate plays a key role in shaping both life history and demographic traits in the sifaka population.

Population genetics. Lawler et al. (2003) genotyped 444 sifaka to assess population structure and patterns of reproduction. The genetic structure of the population mimicked the dispersal and sex-ratio pattern first observed by Richard et al. (1991, 1993). Specifically, within social groups, both average and pair-wise genetic relatedness was higher for females than for males. This makes sense given that female sifaka are mostly philopatric, whereas males disperse from their natal groups on reaching sexual maturity (Richard et al. 1993; see also Kappeler and Fichtel 2011). This results in genetically distinct matrilines across social groups and creates a population more strongly structured through female lineages than male lineages. Similarly, offspring are more genetically distinct than adults across the population, because those in any given group can share the same father but have different mothers. Thus, offspring cohorts are united through paternal alleles within social groups, but across the population each cohort of offspring is genetically different.

However, as Richard et al. (1991, 2002) have documented, most of the infants that survive to 1 year are male (60–70% in most years studied). When males reach sexual maturity they disperse, somewhat randomly, into adjacent groups. At the genetic level, this randomizes the genetic structure of the offspring cohort and results in adults within social groups retaining less genetic structure than offspring. These results also show that the sex ratio, in addition to genetic relatedness, is an important factor with respect to the evolution of social behavior. For example, Richard et al. (2002) argued that the behavioral effects of a male-biased sex ratio include intense competition between females, heightened importance of female mate choice, and female social dominance.

Genetic data coupled with phenotypic and demographic data can elucidate reproductive strategies. Lawler et al. (2005) analyzed paternity and combined phenotypic data with information on reproductive success to measure the strength of intrasexual selection on male traits relevant to male–male competition during the mating season. They found that directional selection targets leg length and size, while stabilizing selection targets body mass. That is, males with longer, stronger legs, and an intermediate body size were more successful at reproduction. These results suggest that traits related to chasing are more important to male fitness than traits related directly to fighting involving physical contact (e.g., overall body size, canine size) and provide one possible explanation for the sexual monomorphism in body mass among male and female sifaka (Fig. 3.4). During male mating competition, there is no intrasexual directional selection acting to increase male body mass relative to that of females (see Lawler 2009).

Lawler (2007) also examined male reproductive success from a population-wide perspective. Specifically, he decomposed variation in male fitness (i.e., total reproductive output) into three components: reproductive lifespan, fertility (i.e. the per-year reproductive output), and infant survival. These components were estimated for males reproducing in their resident groups and those who reproduced outside of their resident groups. The results reveal that fertility makes the greatest contribution to variance in male fitness, followed by reproductive lifespan, and offspring survival. Factors that enhance opportunities for extra-group mating include female choice, a high density of social groups with overlapping home ranges, and a restricted mating season (Lawler 2007). Thus, long-term genetic studies provide a powerful complement to behavioral-ecological studies, since they can reveal the fitness consequences of particular behaviors that occur during an animal's lifetime.

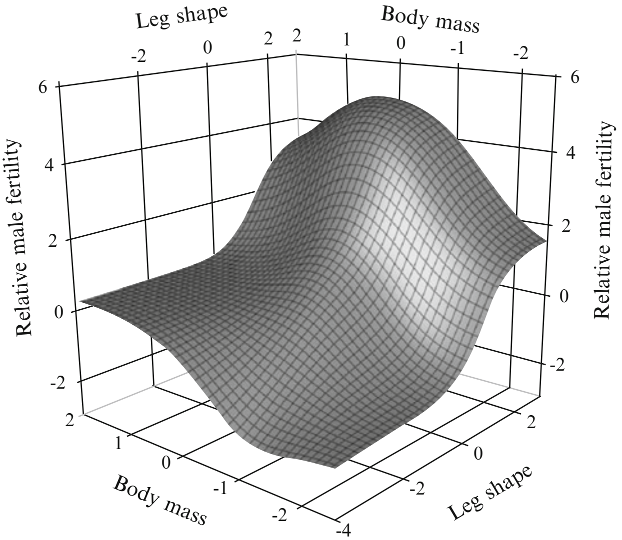

Fig. 3.4 Fitness surface showing relationship between male fertility and body mass and leg shape: Lawler et al. (2005) found that directional selection acts on leg length and thigh circumference, whereas stabilizing selection acts on body mass

3.4 Conclusions

Compared to other mammals, primates are characterized by delayed maturation, slow rates of growth, complex social behavior, and long lifespans. Because of these characteristics, many field studies of wild primates have traditionally focused on documenting behavioral interactions among one or a few individuals throughout their lives. This approach emphasizes the collection of longitudinal data on the careers of individuals rather than the collection of data on numerous individuals that comprise a population. The multidisciplinary studies of ringtailed lemurs and sifaka discussed above show that it is possible to obtain long-term data on careers of individual animals along with extensive data on many animals in multiple social groups and even on entire populations. These data have been, and continue to be, analyzed from various perspectives, thus providing important new insights into the demographic, socioecological, anthropogenic, and epidemiological factors that shape an evolving population.

The following are a few specific examples of research highlighting the benefits of long-term research at Beza Mahafaly:

1. Knowledge of the demographic structure of the ringtailed lemur population in the reserve over the long-term allowed us to determine the effects of a severe drought on the population and the factors that enabled the population to recover.

2. Research on hormone levels in ringtailed lemur males has revealed that male–male aggression and testosterone levels rise at the beginning of mating season. However, these levels fall to non-breeding baseline levels immediately after the early mating season, thus offsetting the high cost of stress related to high testosterone and high levels of aggression. Furthermore, fT levels are not affected by the number of males in a group, nor are there rank or age effects.
3. The parasite loads, types of parasites, and dental health of the ringtailed lemur and sifaka populations, both inside and out of the reserve, are affected directly by habitat structure, dietary differences, and amount and type of interaction with humans.
4. Female sifaka reproduce later and live longer, in relation to body size, than any other primate species, thus displaying a life history strategy in which the pace of reproduction and growth is slowed down to mitigate the negative effects of extreme fluctuations typical of southern Madagascar.
5. Male sifaka exhibit hormonal responses to socially disruptive events during the birth season, including marked fCG elevations in the presence of newborns associated with increased group takeovers and infanticide risk.
6. The combination of long-term genetic, phenotypic, and demographic studies allowed measurement of the strength of sexual selection in a wild primate. Specifically, sifaka males with longer, stronger legs were more successful at reproduction than were males with larger body mass, thus suggesting that traits related to chasing and locomotion were more important to male fitness than those related directly to fighting (e.g., body mass).

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Chapter 4
Long-Term Lemur Research at Centre Valbio, Ranomafana National Park, Madagascar

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Please note the erratum to this chapter at the end of the book.

Abstract We present findings from 25 years of studying 13 species of sympatric primates at Ranomafana National Park, Madagascar. Long-term studies have revealed that lemur demography at Ranomafana is impacted by climate change, predation from raptors, carnivores, and snakes, as well as habitat disturbance. Breeding is seasonal, and each species (except *Eulemur rubriventer*) gives birth synchronously to be able to wean before winter. Infant mortality is high (30–70%)

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and partly due to infanticide in *Propithecus edwardsi,* and perhaps *Varecia variegata*. Diurnal lemurs can live beyond 30 years in the wild and most females reproduce until death. Small-bodied *Microcebus rufus* live up to 9 years without signs of senescence. *Prolemur simus* migrates in search of new bamboo and mates, and related *V. variegata* mothers park their multiple offspring in "kindergartens," protected by others while mothers forage. Interference competition among sympatric lemurs occurs. Anthropogenic factors, such as past selective logging and climate change may influence the declining density of *E. rufifrons*, *P. simus*, and *P. edwardsi* while not affecting the density of pair-living species.

4.1 Introduction

Madagascar ranks as one of the world's top biodiversity hotspots because of its high endemism and high rate of habitat degradation (Myers et al. 2000; Ganzhorn et al. 2001). For primates, Madagascar has the highest conservation priority with 5 endemic families and 15 endemic genera (Mittermeier et al. 2010). Ninety-seven lemur species are now recognized of which 41% are threatened with extinction (8 critically endangered, 18 endangered, and 15 vulnerable), while 42 species remain data deficient (IUCN 2010; Mittermeier et al. 2010). Knowledge obtained from long-term field studies, such as the ones described here, is particularly valuable compared to short-term "snapshots" because long-term data can be especially useful to conservation management efforts. For effective management, park authorities can benefit from understanding the differences between normal fluctuations in population size and real trends over time, patterns which can only be detected with decades of data.

To date there are four long-term lemur research sites in Madagascar: Kirindy Forest in the dry deciduous forest of the west (Ganzhorn and Kappeler 1996; Kappeler and Fichtel 2012), the southern spiny desert reserve Berenty Private Reserve (Jolly et al. 2006; Jolly 2012), Beza Mahafaly Special Reserve (Richard

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et al. 2002; Jolly and Sussman 2006; Sussman et al. 2012), and Ranomafana National Park (RNP) in the southeastern rainforest (Wright and Andriamihaja 2002; Wright 2004). At each site, lemurs have been studied for several decades (Jolly 1966; Sussman 1974; Richard 1978; Jolly and Sussman 2006; Sussman and Ratsirason 2006; Kappeler and Fichtel 2012). In this chapter, we discuss a compilation of the findings of long-term studies of the 13 lemur species found in RNP.

4.1.1 History of Ranomafana National Park

Ranomafana National Park (RNP) is a rainforest park located in southeastern Madagascar (21°16′S, 47°20′E). The landscape is dominated by submontane rainforest, which receives a mean of 3,000 mm of rain per year during the December through March rainy season. The RNP project was initiated in 1986 with the goal of protecting the habitat of a then newly discovered lemur species, the golden bamboo lemur (*Hapalemur aureus*), and the rediscovered greater bamboo lemur (*Prolemur simus*; Meier et al. 1987). From 1986 to 1989, logging concessions were granted by the forestry department and selective logging for valuable hardwood trees was intensive. In 1991, 41,000 ha of the montane rainforest were designated as a national park (Wright and Andriamihaja 2002). The Namorona River and a parallel paved road (Route 25) bisect the park into northern and southern parcels with a third parcel on the western boundary to the north. Patricia Wright, then at Duke University, spearheaded the initial park project, an integrated conservation and development project conducted simultaneously with research on lemurs and other aspects of biodiversity (Wright 1997; Wright and Andriamihaja 2002). Management transitioned to Stony Brook University (SBU) when Wright moved there in 1991. While retaining management of research in RNP, SBU handed park management over to the Association Nationale pour la Géstion des Aires Protegées (ANGAP), the national park system, in 1998. In 2006, the System of Protected Areas of Madagascar (SAPM) replaced ANGAP and incorporated sustainable practices of resource use into park creation and management. In 2009, SAPM became Madagascar National Parks (MNP).

4.1.2 Infrastructure at Ranomafana

The first research station was built in 1989 near the entrance to RNP. This structure was a small, one-story log cabin. In 2003, the station was upgraded to a three-story stone facility adjacent to the park and overlooking the rainforest. The new research station, named the International Centre for Research and Training for the Valorization of Biodiversity (Centre ValBio), is located on Route 25 near the park entrance (Wright 2004). This hub of scientific research and education is managed by a consortium of universities headed by SBU and the Institute for the Conservation of Tropical Environments (ICTE). Founding institutions include SBU and the Universities of Antananarivo, Fianarantsoa, and Helsinki. Currently, the main building houses administrative offices, a small laboratory, a library, and a dining hall that serves 65 people. A second four-story building (15,676 square feet) will open in 2012, and will be equipped with high speed internet, modern hormone, parasite, genetics and infectious disease laboratories, an audio/visual/computer center, and living accommodations for 54 students and researchers. The Centre ValBio has authorization to do research from the Ministry of Forests and Environment of the Government of Madagascar, and works closely with the MNP, especially on conservation management.

Centre ValBio's administration oversees the Departments of Research, Biodiversity Monitoring, Logistics and Management, and Community Outreach including Health and Education. Seventy-two local staff, many trained as lemur technicians and Malagasy biodiversity experts, work at Centre ValBio and live in the villages surrounding the park. The health and education team provides training and outreach programs to 22 nearby villages. Reforestation with native species and medicinal plant gardens managed by traditional healers are two important components of Centre ValBio's outreach efforts (Wright et al. 2005a). Twenty conservation clubs foster appreciation for conservation and a cooperative of artisanal women weavers is a sustainable contributor to village economics.

4.1.3 History of Ranomafana Lemur Research

Ranomafana contains 13 lemur species of which 8 have been subjects of long-term research (Table 4.1). Seven of the 13 species have been subject to taxonomic revision during the 20-year period (Table 4.2). Five species have been redesignated based on genetics and morphology. One new species has been described (*H. aureus*), one taxon has been raised to a new genus (*P. simus*), and one remains to be identified (*Cheirogaleus* sp.).

Twenty-six PhD dissertations and 26 Masters theses on lemurs have been completed since the park's initiation, and an additional eight dissertations are currently in progress. Major foci of these long-term studies have been diurnal lemurs, including behavioral ecology, demography, life history, reproductive biology, stress and reproductive hormones, parasites, feeding and nutritional ecology, morphometrics, predation, communication, and cognition (Table 4.1). Nocturnal lemurs have been studied less intensively, with emphases on reproduction, hibernation, parasites, and vocalizations (Table 4.1). Moreover, research in ecosystem dynamics and conservation with emphasis on lemur seed dispersal, climate, and tree phenology are also ongoing (Dew and Wright 1998; Wright et al. 2005b; Dunham 2008; Dunham et al. 2008, 2010; Ganzhorn et al. 2009).

Researchers have studied lemurs at four sites, each approximately 4 km^2, within the contiguous forest of the park (Fig. 4.1). Three sites (Vatoharanana, Valohoaka, and Mangevo), each with bush camp facilities, are in undisturbed or minimally

Table 4.1 List of RNP lemur species and references to research

Species	Common name	References
Avahi peyrierasi	Peyrierasi's woolly lemur	Harcourt (1987, 1988), Roth (1996), Andriantompohavana et al. (2007a)
Cheirogaleus crossleyi	Crossley's dwarf lemur	Wright and Martin (1995), Blanco et al. (2009), Groeneveld et al. (2011)
Cheirogaleus sp.		Not yet described
Daubentonia madagascariensis	Aye–aye	Sefczek (2009)
Eulemur rufifrons	Red-fronted brown lemur	Meyers et al. (1989), Overdorff (1991, 1993, 1996), Merenlender (1993), Johnson and Overdorff (1999), Overdorff et al. (1999), Johnson (2002), Johnson et al. (2005), Erhart and Overdorff (2008a)
Eulemur rubriventer	Red-bellied lemur	Overdorff (1991, 1993, 1996), Durham (2003), Overdorff and Tecot (2006), Tecot (2008, 2010), Wright et al. (2011), Tecot in press
Hapalemur aureus	Golden bamboo lemur	Meier et al. (1987), Wright et al. (1987), Glander et al. (1992), Tan (1999, 2007), Arrigo-Nelson and Wright (2004)
Hapalemur griseus	Gray gentle bamboo lemur	Meier et al. (1987), Tan (1999), Grassi (2002), Mutschler and Tan (2003), Arrigo-Nelson and Wright (2004), Herrera et al. in press
Lepilemur microdon	Small toothed sportive lemur	Porter (1998), Louis et al. (2006)
Microcebus rufus	Brown mouse lemur	Wright and Martin (1995), Atsalis et al. (1996), Atsalis (1999a, 1999, 1999b, 2000, 2008), Louis et al. (2006), Blanco (2008), Blanco and Meyer (2009), Durden et al. (2010), Deppe (2011)
Prolemur simus	Greater bamboo lemur	Meier et al. (1987), Wright et al. (1987), Tan (1999, 2007), Bergey and Patel (2008), Wright et al. (2008b), CVB census
Propithecus edwardsi	Milne Edwards' sifaka	Hemingway (1995, 1998), Wright (1995), Erhart and Overdorff (1998), Jernvall and Wright (1998), Pochron and Wright (2003), Arrigo-Nelson and Wright (2004), Mayor et al. (2004), Pochron et al. (2004), King et al. (2005, 2011), Pochron et al. (2004, 2005), Arrigo-Nelson (2006), Lehman et al. (2006), Irwin (2007, 2008), Morelli (2008), Bailey et al. (2009), Wright et al. (2009), Wright et al. (2011)
Varecia variegata editorium	Black-and-white ruffed lemur	White et al. (1995), Balko and Underwood (2005), Overdorff et al. (2005), Ratsimbazafy (2006), Baden et al. (2008)

Table 4.2 List of RNP lemurs including recent taxonomic changes with activity pattern: nocturnal (N), diurnal (D), and cathemeral (C); weight in grams; IUCN status

Current nomenclature	Previous	Activity	Status	Weight (g)	References
Avahi peyrierasi	*A. laniger*	N	DD	960	Zaramody et al. (2006)
Cheirogaleus crossleyi	*C. major*	N	DD	350	Groeneveld et al. (2011)
Daubentonia madagascariensis		N	NT	2,500	Feistner and Sterling (1995)
Eulemur rufifrons	*E. fulvus rufus*	C	NT	2,200	Mittermeier et al. (2010)
Eulemur rubriventer	*E. rubriventer*	C	VU	2,400	Mittermeier et al. (2010)
Hapalemur aureus	*New species*	D	EN	1,800	Meier et al. (1987)
Hapalemur griseus ranomafanensis	*H. griseus*	D	NE	990	Rabarivola et al. (2007)
Lepilemur microdon	*L. mustelinus*	N	DD	990	Louis et al. (2006)
Microcebus rufus	*M. rufus*	N	LC	45	Louis et al. (2006)
Prolemur simus	*Hapalemur simus*	D	CR	2,800	Groves (2001)
Propithecus edwardsi	*P. diadema edwardsi*	D	EN	5,800	Mayor et al. (2004)
Varecia variegata editorium	*V. variegata variegata*	D	CR	3,500	Groves (2001)

From IUCN 2010 RedList Guidelines: *NE* Not Evaluated, *DD* Data Deficient, *LC* Least Concern, *NT* Near Threatened, *VU* Vulnerable, *EN* Endangered, *CR* Critically Endangered, *EW* Extinct in the Wild, *EX* Extinct

disturbed rainforest. The fourth is Talatakely located near Route 25, selectively logged by hand from 1986 to 1989, and now accessible to tourists (Wright and Andriamihaja 2002).

Ad hoc transects and surveys have been conducted throughout the park since 1987. Since 2003, researchers conducted lemur surveys along eight 2 km transects, from the edges to the interior (Fig. 4.1). The surveys have led to the identification of new social groups and discovery of new species (Irwin et al. 2000, 2005; Arrigo-Nelson and Wright 2004; Andriantompohavana et al. 2007a, b; Wright et al. 2008b).

4.2 Long-Term Data Collection and Management

4.2.1 Long-Term Research on Focal Species

Most adults from 6 of the 7 diurnal lemur species at each of the main research sites have been marked with tags and collars for individual identification (*Propithecus edwardsi, Hapalemur aureus* and *Prolemur simus, Eulemur rubriventer,*

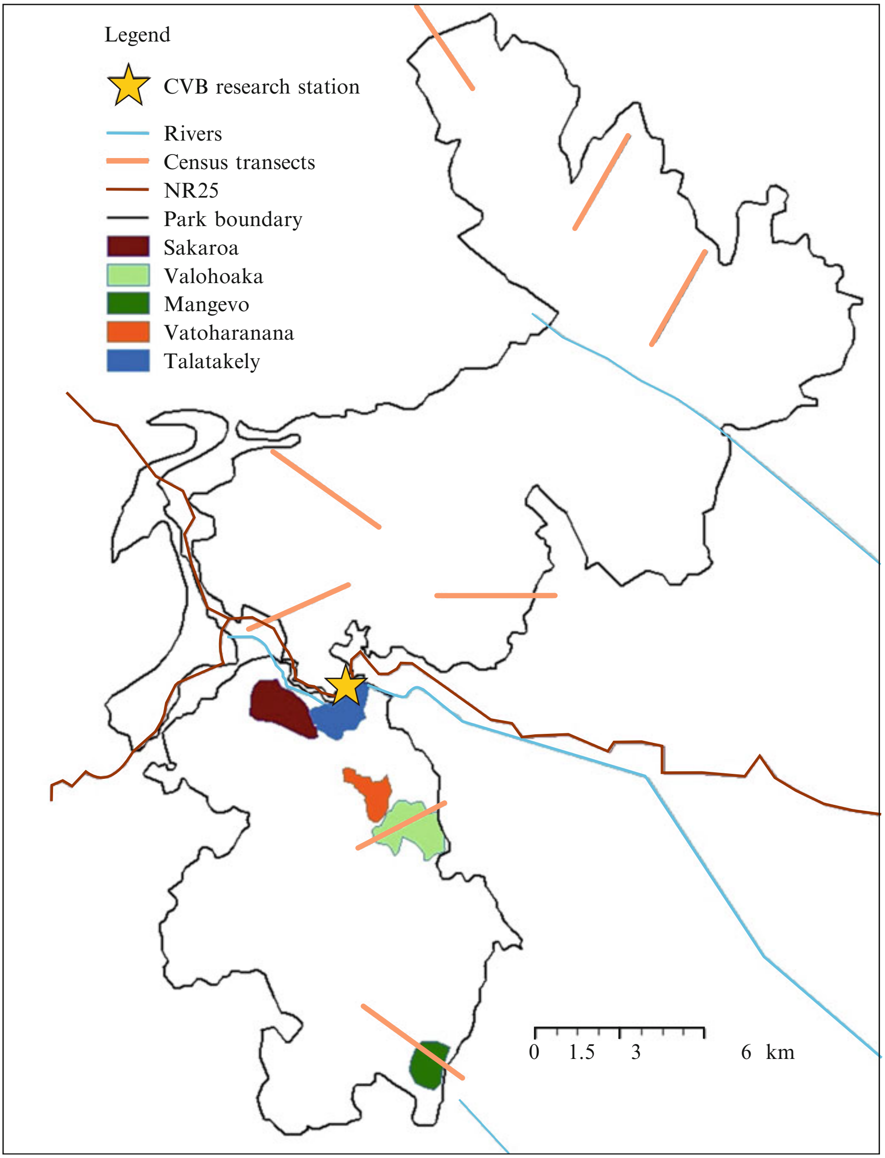

Fig. 4.1 Map of Ranomafana National Park with long-term study sites and long-term transects marked

E. rufifrons, and *Varecia variegata*). Many study groups have at least one member with a telemetry radio-collar for locating groups. Data collection on lemurs has been ongoing in Ranomafana for more than 24 years (Wright 2004; Table 4.1).

4.2.2 Weights, Measures, and Biomedical Data

Beginning in 1987, we established a protocol to obtain morphometric and health data on all seven diurnal lemur species. A trained team of Malagasy technicians capture individuals using remote injection techniques, whereby a Telinject blow gun or CO_2-powered rifle is used to tranquilize individuals with Telazol administered with lightweight darts (Glander et al. 1992; Wright 1995). Researchers, technicians, and veterinarians measure, collect samples from, and mark adult animals with a nylon collar and individual identification tags. Since 1999, captured animals also received a subcutaneous microchip (AVID, HomeAgain®) for permanent identification. While animals are tranquilized, the team uses a checklist developed to record information on general physical condition, body mass, and reproductive state (Glander et al. 1992). Dental molds are taken; physical measurements are recorded; and hair, fecal, blood, and external parasite samples are collected. We used data including body weights, canine eruption patterns, general tooth wear, female nipple length, and presence or absence of descended testes to assign age categories to all known study individuals (Johnson et al. 2005; Baden et al. 2008; Erhart and Overdorff 2008a; Wright et al. 2008a). Actual ages are known for most animals from recorded births. For individuals whose birth date is uncertain (i.e., individuals in the population since before 1986 or immigrants from other groups), Jernvall and King developed an accurate method to determine age by comparing year-to-year tooth wear (King et al. 2005). Beginning in 2003, veterinarians now also conduct detailed health evaluations, compiling biomedical profiles of all lemur individuals (Junge and Louis 2005).

Microcebus rufus and *Cheirogaleus crossleyi* have been intermittently studied since 1990 (Wright and Martin 1995; Atsalis 1999a, 2008). Beginning in 2003, subcutaneously placed microchips have allowed us to monitor individual mouse lemurs during long-term studies (Blanco 2008; Blanco and Meyer 2009; Blanco and Rahalinarivo 2010; Durden et al. 2010; Zohdy et al. 2010; Deppe 2011). Mouse lemurs are captured in Sherman traps baited with bananas, then weighed, measured, and released at the capture site. Over 300 individuals have now been marked. Dental tooth casts reveal ages, and repeated captures allow data collection on body mass fluctuations associated with torpor patterns (Atsalis et al. 1996; Atsalis 2008), reproductive status (Blanco 2008), parasite prevalence (Zohdy et al. 2010), and noninvasive behavioral experiments (Deppe and Wright 2009; Deppe 2011).

4.2.3 Long-Term Phenology, Climate, and Terrestrial Vertebrate Data

Tree phenology, daily rainfall, and temperature data have been recorded since 1987. Tree phenology began with monthly monitoring of 100 trees of 25 lemur fruit species and was expanded in 1995 with monthly monitoring of trees from more than 71 species, representing 26 genera and 19 families (Clark and Clark 2006, 2010). Initially, tree diameter measurements (diameter at breast height, DBH) were taken every 5 years, but beginning in 2004, DBH measurements are taken every 6 months (Clark et al. 2003) to correlate tree growth with rainfall. Maximum and minimum temperature and rainfall data are taken at 06:00 h each day with a team of technicians responsible for accuracy. Camera trap data are taken in distant regions of the park to monitor carnivores and terrestrial vertebrates (Gerber et al. 2010).

4.2.4 Database Management

Long-term data collection and management requires standardized protocols. The following are areas where protocols are in place: (1) permanent identification of individuals for behavioral observation and census, (2) lemur capture data including weights, measurements, and biomedical data, (3) focal lemur sampling, (4) tree phenological data, (5) daily temperature minima/maxima and rainfall, (6) ad libitum observations of predation, reproduction, and intergroup aggression, (7) GIS data for mapping, and (8) lemur fecal sample data. The phenology and climate data are archived and accessible to researchers at Centre ValBio and will soon be available on the ICTE/Centre ValBio website (http://icte.bio.sunysb.edu). Data from projects under the supervision of Dr. Wright are transcribed from field notebooks into Excel spreadsheets, by local research technicians with oversight by the CVB Chief Technical Advisor or US students at SBU with postdoctoral oversight. Data from other projects are the responsibility of the project's principal investigators. Three years after a researcher has terminated data collection, the data can be transferred into the Centre ValBio central database and made available to CVB researchers (with proper citation assured).

4.2.5 Research Highlights from Long-Term Data

Since 1986, the principal goal of primate research at Ranomafana has been to understand the factors driving the behavioral ecology of lemurs in a species-rich community. Our research has focused on particular species that have been the subjects of intensive study over 20+ years, as well as community level analyses to understand the effects of competition, predation, and habitat quality on species richness and on relative abundance. Further, the mixed history of anthropogenic disturbance has allowed comparative work to elucidate the effects of disturbance on lemur physiology, behavioral ecology, and community structure. However, for this chapter we will concentrate on population changes documented over decades of observation.

4.3 Population Ecology

4.3.1 Flexibility of Behaviors

Many social behaviors were not observed until after many years of study. Female takeovers of groups, male lethal aggression from other males, and simultaneous immigrations of related males into groups were not observed in the first 10 years of studying *P. edwardsi*, but were observed in the next decade (Morelli et al. 2009). After years of losing track of focal study groups, continuous long-term observations confirmed that *E. rufifrons* groups seasonally expand their range and travel over 4,000 m to find fruit (Erhart and Overdorff 2008a). Likewise, when *P. simus* group size began to decline in 2003, we began to observe patterns of male disappearance, as well as females' (and their offspring) migrations and wanderings for 3 months before returning to the original territory. This migration behavior was not seen in the first decade (CVB unpublished census data; Wright et al. 2008b). In addition, while breeding out of the birth peak had been observed early on in *E. rubriventer* (Overdorff unpublished data), it was not until almost 20 years of data were analyzed that it was determined that they have been observed to breed in eight different months of the year (Tecot 2010).

4.3.2 Lemur Group Size, Composition, and Social Organization

Social groupings have long been investigated in primates (Crook and Gartlan 1966; Eisenberg et al. 1972; Clutton-Brock and Harvey 1977) by correlating ecological factors to social organization (Janson 1992). For instance, it has been proposed that lemurs' relatively small group sizes may be due to nocturnal ancestry (van Schaik and Kappeler 1996) or smaller crowned fruit trees (Wright 1999). We initially reported that *P. edwardsi* have a multimale, multifemale social organization in groups of 3–9 individuals (Wright 1995). However, by 2003 we had observed every type of social grouping in this species with potential for all different types of mating systems. Moreover, we learned that group sizes can get as large as 11 (Pochron and Wright 2003). In contrast, we consistently found *E. rubriventer* in socially monogamous pairs accompanied by immature offspring (Merenlender 1993; Overdorff and Tecot 2006; Tecot 2008). Although previously described as pair-living (Tan 1999), *H. griseus* and *H. aureus* groups can contain two breeding females in habitats with abundant bamboo (Grassi 2002; Wright personal observation). Using the older mating system terminology did not reflect this flexibility and, as stated by Kappeler and van Schaik (2002), these groupings are really patterns of social organization. With that conceptual framework it makes sense that a high frequency of pair-living and small groups among lemurs may be a response to food resource scarcity and unpredictability (van Schaik and Kappeler 1996; Wright 1999), and may be linked to female dominance (Dunham 2008).

4.3.3 Dispersal

Understanding dispersal is critical to understanding population dynamics, but these data are difficult to collect. Long-term data on multiple groups make it possible to observe dispersal in long-lived primates. For *P. edwardsi,* we initially thought that only males emigrated from natal groups (Wright 1995). We have since observed emigration and immigration by both sexes (Morelli 2008), aggressive group takeovers by females (Morelli et al. 2009), and targeted aggression within and between groups (Wright 1995). Females disperse from their natal groups at a younger age than their male counterparts but male secondary dispersal is more common (Morelli et al. 2009). Male dispersal occurs in the 3–5 months before the breeding season. During this time, males visit other groups and male scent marking frequencies and testicular volume increase (Pochron et al. 2005; Pochron and Wright 2005). Testosterone levels also increase (Tecot et al. 2010). Depending on breeding opportunities, males undergo natal dispersal between 3 and 9 years of age. Most adult *P. edwardsi* males transfer at least three times in their lifetimes (Morelli et al. 2009).

In contrast, *E. rufifrons* males in Ranomafana transfer only once in their lifetimes, typically at 3–5 years old and just before the breeding season. Immigrant males are often accepted without aggression and become social partners of one adult female for 3–6 years, mating preferentially with her (Overdorff 1993, 1998; Erhart and Overdorff 1998). Female dispersal has not been seen in *E. rufifrons*, but groups may fission along matrilineal lines (Overdorff et al. 1999; Erhart and Overdorff 2008b), a behavior which differs from *Eulemur* groups in western Madagascar (Wimmer and Kappeler 2002; Ostner and Kappeler 2004).

Observations of *E. rubriventer* revealed that both sexes disperse from their natal group at 2.5–3 years of age (Overdorff and Tecot 2006). Hostile replacement of resident adult females by nongroup females has been observed, but males have not been aggressively replaced. One dispersing female was seen with a new male in an adjacent territory 15 years later (Overdorff and Tecot 2006). Our data on the genetics of *E. rubriventer* offspring revealed that the resident male consistently fathers the offspring, and there are no data that indicate extra-pair copulations (Merenlender 1993).

Molecular and behavioral data show that dispersal in *Varecia* is not sex-biased, as within-sex relatedness scores were similar for males and females (Baden 2011). Mark–recapture studies of brown mouse lemurs (*M. rufus*) have shown that male membership in the population changes at a higher rate than female membership (Atsalis 2000, 2008), and that males can disperse relatively long distances (Karanewski personal communication; Zohdy personal communication). In all species thus studied, dispersal patterns ensure heterozygosity, an advantage for conservation strategies (Merenlender 1993; Morelli et al. 2009, Bradley and Baden personal communication).

4.3.4 Reproductive Hormones

P. edwardsi, E. rubriventer, and *M. rufus* fecal hormone profiles have been developed (Tecot 2008, Tecot et al. 2009; Blanco and Meyer 2009). In *P. edwardsi* and *E. rubriventer*, estradiol, progesterone, testosterone, dihydrotestosterone, and cortisol are being measured to determine the ovarian steroid fecal metabolites that characterize reproduction. Progesterone levels can reliably indicate pregnancy in these species, and estradiol levels reliably indicate fetal sex (Tecot et al. 2009). As expected, patterns of change in fecally excreted steroid levels during the reproductive season in *M. rufus* showed estradiol (E-2) levels were elevated around estrus, whereas progesterone levels were highest during late pregnancy and around parturition (Blanco 2008; Blanco and Meyer 2009). Blanco (2008) documented moderate estrous synchrony among female mouse lemurs, with clusters of females showing strong estrous synchrony. Two females showing signs of abortion or perinatal death of offspring also showed renewed vaginal swelling in late December, suggesting that some form of polyestry (i.e., as reproductive compensation for fetal loss) exists at RNP (Blanco 2008). With these baselines and proof of concept established, we can now investigate questions associated with development, sexual relationships, and seasonal breeding.

Hormonal studies of dominance rarely investigate inter-sexual relationships. To determine whether female dominance might be mediated by hormonal levels, we investigated androgens (dihydrotestosterone and testosterone) in male and female *P. edwardsi* (Tecot et al. 2009). While DHT levels were higher in males than in females, there was no significant sex difference in testosterone levels. Similar testosterone results were found in *M. rufus*. These results differ from those found for all other mammals studied to date, in which male testosterone levels are consistently higher than female levels, with the exception of the female-dominant rock hyrax (Koren et al. 2006). In other masculinized mammals such as the hyena and ring-tailed lemur, androstenedione is elevated in females, but testosterone levels remain higher in males. This finding may have important consequences for understanding sex differences in lifespan and senescence. Maintaining high testosterone levels may explain why mammalian males frequently have shorter life expectancies than females, but testosterone burden may not explain the sex differences in lifespan in *P. edwardsi*. However, dispersal season testosterone levels increase significantly in both sexes, and if males continue to disperse throughout their lives and females do not, testosterone levels may still contribute to shorter male lifespan (Tecot et al. in prep.).

4.3.5 Reproductive Success

Obtaining lifetime reproductive success data from wild primates is possible for females who have been followed throughout their lifespans (Bronikowski et al. 2011).

By coupling life-long observations with genetic evidence, calculating male reproductive success is now possible. Currently, we have lifetime reproductive success for two females and one male *P. edwardsi*. One female, killed by a fossa at age 32, gave birth to 13 offspring (7 males and 6 females). Five of these animals lived to reproductive age with two males living to emigrate from their natal group (Pochron and Wright 2003; King et al. 2005, 2011). A second female who died at 16 had 7 offspring (3 males and 4 females). Three males and one female survived to reproductive age; the males migrated to breeding groups and the female reproduced in her natal group after her father transferred. Genetic evidence provides a measure of lifetime reproductive success for one male who produced offspring in two groups before he was killed by an immigrant male during a group takeover at age 19. He fathered 14 offspring, 9 females and 5 males, in one group with 4 male and 3 female offspring surviving to reproductive age. Following a second transfer, he sired a 15th offspring, which disappeared, a probable infanticide, after his father was killed. Without continuous long-term data collection we would not be able to have these data on lifetime reproductive success in even these few individuals.

In many primates, heavier females have more surviving offspring (Altmann 1980; Terborgh and Janson 1986). We also see this trend in lemurs. *P. edwardsi* females who were heavier during the previous mating season were significantly more likely to give birth in the following birth season than lighter females (Morelli et al. 2009). Habitat disturbance appears to have a disproportionate impact on the body mass of female *P. edwardsi*. A comparison between Talatakely (logged) and Valohoaka (unlogged) revealed that adult females but not males living within the unlogged forest weighed significantly more than those females living in the disturbed forest (Arrigo-Nelson 2006). When males and females were compared within sites, significant differences in body mass were found only at the disturbed forest site. Given the climatic and reproductive synchrony of the two study sites, and the fact that body mass is positively associated with reproductive success in some primates (Stevenson 2005), these data suggest that differences in *P. edwardsi* feeding behavior and nutrient intake may affect future reproductive success.

4.3.6 Health and Parasites

Although we follow many species daily, we rarely see signs of illness. Over the years, we have seen a wide range of effects of fighting and predation attempts. Wounds are relatively common during the breeding season and we have observed one or both testicles missing in individuals of *E. rufifrons* and *P. edwardsi*. In *P. edwardsi, E. rubriventer*, *E. rufifrons*, and *M. rufus* individuals have been found functioning with sight in only one eye (Erhart and Overdorff 2008a). Older individuals have worn teeth and in two individuals of *P. edwardsi* we have seen healed abscessed teeth (King et al. 2005; Wright et al. 2008a). In *E. rufifrons,* *E. rubriventer,* and *V. variegata* we have captured very old individuals with teeth worn to the gums.

The diversity and prevalence of parasites has been found to influence health and fitness in other mammals (Hart 2007; Price and Kirkpatrick 2009). The variation among individuals and the transfer of parasites among lemur species is presently unknown, as is the incidence of disease that parasites cause. A variety of roundworms and pinworms have been observed in lemur intestines, but further study is necessary (Junge and Louis 2005; Junge and Sauther 2006; Irwin and Raharison 2009). Our initial studies suggest that one species of parasite may be found on many species of these sympatric lemurs, but there are differences in prevalence among species. For example, *Makialges* spp., a parasitic mite, was abundant on *P. edwardsi* (80%), *P. simus* (67%), and *H. aureus* (83%), yet rare on *E. rufifrons* (3%) and *V. variegata* (14%), and absent on *H. griseus* (Wright et al. 2009; Hogg et al. in press). Large group size has been proposed as a factor for higher parasitism (Freeland 1976), but the largest groups in *E. rufrifrons* had the lowest incidence. Large body size might be more attractive for parasites than smaller body size (Freeland 1976), and indeed larger species had the most ectoparasites.

Additionally, lemurs may have species-specific parasites. For example, *M. rufus* is ecto-parasitized by three tick and one louse species. This louse, *Lemurpediculus verruculosus*, is likely a brown mouse lemur-specific parasite (Durden et al. 2010). A new species of wingless, bloodsucking hippoboscid fly, *Allobosca crassipes,* was recently described as a parasite of *P. edwardsi* and *V. variegata* (Vaughn and McGee 2009).

Parasites may increase in primates living in forests with anthropogenic disturbance and be correlated with disease and decreased fitness (Dobson and May 1986; Chapman et al. 2009). We have some evidence that this trend holds true in the Malagasy rainforest. Wright et al. (2009) found that habitat disturbance may account for high ectoparasite loads in *P. edwardsi*. Endoparasite prevalence in *M. rufus* in 2007 was higher in more disturbed habitat than in the less disturbed habitat. In 2008 and 2009 this difference disappeared, and linking habitat disturbance with lemur parasites should be done with caution. Again, long-term studies allowed us to differentiate between minor fluctuations and the consistent correlations with factors such as climate, body size, group size, or habitat disturbance factors.

4.3.7 Mortality: Adults and Infants, and Infanticide

Adult mortality is generally caused by predation, rather than by illness, wounds, or infections (see Sect. 4.4.1). Adult mortality for the lemurs at Ranomafana is low, as would be expected for long-lived primates (Erhart and Overdorff 2008a; Pochron et al. 2004). In contrast, infant mortality is high (overall approximately 50%) and food stress due to environmental unpredictability may account for some mortality (Wright 1999; Richard et al. 2002).

Long-term observations have also allowed us to document infanticides and infanticide attempts. The killing of infants of up to 2 months of age has been observed in *P. edwardsi*, with both immigrant males and females as perpetrators (Wright 1995; Erhart and Overdorff 1998; Pochron et al. 2004; Morelli et al. 2009). Over 24 years, there have been 9 infanticides out of 60 births (15%) associated with immigration in 4 groups of *P. edwardsi* (Morelli et al. 2009). These infanticides have brought the mothers back into estrus a year earlier in a species that gives birth every other year, providing males with the opportunity to improve their reproductive success (Hrdy 1977; Erhart and Overdorff 1998). A potential infanticide attempt may have also been observed when a *V. variegata* male approached and then entered an unguarded nest, knocking two young infants to the ground over 10 m below; neither infant survived the fall. To date, we have not seen infanticide in either *E. rufifrons* or *E. rubriventer* (Durham 2003; Erhart and Overdorff 2008a; Tecot 2008).

4.3.8 Lifespan

Our long-term research has allowed us to document long lifespans (over 30 years old) in individuals of all the diurnal species of wild rainforest lemurs, regardless of body mass (Erhart and Overdorff 2008a; Baden 2011; King et al. 2011). For *P. edwardsi* we documented a dramatic difference in the maximum lifespans of males and females. Since 1986, few old males have been observed whereas three females are known to have lived beyond 30 years of age. Therefore, males cease contributing genetically to the population after about 20 years, whereas we have no evidence that old females cease reproducing (Wright et al. 2008a; King et al. 2011). In *E. rufifrons*, males over 10 years old were peripheralized and replaced in breeding position by younger nonnatal males (Overdorff et al. 1999). Aged males were burdened with handicaps; one had only one eye, another only partial use of the right hand, another had lost both testicles, and two had visible limps (Overdorff et al. 1999; Erhart and Overdorff 2008a).

In *E. rufifrons* older individuals have been seen, and one functioned with only one eye. These scars and wounds are male-biased and indicate violent male–male aggression, which may account for the shorter lifespan of males as observed in many primate species (Bronikowski et al. 2011). In *E. rubriventer* older individuals have been seen, with one female a minimum of 17 years of age (Tecot 2008), though scars and wounds in this pair-bonded species are generally not evident (Tecot personal observation). In *V. variegata*, both older males and older females were observed in the population at Mangevo, suggesting that male–male aggression may not be as pronounced in this species (Baden 2011). These individual life histories add up, over time, into a better understanding of the evolution of social organization in each species.

With new dental technology that has become available in the past 5 years, Zohdy has documented that wild brown mouse lemurs survive up to 9 years of age and do not experience any of the physical symptoms of senescence that are seen in captive congeners (Bons et al. 2006). On the basis of dental wear, we have found that many brown mouse lemurs survive past 5 years (the age of the onset of senescence in captivity) and these aged individuals represent 9% of those captured. It is possible that few mouse lemurs reach old age because of high predation rates (Goodman et al. 1993; Karpanty 2006; Karpanty and Wright 2007; Sefczek 2009; Deppe 2011).

4.3.9 Nutritional Ecology

In contrast with many sympatric monkey diets, rainforest lemur diets are very diverse (Terborgh 1983; Struhsaker 1997). Studying these species over the long term and in different environments revealed the flexibility in diet within certain constraints. Many lemurs have anatomical specializations such as a large cecum or a long foregut to better digest bamboo or leaves from other plants. For example, *Avahi* and *Lepilemur* both eat leaves, but *Avahi* chooses leaves with tannins, whereas *Lepilemur* chooses leaves with alkaloids (Ganzhorn et al. 1985). The three bamboo lemurs all consume nearly 95% bamboo, but two species can tolerate large amounts of cyanide in the shoots (Glander et al. 1992; Tan 1999; Ballhorn et al. 2009). Unlike any other lemur species, *P. simus* with its strong jaws and big teeth has physical capabilities to open the tough culm of the bamboo and eat the pith (Tan 1999; Vinyard et al. 2008; Yamashita et al. 2009), and *H. griseus* eats primarily bamboo leaf petioles. *Daubentonia* eats beetle larvae extracted from dead wood, a niche taken by woodpeckers in other continents (Cartmill 1974). Recently, a comparative study of the four diurnal frugivores revealed that there is much more specialization in fruit choice than previously thought, with the fruit of entire plant families exploited by only one diurnal lemur species in the forest (Wright et al. 2011).

Our most comprehensive dietary studies have been conducted on *P. edwardsi*. Early work by Hemingway (1998) on the Vatoharanana population revealed that they ate leaves, fruits, and seeds in nearly equal proportions. More recent work by Arrigo-Nelson (2006) has added comparative data on sifaka populations at Talatakely (disturbed forest) and Valohoaka (undisturbed forest). Selective logging has altered species composition in the disturbed forest; in response, sifakas have altered their diet by consuming plant taxa in disproportion to their abundance in the forest and by relying more heavily on food from plant life forms other than trees. Disturbance limits the ability of sifakas to consume fruit and seeds, their preferred food and, as they appear to consume leaves in an effort to replace these missing foods, this creates a discrepancy in the nutrient intake of sifakas living within this habitat (Arrigo-Nelson 2006). As fruit availability was found to be lowest during the most climatologically and reproductively harsh months of the year, we hypothesize that this discrepancy may severely impact infant survival and, with it, the reproductive success of sifakas living in disturbed forest habitats.

Habitat differences in diet are evident in *E. rubriventer* as well. In a 19-month study in Talatakely and Vatoharanana, Tecot (2008) found that during the scarce season, dietary overlap decreased and the proportion of the diet composed of fruits, flowers, and leaves differed between the two sites. Seasonal changes in behavior and diet were greater in the undisturbed site, indicating more flexibility in that site. Most notably, during an entire month of the scarce season, animals in the disturbed site spent 100% of their time eating unripe fruit from the invasive Chinese guava (Tecot 2008).

Atsalis (1999, 2008) conducted a 17-month feeding study on *M. rufus* and found that this species fed on a wide variety of fruits, mistletoe berries, and insects, especially beetles. The seeds of *Bakerella* spp., epiphytic semiparasitic mistletoes high in lipids, were present in 42% of fecal samples that contained fruit and this food was consumed year-round irrespective of habitat-wide fruit availability (Atsalis 1999, 2008). This abundant mistletoe is eaten by many lemurs and has been documented to be a fallback food in both disturbed forest areas and forest fragments (Arrigo-Nelson 2006; Irwin 2006).

4.4 Community Ecology

4.4.1 Predators on Lemurs

Predation is a major selective factor in primates and major cause of mortality (Isbell 1994; van Schaik 1983; Zuberbühler 2007). Predators of Ranomafana lemurs include birds, mammalian carnivores, and snakes (Table 4.3). Two raptors,

Table 4.3 Known predation on lemurs in Ranomafana National Park

Lemur species	Carnivore	Boa constrictor	Raptor
Avahi peyrierasi	Not observed	Not observed	*Accipiter*++ *Polyboroides* ++
Cheirogaleus crossleyi	*Galidia*++	Yes	*Accipiter* ++
Cheirogaleus sp. nov.	Unk.	Unk.	Unk.
Daubentonia madagascariensis	Not observed	Not observed	Not observed
Eulemur rufifrons	*Cryptoprocta*+	Not observed	*Accipiter*++
Eulemur rubriventer	*Cryptoprocta*+	Not observed	*Accipiter*+
Hapalemur aureus	Not observed	Not observed	Not observed
Hapalemur griseus	Not observed	Not observed	*Accipiter*+++ *Polyboroides* ++
Lepilemur microdon	Not observed	Not observed	Not observed
Microcebus rufus	*Galidia*++	Yes	*Accipiter*++ *Polyboroides*++
Prolemur simus	Not observed	Not observed	*Accipiter*++
Propithecus edwardsi	*Cryptoprocta*+++	Not observed	Not observed
Varecia variegata editorium	*Cryptoprocta*++	Not observed	*Accipiter*+

Wright et al. (1997), Wright and Martin (1995), Wright (1998); Karpanty and Wright (2006), Erhart and Overdorff (2008a), Baden (2011), Deppe (2011)

+ observed once, ++ 2–14 observations, +++ 15–30 observations

Table 4.4 Changes in *Propithecus edwardsi* population size over time in relation to the observed predation events by *Cryptoprocta ferox*

Time step	Population density	# Predation events	Comments
1990–1995	7 ind/km^2	3	Two adult and three immature members of three groups
1996–2000	5 → 12 ind/km^2	0	No known predation events
2001–2005	12 → 3–6 ind/km^2	5	Two immature, two old-age and one prime-age adults from two groups
2006–2010	6 → 3 ind/km^2	6	Two immature, three old-age and one prime-age adults from four groups; extinction of two study groups in 2007

The oscillation in population size in relation to known predation events indicates that fossa predation is a major cause of population size change for *P. edwardsi*. Data are generated from one study site, Talatakely over 20 years with observations of known groups, direct observations of corpses with indications of fossa predation and long-term census data. *Arrows* within population density column indicate trends in size change within the 5-year interval

Henstii's goshawk (*Accipiter hensteii*) and the Madagascar harrier hawk (*Polyboroides radiatus*) (Karpanty and Wright 2007) eat small-bodied nocturnal (*C. crossleyi, M. rufus,* and *A. peyrierasi*) and diurnal (*E. rufifrons* and *H. griseus*) lemurs. The lemurs preferred by raptors, *A. peyrierasi* and *H. griseus*, weigh approximately 1 kg (Karpanty 2006), suggesting that the body mass, not activity cycle, account for the preference.

A major predator of lemurs is the fossa (*Cryptoprocta ferox)*, a viverrid carnivore that weighs between 8 and 12 kg, is agile in the trees, and hunts diurnally and nocturnally. The fossa has made a major impact on the population of the largest lemur in Ranomafana, *P. edwardsi* (Table 4.4; Wright 1995, 1998; Wright et al. 1997; Irwin et al. 2009) as well as on *V. variegata* in recent years (Baden personal communication). Over 20 years, it seems that predation events happen during temporally clumped periods that cut population densities by up to 50%. Fossa predation has caused the extinction of two long-term study groups and independent censuses of the study population support the tremendous impact on population density (Table 4.4; Irwin et al. 2009; see also Kappeler and Fichtel 2011). *Galidea elegans*, a diurnal mongoose weighing less than a kilogram, has been observed eating and stalking *M. rufus* and *C. crossleyi* (Wright and Martin 1995). Finally, boa constrictors (*Sanzinia madagascariensis*) have been mobbed by *Microcebus* and are known to eat *Cheirogaleus* (Wright and Martin 1995; Deppe 2011). Data on all of these rare events can only be accumulated during long-term studies.

4.4.2 Interspecific Aggression

Interference competition by close relatives has been cited as an important selective force in animal behavior (Case and Gilpin 1974; Terborgh 1983), and in a rainforest with 13 sympatric lemurs we would expect this to be the case. Results from observations over 25 years show that one strategy is for each lemur species to specialize on different fruit species (Wright et al. 2011). Yet interspecific aggression among lemurs exists, including agonistic vocalizations, chasing, and biting. These interactions occur during the season of ripe fruit availability (Overdorff and Tecot 2006; Wright personal observation). Since 88% of agonistic interactions among *E. rufifrons*, *E. rubriventer*, *P. edwardsi,* and *V. variegata* occurred over ripe fruit during the high season for fruit availability (Overdorff et al. 2005; Overdorff and Tecot 2006), interference competition for high quality fruit is the most likely driver of this agonism. *E. rubriventer* retreated in every case in the resource abundant season, but did not retreat in the few agonistic encounters which occurred with *P. edwardsi* and *E. rufifrons* during the scarce fruit season (Overdorff and Tecot 2006). *V. variegata* will often successfully defend fruit trees against all other lemur species (Balko 1998; Andrea Baden personal observation; Iris de Winter personal communication). The ruffed lemurs are most often the winner of any competition (the raucous barking of a whole group deters other species), even though the sifakas are twice their size. Congeners seem to compete most, and *E. rubriventer* and *E. rufifrons* have 0.04 aggressive interactions/hour, while *V. variegata* and *E. rubriventer* contest 0.006/h and *P. edwardsi* and *E. rubriventer* contest 0.003/h. The hierarchy established by % contests won is *V. variegata* (obligate frugivore), *E. rufifrons*, *P. edwardsi,* and *E. rubriventer* (Overdorff and Tecot 2006). During 3 months of fruit scarcity in 2010, *E. rufifrons* initiated and won 7 out of 7 contests with *E. rubriventer*, and 6 out of 7 aggressive interactions were adjacent to fruit trees (Iris de Winter personal communication).

Interference competition may also be playing a role in the population dynamics of *Eulemur* species. Across three long-term study sites, population density changes are inverse between *E. rufifrons* and *E. rubriventer*; when *E. rufifrons* population densities increase, *E. rubriventer* density decreases and vice versa (Fig. 4.2). Further evidence that competition for food resources is driving interspecific behavior, not predation, is that polyspecific associations are rare. This is contrary to observations of rainforest monkeys in Africa and South America where several species often feed together for protection against predators (Terborgh 1983; Holenweg et al. 1996).

4.4.3 Seasonal Breeding

Seasonal breeding is one female strategy to limit extra-pair copulation by males (Wright 1999). In the first decade, Ranomafana researchers suggested strict seasonality in lemur breeding (Wright 1999). Long-term results revealed that in *P. edwardsi, P. simus, V. variegata,* and *E. rufifrons* all females in a group and usually all those in the [study] population come into estrus within the same week for a day or two, with older females breeding first. In contrast, Tecot (2010) found that reproduction in *E. rubriventer* is not strictly tied to photoperiod, with births

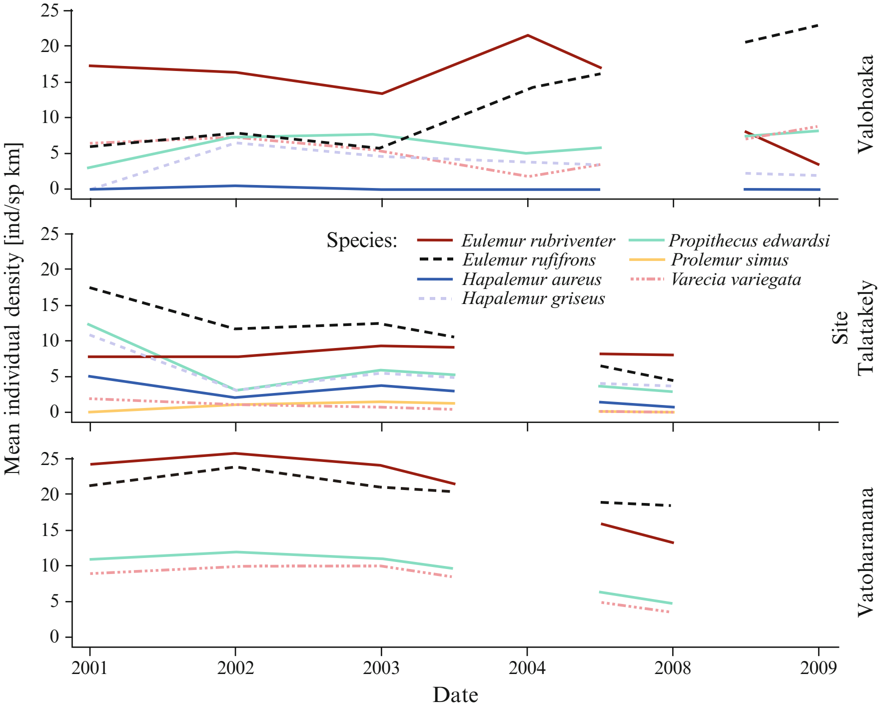

Fig. 4.2 Population densities of diurnal lemurs in Ranomafana National Park from 2001 to 2009 in three different study sites (Talatakely, Vatoharanana, and Valohoaka) within the park

occurring in eight different months. However, only infants born in the "seasonal breeding" window (with food abundance prebreeding) actually survived.

Another selective advantage to infants born at the same time is that synchronous births could be a successful strategy to satiate predators (Boinski 1987). *Varecia variegata* are strict seasonal breeders (Baden 2011) and use a boom or bust strategy (Ratsimbazafy 2006; Baden 2011). At Mangevo, a population of over 80 individuals, *V. variegata* reproduction was only observed once in 6 years of continuous observation. In 2007, 6 out of 7 adult females in the Mangevo population gave birth to twins or triplets (Baden 2011). This synchronous breeding at 6–8 year intervals has been observed in *Pongo pygmaeus* and was associated with fruit masting (Knott 1998). Preliminary analysis of plant phenological data from Ranomafana suggests that fruit availability is also the driver of *V. variegata* synchronous breeding (Wright unpublished data).

M. rufus has a breeding season from mid-October to mid-November, during which females have estrous periods of 5 days or more (Blanco 2008; Blanco and Rahalinarivo 2010), although some variation in the timing of breeding exists. Most females are gestating by mid- to late November (Atsalis 2008), although some are not gestating until December (Blanco 2008). Thus, the onset of estrus may not be completely controlled by photoperiod (Perret and Aujard 2001). There is no evidence for more than one litter a year (Atsalis 2008; Blanco 2008; Blanco and Rahalinarivo 2010).

4.4.4 Habitat Disturbance

To understand the effects of habitat disturbance on lemur demography, we compared life histories of lemurs at sites within the park with high and low levels of human disturbance. The high level disturbance site (Talatakely) was selectively logged for valuable hardwoods between 1986 and 1989, with the intrusion of invasive plant (Chinese guava) and animal (*Rattus rattus*) species (Arrigo-Nelson 2006; Brown and Gurevitch 2004; Laakkonen et al. 2003). The intermediate disturbance site (Vatoharanana) had less than 1% of the study area trees removed during the 1986–1989 period (approximately 1,000 trees; Balko 1998). The low level site (Valohoaka) is considered sacred by local villages and no known timber extraction has occurred (Herrera et al. 2009; Balko 1998). In contrast to the forests north of the park boundaries, there has been very little hunting within Ranomafana forest since the park was established (Lehman et al. 2006; Golden 2009).

The strictest frugivore, *V. variegata*, did not occur in the high disturbance level site (Talatakely) where the big canopied fruit trees were removed (Balko and Underwood 2005). Compared to forests in South America and Africa, Madagascar rainforest tree growth is slow (Struhsaker 1997; Ganzhorn et al. 1999; Clark and Clark 2010), and this delayed regeneration of the forest may impact lemur demography for decades. In the 20 years since selective logging, no one group of *V. variegata* has since arrived in the high disturbance site. Similarly, 10 years postselective logging, the effects on the physical structure of the forest, its species composition, and availability of *P. edwardsi* foods have continued at the highly disturbed site (Arrigo-Nelson 2006). Sifakas in the disturbed forest consumed foods from tree taxa in disproportion to their abundance and relied more on vines and epiphytes than counterparts at the unlogged site. As a consequence, intake of fats and sugars was lower for sifakas at the previously logged site. These differences in food availability and nutrient intake are reflected in significant differences in the body weights of female sifakas between sites and significant male–female differences in body mass in previously logged forest. Sifakas in the disturbed forest spent significantly less time interacting socially and significantly more time feeding and self-grooming than animals in the undisturbed forest. That all of these differences were greatest during lean season only makes their potential impact on the sifaka population of greater consequence. In the long term, these differences may lead to differences in group cohesion, survival, and/or reproductive success (Arrigo-Nelson 2006).

To investigate the impact of habitat disturbance on *E. rubriventer* demography, Tecot (2008, in press) collected data simultaneously on the red-bellied lemur populations in heavily logged and minimally logged sites. Results again indicate that logging has reduced the structure, species composition, abundance, and predictability of red-bellied lemur foods within the disturbed forest site. Additionally, red-bellied lemurs at the disturbed site were less active (Tecot 2008), bred out of peak season, and had higher infant mortality (Tecot 2010, in press).

High levels of cortisol have been implicated in reduced fitness (Bonier et al. 2009), and the effects of stress on lemur demography is being investigated (Tecot 2008). In a comparative study of stress hormones in adult *E. rubriventer* in selectively logged versus minimally logged sites, patterns of cortisol excretion were similar in both sites, but those in the undisturbed site showed little response to variation in food availability and rainfall. In contrast, at the disturbed site, fecal cortisol levels were significantly higher when fruit was scarce (parturition and early lactation) compared with when fruit was abundant (prebreeding season). Contrary to the Cortisol-Fitness Hypothesis (Bonier et al. 2009), cortisol levels were higher in the undisturbed site. Lower cortisol levels, minimal changes in hormones and behavior (Tecot 2008), and higher infant mortality (Tecot 2010) in the disturbed site indicate that there may be down-regulation of the cortisol stress response where environmental stress is prolonged (Tecot 2008, in press).

4.4.5 Trends in Population Densities of Lemurs

Over the past 20 years, we have documented population size changes across three sites with different histories of anthropogenic disturbance (Table 4.5; Fig. 4.2). These data allow us to determine changes, rather than trends, in population size over time. Our results indicate that changes in population size vary across sites, as

Table 4.5 Estimated population size of lemurs in Ranomafana National Park

Lemur species	Estimated density (ind/km^2) ± SE	Estimated population size (ind/330 km^2 of RNP forest)	Estimated biomass (kg/330 km^2)
Avahi peyrierasi	9.65 ± 1.92	3,185 ± 633	3,058 ± 607
Cheirogaleus crossleyi	13.48 ± 3.91	4,448 ± 1,291	1,557 ± 452
Daubentonia madagascariensis	rare	200 ± 50	600 ± 150
Eulemur rufifrons	6.75 ± 1.63	2,228 ± 537	4,902 ± 1,181
Eulemur rubriventer	5.46 ± 0.70	1,802 ± 231	4,325 ± 554
Hapalemur aureus	0.21 ± 0.14	69 ± 47	124 ± 85
Hapalemur griseus	2.48 ± 0.48	818 ± 159	614 ± 119
Prolemur simus	0.85–1.23 at one site in 2002–2003	20 ± 5	56 ± 15
Lepilemur microdon	0.99 ± 0.37	327 ± 128	327 ± 128
Microcebus rufus	23.52 ± 4.07	7,762 ± 1,343	233 ± 40
Propithecus edwardsi	4.73 ± 0.76	1,561 ± 251	9,366 ± 1,506
Varecia variegata	2.23 ± 0.81	736 ± 267	2,429 ± 1,082

These data are based on transect surveys from 2004 to 2009 (S.E. Johnson, F. Ratelolahy, P.C. Wright, J.P. Herrera). Species in bold are critically endangered (IUCN Redlist) would be expected of meta-populations in a varying landscape (Hanski and Gilpin 1991; Table 4.5). Oscillating population densities of *E. rufifrons* and *E. rubriventer* suggest that these changes in population density may reflect some degree of congeneric competition (Overdorff et al. 1999; Erhart and Overdorff 2008a). In comparison, in Vatoharanana, the density of *E. rubriventer* and *V. variegata* increased over the study years from 15 to 25 individuals per km^2 and from 2 to 10 individuals per km^2, respectively, while the density of *P. edwardsi* remained at 11 individuals per km^2. Similar trends have been observed in the critically endangered *V. variegata*. In the low disturbance site, their population density has oscillated but increased slightly overall. Population density in the intermediate disturbance site increased gradually between 1990 and 2003, but seems to have declined again by 2008. Overall population densities are low (2–10 ind/km^2). In *P. edwardsi* and *V. variegata*, we have seen an increase in population densities at Valohoaka, but population densities appear to be declining at the intermediate and high disturbance sites, which can perhaps be partly attributed to predation events or fruit scarcity (Arrigo-Nelson 2006; Irwin et al. 2009). Long-term data show that the species with declining populations in normal circumstances have larger home ranges and larger group sizes (Morriss et al. 2009). Theoretically this suggests that food constraints are more important than predation, as larger group size provides more eyes and ears for detecting predators (Hamilton 1964; van Schaik 1983; van Schaik et al. 1983).

4.5 Conservation

4.5.1 Successes and Ongoing Problems

RNP has been designated as a conservation priority (Kremen et al. 2008) and in 2007 was declared a World Heritage Site. We have successfully integrated education, health, and economic assistance programs with biodiversity research and habitat protection goals (Wright 1997; Wright and Andriamihaja 2002; Lovejoy 2006). An evaluation of the educational impact has shown that local people have experienced a change in attitude (Korhonen 2006). Attempts to correlate human impact on lemur populations have shown that human immigration into the park's peripheral zone is correlated with increased deforestation rates (Brooks et al. 2009). Villages which are the farthest from the road tend to encroach further into the park than do the on-road villages (DeFries et al. 2010). Moreover, the park itself has maintained edges with minimum invasion by exotic plants (Brown et al. 2009). Eco-tourism to visit the park has been a great boon to the local economy. However, the 30,000 tourists do have negative consequences on habitat and breeding birds (Razafimahaimodison 2003). Better management of tourism is in process. Satellite photos suggest that there is minimum forest destruction since 1991, when the park was gazetted, but the recent political instability is worrisome.

4.5.2 *Implications of Climate Change*

Long-term data enable better understanding of the effects of climate change on rainforest ecology and lemur populations. Indeed, lemur observers with long-term research projects were among the first to gain evidence of the effect of climate fluctuations on mammal populations (Gould et al. 1999; Wright 1999, 2006). Using Madagascar climate data and the Centre ValBio long-term rainfall and temperature database, we discovered that dry seasons have become longer, and cyclones more frequent (Wright 2006). In particular, the November temperatures in 2007, 2008, and 2009 were over 30°C, much higher than ever previously recorded, and the gap between minimum and maximum temperatures has increased. But does this have an effect on lemur demographics?

Long-term demographic data show that older *P. edwardsi* mothers lose infants in years with extended hot, dry seasons (King et al. 2005). Further analysis shows that the average fecundity of lemurs was over 65% lower in El Niño years (Dunham et al. 2008). As El Niño years become more erratic and frequent (Fedorov and Philander 2000) this could lead to more extreme weather and increased impacts on biodiversity. The southern oscillation (ENSO) related to El Niño is known to cause drought (Thomson et al. 2003) and changes in vegetation indices (Ingram and Dawson 2005). Dunham et al. (2010) found that cyclones, ENSO phases, and rainfall levels affected the reproductive rates of *P. edwardsi*. Overall fecundity (defined as the number of offspring per female per year surviving to 1 year of age) was negatively associated with cyclone presence during gestation, and positively associated with colder ENSO phases during the second 6 months of life and during the period faced by mothers preceding conception. Wet season rainfall and intensity during gestation was negatively related to birth rates, and the number of drought months during lactation was negatively associated with first year survival. Finally, fluctuations in lemur stress hormones show an elevation of cortisol during the dry season (Tecot 2008; Tecot in press), which may ultimately impact reproduction. Longer dry seasons in consequent years could impact lemur populations negatively (Wright 2006; Dunham et al. 2008, 2010). The effects of ENSO events on population dynamics has also been seen in many species of New World monkeys (Wiederholt and Post 2010).

4.6 Summary and Conclusions

Most of the lemur species in Ranomafana were data deficient before we initiated our first studies in 1986. The virtue and vice of long-term research is that it is never complete. Here we have compiled a list of essential findings, the product of long-term research that has many times resulted in the reevaluation of earlier findings. Thus, over the years we established the number of species residing in RNP through the rediscovery of *P. simus* and the discovery of *H. aureus* and a potentially new species awaiting description: a high altitude species of *Cheirogaleus*. We have established demographic changes through time including life history events, mortality, lifespan, and dispersal patterns for *P. edwardsi*, *E. rufifrons*, *E. rubriventer*, *V. variegata*, *H. aureus*, *H. griseus*, *P. simus,* and to a lesser extent *M. rufus*. We have documented variability of social organization in each species, and we have described how populations recover after cyclones and droughts.

Furthermore, we have confirmed that lemur population densities vary over time, and that predation by raptors and mammalian carnivores can have a major impact on local lemur populations. We know that many lemur species are important to seed dispersal and thus to forest dynamics. Monitoring and measuring the long-term effects of habitat disturbance on lemur populations, we have evidence that selective logging may negatively impact population densities of *E. rufifrons, V. variegata*, and *P. edwardsi*, even a decade after the last logging disturbance. We have also determined that fertility of *P. edwardsi* females decreased during ENSO years and infants of older *P. edwardsi* females died in years with extended dry months.

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Chapter 5
A 15-Year Perspective on the Social Organization and Life History of Sifaka in Kirindy Forest

Peter M. Kappeler and Claudia Fichtel

Abstract In this chapter, we summarize some fundamental demographic and morphometric data from the first 15 years of a long-term study of Verreaux's sifaka (*Propithecus verreauxi*) at Kirindy Forest in Western Madagascar. We first describe this research site, its history, and infrastructure, as well as the methods employed to study a local sifaka population. Regular censuses, behavioral observations, and systematic captures of members of up to 11 groups began in 1995 and yielded a data set on demography and life history that can contribute comparative insights about sifaka life history. Our analyses revealed that average group size fluctuated very little around a mean of six individuals across years. Group composition was modified by dispersal (mostly male transfers) or disappearances, births, and deaths. Predation and female transfer were the main mechanisms triggering group extinctions and foundation of new groups ($N = 5$ cases in 149 group years). These exceptional cases of female transfer were most likely motivated by female competition or inbreeding avoidance. One female was a member of at least four different groups. Median age at first birth was 5 years. All females gave birth to single infants, but the proportion of adult females reproducing varied between 25 and 85% across years. The mean interval between 112 births was 15.1 months. Loss of an infant before weaning reduced the subsequent inter-birth interval only by about 1 month. The probability that individual females reproduced successfully decreased as the number of adult females per group increased, implying that subtle forms of female competition limit group size. Mortality is especially high (62%) in

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the first 2 years of life. Predation by the fossa (*Cryptoprocta ferox*) is the main cause of death. Maximum female reproductive lifespan is at least 15 years, but longevity is still impossible to estimate. These analyses revealed new insights into female reproductive strategies and their interaction with social organization that were only possible because of the long-term nature of the study, but problems of small sample size still limit the analysis of many vital statistics.

5.1 Introduction

Sifakas (*Propithecus* spp.) represent a genus of lemurs that has played an important role in the history of primatology in Madagascar for at least two reasons. First, sifakas include some of the largest extant lemurs, and they are diurnal and group-living. Because all these traits facilitate behavioral observations, sifakas were among the first lemurs to be studied in the wild (Jolly 1966; Richard 1974a,b; Albignac et al. 1988), and some of the most detailed and long-term lemur data sets are available from several sifaka populations, notably from Beza Mahafaly (*P. verreauxi*: Richard et al. 1991, 1993, 2002; Sussman et al. 2012) and Ranomafana (*P. edwardsi*: Wright 1995; Pochron and Wright 2003; Pochron et al. 2004; Morelli et al. 2009; Wright et al. 2012). [With long-term, we refer not only to periods that far extend typical Ph.D. field projects of 1 or 2 years but also to periods exceeding species-typical ages of first reproduction or dispersal]. Second, recent phylogenetic analyses indicated that diurnality and group-living in sifakas evolved independently from other lemurs and primates (Horvath et al. 2008). Sifakas therefore present a valuable opportunity to study fundamental adaptations to primate sociality from a comparative perspective. Interesting levels of comparison include analysis of variation among groups within populations, among populations of the same species, among different sifaka species, and ultimately between sifaka and other group-living lemurs in the family Lemuridae, and between sifakas and ecologically similar anthropoids. The latter comparative perspectives are beyond the scope of the present chapter, however.

At present, nine species of sifaka are recognized (Mittermeier et al. 2010). They inhabit most remaining dry and rain forests around the island where they feed on flowers, leaves, and fruits (Richard 2003). Sifakas are strictly diurnal (Erkert and Kappeler 2004). At night, they often retreat into emergent trees. During austral winters, they may begin the subsequent day with a sunbath because they lower their body temperatures overnight to conserve energy (Richard and Nicoll 1987). Sifakas range in body mass from about 3 to 9 kg and locomote mostly by vertical leaping. Their main predators include the fossa (*Cryptoprocta ferox*), Harrier hawk (*Polyboroides radiatus*), and boas (*Acrantophis* spp.; Rasoloarison et al. 1995; Wright 1998; Burney 2002; Karpanty 2006), to which they represent some of the most profitable prey because of their size and density. They live in groups of 2–12 individuals that typically contain multiple adult males and females. Females tend to be slightly larger than males, and they dominate them socially (Richard 1974a;

Kappeler 1991; Pochron et al. 2003). Home ranges vary between just a few to about 200 ha among study sites. Mating is confined to a few days within a brief annual season of a few weeks (Richard 1974b; Brockman and Whitten 1996). The single infants require 3–5 years to attain sexual maturity (Richard et al. 2002). Dispersal is primarily by males (Richard et al. 1993), but female dispersal has also been documented (Morelli et al. 2009). Infant mortality is high, but longevity has been projected to exceed 30 years (Richard et al. 2002; Wright et al. 2012). Sifakas communicate with scent marks and several vocalizations (Fichtel and Kappeler 2002; Lewis 2005; Pochron et al. 2005; Fichtel 2008), one of which is responsible for their onomatopoetic name.

Verreaux's sifakas (*P. verreauxi*) have been studied at Beza Mahafaly Special Reserve for more than 3 decades (Richard et al. 2002; Sussman et al. 2012). Results of this long-term study of marked individuals were instrumental in characterizing the ecology, demography, and social behavior of this species. Because *P. verreauxi* has the largest distribution of all sifakas, ranging from the dry spiny forests of the far south to the deciduous baobab forests of the central west, opportunities to identify intraspecific behavioral flexibility and fine-grained adaptations across habitat gradients exist (Richard 1978; Fichtel and Kappeler 2011). In this chapter, we summarize the first 15 years of research on a *P. verreauxi* population at Kirindy Forest to contribute to the comparative approach outlined above.

5.2 The Study Site: Kirindy Forest

Kirindy Forest is one of the largest remaining tracts of dry deciduous forest in Madagascar. The infrastructure for long-term studies of lemur ecology and behavior was established there by the German Primate Center (DPZ) in 1993. In this section, we briefly characterize the study site, outline its history as a lemur study site, and describe the current research infrastructure and methods.

5.2.1 Forest Characteristics

The DPZ research station is located at 44°39′ E 20°03′ S near the center of Kirindy Forest in the central Menabe region of western Madagascar, about 20 km inland from the Mozambique Channel. A 12,500-ha forest concession forms the core of Kirindy Forest. It is (still) connected by a narrow forest corridor to Ambadira Forest to the north (Fig. 5.1). These two forest blocks form the heart of a future protected area (Aire Protégée Menabe Antimena), but it remains officially unprotected as of 2011 (N.B.: Kirindy is sometimes confused with Kirindy-Mitea National Park, which is located south of Morondava). This area is characterized by a hot wet season from November to March and a dry season that can last up to 9 months (Fig. 5.2). The mean annual maximum temperature is 35.8°C and mean annual

Fig. 5.1 Map of Kirindy Forest (© Google maps)

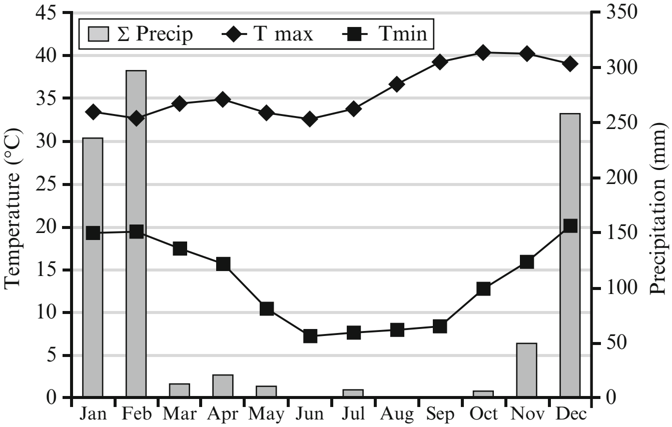

Fig. 5.2 Climate at Kirindy. Mean monthly maximum (*diamonds*) and minimum (*squares*) temperature as well as monthly precipitation (*bars*)

rainfall is 900 mm. Mean annual minimum temperature is 13.5°C, but individual nights during the dry season can get very cold (recorded minimum, 3°C).

Kirindy forest grows on predominantly sandy red and yellow soils just above sea level. It is home to more than 200 species of trees (Rakotonirina 1996). With the exception of a few emergent trees (10–50 trees/ha with >25 cm DBH) along riverbeds or in other humid sites, the vast majority of trees at Kirindy do not exceed 25 m in height. In fact, mean canopy height is 12–18 m. Most canopy layer trees are deciduous, and other plant adaptations to water stress, such as small leaves, spines or thickened stems are common. Visually, three species of baobab (*Adansonia* spp.) as well as *Commiphora*, *Poupartia*, *Colvillea*, and *Terminalia* trees stick out. Near the ground, the forest is very dense with 5,000–19,000 stems/ha with <10 cm DBH and 300–400 trees/ha with a DBH between 12 and 25 cm (Sorg et al. 2003). Depending on the locally prevalent soil type (yellow, red, brown, black, rock), forest structure and composition are very heterogeneous and can change dramatically over distances of a few dozen meters. The phenology of 55 tree species, including all commercially valuable ones, has been studied in great detail (Sorg and Rohner 1996).

Various surveys have revealed the local presence of 15 species of amphibians, 45 species of reptiles, 82 species of birds, and 35 species of mammals, 8 of which are lemurs (Ganzhorn and Sorg 1996). This vertebrate community contains several endangered and locally endemic species, such as the Madagascar jumping frog (*Aglyptodactylus laticeps*), the flat-shelled tortoise (*Pyxis planicauda*), the white-breated mesite (*Mesitornis variegata*), the giant jumping rat (*Hypogeomys antimena*), and Madame Berthe's mouse lemur (*Microcebus berthae*).

5.2.2 History

The Centre de Formation Professionnelle Forestière de Morondava (CFPF) was established by the Malagasy government in 1978 to develop sustainable silvicultural practices for the selective logging of the forests in the Menabe region. To this end, the CFPF installed a forestry concession in Kirindy Forest. The center's activities were coordinated with Swiss development (Coopération Suisse) and research (ETH Zürich) activities. Apart from the training of forestry personnel, the initial period of semi-mechanized logging (1978–1984) was characterized by research projects focusing on forest ecology, silviculture, and methods of forest exploitation and reforestation. In a second phase (1984–1992), silvicultural research was extended to agroforestry experiments outside the forest. After 1992, more emphasis was put on developing ways to use the land and wood resources around the forest area sustainably. In 1995, forestry-related activities inside the forest were reduced, and the CFPF established an ecotourism site that relied to a large extent on the initial forest camp infrastructure. In 2008, the CFPF was formally replaced by the Centre National de Formation, d'Etudes et de Recherche en Environnement et Foresterie (CNFERF), which has a national mission in environmental and forestry training and research and which manages the concession today, including a popular ecotourism site with bungalows and a restaurant.

Research on the fauna of Kirindy began in 1987, when Jörg Ganzhorn (then at the University of Tübingen, Germany) first visited Kirindy Forest. In the following years, he returned annually with some students to explore the effects of selective logging on lemurs and the small mammal fauna (Ganzhorn et al. 1990, 1999; Ganzhorn 1995). Construction of a simple research camp next to the CFPF field camp began in early 1993, after Jörg Ganzhorn had taken up a position at the German Primate Center (DPZ) in Göttingen as the head of a newly created research unit on primate behavior and ecology. Jutta Schmid was the first Ph.D. student (studying mouse lemur energetics: Schmid 2000; Schmid et al. 2000), and Peter Kappeler took up a postdoc position in that group. In 1997, Jörg Ganzhorn left the DPZ for a professorship in Hamburg, and Peter Kappeler took over the management of the research station. Rodin Rasoloarison subsequently joined the team to support the project administration at the national level while also conducting lemur biodiversity research (Rasoloarison et al. 2000; Yoder et al. 2000, 2005; Mittermeier et al. 2008; Groeneveld et al. 2009; Weisrock et al. 2010). Léonard Razafimanantsoa became the station manager in 1998, when the first four permanent local field assistants were also employed and trained. Today, the project employs 15 assistants, including cooks, guardians, and a driver. By 2011, field work for 28 Ph.D. and 75 Master's projects by students from nine countries has been conducted at Kirindy, and regular field courses for students from Göttingen and the University of Antananarivo, as well as the Tropical Biology Association (Cambridge) take place there.

5.2.3 Research Infrastructure

The DPZ research camp at Kirindy was renovated and enlarged in 2004. Today, it offers room for eight researchers, who live in tents on platforms in the forest surrounding the central camp facilities. The core station facilities include brick buildings for the five permanent field assistants, associated staff, a kitchen, several storage buildings for research materials, and a simple laboratory. Electrical power is provided by solar panels; all water and food has to be brought in with a project vehicle from a nearby village (Beroboka) or the provincial town (Morondava), respectively. A base camp ("Villa Mirza") in Morondava provides facilities for the storage of equipment, data management, and recreation. The long-term maintenance and perspective of this site are due to financial support by the DPZ, who provides an annual budget for all local salaries, infrastructure, and basic operating costs.

Animal research at Kirindy has focused on the behavior and ecology of its eight sympatric lemur species (*Microcebus berthae, M. murinus, Cheirogaleus medius, Mirza coquereli, Phaner pallescens, Lepilemur ruficaudatus, Eulemur rufifrons,* and *Propithecus verreauxi*). Lemur research in this dense forest was facilitated by

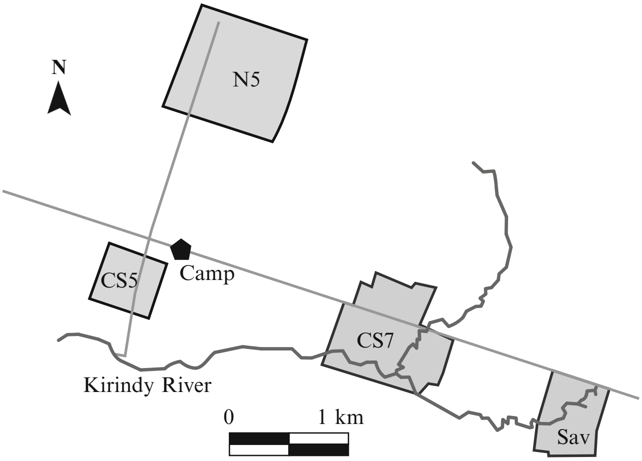

Fig 5.3 Map of local study areas at Kirindy Forest

establishing several trail systems. Checkerboard-like systems of foot trails were established in four areas between 1993 and 2010 (Fig. 5.3). In most cases, trails intersect every 25 m. In total, about 128 km of trails provide access to about 181 ha of forest. All trails are mapped, and all intersections are marked with a small plastic tag. The two oldest grid systems (locally known as N5 and CS7, respectively) also include phenology transects that include several hundred individually marked trees that are checked twice a month.

The Verreaux's sifakas inhabiting the core area (about 50 ha) of the grid system CS7 situated along the Kirindy river were first captured and marked in March 1995. Enafa, an adroit field assistant of the Beza Mahafaly project (Sussman et al. 2012), has been darting the Kirindy sifakas with a blowgun ever since 1995. The anesthetized animals are weighed, permanently marked with a subdermally implanted transponder and subjected to standard morphometric field measurements. A small skin biopsy from the ear is stored in ethanol and used for later DNA extraction. Mitochondrial DNA has been sequenced to study group structure and histories (Kappeler et al. in prep), and variation in nuclear microsatellites has been used to determine paternities (Kappeler and Schäffler 2008). Finally, all individuals are fitted with small nylon collars, each with a unique pendant. One individual per group is fitted with a radio collar. Juveniles, who are born in July/August, are captured in March/April of the subsequent year together with any immigrants. Radio collars (Holohill, Canada) were initially replaced annually; nowadays, battery life is 3 years. The composition and location of all marked sifaka groups are monitored by Tiana Andrianjanahary several times a week, so that all important demographic events, including births, predation events, and disappearances or dispersal events can be dated to within several days. Several Master's (Hussmann, Rümenap, Carrai, Kraus, Randriamanalina, Dill, Rakotondravony, Dirac, Trillmich, Scholz, Benadi) and Ph.D. studies (Carrai, Fichtel, Lewis, Mass, Koch) on sifaka ecology or behavior have yielded additional behavioral data on most groups over the years. Demographic, morphometric, genetic, and behavioral data have been centralized and are currently being transferred from Excel files into a data bank.

5.3 Kirindy Sifaka

During the initial capture in 1995, 24 individuals from six groups (A–F) were marked within a 25-ha grid. With the eventual extension of the grid system, additional groups were added to the study population over the years, and a total of 213 individuals were captured at least once. After several group extinctions, fissions and fusions, there are currently 9 groups with 52 marked individuals. In the intervening 149 group years, 141 infants were born into these study groups and 154 animals disappeared or died. In this section, we summarize some of the basic demographic events of these first 15 years of our study, focusing on some rare events as well as on births and deaths.

5.3.1 Group Size and Composition

The average group of Kirindy sifaka contains 1.6 ± 0.8 (mean ± SD) adult females, 1.9 ± 0.8 adult males, 0.7 ± 0.8 juvenile females, 0.8 ± 0.9 juvenile males, 0.1 ± 0.3 unsexed juveniles, 0.3 ± 0.5 female infants, and 0.4 ± 0.6 male infants (unsexed infants 0.3 ± 0.5). Group size fluctuated very little around a grand mean of 6.1 (±1.8) over 149 group years. For the present analyses, we used group composition in April of every year to determine the number of adults, juveniles, and infants present. Infants were captured for the first time in March or April, i.e., when they were still within their first year of life and about 8 months old. Infants who disappeared before this first capture could not be sexed, and typically, no material for paternity analyses was available. Individuals in their second and third year were classified as juveniles because (female) sexual maturity and the earliest age of first reproduction were observed at age 4 (see below). Characteristics of the average growth pattern could be used to age unknown individuals below 3 years of age reliably (see Sect. 5.3.5). All other animals were classified as adults.

5.3.2 Group Histories

The histories of some groups were characterized by extinctions or fusions, but we also witnessed the establishment of new groups. Predation and female transfer were the key mechanisms in these events. We operationally define groups as bisexual units, i.e., they consisted of at least one adult male and female. In 149 group years, only five events that resulted in changes in the number of study groups occurred. Below, we describe the circumstances of these rare but important events in detail.

Two groups essentially went extinct following confirmed fossa predation. First, group D was among the groups captured in 1995. It consisted of an adult pair (DFRom and DMMil) and their juvenile son (DMNap; acronyms denote group (in which an animal was born or first captured)* sex* individual ID). They were also regularly visited by a roaming male (AMPin). In July 1995, a female infant (DFPis) was born. On July 22, 1996, DMMil was killed by a fossa. The 1996 infant of DFRom disappeared within a week after its birth on July 24. Its disappearance was likely due to infanticide as it coincided with the immigration of a new adult male (DMFir) between the 25th and 30th of July 1996. On August 14, 1996, DMNap was killed by a fossa. For most of the following year, group D consisted of DFRom, DFPis, DMFir, and AMPin. On August 10, 1997, DFRom gave birth to another infant. On August 27, 1997, she disappeared together with her new infant; circumstances also imply fossa predation as the cause of their disappearance. In October 1997, the 2-year-old DFPis emigrated (together with AMPin) into the neighboring group H, where she stayed until March 2001. DMFir was left behind by himself. He paired up with another solitary adult male (BMBer) between February and June 1998, but then became solitary again and stayed alone until he was last seen in October 1998. Thus, group D dissolved following emigration of a juvenile female after all of her relatives were killed by fossa within a year.

Second, group K was also exterminated by fossa predation. In 2006, it consisted of two adult females (KFAlm and KFJal), an adult male (KMChe), a juvenile male (FMGor) who disappeared on 8 June, and KFAlm's infant KMCha. On July 29, 2007, KFAlm, and her infant (born on 16 July) were killed by a fossa. KFJal was last seen on the same day. KMCha was last seen together with his father KMChe on August 4, 2007. After a last solitary sighting on August 6, the yearling disappeared. KMChe was still solitary in August 2010. Thus, presumably, a single fossa attack ultimately led to the extinction of this group.

In three other cases, female transfer significantly modified group compositions and ultimately changed the number of groups. In one example, the female members of group A voluntarily joined one of their neighboring groups. In 2006, group A consisted of two closely related adult females (AFSil and AFSis), an immigrant adult male (FMPho), a 3-year-old natal male (AMAnt), a same-aged juvenile female (AFRos), and the 2006 infant of AFSil. In early January 2007, two males from neighboring group F, 9-year-old FMChi and 4-year-old FMFra, immigrated into group A. On January 8, 2007, AFSil was attacked by a fossa and disappeared shortly thereafter. Her 2006 infant disappeared on the same day. FMFra went back to his natal group in April 2007. FMPho, the half brother of FMChi and father of AFRos, disappeared on June 18, 2007. On September 29, 2007, EFSis emigrated into neighboring group E, which had lost its sole adult female EFAli together with her 2007 infant in a fossa attack on September 16, 2007, leaving 4 males (EMDar and his sons, 7-year-old EMHar, 4-year-old EMMel, and 3-year-old EMAlb) behind. AFRos followed 2 days later, leaving behind AMAnt and FMChi, who stayed together until they immigrated into FMChi's natal group in March 2008. Group A therefore ceased to exist because its two females emigrated. Inbreeding avoidance (AFSis and AFRos) and, perhaps, other reproductive interests led to voluntary female emigration that was facilitated in this case because the target group contained no other females at the time of fusion.

Female transfers also led to massive changes in the composition of group F and ultimately to the formation of the new group F1. In 2005, group F consisted of two adult females (FFDal and her daughter FFSav), immigrant adult male FMJun, natal adult male FMChi, three juvenile males (FMFra, FMDet, and FMRal), and juvenile female FFTam. FFDal was the mother of all natal group members, except for FMDet, who was FFSav's son. On October 18, 2005, FFSav and FFDal were first seen with a group of four unmarked males about 150 m away from the rest of group F. On October 25, they were back with FMJun and their offspring. On October 28 and 30, the two females were again with the new males. On 31 October and 1 November, FFSav was with the new males, whereas FFDal was back with FMJun and her sons. On November 2, both females were with the new males; on November 9, both of them were back in group F. On November 13, FFSav was again with the new males; on the next day, her mother had followed. On November 19, both were again in group F; on the 22nd both were with the new males. On November 23, FFDal and FFSav were seen with the males of group F for the last time. The four unmarked animals were captured on April 4, 2006. FFDal and FFSav both gave birth on July 7, 2006. FFDal and her infant disappeared on July 17, 2006. The new group remained in a distinct area to the east of group F's range and was named F1. [FFSav had given birth to her first infant in 2003. It was one of the very few infants sired by a nonresident male. She had another infant in 2004 (FMDet) and none in 2005]. As all males in her natal group were close relatives, inbreeding avoidance might have triggered her emigration; why her mother followed remains unknown, however. Throughout 2006, FMJun and his two sons FMChi and FMFra stayed together in their habitual home range. On October 17, 2007, they were joined by an unmarked adult female (FFOma), who gave birth to an infant in July 2008.

Groups I and C represent two other related cases in which the same adult female (IFCal) formed a new group. She appeared in the study area in February 1998 as a fully adult female and was first captured on September 8. She had been joined by two adult males from different groups, EMSyd (on February 20, 1998) and BMBer (on June 7, 1998) to form group I. In January 1999, BMBer left group I and led a solitary life until he was last sighted on May 28, 1999. On that day, IFCal and EMSyd immigrated together into group C. Group C's matriarch CFAnt (together with her infant of 1998) had been killed by a fossa on October 11, 1998. The only other resident female, CFTam, left her group on the next day, leaving two natal juvenile males (CMMaf and CMBel) and three adult immigrant males (CMTul, CMAnt, and CMDau) behind. Beginning on October 26, 1998, one of two adult females of group B (BFFul), one of group C's neighbors, associated with the five males of group C. She was last seen in group C on April 27, 1999 before returning to group B. CMAnt and CMDau emigrated into group E in March 1999. Thus, group C consisted of two juvenile and one adult male when IFCal and EMSyd joined them.

EMSyd left group C again on July 5, 1999 and was by himself until he was last seen on July 17, 1999.

More than a year later, on September 16, 2000, IFCal left group C and joined five unmarked animals. She did not have an infant in 2000. It turned out that her new group (L) consisted of one adult (LFPat) female and two juvenile females (LFDel and LFMad) living with two adult males (LMBha and LMBom). The three initial resident females of group L disappeared in August 2001, July 2002, and October 2003, respectively. IFCal had her first infant in 2002 and subsequently five more infants before she disappeared on April 7, 2009. Thus, the circumstances triggering this exceptional female's dispersals remain unclear, but her case shows that females can initiate new groups by attracting males, and that females who have left their natal groups can disperse repeatedly – in this case three times.

5.3.3 Reproduction

Mating in Kirindy sifaka is limited to a few weeks in January and February. Direct observations of matings are extremely rare, despite considerable effort by some students (e.g., Kraus et al. 1999; Lewis 2004; Mass et al. 2009). For one thing, they occur at the peak of the rainy season, when observation conditions are very difficult. Moreover, they tend to be very uneventful and short. A study relying on fecal hormone analyses to determine the timing of female reproductive periods confirmed that fertile periods of individual females are limited to 2–4 days and that the fertile periods of co-resident females rarely overlap (Mass et al. 2009).

Births occur about 6 months later, i.e., in July and August. Only single infants have ever been born. Between 1995 and 2009, a total of 29 different females gave birth to a total of 141 infants. The sex ratio of infants that survived long enough to be captured and sexed ($N = 102$) did not differ from unity (1.37; 59 males, 43 females, $X^2 = 0.96$, $df = 1$, ns). However, the proportion of females giving birth differed notably among years, varying between 25 and 85% (Fig. 5.4). This proportion is not significantly correlated with total annual rainfall ($r = 0.35$, $N = 14$, ns) or other climatic variables.

Eleven females born into the study groups had reached reproductive age by 2009. Their median age at first birth was 5 years (range 4–6). Twenty-four females gave birth at least twice, so that 112 inter-birth intervals were available for analysis. The mean inter-birth interval was 15.1 months (±5.4). If the infant survived to post-weaning (i.e., the following April; $N = 93$), mean inter-birth intervals were only slightly longer (15.3 months ±5.7) than if it died during its first 9 months of life (14.7 months ±4.9). Early loss of an infant thus did not increase the probability of subsequent conception (Fisher's exact test, $p = 0.47$).

The number of adult females per group varied between 1 and 4 (Fig. 5.5). In 64% of 64 group years in which only one adult female was present, this female reproduced. When a group contained two adult females (66 group years), the probability that both of them reproduced was reduced to 39%; in 41% of these

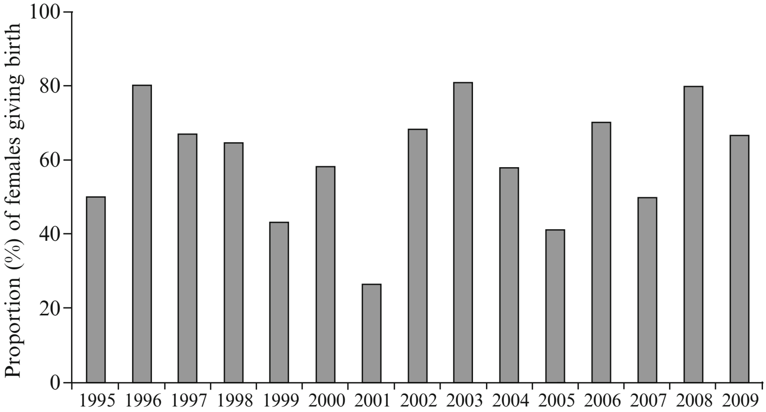

Fig. 5.4 Proportion of sifaka females giving birth between 1995 and 2009

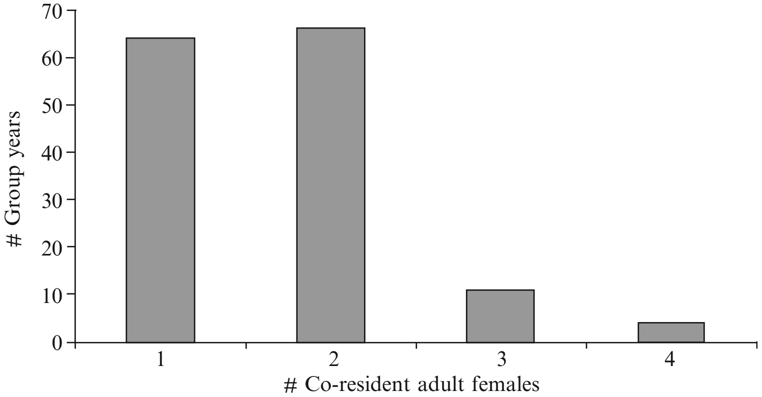

Fig. 5.5 Number of co-resident sifaka females per group over 149 group years

cases, at least one female reproduced. In none of 11 group years with three adult females present did all three produce an infant; in 55% of these years, there were at least two infants. Finally, in the two group years with four adult females, a maximum of two females had an infant in one of those years (50%). Assuming that no other factors play a role, the probability of individual reproduction therefore decreased with the number of females per group from 64% ($N = 1$ female) to 40% ($N = 2$ females), to 37 % ($N = 3$ females), to 25% ($N = 4$ females). Thus, competition among females appears to limit reproductive opportunities in these Verreaux's sifakas.

Paternities were determined for 54 surviving infants born between 1995 and 2003 by comparing patterns of individual variation at 15 microsatellite loci (Kappeler and Schäffler 2008). More than 91% of all infants were sired by the dominant adult male of a group when a group contained two or more non-natal adult males. Only one infant was the result of an extra-group mating. The youngest confirmed male fathering offspring was 4 years and 7 months old at the time of conception.

5.3.4 *Disappearances*

Between 1995 and 2010, 154 individuals disappeared. Animals that disappeared could have emigrated or died. Evidence for mortality ($N = 31$) was most often due to confirmed cases of fossa predation (Fig. 5.6). Kirindy harbors a dense population of fossas that heavily prey on sifakas, especially in the second half of the dry season (June–October), when most alternative prey hibernate (see also Rasoloarison et al. 1995). In some cases, hunts were directly observed. Some of the fossa hunts were cooperatively (Lührs and Dammhahn 2010). In all other confirmed cases, corpses or at least the animal's nylon collars together with some fur and blood were found. Predation by the Harrier hawk, other raptors, or snakes has not been observed or inferred (cf. Karpanty and Goodman 1999). Infanticide by strange males has been observed or suspected as the cause of some infant deaths (see above; Lewis et al. 2003). Several infants have died within the first weeks of life, presumably from maternal neglect (observed in several cases) or failure to produce enough milk. Juvenile or adult sifakas dying from disease or other causes were never discovered.

About a third of all newborns did not survive their first year of life, and 62.4% of individuals died within the first 2 years (Fig. 5.7). Female dispersal was extremely rare (12 cases in 149 group years). The majority of disappeared females and juvenile males are therefore most likely dead and did not emigrate. Thus, a

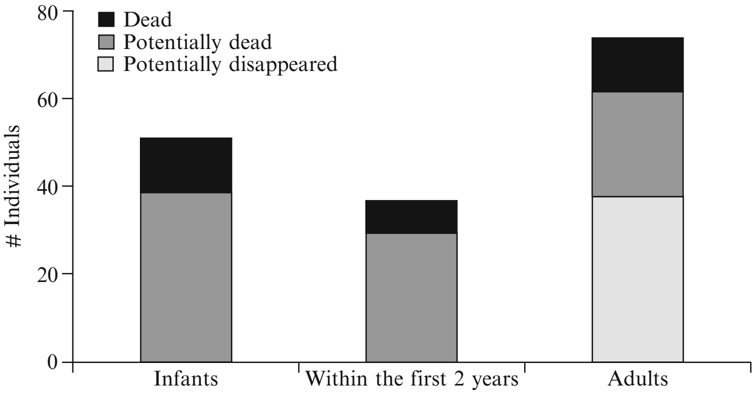

Fig. 5.6 Number of infants, juveniles within the first 2 years, and adults that either died are potentially dead or potentially disappeared. Individuals that disappeared at an age under the average age of natal dispersal (males median 60 months (IQR 12); females median 54 months (IQR 18)) were considered as potentially dead; all other individuals were classified as potentially disappeared

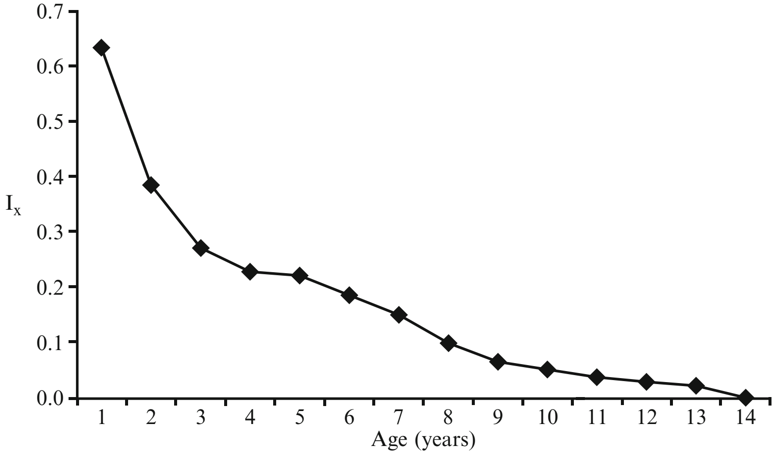

Fig. 5.7 Age-dependent survival of sifakas at Kirindy Forest

minimum of 38 and a maximum of 54 of the disappeared individuals presumably died.

Longevity is still difficult to estimate 15 years into the study. Of the 11 oldest animals with known ages (born in 1994 and 1995), none are still alive today. The oldest ones disappeared at age 14. Currently, the oldest female alive with known age is 13, and three males are of the same age. However, one female first captured in 1995 as a young adult (BFCol) had an infant in 1996 and was killed by a fossa in September 2010. If the 1996 infant was her first one, she was most likely born in 1991 (±1 year), and was thus in her 20th year. She had an infant (her 13th!) on July 29, 2010, but abandoned it on 13 August. Thus, maximum female reproductive life span is at least 15 years.

5.3.5 Growth

Newborn and immigrant individuals were captured at least once a year. In addition, dead radio collars or broken nylon collars were replaced whenever possible (i.e., if the bearer was not a pregnant or lactating female). As a result, we have accumulated a mix of cross-sectional and longitudinal data on body mass and other standard morphometric measurements (skull length and width, canine and testes size, body and tail length) for 184 individuals of different age and sex classes whom we captured a total of 384 times across the years. Here, we present some growth data that have helped us to age unknown individuals. Because of the seasonality of reproduction, identifying an individual's year of birth is equivalent to reconstructing its age to within a month.

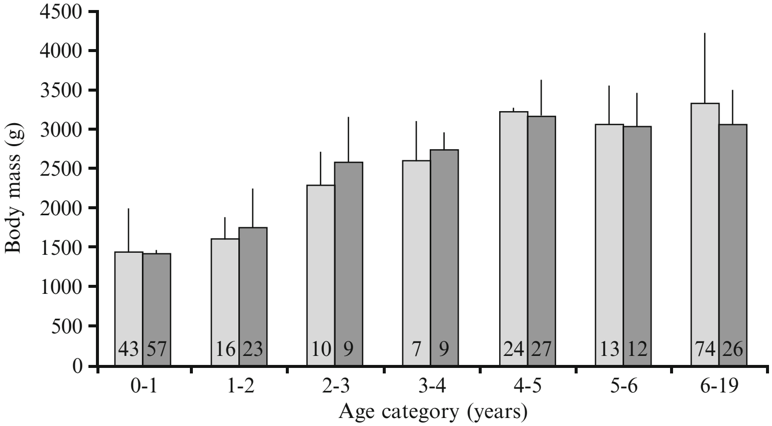

Fig. 5.8 Mean (±SD) body mass of female (*light*) and male (*dark*) sifakas per age category. Numbers inside bars denote sample size. Please note that most individuals were weighed repeatedly at different ages

The lightest individual ever weighed was a 15-day-old infant that was abandoned by its mother when it weighed 58 g. Of the individuals with exactly known ages, the heaviest (3,700 g) was a 6-year-old female. The heaviest female ever captured weighed 4,400 g; the heaviest male weighed 3,850 g. At first capture (mean age 241 days), recently weaned individuals had a mean weight of 1,381 ± 28 g (both N's = 89; Fig. 5.8). During their second year of life (mean age 441 days), juveniles weighed on average 1,601 ± 530 g ($N = 32$). During their third year (mean age 855 days), 11 juveniles had a mean weight of 2,331 ± 594 g. Between ages 3 and 4, the mean weight increased to 2,626 ± 221 g ($N = 8$). Adults between 4 and 13 years old weighed an average of 2,973 ± 124 g ($N = 34$). Animals without known ages (immigrants, first capture of a group) with a body mass of >3,000 g were therefore assigned a minimum age of 5 years, so that their subsequently obtained data could be included into future analyses.

5.4 Comparative Aspects Based on Long-Term Data

This first summary of the social organization and life history of the Kirindy sifaka provides a basis for comparisons with other studies of sifaka, in particular, that of the population at Beza Mahafaly. At Beza, groups also contain about 6 individuals on average (Fig. 2 in Richard et al. 1993), with a slight average preponderance of males (Fig. 4 in Richard et al. 1993). Dispersal is also male biased, with all 17 males aged 3–6 years of one particular study cohort emigrating from their natal groups; in most cases, into neighboring groups (Richard et al. 1993). As at Kirindy, female transfer at Beza was rare (Sussman et al. 2012). During a 7-year period, only two neighboring females switched home ranges and males. In six additional cases, an adult pair formed a new group, but the circumstances of the departures of these adult females from their original groups were unknown (Richard et al. 1993). Population genetic analyses of the Beza population reflected the genetic consequences of this sex bias in dispersal (Lawler et al. 2003; Sussman et al. 2012). Thus, the overall pattern of social organization of sifakas at both sites is rather similar.

In contrast, the demographic structures of the two populations appear very different, despite great similarities in female life history parameters. The youngest females to give birth at Beza were 3 years old, but no infants of females younger than 5 years survived to 12 months (Richard et al. 2002). Five years is the age at which Kirindy females also begin to reproduce regularly. Even though female fertility declined after the age of 18 at Beza, females continued to give birth until at least the age of 28 (Richard et al. 2002), whereas we have so far only evidence that a single female in the Kirindy population is even close to being 20 years old. Close to 60% of females at Beza reproduced successfully within 1 year of a surviving birth, indicating that average inter-birth intervals are similar at the two sites. Infant survival during the first year is slightly lower at Beza (51 vs 55%), but later mortality is substantially lower, with many animals surviving well into their twenties (Richard et al. 2002). Infanticide is similarly rare at both study sites. However, during the 15 years on which they based their analysis, Richard and colleagues (1992) found 28 decomposing sifaka corpses (compared to zero at Kirindy), and report only a single probable episode of fossa predation and no attacks by the Harrier hawk. Predation by introduced wild cats (*Felis sylvestris*) is rare and apparently ecologically insignificant (Brockman et al. 2008). Thus, it appears likely that different predation rates, particularly by fossa, underlie a major component of the observed differences in demography between the two study sites.

Propithecus edwardsi at Ranomafana National Park exhibit some interesting contrasts and similarities with the two *P. verreauxi* populations. Groups of this rainforest species consist of 4.6 individuals on average, including 1.44 adult females and 1.46 adult males (Pochron et al. 2004). Female dispersal is much more common in *P. edwardsi*, however, and even equaled dispersal rates among males in a small sample (Morelli et al. 2009). Inbreeding avoidance appears to be a major cause of female dispersal, but dispersing females also commit infanticide in their new groups and evict the corresponding mothers (Morelli et al. 2009). Thus, reproductive opportunities for females appear to be limited, and dispersal may represent the main behavioral mechanism that females use to gain breeding positions (see also Wright et al. 2012).

Female *P. edwardsi* also begin reproducing as early as age 4, but substantial fertility is only achieved after age 6. Reproduction continues until age 18, with an average inter-birth interval of 1.56 years, but early infant death results in a significant reduction of the average inter-birth interval to 1.1 years (Pochron et al. 2004). Life expectancy at Ranomafana also declines at age 15 and ends before age 20. As in *P. verreauxi*, half of the newborn (female) infants fail to survive their first year of life. Infanticide is a more common cause of infant death (12% of young females' deaths; see also Morelli et al. 2009) than in either *P. verreauxi* population, but, importantly, as in Kirindy, predation by fossa is responsible for a large proportion (64%) of deaths for which the causes are known (Wright et al. 1997; Pochron et al. 2004). Thus, high predation pressure by fossa has resulted in similar demographic structures of the sifaka populations at Kirindy and Ranomafana, both of which clearly differ from that at Beza Mahafaly.

5.5 Conclusions: Limitations and Highlights of a Young Long-Term Study

This summary of some aspects of our sifaka study both reveals some of the major limitations of our research thus far and highlights a few findings that were only possible because of the long-term nature of the study.

A 3-kg sifaka is a small-to-medium-sized mammal. However, to describe even the cornerstones of its social organization and life history, studying >150 individuals over 15 years turned out to be far from sufficient. Relatively low birth and developmental rates characteristic of most primates, and sifakas in particular (Richard et al. 2002), limit sample size for other analyses considerably. Most importantly, even after 10 or more years of study, small sample size hampers many aspects of life table analyses (see Alberts and Altmann 2003). For example, the sample size for female age at first reproduction – the key functional life history variable – is still so small that it is statistically not justified to calculate an arithmetic mean. Thus, studying multiple groups in species with such small average group sizes as sifaka is essential for capturing natural variation across groups and time, and a long-term approach is the only way to reduce these natural limitations.

The specific highlights of our insights into sifakas sociality due to the long-term nature of our study mainly concern rare but important events, of which female transfer is clearly the most important one. Female transfer happens so rarely, quickly, and uneventfully that it is extremely easy to miss in short-term studies. Whereas genetic analyses allowed us to infer its occurrence (see also Di Fiore et al. 2009), only regular observations have permitted us to identify some of the potential ultimate causes motivating it (see also Morelli et al. 2009). Because it has been known for some years that females of group-living Lemuridae evict other females from their group, even though they are close relatives by anthropoid standards (Vick and Pereira 1989), we initially suspected that these rare dispersing females might also be victims of targeting aggression in their natal groups. However, as our long-term analyses of female reproductive success as a function of natural variation in female group size revealed, female competition in sifakas appears to be ubiquitous despite peaceful coexistence of two or more adult females. Unlike those species of Lemuridae that form stable social groups, active expulsion of female competitors has never been observed among the Kirindy sifaka. Exploiting opportunities for reproduction in groups that have lost adult females to predation or other events may instead trigger many of these unusual female dispersals.

A second, related point concerns the importance of knowing the genealogical relationships among all group members, especially because these cannot be determined with precision from genetic analyses alone (Harris et al. 2009). In some of the documented cases of female dispersal in this study, female transfer can be reasonably interpreted as an attempt to avoid incestuous matings with closely related males.

Given the low reproductive rates of sifakas in combination with high rates of early infant mortality, a long-term approach to studying the distribution of paternities among males was also necessary because the sample sizes required for meaningful analyses accumulated very slowly. Only after more than 10 years did we have a sufficient number of infants who survived long enough to be captured to obtain a tissue sample for genetic analyses (Kappeler and Schäffler 2008). The results of this study contributed to the illumination of a long-standing problem in the study of lemur sociality related to the male-biased adult sex ratios (Kappeler et al. 2009). The relative reproductive success of males pursuing apparently different reproductive tactics could also be only determined after witnessing a sufficient number of group take-overs or knowing individual dispersal strategies (Kappeler and Schäffler 2008). These data now provide an opportunity to examine interesting intraspecific variation in male reproductive strategies because paternity analyses of the Beza sifaka revealed that the higher population density there, combined with more strongly overlapping home ranges during an equally short mating season, has resulted in greater opportunities for male extra-group mating opportunities (Lawler 2007; Sussman et al. 2012) and presumably smaller male reproductive skew, suggesting that sifaka males at Kirindy appear to be better able to mate-guard receptive females (Mass et al. 2009).

Finally, the combination of results from long-term studies at different sites made it possible to begin explaining other differences among populations. A qualitative comparison of sifakas demography showed Beza Mahafaly to be unusual, especially with respect to its age structure and mortality schedules, compared to Ranomafana and Kirindy. The absence of fossa predation at Beza can account for this demographic difference, something that provides a natural experiment to study the behavioral and long-term demographic consequences of the changes in one key ecological variable.

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Part III
America

Chapter 6
The Northern Muriqui (*Brachyteles hypoxanthus*): Lessons on Behavioral Plasticity and Population Dynamics from a Critically Endangered Species

Karen B. Strier and Sérgio L. Mendes

Abstract Since its onset in the early 1980s, our ongoing field study of the northern muriqui in southeastern Brazil has yielded original data on the behavioral ecology, reproductive biology, and life histories of one of the most critically endangered primates in the world. At the same time, a sixfold expansion in the size of our study population has provided insights into the plasticity of behavior and life history patterns that have important implications for muriqui conservation as well as for comparative models of primate socioecology. In this review of the history, growth, and diversification of our long-term study, we describe the transformation of our field site into a federally protected private reserve, the progression of the research questions as our knowledge has increased, and our predictions about the effects of increased population density on key demographic and life history variables. We also reiterate the need for more comparative studies of other muriqui populations, and reflect on the essential role that long-term, international collaborations have played in advancing the scientific and conservation agendas we have pursued from the start.

6.1 Introduction

Like most other members of the Atelinae, the northern muriqui (*Brachyteles hypoxanthus*) is a large-bodied New World monkey characterized by slow, ape-like life histories and a social system that includes male philopatry and female-biased dispersal (Strier 1992a, 1999a; Nishimura 2003; Di Fiore et al. 2011;

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Fig. 6.1 Male northern muriquis (*Brachyteles hypoxanthus*) at the RPPN-Feliciano Miguel Abdala, Minas Gerais, Brazil. Photo © Carla B. Possamai

Fig. 6.1). Unlike the other three genera of Atelinae (*Ateles, Lagothrix,* and *Oreonax*), muriquis are endemic to the Atlantic Forest of southeastern Brazil, with the southern muriqui (*Brachyteles arachnoides*) found in the states of Rio de Janeiro and São Paulo and in forest fragments in Paraná (Aguirre 1971; Koehler et al. 2002), and the northern muriqui, restricted to only a dozen of the remaining forest fragments in the states of Minas Gerais and Espírito Santo (Mendes et al. 2005a). With a known population of less than 1,000 individuals, the northern muriqui is one of the most critically endangered primates in the world (Mittermeier et al. 2006).

Concern for the muriqui's conservation status dates back more than 40 years, when it was still considered to be a monotypic genus and virtually nothing about its behavior and ecology was known (Aguirre 1971; Coimbra-Filho 1972). Subsequent analyses of the morphological and genetic differences between northern and southern populations led to their reclassification as separate species (Rylands et al. 1995; Groves 2001; Rylands and Mittermeier 2009). The two muriqui species face different kinds of primary threats from habitat loss and hunting, respectively (Strier and Fonseca 1996/1997).

The elevation of the northern muriqui to separate species status is only one of the many changes we have witnessed since 1982, when unbeknownst to us and by independent paths, we had separately visited the same small patch of privately owned Atlantic Forest, located on Fazenda Montes Claros in the municipality of Caratinga, Minas Gerais, and had each caught our first glimpses of a wild muriqui. One of us (K.B. Strier) had gone there with the explicit goal of assessing the feasibility of studying muriquis; the other (S.L. Mendes) went to evaluate the prospects for a study of the sympatric brown howler monkey (*Alouatta guariba*; previously, *Alouatta fusca*), another species endemic to the Atlantic Forest and just as poorly known as the muriqui. We both opted to return to the forest to pursue our respective studies in 1983, which thus marks the beginning of what has developed into the longest-running field study on the northern muriqui, as well as our mutual enduring interest in the future of this forest and the endangered primates it supports.

We begin this chapter by reviewing the history of our long-term study site and the administrative and ecological changes it has undergone as a result of international and Brazilian conservation efforts mediated through some key nongovernmental organizations (NGOs) and the conservation initiatives taken by members of the family that owns the forest. We then summarize some of the main findings that have emerged from the nearly 30 years that this muriqui population has been systematically monitored. As is true for most long-term field studies, the focus of our research has shifted from initial quantitative depictions of basic behavior and ecology to analyses of reproductive patterns and life history strategies, which are only possible to investigate with data and perspectives obtained over the course of multiple generations in the muriquis' lives (Strier 2003a, 2009; Strier and Mendes 2009). Our key findings thus include the insights into the behavioral consequences of demographic changes that could not have been made during a shorter study period. We also discuss some of our predictions about the effects of demography on fundamental variables such as female dispersal and male maturation. We conclude by reflecting on the synergy between the two driving forces – conservation and research – that have fueled the long-term study from its inception.

6.2 History and Ecology of the Study Site

In 1944, Sr. Feliciano Miguel Abdala purchased a plot of land about 60 km south of Caratinga, Minas Gerais, a town that sits at the crossroads between the transnational highways that connect São Paulo in the south with Bahia in the north, and Belo Horizonte in the west with Vítória in the east. The land, known as Fazenda Montes Claros, was a productive coffee plantation and cattle ranch, but also included what has remained one of the largest privately owned tracts of Atlantic Forest in the region. According to local history, Sr. Feliciano promised the fazenda's previous owner that he would preserve the forest and protect its inhabitants (Abdala Passos 2003). The area is known today as the Reserva Particular do Patrimônio Natural (RPPN)-Feliciano Miguel Abdala; its persistence as a federally recognized "Private Natural Heritage Reserve" is a testimony to Sr. Feliciano's honored promise (Castro 2001).

The presence of muriquis at this site was first reported to the scientific community by zoologist Álvaro Aguirre in 1971. By the late 1970s, zoologists from the Universidade Federal de Minas Gerais (UFMG), led by the indefatigable Professor Célio Valle, had initiated a campaign for the protection and scientific study of this area. Japanese primatologist Akisato Nishimura (1979) visited the site and provided some of the first observations of muriqui behavior. Other primatologists and conservationists, stimulated by Russell A. Mittermeier, Adelmar F. Coimbra Filho, and Ibsen G. Câmara, joined Célio Valle's group from UFMG in an international collaborative effort to study and preserve the local biodiversity (Mittermeier et al. 1982). Besides the presence of brown howler monkeys and muriquis, the discoveries of another endangered primate, the buffy-headed marmoset (*Callithrix flaviceps*), and of a large population of tufted capuchin monkeys (*Cebus nigritus*) signaled the forest's unusual potential to become a major site for field research on wild primates in the Atlantic Forest of Brazil. To help realize this potential, Sr. Feliciano donated a small house at the edge of the forest, and in collaboration with the UFMG, the World Wildlife Fund (WWF), and the Brazilian Foundation for the Conservation of Nature (FBCN), the Estação Biológica de Caratinga (EBC) was inaugurated in May 1983.

The EBC provided essential infrastructure for researchers and was thus critical for establishing our long-term study (Strier and Mendes 2003). Although the accommodations are simple, the house has undergone many improvements over the years, including the acquisition of electricity from nearby power lines, the expansion of living space for researchers and visitors, and the construction of a laboratory for storing and processing materials such as plants (Boubli et al. in press) and feces used for the noninvasive analyses of muriqui gastrointestinal parasites (Stuart et al. 1993; Santos et al. 2004), steroid hormones (e.g., Strier and Ziegler 1997, 2000), and genetics (Fagundes et al. 2008). The EBC has also undergone transitions in its administration, which passed from the FBCN to Fundação Biodiversitas, then to Conservation International-Brasil, and, in 2001, to the Sociedade para a Preservação do Muriqui, or SPM, established by the Abdala family to administer the activities in their Reserve.

Consistent with Sr. Feliciano's conservation vision for his forest, the Reserve's most important function continues to be the sanctuary it offers to its endangered flora and fauna. The natural regeneration of nearly 100 ha of pasture and agricultural land within and surrounding the Reserve has provided additional habitat that all four species of primates increasingly exploit (Strier and Boubli 2006). In addition, plans to create corridors to link the Reserve with some of the smaller forest fragments that remain on other privately owned properties surrounding it are underway; once established, the corridors will increase the available habitat for muriquis and thus should permit the population's continued expansion (Strier et al. 2005; Tabacow et al. 2009b).

The local predator community has increased in diversity along with the increased habitat protection and expansion over the past three decades. Suspected muriqui predators include tayra and large hawks (Printes et al. 1996), and possibly semi-feral dogs (Mourthé et al. 2007). The first ocelot since the onset of the study was sighted in 1990 (Strier 1999b), and scat analyses have since confirmed that muriquis in our study population are among their prey (Bianchi and Mendes 2007).

Over the past three decades, many of the plants and animals, and all four species of primates, have been the targets of systematic field studies. The integration of research with conservation efforts, like our own work with the muriquis, has characterized many of these other projects and benefitted from the strong international collaborations that were initiated decades ago when the value of the forest for conservation and for science was first recognized. These collaborations, along with our mutual commitment to capacity building, have been critically important to the continuity of our long-term study. Since 1983, some 45 Brazilian students have participated in the muriqui project alone, and many of these students have gone on to pursue scientific and conservation-oriented careers (Strier and Mendes 2003, 2009; Strier and Boubli 2006).

6.3 Demography, Group Dynamics, and Life Histories

Systematic studies were initiated on one of the two original muriqui groups (Matão group) present in the forest in 1982, yielding detailed individual life history data since July 1983. Systematic studies on the other groups in this population were initiated in 2002, yielding demographic and life history data on the entire population from 2003 through the present. One of these groups (Jaó) was present in 1982; the other two groups were established when the Jaó group fissioned in 1988 (M2 group) and 2002 (Nadir group) (Strier et al. 1993, 2006). Thus, as of June 2010, our accumulated demographic and life history data span a 28-year period on the Matão group and the last 7 years on the entire population.

All individuals in this isolated population can be identified by their natural markings and are monitored by teams of trained Brazilian students who are in the forest on a near-daily basis. This has made it possible to follow known individuals from their birth through maturity, and to track females after they disperse from their natal groups (Strier and Mendes 2009).

6.3.1 Population Expansion

The Matão group has increased steadily from 22 to 107 individuals between July 1982 and June 2010 (Fig. 6.2). Some of its original members are still alive, including five adult females estimated to be >35 years old. The increase in this group's size and in the number of muriqui groups (from 2 to 4) can be attributed to the increase in the population's size and density during its recovery from past disturbances that included the forest's initial fragmentation, selective logging, and fire (Strier 1999b; Strier and Boubli 2006). In the late 1960s, the muriqui population was estimated at 20–25 individuals (Aguirre 1971) and by the early 1980s, it was estimated at 40–50 individuals (Valle et al. 1984); as of June, 2010, the population included 288 individuals. This sixfold size increase in less than 30 years has offered us an unanticipated opportunity to document the muriquis' behavioral responses to demographic changes (e.g., Dias and Strier 2003; Strier et al. 2006; Tabacow et al. 2009a; Strier 2011).

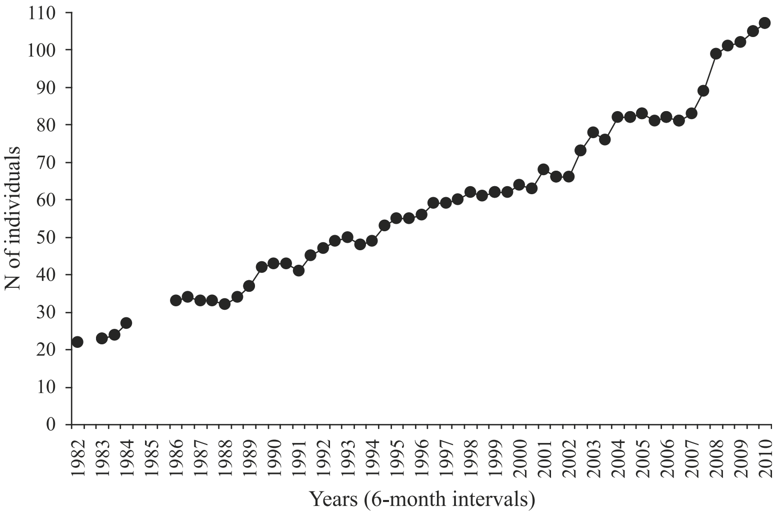

Fig. 6.2 Changes in the size of the Matão group. Group counts are shown at 6-month intervals, beginning in July 1982; gaps indicate missed counts. Updated from Strier (2005)

6.3.2 Behavioral Stability and Plasticity

Despite the group and population expansion, there have been no changes in the unusually peaceful, egalitarian relationships that distinguish the societies of northern muriquis from those of other primates (Strier 1990, 1994; also reviewed in Di Fiore et al. 2011). There is no overt evidence of dominance relationships among or between males and females, and both the rates and intensity of intragroup aggression have remained relatively low (Strier 1992b; Strier et al. 2000). Philopatric males maintain particularly close spatial associations and do not interfere with one another's access to fertile females, who routinely mate with multiple partners at times in their cycles when they are most likely to conceive (Strier 1997a; Strier and Ziegler 1997; Strier et al. 2002; Possamai et al. 2007). Despite more than 28 years of near-continuous field observations in our main study group, there has never been any indication of the kind of lethal aggression that has been observed in spider monkeys, which also show male philopatry (Campbell 2006), and in one population of southern muriquis living under different ecological conditions than those at our study site (Talebi et al. 2009).

Nonetheless, other behavioral changes can be directly attributed to the dramatic demographic changes the population has undergone. For example, within 15 years after the systematic monitoring had begun, the size of both the Matão group and its home range had roughly doubled. Although there was no corresponding increase in their daily travel distances, the group's previously cohesive pattern of association shifted to more fluid associations involving variably sized parties (Dias and Strier 2003) like those seen in other primates in which fission–fusion sociality is associated with the avoidance of direct feeding competition (Aureli et al. 2008). Indeed, shifts from cohesive to fluid grouping patterns appear to be a consistent response to increasing group sizes that distinguishes primates living in patrilocal societies from those living in matrilocal societies (Strier 2009).

The fluid grouping patterns that now characterize the Matão group may be responsible, at least in part, for the persistence of this group despite its continued (and ongoing) growth. In contrast to the Jaó group, which has undergone two prior fissioning events since the onset of the population monitoring in 1982 (Strier et al. 2006), the Matão group has maintained its integrity as a group, as evidenced by the routine reuniting of subgroups as well as by its fidelity to a common home range. Previous predictions about the Matão group's fate have focused on the effects of group size, age and sex composition, and intra- and intergroup male relationships (Strier et al. 1993; Strier 2011). For example, increasingly male-biased adult sex ratios might lead to higher rates of male–male aggression or even favor male dispersal if the sex ratios in other groups are more favorable than those in their natal groups (Strier et al. 2006). Evaluating these predictions is an empirical question that only ongoing observations over the long term will be able to resolve.

With roughly 0.30 muriquis per hectare, our study population's density is now one of the highest known for this species (Mendes et al. 2005a). Extensive home range overlap among the four groups that now occupy the forest (Boubli et al. 2005) and a decline in the density of sympatric brown howler monkeys, whose diets overlap with those of muriquis (Almeida-Silva et al. 2005), provide indirect indications that our study population might be approaching the carrying capacity of this forest. In addition, the documented increase in the use of terrestrial substrates by members of the Matão group may reflect an expansion in their vertical niches (Mourthé et al. 2007; Tabacow et al. 2009a). Moreover, recent sightings of nulliparous females from our study population moving between the Reserve and some neighboring forest fragments located adjacent to the Reserve suggest that they may be seeking new habitat to colonize as the population density of muriquis inside the Reserve has increased (Tabacow et al. 2009b).

Although much of our ongoing research is now focused explicitly on understanding the effects of habitat saturation on the muriquis' behavior and ecology, there are also some intriguing illustrations of the synergistic interactions between behavior and population dynamics that we are simultaneously pursuing. For example, the increase in terrestrial behavior in our main study group appears to have occurred along two dimensions: The first involved the expansion from essential activities, such as feeding and drinking, to include nonessential activities, such as resting and socializing; the second involved the spread of the behavior along male social networks and subsequently to females including recent female immigrants to the group (Tabacow et al. 2009a). The terrestrial behavior of the Matão group can be considered a new local tradition according to the criteria applied to other types of traditions in other organisms (see Perry et al. 2011): it was socially transmitted and adopted by the all or most group members, and it has endured over time (Tabacow et al. 2009a). Consequently, we are now investigating whether females who have acquired this terrestrial tradition in their natal Matão group import it into the groups into which they disperse, and thereby effectively diffuse the custom of engaging in nonessential terrestrial activities throughout the population.

6.3.3 Habitat Saturation and Female Dispersal

We can expect flexibility in life history components in response to density dependent effects associated with habitat saturation. For example, the effects of high levels of intragroup competition in large groups might include delays in the maturation of philopatric individuals and earlier dispersal ages in the dispersing sex, whereas high levels of intergroup competition in saturated habitats can result in delays in dispersal age and in extreme cases may lead to the permanent retention of both sexes in their natal groups (e.g., Alberts and Altmann 1995; Ferrari and Digby 1996; Altmann and Alberts 2003; Charpentier et al. 2008).

Plasticity in dispersal provides a mechanism for adjusting the size and sex ratio of breeding groups relative to those of other groups in the population (Moore 1992; Strier 2003b). Dispersal costs previously documented for female muriquis include reduced survivorship, with 28.4% mortality estimated for 38 females of dispersal age (5–7 years) from 2002 to 2007 compared to 4.55% mortality for philopatric males in the same age class. There was also significantly later ages at first reproduction compared to females that remained and reproduced in their natal group. Specifically, natal Matão females have dispersed at 5.25–7.85 years of age (mean $= 6.15 \pm 0.60$ years, $N = 34$; updated from Strier et al. 2006), prior to the onset of sexual activity or hormonal evidence of puberty (Strier and Ziegler 2000). Age at first reproduction was significantly earlier in the Matão females that reproduced in their natal group (7.77 ± 0.72 years, $N = 3$) compared to females that dispersed from the Matão group and whose first reproductions in their new groups have been documented (9.58 ± 0.87 years, $N = 9$; $z = 2.40$, $p < 0.02$); this difference can be attributed to the earlier onset of puberty in the non-dispersing females instead of shorter cycling-to-first conception delays (Martins and Strier 2004).

Delayed reproduction associated with dispersal has been documented in red howler monkeys (*Alouatta seniculus*), where it may be associated with eviction from their natal groups (Crockett and Pope 1993), but not in mountain gorillas (*Gorilla beringei*), where the voluntary dispersal of nulliparous females from their natal groups (Robbins et al. 2009) more closely resembles that of muriquis to date (Printes and Strier 1999). Nonetheless, fluctuations in group and population conditions in our study population could alter both the contexts under which females disperse and the consequences of dispersal for reproduction. For example, if females are sensitive to levels of intragroup competition, then we might expect the age at dispersal of female muriquis to decline as the size of their natal group increases. However, there is no evidence that this has occurred over the decades during which the Matão group has been monitored (Fig. 6.3).

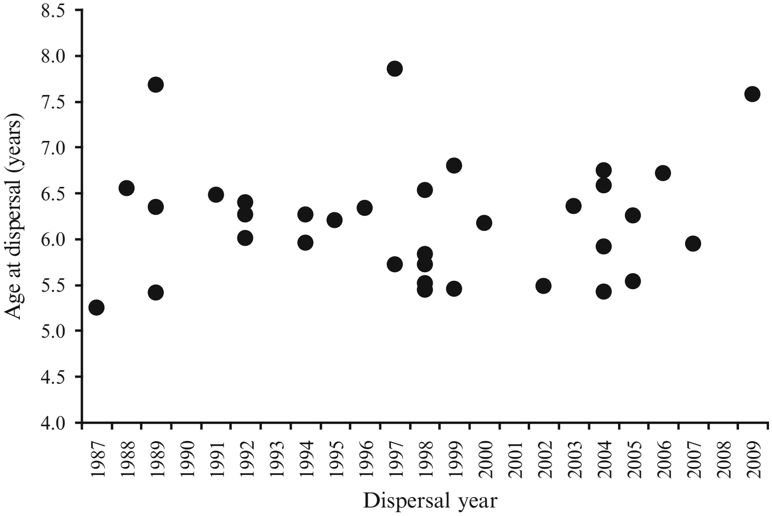

Fig. 6.3 Female dispersal age over time. Natal Matão group females (*N* = 34) have dispersed between 5.25 and 7.85 years of age, and there is no evidence for changes in female dispersal age despite increases in group size, population size, and population density over time

Alternatively, if females are sensitive to intergroup competition associated with population density, then they might postpone dispersal from their natal groups, and experience higher levels of aggression from females in the groups they try to join and higher mortality costs during dispersal as population density increases. Although high population density should facilitate encounter rates with other groups (Strier 2000a), increased competition and aggression should make joining these groups more difficult now than it has been in the past. However, although we found early on that the rate at which females received displacements from other female was higher for new immigrants than for long-term residents (Printes and Strier 1999), this difference has not increased, nor have we seen increases in the rate of aggression directed at immigrants.

6.3.4 Male Maturation and Philopatry

Changes in female dispersal and maturation can have significant implications for breeding sex ratios as population density has increased, and thus affect levels of male competition within and between groups, particularly in species in which males remain in their natal groups (Strier 2000b, 2011). To date, males in the Matão group become sexually active between 4.10 and 8.27 years of age (mean = 6.18 ± 1.04, *N* = 26) and when they have reached sexual maturity, defined behaviorally by their first observed copulation that culminates with ejaculation, between 5.21 and 8.36 years of age (mean = 6.81 ± 0.86, *N* = 25). Males in the Matão group have thus entered the potential breeding population about 0.3 years (4 months) younger, on average, than the age at which the females that have (atypically) remained in their natal groups have conceived (7.10 years; calculated from subtracting the hormonally determined mean gestation length of 216 days, or 0.59 years; Strier and Ziegler 1997), and more than 2.2 years earlier than the average age at which dispersing females have conceived.

Despite more than a 3-year range of variation in age of male sexual maturity, there has been no pattern of change in the variation over time (Fig. 6.4). This consistency in the age of sexual maturation in male muriquis might reflect a balance between demographic pressures that should delay maturation on the one hand, and the effects of increased competition on survivorship that should favor faster maturation on the other hand (Janson and van Schaik 1993). Alternatively, it could reflect a lag between the effects of group size and density effects, such that social pressures have not yet begun to exert the expected delaying effect on male life histories (Joffe 1997). As operational sex ratio in the Matão group becomes increasingly male-biased (Strier et al. 2006) and scramble competition for access to females correspondingly increases (Strier et al. 2002; Strier 2003b), we expect increasing delays in the onset of male sexual maturity and possibly dispersal to groups with more favorable breeding sex ratios. Extraordinary demographic conditions may underlie other examples of deviations from male philopatry, such as in an isolated chimpanzee community at Bossou, New Guinea (Sugiyama 2004), in the case of male bonobos thought to have transferred into a community with more favorable sex ratios (Hohmann 2001), and in one group of wooly monkeys in a population that might have been affected by past hunting (Di Fiore and Fleischer

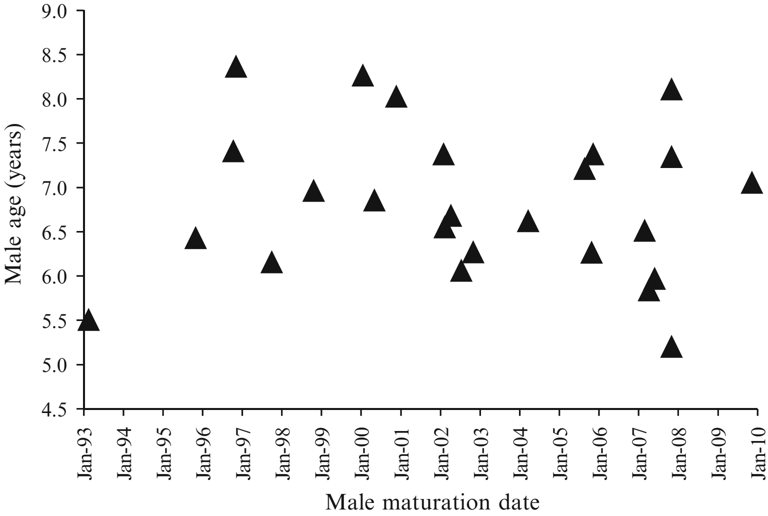

Fig. 6.4 Male age at sexual maturity over time. Matão males ranged from 5.21 to 8.36 years ($N = 25$) and there was no obvious change over time despite increases in group size, population size, and population density

2005; Di Fiore et al. 2009). Indeed, the social flexibility seen in both woolly monkeys and northern muriquis may extend to their dispersal patterns (Di Fiore and Strier 2004), and thus provide a mechanism to offset the predicted effects of increased social and ecological competition on male maturational stages.

6.4 Past Perspectives and Prospectives

After nearly 30 years of field research on the northern muriqui, we have gained some clear insights into features of the behavioral ecology, reproductive biology, and life histories of our study population. Although our understanding of other muriqui populations is still limited, both the changes and the equally important lack of changes we have documented in our study population provide a crucial comparative context for research on these populations. Neither the extent of the population expansion nor the corresponding behavioral changes that our study has tracked were anticipated aims of the project from the onset. Yet, in many respects it has been this first-hand glimpse into the dynamics of the muriquis' lives that has captured – and continues to hold – our attention.

Reflecting on the history of our long-term field study, five particular points come to mind, and all are connected in one way or another to the northern muriquis' critically endangered status. Perhaps the most obvious of these has been the methodological choices we have made to minimize the impact of our research on the animals. Thus, we have restricted ourselves and our students to observational studies instead of field experiments, even though the careful deployment of feeding platforms or of controlled playback techniques might have permitted us to discriminate between correlated and causal responses. We have also opted to restrict investigations of muriqui parasites, hormones, and genetics to what could be gleaned from analyses of their dung. This has sometimes meant greater costs and longer delays than we might have incurred, for example, if we had captured the muriquis to obtain samples of their blood for genetic analyses before the techniques for extracting and amplifying DNA from dung were developed. Yet, even with these self-imposed constraints, we are cautious about the possible impacts of our long-term research presence (Strier 2010).

A second major consideration pertains to the demographic fluctuations and behavioral plasticity we have documented. The increases in the size of our main study group and the entire study population have clearly shown that primate groups and populations are not static entities with fixed properties, but instead, that they have group and population histories of their own (Strier 1997b). This realization raises all kinds of questions about how much we can conclude about the behavioral adaptations of northern muriquis – or any other primates – that are currently living under what are likely to be highly altered ecological and demographic conditions (Strier 2003b, 2009). Indeed, after all of these years, we cannot determine what group size or population density would be typical for this species or the extent to which these vary among populations. Nonetheless, we think that questions about how much of the behavior we observe in our study subjects today reflect adaptations as a result of past selection pressures versus mismatches between past and current conditions that could negatively impact their survival are important and interesting, not only for northern muriqiuis, but for all other primates whose futures are threatened (Strier and Mendes 2009).

Demographic changes in our main study group were responsible for a third significant shift in our perspective, for as the number of natal female emigrants began to exceed the number of female immigrants, our focus expanded from studying a single group to studying the dynamics of the entire population (Strier 2005; Strier et al. 2006). This catapulted the importance of this particular population – and of this particular forest, which supports nearly 30% of the entire species – into a broader perspective, stimulating our interest in facilitating new research initiatives on the vegetation and ecology of the forest (Strier and Boubli 2006; Boubli et al. in press) and our ongoing collaboration with the NGO that now administers the protected reserve.

The expansion and diversification of research contributed to a fourth major advance, which involved the launching of comparative field studies of other populations of northern muriquis. This includes one at the municipality of Santa Maria de Jetibá (SMJ), Espírito Santo State (Mendes et al. 2005b) that is particularly valuable because the demography of that population differs greatly from that at the RPPN-FMA. Whereas our study population includes multiple large social groups in a single isolated forest of nearly 1,000 ha, the SMJ population is represented by at least 13 single small groups of 2–20 individuals occupying forest fragments of 60–350 ha, where opportunities for dispersal are limited (updated from Mendes et al. 2005b). Although the behavioral and ecological comparisons between these populations hold great theoretical potential, our greatest concern at the moment is how to apply what we have learned about northern muriquis so far to insure the survival of both of these – and other – remaining populations.

A final reflection that we are in a privileged position to make involves our ongoing appreciation for the synergy that can come from a true international collaboration (Strier and Mendes 2009). The continuity in our long-term study of the northern muriqui would not have been possible without it.

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Chapter 7
The Lomas Barbudal Monkey Project: Two Decades of Research on *Cebus capucinus*

Susan Perry, Irene Godoy, and Wiebke Lammers

Abstract The Lomas Barbudal Monkey Project began in 1990 with the study of a single white-faced capuchin monkey (*Cebus capucinus*) group, and has since expanded to 11 groups. Social behavior has always been the primary focus of our research, with emphasis on communication, social learning, and life history strategies. Genetic analyses in the context of this long-term study have enabled research of many standard behavioral ecology topics such as kin-based altruism, reproductive skew, and inbreeding avoidance. Long-term research on numerous groups, and collaboration with researchers at other *C. capucinus* sites, has permitted the documentation of social traditions regarding both communicative rituals and foraging techniques.

7.1 The History and Infrastructure of the Study Site

7.1.1 History

The Lomas Barbudal Monkey Project began with my (SP's) dissertation work on the evolution of intelligence. I was looking for a stable country where I could begin a long-term project investigating social relationships and social intelligence in capuchin monkeys, which were known for their large relative brain sizes. Costa Rica, with its friendly policy toward researchers, excellent environmental record, superb medical system and lack of an army, was the obvious choice. Following the

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advice of Colin Chapman, who had censused monkeys in Guanacaste province, I settled on Lomas Barbudal as a study site and conducted a pilot study in 1990.

Lomas Barbudal Biological Reserve is a tropical dry forest site located in Guanacaste Province, northwestern Costa Rica. It was established as a reserve by UC-Berkeley entomologist Gordon Frankie, who has described the vegetation structure (Frankie et al. 1988). The monkeys range well outside the reserve into other public and private lands. This highly disturbed forest includes riparian forest, dry deciduous forest, mesic forest, and regenerative forest. Lomas receives 1,000–2,200 mm of rain annually between the months of May–November (Frankie et al. 1988), and fires are common in the dry season. Lomas Barbudal is approximately 55 km away from the better-known Santa Rosa National Park, which also hosts a long-term study of white-faced capuchins (see Fedigan and Jack 2012). The two sites have similar ecologies and plant lists (Panger et al. 2002); however, the Lomas monkeys have plenty of access to fresh running water, whereas the Santa Rosa monkeys rely heavily on waterholes in the dry season.

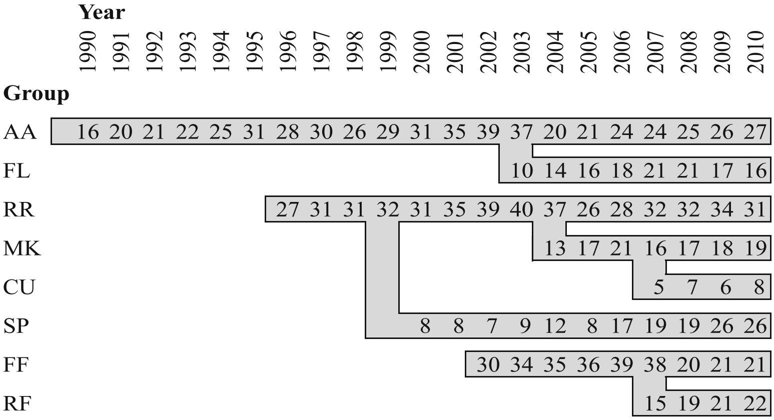
In 1991, the year following my pilot study, Joseph Manson and Julie Gros-Louis joined me as field assistants for my thesis research and became co-founders of the site, assisting me in the set-up of the site and co-managing it with me until the end of 2001. For the first 4 years, we documented the social behavior of a single group, Abby’s group (AA).

Following my thesis research, Joe Manson and I received half-time tenure track jobs at UCLA, and began developing plans to make Lomas a long-term project. Our UCLA startup funds allowed for the purchase of a 1977 LandCruiser and a tent, and funds from my postdoctoral fellowships purchased Psion handheld computers, to streamline data collection. From 1994 to 1998, we pitched our tents on a rice farm owned by some *campesino* friends (the Rosales family) and ran our laptop computer on a truck battery powered by solar panels. In the meantime, Julie Gros-Louis began her dissertation research and was primarily responsible for the habituation of a second study group (Rambo’s, RR). Because all of us had commitments teaching or taking classes at our respective universities, there were periods of time when no one could be present at the site. We initially attempted to solve this problem by inviting graduate students from other universities to work there in exchange for contributing to the demographic database. This, however, was a failure in terms of the long-term goals of the project; visiting students were not willing to invest the time to learn the identities of young monkeys who were not their focal subjects, or to track the movements of migrating males. And it was difficult to persuade anyone to continue data collection through the worst of the rainy season. It became clear that obtaining an accurate demographic database required employing someone whose sole responsibility was to collect these data for the project during our absence.

By 2001, things were not looking good for the future of the field site. The rice farm where we lived had been sold. Julie was finishing her final field season for her doctoral research. To ensure proper management of the site and the long-term database, it was imperative that I maintain a continuous presence at the site, and this was not possible while I was employed by UCLA. At this critical juncture, I was fortunate to be appointed director of the Cultural Phylogeny research group at the Max Planck Institute for Evolutionary Anthropology (MPI-EVAN) in Leipzig. Germany. This job allowed me to devote all of my time to research and to hire a large crew to run the project when I was in Germany for 6 months of each year. The project rented two adjacent houses in the nearby town of Bagaces (35 min from the forest where we work), which had electricity, running water, and even internet access, so that I could supervise my crew's work remotely. The modernization of the site made it possible to attract field assistants who would stay for a year or more.

During the MPI phase of the project, we employed 6–9 interns per year, plus a permanent staff of seven people. The MPI-EVAN job ended in 2006, at which time I returned to my half-time job at UCLA. Thus far we have succeeded in keeping the project running on far less funding than was available at MPI, via short-term grants from NSF, the Leakey Foundation, and the National Geographic Society. We still maintain a staff of six interns, two full-time permanent staff and two part-time permanent staff. But now that we lack the security of long-term funding from MPI, we are extremely vulnerable to funding crises that could suddenly end the project at any time. This insecurity makes it harder to retain valuable staff members.

Beginning in January 2002, we completed habituation of a third study group (Pelon, FF) and were able to monitor all of our groups for up to 25 days/month year-round. These groups grew and fissioned (see Fig. 7.1), and males migrated to new groups. Currently, we have 11 study groups, nine of which we follow for several days per month, and two of which we visit more sporadically. Since 1994, we have collected fecal samples for genetic analysis from virtually all members of the study groups (aside from infants who die before we can obtain samples), and since 2006 we have been collecting fecal samples for hormonal analysis (fecal corticosteroids and testosterone). Our genetic and hormonal work has been carried out by graduate



Group	1990	1991	1992	1993	1994	1995	1996	1997	1998	1999	2000	2001	2002	2003	2004	2005	2006	2007	2008	2009	2010
AA	16	20	21	22	25	31	28	30	26	29	31	35	39	37	20	21	24	24	25	26	27
FL														10	14	16	18	21	21	17	16
RR							27	31	31	32	31	35	39	40	37	26	28	32	32	34	31
MK															13	17	21	16	17	18	19
CU																		5	7	6	8
SP											8	8	7	9	12	8	17	19	19	26	26
FF													30	34	35	36	39	38	20	21	21
RF																		15	19	21	22

Fig. 7.1 Maximum group sizes during each year of observation, and timing of fissions. For fission years, we report the size of the group right before the fission for the larger fission product, and the size of the group right after the fission for the smaller fission product

students working in the MPI-EVAN laboratories of Linda Vigilant and Tobias Deschner.

The topics of investigation have always centered on social behavior. The first few years of the project were devoted to documenting basic natural history of social communication and the structure of social relationships (Perry 1996a, b; 1997; 1998a, b; 2003; Manson et al. 1999; Gros-Louis et al. 2003; Perry et al. 2004; Perry and Manson 2008). Between 1995 and 2001, we investigated communication (vocal, gestural and olfactory) in greater detail and became particularly interested in the way in which individuals negotiate their social relationships (Manson et al. 1997, 2004a, 2005; Manson 1999; Manson and Perry 2000; Gros-Louis 2002, 2004a, b, 2006; Fichtel et al. 2005; Campos et al. 2007; Gros-Louis et al. 2008; Perry and Manson 2008). Our discovery of group-specific communicative rituals launched me on a multi-year study of social learning and social traditions (Panger et al. 2002; Perry et al. 2003a, b; Rose et al. 2003; Perry and Ordoñez Jiménez 2006; Perry and Manson 2008; Perry 2009). The interest in social learning spurred me to begin a developmental study of 46 infants in 2001 that continues to the present (Perry 2009). The availability of genetic data has enabled us to answer basic questions in behavioral ecology about issues such as kin-based altruism, inbreeding avoidance, and mating systems (Muniz et al. 2006, 2010; Perry and Manson 2008; Perry et al. 2008). This knowledge contributes to our long-term study of life history strategies.

7.1.2 Data Collection Methods

In the early years of the study, a team of observers (a narrator and a spotter, to check ID's) collected data, and data were narrated directly onto microcassette recorders. This method was essential in the early days, due to the richness of the behavioral repertoire, which had not yet been thoroughly documented. In 1997, we switched to using Psion palmtop computers, and I developed an elaborate system for rapidly coding behaviors in fine detail. We still switch to microcassette recorder when the action is extremely rapid or complex (e.g., when there are coalitionary fights or multi-party play bouts, or when the animals innovate and we have no codes to describe their actions accurately). These inserts are transcribed into the data after they are transferred into Excel spreadsheets at the end of the day. During data collection, one person types and double-checks IDs while the second person narrates the action and constantly watches the focal animal. Focal follows are the top priority in data collection, and these vary in length from 10 min to 12 h, depending on the topic of investigation. During these follows, we collect activity data and proximity data during point samples every 2.5 min, and continuous data on all social interactions, vocalizations, object handling and foraging events. We also conduct group scans approximately every 30 min, in which activities, food type (for foraging activities) and proximity to other animals are recorded. *Ad libitum* data on predator encounters, fights, agonistic interactions, sex, grooming, and innovative or traditional behaviors are also collected. Census sheets are filled out daily, reporting who was in each group, health and wounding status, and reproductive states. At the end of each year of employment with the project, each observer fills out a 26-item personality questionnaire on the animals they studied. During some years, there are special protocols in addition to these core protocols, which can include recording (audio or visual), field experiments of various types, and food processing protocols that note processing techniques, proximity between foragers, and gaze directed toward other foragers. Fecal samples are collected for both genetic and hormonal analysis. We have used a variety of methods for collection of genetic samples (Muniz and Vigilant 2008), all of which have worked: collection in (a) 96% ethanol, (b) silica, (c) RNA-later, and (d) a two-step process involving first ethanol and then silica. We dry and grind feces in the field for hormone analysis and mail them to a lab for extraction.

7.1.3 Current Infrastructure and Logistics of the Site

The bulk of the core data collection is performed by a crew of six or more interns. Most are people who have just finished a bachelor's or master's degree and are seeking fieldwork experience before continuing to a Ph.D. program or a career in conservation. Two Costa Ricans (Alex Fuentes Jiménez and Juan Carlos Ordoñez Jiménez) have been employed by the project for a number of years to help with data collection, logistics, and plant identification. Two managers aid me in the running of the site. One lives in the project house and is responsible for the training of assistants, monthly inter-observer reliability checks, scheduling, maintenance of the house and project equipment, and the running of the fecal sample laboratory. The other (Wiebke Lammers) is in charge of data organization, project purchasing and accounting, and the environmental education program. This second manager and the Costa Ricans are invaluable in coordinating conservation efforts and meeting with government officials when I am out of the country. The managers and I remain quite active in data collection, so that we can reliably identify all animals and maintain continuity in the demographic database. In addition to this core staff, who are primarily responsible for the long-term database, there are typically one or two graduate students or postdoctoral scholars who are doing independent research, and they also have field assistants. Most of the graduate students have previously served as field assistants.

In a project of this size that involves a collective attempt to produce a complex data set, inter-observer reliability is always a concern. Before anyone is cleared to collect usable data, they must pass code and syntax tests, speed typing tests on the Psion Workabout handheld computers, shadow follows (in which a trainee follows a trained team of observers and types along, and the two sets of records are compared), monkey ID tests, and vocalization recognition tests. It typically takes 6 weeks to 3 months for an intern to be considered fully trained enough to be the senior member of a two-person data collection team. Every line of data is tagged by spotter and typist ID so that if any errors are discovered later, the relevant data can be fixed or discarded. Each month, all observers are retested on their knowledge of codes, syntax, and vocalization recognition. If there is reason to suspect that someone's typing speed has declined since the initial training, then typing speed tests are retaken as well. Because we rotate work partners regularly, and work partners constantly double-check one another's monkey IDs, there is not much chance for errors to creep into monkey IDs. Whenever there is lack of agreement about monkey IDs or about what behaviors occurred, the follow is aborted and discarded. Whenever there is doubt about plant identification, a sample is collected and brought back to the Costa Rican botanist. We have a short staff meeting every night during dinner to discuss any doubts about protocol that have arisen during the day's data collection. Vocalization tests are always the hardest for achieving inter-observer reliability, so we just keep training records regarding which observers reliably recognize each vocalization and only analyze vocal data from those observers who are reliable for that call type.

Currently the project has amassed approximately 70,600 h of behavioral data, stored in the form of Excel spreadsheets. With this amount of data, the analysis process has become unwieldy, and so we are in the process of constructing a MySQL relational database to aid in the analysis process, modeled roughly after Babase, the database created for the Amboseli Baboon Project (Alberts and Altmann 2012).

7.2 Demography

7.2.1 Dispersal Patterns

Female capuchins at Lomas Barbudal are philopatric, as at other sites where this species and genus have been studied (Fragaszy et al. 2004; Perry et al. 2008; Jack and Fedigan 2009). Although we have directly observed immigrations or immigration attempts by 85 males (many of these migrating multiple times), we have still never witnessed a migration by a female (but see Jack and Fedigan (2009) and Fedigan and Jack (2012) for a few exceptions to this pattern at Santa Rosa). There have been 90 adult females above age 5 observed in our study for a period of up to 20 years. We have witnessed females interact non-aggressively with females from other groups only three times in 20 years and have never seen females seriously attempt to join other groups. In two cases, the females were separated from their own groups briefly following an intergroup encounter, and in the third case, it appeared that an estrous female and a male wandered away from their group and temporarily joined a neighboring group for half a day, until there was an intergroup encounter between the two groups and they returned to their normal group.

Typically females only remove themselves from close proximity with female kin when their group becomes so large that coordination of group movement becomes difficult (i.e., group size of >30). In these cases, groups fission fairly neatly along matrilines, so that the average relatedness among females is higher in the fission products than in the original group (Muniz 2008). The fission process may take up to 3 months, during which the two subgroups apparently try to stay together, but finally they decide who will be in which subgroups and adopt hostile relations toward the members of the other subgroup. For the first several months after the fission, intergroup relations are actually more hostile than is typical in intergroup encounters, and even females physically attack one another (whereas in typical intergroup encounters, active participation is almost exclusively by males). Figure 7.1 shows the history of group fissions at Lomas, with the number of monkeys that was present in each group at the time the fission occurred.

Males can either migrate singly or in groups of 2–8. Often co-migrant males are kin, and co-migration with kin can occasionally result in higher relatedness among adult males than among adult females. However, in 10 out of 11 demographic situations analyzed from three social groups at Lomas at different time periods, adult females had higher average relatedness than adult males (Muniz 2008). Males born into our three primary study groups, (AA, RR and FF) tend to make their first migration at age 92 months, regardless of whether we use a sample of 21 males from our developmental study whose birthdates and migration dates are fairly accurately known, or a sample of 44 males from the broader study whose birthdates and migration dates are somewhat less accurately estimated. The three youngest males to migrate were 4 years old, and they migrated in the context of a fission and/or an alpha male takeover in which a large all-male group composed of their male relatives formed. It is likely that they would not have migrated so early if the fission had not occurred. The seven oldest males to leave their natal groups were 11 years old. Additionally, one 11-year-old remains in a fission product of his natal group (but does not reside with either parent). This male is missing a hand, which may inhibit him from migrating, though he did accompany some of his brothers on a visit to a neighboring group once.

This mean age of migration (7.6 years) is considerably higher than that seen at the nearby site of Santa Rosa National Park, where males tend to make their first migration at a mean age of 4.17 and never remain in natal groups past age 8 (Jack and Fedigan 2004; Fedigan and Jack 2012). It is not clear why this difference between the two nearby, ecologically similar sites exists. Possibly the apparently higher rate of lethal coalitionary aggression at Lomas Barbudal (Gros-Louis et al. 2003) makes migration more dangerous, but the exact rate of such killings at Santa Rosa has not yet been reported. Males at Lomas tend to co-migrate more often than Santa Rosa males do, and so many males may spend extra years in their natal groups waiting for close kin to mature to migration age so that they can move together. Every one of the 44 males born into our study groups whom we have seen to migrate has migrated with other natal males, at least initially (though sometimes the co-migrants do not remain with their co-migration partners after one male has claimed the alpha position). In contrast, only 71% of males at Santa Rosa co-migrate (Jack and Fedigan 2004). We do see occasional solo migrations at Lomas, but thus far it has always been males from unhabituated groups who have migrated alone into our study groups; therefore, we know nothing about the migration options for these males.

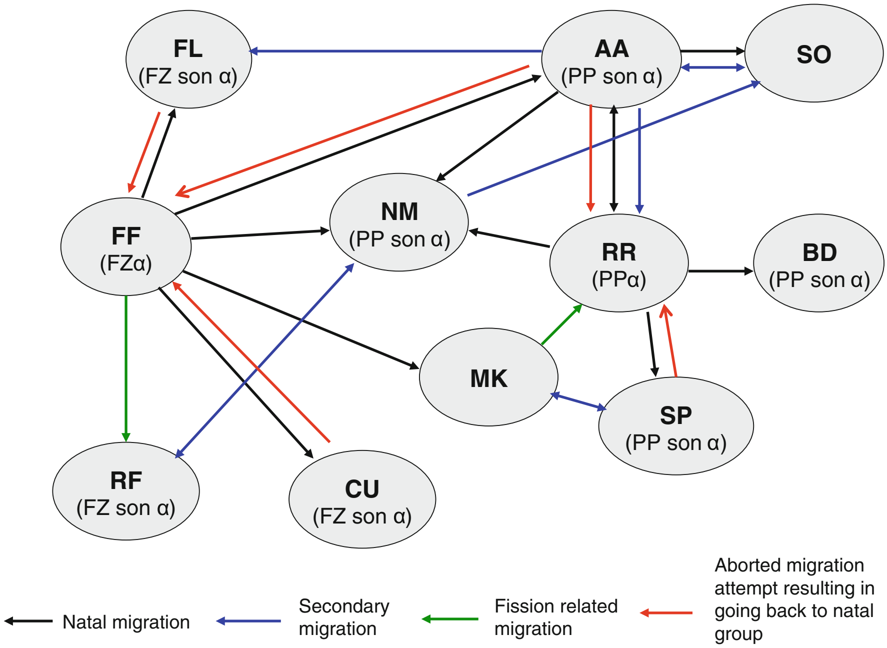


Fig. 7.2 Diagram of male migrations. Each oval represents a social group. Two long-term alpha males are noted, as are their alpha male sons. See text for the four types of migrations, which are denoted by different types of *arrows*

Figure 7.2 demonstrates the patterning of male migration. There are four basic types of migration or transfer: (a) natal transfer (i.e., transfer from the natal group to another group), (b) secondary transfer (transfer from one non-natal group to another non-natal group), (c) “fission transfer” in which males initially go with their mothers during a fission, but later move to the other fission product that has less closely related adult females, and (d) “returning home” transfers, in which males first transfer to a non-natal group and then return to the natal group.

Some males make many false starts; that is, they transfer to non-natal groups, but return to the natal group for extended periods between each transfer attempt; in these cases, we counted all emigrations out of the natal group as natal migrations for the purpose of Fig. 7.2. We only included multi-male/multi-female groups in this diagram, but there are also many all-male groups in the study area that shift composition at high rates. Males often spend prolonged periods in these groups in between periods of residency in groups containing females. Some of the secondary migrations reported in Fig. 7.2 might not have been direct migrations, but rather involved visits to all-male groups and perhaps even other multi-male/multi-female groups in between. Males typically transfer to an adjacent group with females or to an all-male group, at least initially.

It has been proposed (Schoof et al., 2009) that one of the reasons males engage in parallel dispersal is because it gives them access to willing coalition partners who can enhance their competitive ability in within-group and between-group competition. One of the arguments for why males are expected to engage in parallel dispersal is to keep male kin together so that they can engage in kin-selected altruism (Schoof et al. 2009). Indeed, at Lomas there is a tendency for male co-migrant dyads to be more closely related than randomly selected male–male dyads from a given group (Wilcoxon signed ranks test: $Z^+ = -2.132$, $p = 0.016$, $N = 13$ migration events; Muniz 2008). At Lomas, it is definitely true that males aid one another in defending the group from intruders (Perry 1996b; Perry and Manson 2008), and that they regularly aid one another in takeovers of other groups (Perry and Manson 2008, unpublished data). It is less certain whether co-migrants aid one another in within-group coalitionary aggression in their new groups more often than do pairs of males who are not co-migrants; this topic will require further research. Certainly we do see many cases in which co-migrants side against one another in within-group coalitionary aggression. Once a takeover has been achieved, we sometimes see cases in which co-migrant males engage in fierce battles over the alpha position with their own brothers, inflicting severe wounds. Strong circumstantial evidence from Lomas indicates that males sometimes kill their brothers and their brothers' infant offspring in disputes over the alpha position, despite their close genetic relatedness (unpublished data).

7.2.2 Genetic Structure of the Population

The Lomas Barbudal capuchins are noteworthy for often having quite long alpha male tenures, lasting up to 18 years. These long tenures, combined with high reproductive skew, mean that natal individuals are often related both through the maternal and the paternal line. Out of 2,111 dyads analyzed from five social groups, 4% were full siblings, 5% were maternal half siblings, and 24% were paternal half siblings (Muniz 2008). Another unusual feature of capuchin social structure imposed by long alpha male tenures is the high frequency with which alpha males co-reside with their daughters and grand-daughters. In most mammalian populations, father–daughter inbreeding is avoided by having one sex disperse. But capuchins avoid father–daughter inbreeding even while co-residing (Muniz et al. 2006). Paternity data on 97 infants born during 15 stable alpha male tenures show that in the years before an alpha male's daughters have started to mature, the alpha males have sired 96% of all offspring (data from Godoy 2010; Muniz et al. 2010). However, subordinate males who have been helping an alpha male defend his group's females from extra-group males experience greatly increased breeding opportunities when the alpha male's female descendents finally mature. Subordinate males have sired 94% (31/33) of offspring produced by females that were the daughters or granddaughters of their groups' current alpha males (Godoy 2010; Muniz et al. 2010). Thus, the longer an alpha male remains in place, the lower the degree of reproductive skew, due to the increasing numbers of his female descendants.

Figure 7.3 shows the breeding histories for the males in Rambo's group from 1991 to 2008. This pattern is similar to what we observed during two other long-term tenures. At the start of the study, alpha male Pablo (PP) co-resided with two other immigrant

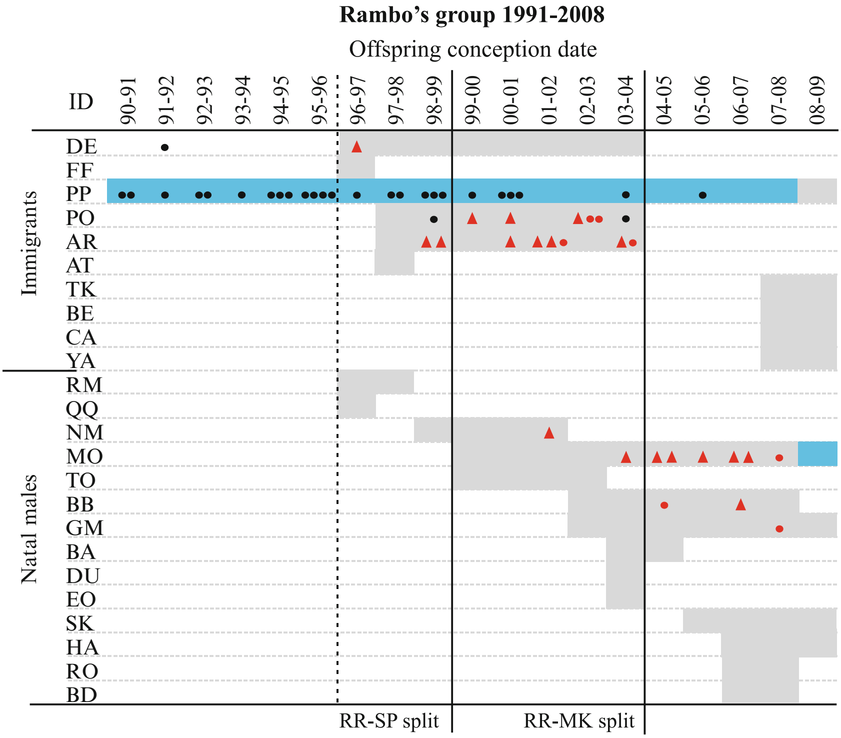


Fig. 7.3 Distribution of paternity over time in Rambo's group. All males residing in a group during a particular year are shaded in grey, with the alpha male having *blue* shading. Offspring of the current alpha males' daughters are represented by *red triangles*, and offspring of the alpha male's granddaughters are represented by *red circles*, while offspring of all other females are represented by *black circles*. Vertical dashed lines indicate the beginning of direct observations

males with whom he had non-antagonistic relationships. In 1997, a trio of migrant males immigrated relatively peacefully and did not attempt to overthrow PP. Again in 2008, four migrant males who had known one another in AA group immigrated peacefully. At the end of 2008, PP was overthrown by MO, who was the offspring of PP's former ally DE. Aside from MO, RM and QQ, all other natal males in the group were PP's sons or grandsons. PP remained in RR group after losing alpha status.

PP sired 25 out of 30 offspring (83% of offspring) born to females who were not his direct descendants; the remainder were sired by immigrant males. Of those offspring born to PP's daughters and granddaughters, 12 were sired by immigrant males, 4 were sired by PP's sons (i.e., his sons bred with their paternal half sisters or nieces), and 7 were sired by MO, a natal male who was unrelated to PP and only distantly related to most of the females with whom he bred. Thus, PP did not breed with any of his daughters or granddaughters.

Long-term alpha males have far more reproductive influence in the population than is apparent just by examining the patterns of reproduction in the groups in which they reside. This is because long-term alpha males have ample opportunity to produce sons, who then migrate and often become alpha males themselves, monopolizing reproduction in other groups. Figure 7.2 shows which adjacent groups have alpha males who are sons of the long-term alpha males PP (of RR group) and FZ (of FF group). These males may have additional sons who are alpha males in groups outside our study area. To the best of our knowledge, PP has sired at least 25 offspring, 83 grandoffspring, and nine great-grandoffspring at the present time (and of course the numbers of his second and third generation descendents will continue to increase after his death).

7.2.3 Sources of Mortality and Ages at Mortality

Although white-faced capuchins can live to 55 years of age in captivity (Hakeem et al. 1996), maximum life span is in the wild is unknown because no field study has come close to spanning that amount of time. Certainly, however, it is rare for capuchins to live that long. Based on genealogical data, we estimate that our oldest living monkey is 36 years old. Of the 24 monkeys who were members of AA group during the first 3 years of our 20-year study, only 2 females are still living.

Mortality rates at Lomas Barbudal were calculated using individuals with birthdates known to an accuracy of plus or minus 3 months ($N = 262$). We assigned two values for age at death to those individuals presumed dead ($N = 108$); these incorporated inaccuracy in both birth and death dates. We used these values to generate two curves for mortality rates across time (Fig. 7.4a), one using the lowest possible value for age at death and second curve using the highest possible value. Since birth dates were relatively accurate, the two curves produced similar results. We also included in this analysis stillborn infants and obvious miscarriages (when it was clear that a female was pregnant based on the size and shape of her abdomen, and then she suddenly decreased in size). Because mortality was highest in the first year (26–30%), we generated a separate graph to describe mortality rates within that year in four 3-month increments (Fig. 7.4b).

The principle cause of mortality for infants under 1 year of age seems to be infanticide. The mean interbirth interval for those cases in which the first infant lives until the next infant is born is 749 days ± 145 ($N = 41$ IBI's for which birthdates were known to an accuracy of 1 week). This is slightly shorter than the 2.25-year (~821-day) interbirth intervals reported for Santa Rosa (Fedigan and Jack 2011). However, when the previous infant dies or is abandoned before the second is conceived, the mean interbirth interval is 444 days ± 168 ($N = 21$), i.e., significantly shorter than when the previous infant lives (two-sample t-test with unequal variance, $t = 7.09$ (37), $p < 0.0001$). The mean time to conception following an infanticide was 478 days ± 212 ($N = 6$), or 271 days shorter than in cases where infanticide was not committed.

We analyzed the effects of adult male migrations and alpha male turnovers on infant mortality rates using a sample of 210 births for which we had accurate birthdates. For each birth, we scored whether a male migration or a turnover in the alpha male position occurred within 6 months before or 1 year after the infant's

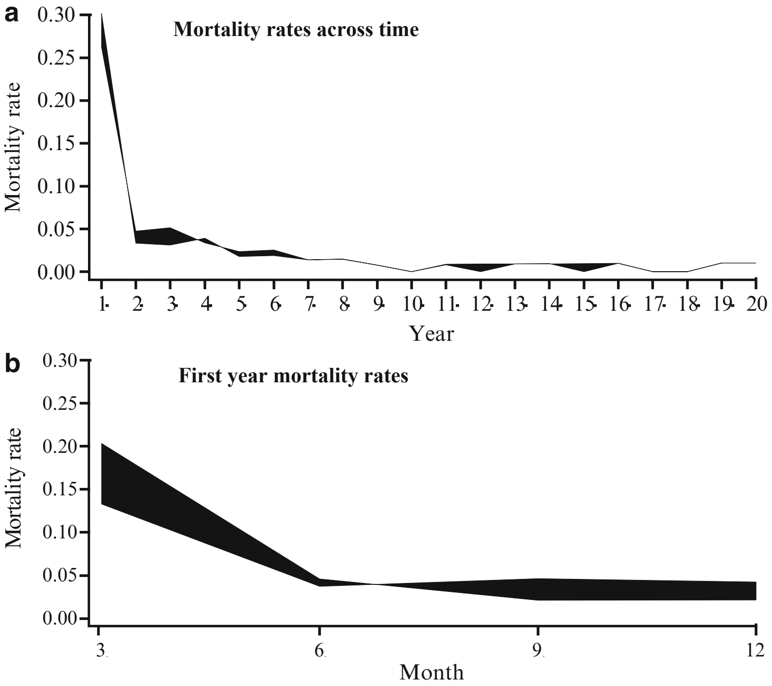


Fig. 7.4 Mortality rates over the life span. (**a**) Shows the mortality rates over the first 20 years of life; (**b**) shows the timing of deaths during the first year of life. *Shaded areas* in both graphs denote the upper and lower bounds of mortality rates

birth. Only 18% of infants died in periods characterized by stable alpha males, whereas 49% of those infants born in alpha male turnover periods died before reaching 1 year of age. This is a significant difference (Pearson's $\chi^2 = 23.38$, 1df, 1-tailed $p < 0.001$), and replicates similar findings from the Santa Rosa capuchins (Fedigan 2003; Fedigan et al. 2008). We witnessed 20 peaceful immigrations, i.e., migrations in which no alpha male turnover occurred. The mortality rate for infants born during times of peaceful male immigration (25%) did not differ significantly from that for infants born during periods in which no male immigrated (23%) (Pearson's $\chi^2 = 0.038$, 1df, 1-tailed $p = 0.845$). We do not always witness infant deaths, so we cannot be certain what proportion are due to infanticide. We directly observed six infanticides, and in five other cases we witnessed the alpha male stalking the infant for days previously, and/or the mother alarm-calling at the alpha male right after the infant was killed (Manson et al. 2004b; Perry and Manson 2008). In another four cases, infants disappeared in the middle of an infanticide spree when a new alpha was seen to kill other same-aged infants. In another 11 cases, a female was pregnant on the last day of observation during one month, but when next seen was no longer pregnant and had no infant; it was impossible to know whether there was a miscarriage or an infanticide. Thus, although we cannot give a precise rate, infanticide is clearly the biggest source of infant mortality at our site.

7.2.4 Age at First Reproduction for Each Sex

Females at Lomas Barbudal give birth for the first time at a mean age 6.22 years (SD = 0.58). This sample is based on 30 females for whom the age of their own birth and the age of their first infant's birth is known to an accuracy of ±3 months. It includes three miscarriages. If we look only at the age of first live birth, then the mean age of first birth increases to 6.30 (SD 0.62). The youngest female to give birth was 5.50 years old.

Determining the age of first reproduction for males is much more difficult because there is such high reproductive skew that very few males actually reproduce. Only 27 males in our population are known to have sired offspring, and we only had reasonably accurate birthdates (+3 months) for two of these, since it is primarily the older males who reproduce. Of these two males, one conceived his first offspring at 7.3 years of age, and the other conceived his first offspring at 9.0 years. Based on our much rougher age estimates for other sires, we suspect that the typical age at which males first conceive an offspring is much later, however.

7.2.5 Birth Seasonality

67.1% of births at Lomas Barbudal ($N = 173$ births, during years for which we have continuous demographic monitoring) occurred between April and July, though some births occurred during all months but October. Thus, the birth season straddles the end of the dry season and the start of the rainy season, which typically begins in mid-May. Figure 7.5 shows the distribution of births across years, using

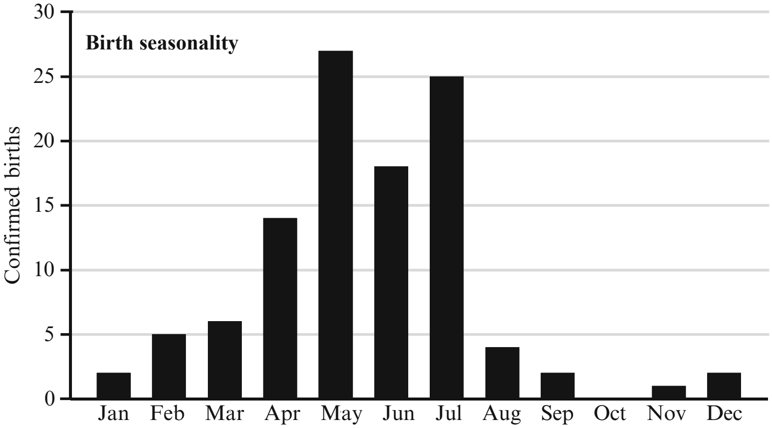


Fig. 7.5 Number of births in each month in a sample of 106 births for which birth date was known accurately enough to assign it to a particular month

only those births for which we knew the precise month ($N = 106$). The timing of this birth season corresponds roughly to that of Santa Rosa (see Fig. 8.2 in Fedigan and Jack 2011), where 40% of births occur in April–June.

7.3 Topics We Could Not Have Studied Without Long-Term Research: Social Learning and Traditions

Lack of temporal depth in datasets from wild animal populations usually prevents researchers from identifying *traditions*, defined as “enduring behavior patterns shared among members of a group that depend to a measurable degree on social contributions to individual learning, resulting in shared practices among members of a group” (Fragaszy and Perry 2003). Simply knowing that a behavior pattern varies across sites in cross-sectional samples is insufficient to conclude that the behavior is a tradition, because many factors, including between-site genetic and ecological variation, can affect behavioral variation. To determine whether a behavior pattern is a true tradition, it is useful to know whether and how it varies over time. Two forms of long-term temporal patterning strongly suggest that social learning affects the acquisition of a behavior. First, a behavior may appear suddenly in an individual (i.e., as an innovation) and then spread, in a transmission chain, through that individual’s social network. Second, a general behavior pattern may occur universally in a population, but exhibit discrete variant forms, and immature individuals may preferentially acquire the variants favored by their close spatial and social associates. We have documented both patterns over multi-year periods at Lomas Barbudal, the first with respect to dyadic social rituals and the second with respect to foraging techniques.

7.3.1 Social Conventions

Early in the history of the project, SP began visiting other field sites and communicating with the researchers who worked at these sites. It soon became apparent that some of the more bizarre behaviors we witnessed were not common features of the repertoire of capuchins everywhere, and we decided to coordinate our methods so that we could more rigorously investigate the hypothesis that capuchins exhibit social conventions – i.e., dyadic communicative rituals that are unique to particular cliques or social groups. We made a list of candidate traditions by identifying forms of social behavior that were practiced in some social groups at a rate of at least once per 100 h of observation, but were absent in others that had been studied for at least 250 h. We also kept track of which individuals practiced the behaviors and of how long the behaviors persisted in each group’s repertoire, for all cases in which the timing of the field seasons permitted documentation of the innovation event and included the periods during which it could have spread and, where relevant, when it became extinct.

In our original study, which included 19,000 h of behavioral observations on 13 social groups from four sites in Costa Rica over a 13-year period, five behaviors qualified as traditions according to our operational criteria (Perry et al. 2003a). One of these, handsniffing, involved the insertion of a finger into the nose of another monkey; this behavior was often mutual and exhibited many minor variations in form. Handsniffing was common for a period of 1–7 years in five out of the 13 groups we studied and at three of the four study sites. The sucking of body parts (ears, tails or fingers) was common in two of our study groups for periods of 6 months or more. Three "games" were invented by a single monkey (Guapo of Abby's group at Lomas Barbudal) and had roughly the same format, in which one monkey has something in its mouth that the partner tries to remove from the mouth (a finger or a tuft of hair from the partner, or an inanimate inedible object such as bark or a stick). The mouth is pried open using hands, feet, and perhaps the mouth, and the object is passed back and forth from mouth to mouth.

In the case of the three games ("finger-in-mouth", "hair" and "toy"), we could construct social transmission chains. The "toy" game was invented in 1991, and the other two were invented in 1992. The "toy" game had 13 practitioners and three links in the transmission chain and lasted 9 years. The "finger-in-mouth" game and hair-passing games both lasted for 10 years and had 11 and 14 practitioners, respectively. The finger-in-mouth game had two links in its transmission chain, whereas the hair-passing game had three. In the games, adult male-juvenile males were the primary participants. The games persisted in group repertoires for 2–3 years after the innovator (a subordinate male) became alpha male and stopped participating. Some of the main practitioners continued to play these games together even after co-emigrating.

In subsequent years, we have continued to document the innovation and spread of social conventions. The larger the data set grows, the more often we find that similar innovations occur. For example, the males in Flakes group have independently invented all three of the games that were previously played in Abby's group. Despite the fact that Flakes is a fission product of Abby's group, none of the current game players were resident in the group at the time these games were played in Abby's group, so we believe them to be independent inventions. We have also observed the invention of a rare, new variant of handsniffing that includes the insertion of the partner's finger deep into the eye socket, up to the first knuckle in some cases. This variant has been slower to spread than most traditions and also not quite common enough to meet all of our operational criteria for tradition in the original study, but it nonetheless appears to be socially learned.

As the study continues and the cumulative number of observation hours per group increases, we are discovering that (a) there are more observations of groups that exhibit temporal variation in their behavioral repertoires, and (b) many groups that formerly exhibited a total absence of particular traditional behaviors now have an occasional observation of a behavior thought to be unique to another group, even if it does not spread to other group members or become common in the repertoire. The longest-studied group, Abby's group, has exhibited particularly interesting variation in the expression of handsniffing over the past 20 years. This behavior was not observed in 1990. From 1991 to 1997, it was commonly practiced by up to

12 individuals and 13 dyads in any given year. From 1998 to 2001, it was never seen, but females often sniffed their own hands. During 2002–2003, when there were frequent migrations, dyadic handsniffing was practiced at low frequency by 14–16 individuals and 15–16 dyads per year. The practice dwindled until by 2008, dyadic handsniffing had once again vanished from the group's repertoire, though solo handsniffing remained. The solo handsniffing in Abby's group and its fission product (Flakes) is never seen in three of our other study groups (MK, CU, NM) and occurs roughly an order of magnitude less often in the neighboring RR group.

7.3.2 Social Learning About Foraging Techniques

Short-term studies of *C. capucinus* have demonstrated between-site differences in the ways foods are processed (Panger et al. 2002). Providing conclusive evidence for a substantial role of social learning is impossible in such cross-site studies, although the fact that all of the sites in this study were tropical dry forest sites in northwestern Costa Rica makes a major role for ecological or genetic variation unlikely. Within-site studies are highly suggestive of a role of social learning of food-processing techniques. White-faced capuchin monkeys are more prone to observe group-mates foraging at close range when they are foraging on foods that require multiple steps to process before ingestion (Perry and Ordoñez Jiménez 2006). However, showing that monkeys observe one another does not mean that they necessarily learn from the observations. At Lomas Barbudal (Perry and Ordoñez Jiménez 2006), Palo Verde (Panger et al. 2002) and Santa Rosa (O'Malley and Fedigan 2005), pairs of monkeys who frequently associate are more prone to share the same food-processing techniques than pairs who associate less often, but the results of these comparisons are generally only marginally significant.

A longitudinal approach is preferable to a cross-sectional approach to this issue because it allows researchers to document the association patterns at the time when young animals are acquiring their food-processing techniques and are most subject to social influence, rather than simply measuring association patterns in adulthood and assuming that these represent the patterns that held when the monkeys acquired their current techniques. It is time-consuming and costly to conduct longitudinal studies of the development of large numbers of juvenile primates in the wild, so such studies are rare. We have conducted the largest such study to date, focusing on the acquisition of techniques for processing *Luehea candida* fruits, a staple item that contributes up to 15.4% of the diet during the peak fruiting period (Perry and Ordoñez Jiménez 2006). This fruit consists of a woody capsule with five cracks, from which small but nutritious wind-dispersed seeds can be extracted either by pounding or scrubbing the fruit. Both techniques are approximately equally efficient (Perry 2009). The lack of difference in efficiency means that individuals are probably less likely to select a technique on the basis of individual trial and error learning, as opposed to social learning.

All of the social groups included in the study (three groups and three of their fission products) had some group members who were primarily pounders and others who were primarily scrubbers. However, some between-group differences in the tendency to pound or scrub existed, particularly for the philopatric sex. For example, currently nine of the 10 adult females in AA group are scrubbing specialists (the youngest female still combines pounding and scrubbing), whereas in RR group, all of the six adult females are pounders.

During the first developmental year (i.e., the first year in which the infants have exposure to *Luehea* fruits and are off the mother's back during part of *Luehea* season), most infants do not regularly process *Luehea* fruits, although they handle them and eat the seeds protruding from the ends. In their second year of exposure to the fruits, they employ a variety of techniques (about four per monkey), including both pounding and scrubbing (Perry 2009). As juveniles mature, they select a preferred technique and use it increasingly until they reach adulthood (Fig. 7.6). By 3 years, inefficient techniques have largely been eliminated from individual repertoires, and individuals use their dominant technique 82% of the time ($N = 49$ individuals), and by age 7 years, they use the dominant technique 95% of the time ($N = 27$).

Infants remain on their mothers' backs for most of the first 3 months of life. During months 4–6, they spend increasing amounts of time with alloparents, and by 6–9 months of age, they are within 40 cm of their mothers only 10% of the time (Perry 2009). Even after becoming largely independent of their mothers, they spend much time within observation range of other monkeys, and by age 5 years, they still spend 73% of their time within 4 m of at least one other monkey. Juvenile males and females do not differ significantly with regard to the amount of time they spend in proximity to their mothers, time spent alone, or time spent observing other foragers (Perry 2009).

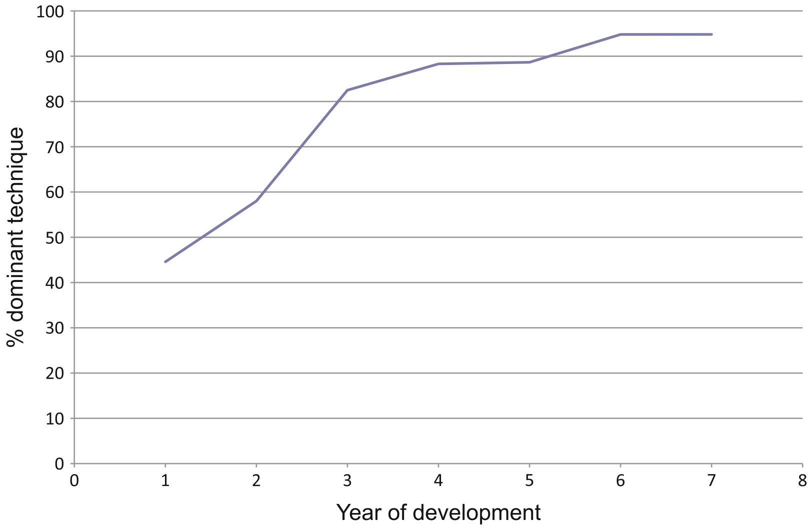


Fig 7.6 Percentage of Luehea processing incidents in which the individual's dominant (favored) processing technique is used during each year of development

We collected data on the *Luehea* processing techniques of all members of our study groups over a period of 7 years, which allowed us to follow 48 immature monkeys (21 females and 27 males) during the first 5 years of their lives. In many cases we had to drop particular monkey-years from the data set due to inadequate sample sizes for (a) number of fruits processed by the focal monkey, or (b) opportunities for the focal animal to observe others' foraging techniques. Once these cases were eliminated, we had 79 cases (i.e., monkey years) in the sample (see Perry 2009 for further details). Whenever a monkey entered a *Luehea* patch, we recorded the technique(s) used to process each fruit, the distance between the focal animal and other individuals who were processing *Luehea*, the gaze directions between animals, and the techniques being used by other animals in the same patch.

I analyzed the data using a Poisson regression model, adjusting the standard errors for within-subject correlation (see Perry 2009 for details of measurement and analysis). The primary predictor variable was the technique to which the focal subject was exposed, which is a measure of the relative exposure to pounding as opposed to scrubbing in foraging neighbors (see Perry 2009 for details of measurement and analysis). Sex was also a predictor variable. The outcome variable was the proportion of *Luehea* fruits that the focal monkeys processed by pounding them (i.e., number of fruits pounded, divided by the sum of number of fruits pounded and number of fruits scrubbed). Developmental years were control variables.

Figure 7.7 shows the effect of observed technique on the practiced technique for males vs. females across the first five developmental years. In Fig. 7.7a, only observations of maternal foraging are included in the independent variable. Figure 7.7b includes only observation of non-maternal foraging in the independent variable. In both cases, the impact of observed techniques on practiced techniques was greatest in the second year of development. Females were more strongly influenced by observed technique than were males, across all years of development. Non-maternal influence is slightly greater than maternal influence for both males and females.

In a separate analysis (Perry 2009), I used a broader data set ($N = 106$ monkeys) in which I also included adults and included all cases for which we had adequate behavioral data to characterize individuals' techniques during the most recently available processing season and also knew the mothers of the subjects. Females were significantly likely to use the same technique as their mothers (Fisher's exact $p = 0.002$, $N = 48$), but males were not ($p = 0.18$, $N = 58$). This result parallels findings by Lonsdorf et al. (2004) at Gombe, in which the acquisition of termiting techniques was studied in 14 immature chimpanzees over a period of 4 years. In their study, daughters were more likely than sons to adopt a termiting tool length similar to the mother's; daughters acquired the technique earlier than sons and were more efficient termite-fishers. Lonsdorf et al. found that this sex difference could be explained by the fact that sons paid less attention to the mothers than the daughters did when the mother was termiting. However, in the Lomas capuchins, there are no differences between sons and daughters with regard to time spent in proximity to the mother (or other group members) or in the tendency to visually focus on the model during demonstrations of the *Luehea* processing technique. It may be that

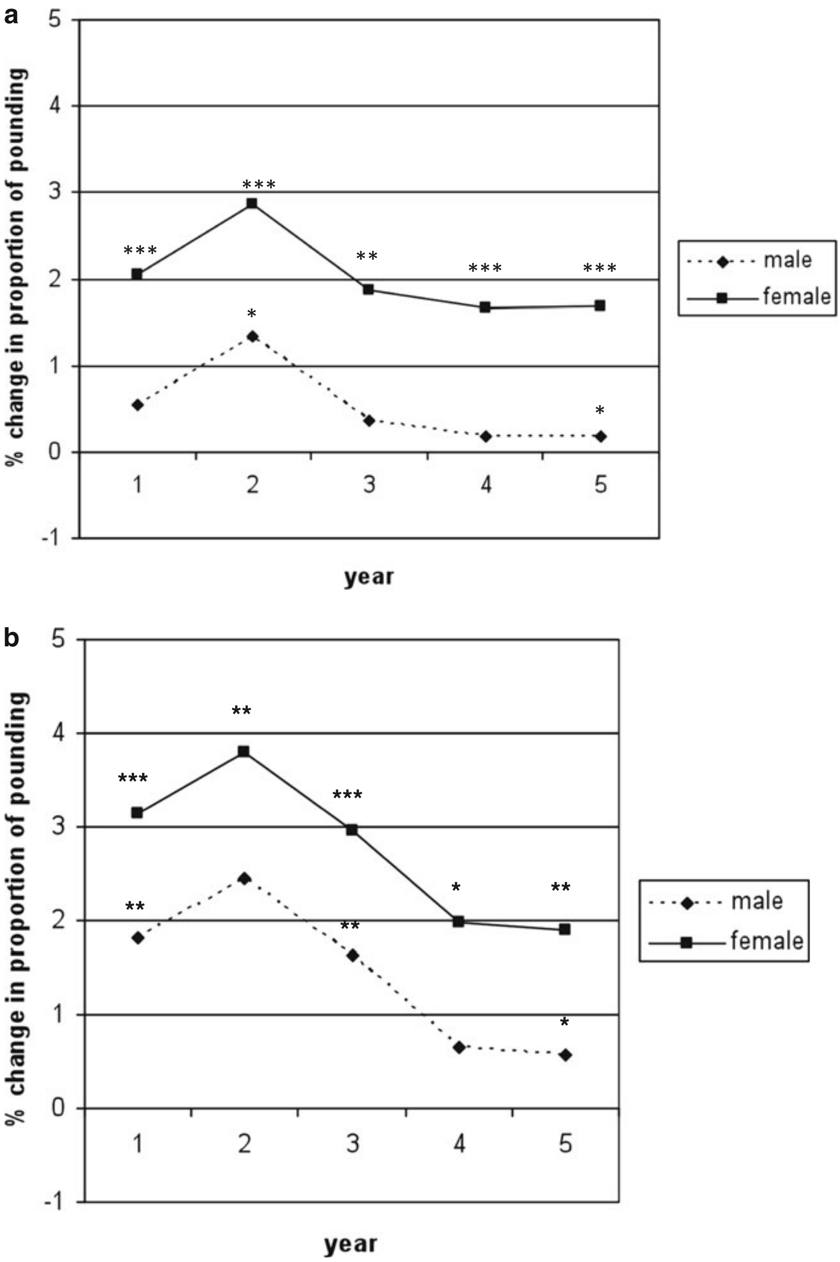


Fig 7.7 Impact of (**a**) maternal influence and (**b**) non-maternal influence on practiced technique for processing *Luehea* fruits. Y-axis is "% change in proportion of pounding practiced" resulting from a 1% change in observed technique. These two figures are slight modifications of Fig. 3b, c in Perry (2009) *=$p \leq 0.05$; **=$p \leq 0.01$; ***$p \leq 0.001$

female capuchins, being the philopatric sex, are more inclined to identify with their closest associates in the group, and hence conform to their techniques, in accordance with de Waal's "Bonding and identification-based learning model" (de Waal 2001).

7.4 Conclusions

The most interesting pieces of information that have emerged from our project are findings that were only possible to obtain via long-term study and extensive inter-site collaboration. To gain a deeper understanding of the social strategies of these long-lived animals, we needed to integrate data from multiple social groups and sites for hundreds of individuals over a period of 20 years, and even now, we are far from having complete life histories for many individuals in our sample. The discovery of father–daughter and grandfather–granddaughter inbreeding avoidance was possible only by obtaining genealogical data for multiple generations. Migration strategies can only be documented by knowing the natal groups of males and following them for multiple decades as they migrate repeatedly under changing demographic circumstances. The role of social learning in acquiring foraging skills was documented by collecting extraordinarily detailed observations at high density for a 7-year period in multiple groups. Finally, the documentation of group-specific communicative rituals was possible only by collecting long-term data on transmission chains, changes in groups' behavioral repertoires over multi-year periods, and comparative data from multiple sites.

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Chapter 8
Tracking Neotropical Monkeys in Santa Rosa: Lessons from a Regenerating Costa Rican Dry Forest

Linda M. Fedigan and Katharine M. Jack

Abstract The Santa Rosa primate project began in 1983 and we have studied the behavioral ecology of the resident primate species (*Cebus capucinus*, *Alouatta palliata* and *Ateles geoffroyi*) continuously since then. Most of our research has concentrated on the behavior, ecology, and life history of multiple groups of capuchins and on documenting the effects of forest protection and regeneration on the howler and capuchin populations. Our examination of capuchin life histories has shown that they lead complex and intriguing lives, many aspects of which are affected by the frequent movement of adult males between social groups throughout the course of their lives. Over the past 28 years, we have documented increases in both the capuchin and howler populations. However, the howler population apparently reached carrying capacity in 1999, whereas the capuchin population continues to grow, probably because of their ability to occupy early-regeneration habitats. Our long-term examination of the population structure and life history of these two species clearly demonstrate that many species-specific aspects of biology and behavioral ecology differentially influence patterns of primate population recovery. It is only after decades of research that we can begin to understand the underlying constraints and variability in the lives of these animals.

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8.1 History and Infrastructure of the Santa Rosa Monkey Project

In the early 1980s, I (L.M. Fedigan) began searching for a site to conduct long-term studies of primates. My wish list of ideal field site characteristics included the following: the site would be in a stable sociopolitical setting where I could safely bring students; the habitat would contain multiple primate species, at least one of which was relatively unstudied; the flora and fauna would be protected; the terrain would not be too formidable and the primates would be accessible for study and amenable to habituation. After a false start in one country where the monkeys were accessible and protected but the political situation was not stable, and in another where the government was stable but the primates were poorly protected, I made a trip to Costa Rica in 1982. After checking out many Costa Rican reserves and parks, I visited Santa Rosa National Park, home to white-faced capuchins (*Cebus capucinus*), mantled howlers (*Alouatta palliata*) and black-handed spider monkeys (*Ateles geoffroyi*). Not only was Santa Rosa an ideal location, but the three primate species, which all form multi-male, multi-female groups, display a range of dispersal patterns, dietary specializations, and social systems exhibited by polygynandrous primates, making them ideal for comparative studies. I knew immediately that I had found a place that met my criteria and where I could establish a stable long-term primate field site.

Santa Rosa National Park (SRNP) was created in 1971. The history of the park is a fascinating story in itself, far too long for this chapter, but well described in Evans (1999) and Allen (2001). SRNP was one of the first parks established by the fledgling Costa Rican National Park Service. It constitutes about 100 km^2 of tropical dry forest in Guanacaste Province and was chosen for early park designation mainly because its large central ranch house was the site of a famous 1857 battle in which a volunteer army of Costa Ricans repelled an invasion by American mercenaries. At the time of the park's establishment, the area was overrun with squatters, shacks, and roaming cattle owned by absentee landlords who planted African grasses that they burned annually to create pastureland. Soon after the park was established, the squatters were removed, hunting and logging were banned, a small complex of cement block buildings was constructed for park personnel, and the guards were given guns and horses (but no uniforms or vehicles!) to drive the poachers and the neighboring ranchers' cattle out of the park. Throughout the 1970s and 1980s, efforts were made on a shoestring budget to attract visitors and control the major forms of anthropogenic disturbance: poaching, logging, grass fires and grazing by cattle.

In the mid-1980s, Dan Janzen, a renowned tropical ecologist who first visited Santa Rosa before it became a park and who has made it his lifetime study site, convinced the park service and Costa Rican government to establish a large mega-park, now called Área de Conservación Guanacaste (ACG; Janzen 1988, 2000, 2002, 2004). Dr. Janzen created a non-profit conservation organization (Guanacaste Dry Forest Conservation Fund) that initially raised funds to purchase the properties surrounding Santa Rosa, in order to connect it to the small nearby parks and reserves. More recently, ACG has expanded further, as the Conservation Fund purchases cloud forest and Atlantic rainforest habitat on the eastern slopes of the mountains. Santa Rosa has now become a "sector" in the mega-park and is the core of a much larger protected zone (163,000 ha and counting) that covers nine Life Zones from the Atlantic rainforests of the east, to the volcanoes at the tops of the mountain range that runs along Guanacaste like a backbone, and into the Pacific Ocean on the west. ACG was declared a UNESCO World Heritage Site in 1999. The park now has ten sectors, most with their own buildings and staff. ACG also has a professionally-trained fire fighting team, locally-trained park researchers, police protection service, ecotourism office and outreach educational programs. Although far from wealthy and still dependent on donations from conservationists, the park has come a long way from the days when a small and poorly funded group of rangers tried to protect and maintain the land. Under Janzen's visionary guidance, the goal of ACG is not only to protect the old growth rainforest and cloud forest that remain in the mountainous regions of Guanacaste Province, but also to engage the local populace in efforts to regenerate the severely endangered tropical dry forest that was the original habitat type of the western lowland areas. Over the past two decades, major fires have become a thing of the past in Santa Rosa, the introduced African grasses have mostly died out, and the pastures are transforming into newly regenerating dry forest (Janzen 2002, 2004).

When I first requested a research permit from the Costa Rican National Park Service in 1983, the administrators made it clear they wanted me to monitor how the monkey populations were faring in the park. No counts of the primate populations had occurred in Santa Rosa since Curtis Freese, a Peace Corps volunteer had censused the monkeys in 1972, 1 year after the area came under protection (Freese 1976). Therefore, along with my plans to study the life histories and behavioral ecology of the monkeys, I agreed to monitor the park-wide populations. Beginning in 1983, my students, field assistants and I conducted annual censuses in May/June of every year for 6 years, after which we switched to less frequent park-wide censuses with a goal of at least one census every 4 years.

In 1984, I also selected three groups of capuchins, four groups of howlers, and one community of spider monkeys to be habituated and closely tracked as our "study groups." We found it difficult to distinguish individual howler monkeys and to track the rapidly-moving spider monkeys around their large home ranges. Therefore, with the help of Glander et al. (1991) we captured, marked, measured, and released many individuals in our howler study groups and several in our spider monkey community (Fedigan et al. 1988). In 1985, we started to systematically observe recognizable individuals in all three species in order to record births, deaths, disappearances, and dispersal, as well as foraging and social behaviors. The official "start" date for our life history data is June 1986, because it took us nearly a year to develop standardized and efficient methods for reliable data collection.

In the mid-1990s, I made the decision to concentrate my research on five groups of capuchins (Fig. 8.1), except for the park-wide censuses of monkey populations in

Fig. 8.1 A subadult female from one of our study groups carrying her infant sister (© Fernando Campos). Alloparenting, including extensive allonursing is very common in this species

May/June of designated census years. I maintained my focus on long-term life history data and started to direct and oversee many shorter-term (6–12 month) behavioral ecology projects carried out by graduate advisees.

Graduate students were actively involved in the Santa Rosa monkey project from the beginning. Dr. Colin Chapman was part of our original census team in 1983 and continued research in our park until 1989, focusing on the spider monkeys latterly (e.g., Chapman 1989, 1990; Chapman et al. 1988, 1989a, b). A young Costa Rican biologist, Rodrigo Morera Avila, worked as my local project manager for 10 years, until he completed his master's degree in wildlife management at the National University of Costa Rica and took up a post at the University of Costa Rica in Heredia. Since 1984, 30 graduate students from 12 universities and 6 countries have pursued and/or completed thesis projects on the monkeys of Santa Rosa (see partial list at http://people.ucalgary.ca/~fedigan/fedigan.htm). In 2000, Drs. Filippo Aureli and Colleen Schaffner initiated a long-term project on the spider monkeys of Santa Rosa. In 2004, I invited a former graduate advisee, Dr. Kathy Jack, now of Tulane University, to join me as co-director of the Santa Rosa capuchin project. Dr. Jack and her graduate students focus on capuchin behavioral ecology and life histories from the male perspective whereas my team addresses similar questions from the female perspective. We conduct many behavioral projects and all project data collection collaboratively.

Another major event in the history of our project was the creation of the Santa Rosa Database in June 2001 by Dr. John Addicott. This research tool is essential to our overall endeavor, although it will forever be a work-in-progress. It includes ~33 linked tables covering not only census and life history information, but also data on genetics (e.g., opsin genes, microsatellite DNA), climate (temperature, rainfall), phenology, food lists, dominance hierarchies, researcher names and other data

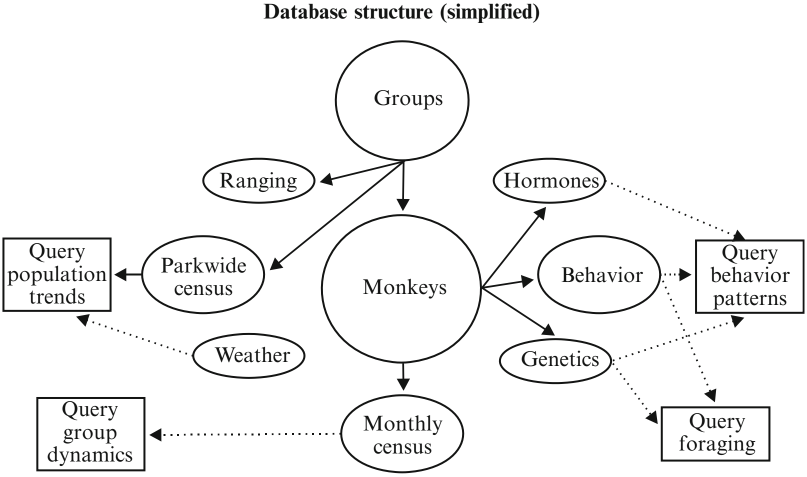

Fig. 8.2 Schematic diagram of selected linked tables that make up the Santa Rosa database. For additional information on the data included in each table, please contact the authors

(Fig. 8.2). We are putting this database on a server that will be remotely accessible by any user with appropriate permission.

Over the 28 years of this project, we have been variously housed: in tents, in an original 1971 park administration building, in a house outside of Santa Rosa that played a role in the "Iran-Contra" scandal, and in a more modern "dormitory" built in 1994. As of March 2011, we live in a designated "casa carablanca" that we built in the park with our own funds and grants from the Zemurray Foundation. This multi-roomed building is owned by the park but largely managed and maintained by our monkey research team.

8.2 Life History Parameters, Dispersal and Reproductive Success in the Santa Rosa Capuchins

Here we briefly review a few of the many aspects of capuchin life history, reproductive patterns, and socio-ecology that we could not have documented or understood without longitudinal data collection (see also Perry and Manson 2008; Perry et al. 2011). Table 8.1 summarizes capuchin reproductive and life history parameters at Santa Rosa. It did not take us long to discern that white-faced capuchins conformed to the *Cebus* pattern of male dispersal and female philopatry. However, only after many years could we determine the average age at which natal dispersal occurs, discover that males continue to change groups throughout their lives (Jack and Fedigan 2004b), and realize that adult females also disperse under some circumstances (Jack and Fedigan 2009). Although white-faced capuchins are best described as residing in multi-male/multi-female groups (current average

Table 8.1 Summary of life history parameters for white-faced capuchin monkeys in Santa Rosa National Park, Costa Rica between 1986 and 2010

		Value	Range	*N*
Gestation (days)		158 ± 8[a]		6
Sex ratio at birth (proportion male)		0.605[b]		119
Infant survival to age 1 (proportion)	All infants of known sex	0.823		119
	Females	0.914		47
	Males	0.763		72
	All infants (incl unknown sex)	0.680		144
Mean age at first birth (years)	Females	6.50	5.80–7.90	19
Mean interbirth interval (years)	First infant dies before age 1	1.05	0.67–1.75	22
	First infant survives to age 1	2.25	1.48–5.58	52
Mean age at 1st dispersal (years)	Females	≥7[c]		5
	Males	4.5		30
Mean age at death (years) for individuals surviving to at least age 1	Females	9.41		18
	Males	2.96[d]		14
Oldest age at death (years)	Females	27[e]		
	Males	24.70[d, e]		

[a] Sarah Carnegie unpublished data, based on ovarian hormone analyses

[b] Of the 144 infants born in our study groups, 25 (17%) were not sexed prior to their neonatal death

[c] All five females that immigrated into our study groups were considered adults (all but one was parous)

[d] For males, death is not easily distinguished from dispersal

[e] Birth dates of monkeys alive at the start of the study or immigrating into study groups are estimated

group size: 15.2, Table 8.2), their social structure varies and we have documented small uni-male/multi-female groups, and in one case, a group that had no resident adult, or even subadult, male for 10 months.

Even though the number of adult males per group varies across our five study groups and 48 census groups, all groups contain multiple, usually closely related, females and their immature offspring. Ovarian hormone analyses from fecal samples show that gestation length in our females is approximately 5.5 months, and that females typically experience only one or two cycles before they conceive (Carnegie 2011). Females appear to provide no visible cues to ovulation and often approach and direct proceptive signals to subordinate males when they are not fecund and even when they are pregnant (Carnegie et al. 2005). The occurrence of female-initiated, non-conceptive mating with subordinate males may explain why we see all resident adult males copulate, but genetic data show that the alpha males father most of the infants (Jack and Fedigan 2006).

Age at first birth for a female is usually around 6.5 years (Table 8.1), reflecting the slow life history of this species relative to its body size (♂ = 3.7 kg, ♀ = 2.7 kg; Ford and Davis 1992). In captivity, capuchins may live into their fifth decade (Fragaszy et al. 2004), but in the wild, mortality rates at our site are such that female

Table 8.2 Census data for (a) Capuchin monkeys and (b) Howler monkeys in Santa Rosa National Park, Costa Rica between 1972 and 2007

Year	# Monkeys counted	# Groups counted	Average group size	Estimated # groups	Estimated population size[a]
(a) Capuchins					
1972	?[b]	1	17.5	17	297
1983	226	20	11.5	28	318
1984	338	25	13.6	28	378
1985	175	13	14.8	28	397
1986	284	18	16.4	28	448
1987	173	10	16.7	28	474
1988	140	8	16.4	28	468
1990	314	18	17.7	28	491
1992	541	30	18.0	30	541
1999	521	31	16.8	35	588
2003	655	49	13.4	49	655
2007	594	39	15.2	48	716
(b) Howlers					
1972	65	8	8.1	10	85
1983	217	19	11.4	24	274
1984	295	23	12.8	25	321
1985	262	19	13.8	26	359
1986	315	19	16.6	28	464
1987	181	16	11.3	30	339
1988	212	12	17.7	31	548
1990	432	27	16.0	33	528
1992	563	35	16.1	34	547
1999	545	46	11.8	50	592
2003	529	44	12.0	49	589
2007	463	41	11.3	54	610

[a] Estimated population size was computed as: # Monkeys Counted + ((Estimated # Groups − # Groups Counted) × Average Group Size))

[b] Freese (1976) did not state how many capuchins he counted. Instead he estimated 15–20 groups of capuchins in Santa Rosa. The one group he tracked over time had on average 17.5 members

life expectancy at age one is only around 9 years whereas male life expectancy at age one is much lower, around 3 years (Table 8.1; Bronikowski et al. 2011). Santa Rosa has a large and intact predator community (cats, canids, mustelids, raptors, snakes; Janzen 1988) and we have seen capuchins killed by a *Boa constrictor* (Chapman 1986) and a puma (McCabe unpublished data), as well as observing predators stalking the monkeys. Other documented and inferred sources of mortality are intra-specific aggression, parasites, and contagious diseases (Fedigan 2003; Parr 2011). Obviously, some individuals live much longer than 3–9 years and we estimate that the oldest females in our study groups are about 27 years of age and the oldest males approximately 25 years. Estimating the life expectancy of capuchin males is problematic as it is often difficult to distinguish death from dispersal in this sex. At Santa Rosa, males disperse from their natal groups at around 4.5 years of age (Jack et al. 2011, but see Perry et al. (2012) for an older average male age at natal dispersal, 7.6 years) and they continue change groups at approximately 4-year intervals throughout their lives (Jack and Fedigan 2004b).

Infant mortality in the first year of life is quite variable from year to year, but averages around 30%. If a female's infant dies, she is likely to produce another infant in about a year, whereas if her infant survives, her interbirth interval averages 2.25 years. We examined the factors that may affect length of interbirth interval and infant survival, using 21 years of data, 24 adult females, and 74 completed interbirth intervals (Fedigan et al. 2008). In brief, we found that the pace of a female's reproduction can be predicted by the number of matrilineal kin in her group (sources of supportive allomothering and coalitions) and by the availability of resources, as inferred from the amount of rainfall that occurred in the 12 months subsequent to each infant's birth (see justification for use of rainfall as a proxy for food availability in Murphy and Lugo 1986; Fedigan et al. 2008). But the strongest predictor of the length of interbirth intervals is whether or not the first infant in the interval survives. In turn, the survival of infants is best predicted by whether male membership in the group is stable at the time of birth or whether there is a take-over in the first year of the infant's life. Infant survival is also affected by sex – a higher proportion of female than male infants make it through their first year (Table 8.1). Somewhat surprisingly, the mother's dominance rank at the time of the infant's birth affects neither its survival nor the length of interbirth intervals. Thus, dominance rank does not influence female reproductive success, whereas we have found such a relationship for males (Jack and Fedigan 2006).

Santa Rosa is a highly seasonal tropical dry forest and white-faced capuchins prefer to drink water every day. Rainfall amounts vary greatly across the months of the year as well as across years (range: 818–4,012 mm per annum). The rainy season typically occurs between mid-May and mid-November, during which an average of 1,792 mm of rain falls. Between mid-November and mid-May, especially from January through April, virtually no rainfall occurs, most trees drop their leaves, all the streams dry up, and most sources of standing water disappear. In tropical dry forests, rainfall is a major influence on plant and insect productivity and thus available food energy (Murphy and Lugo 1986; Fedigan et al. 2008). Therefore, we have been interested in the extent of seasonality in capuchin conceptions and births. Analyses of 144 birthdates for capuchin infants in our study groups over many years show that births are significantly more likely to occur in the late dry/early wet season (Fig. 8.3; Fedigan 2003; Fedigan and Jack 2004). Given a 5.5-month gestation period, this indicates that conceptions are clustered in the second half of the wet and early part of the dry season (Carnegie et al. 2011). With 44% of infants born within the 3-month period of May through July (and therefore conceived within a 3-month period), the Santa Rosa white-faced capuchins display moderate breeding seasonality (see van Schaik et al. 1999 for classification overview). Although white-faced capuchins do not show strict birth seasonality, as has been demonstrated for the black capuchins (*Cebus nigritus*) of Iguazu National Park, Argentina, studied by Di Bitetti and Janson (2000), (see also Janson and

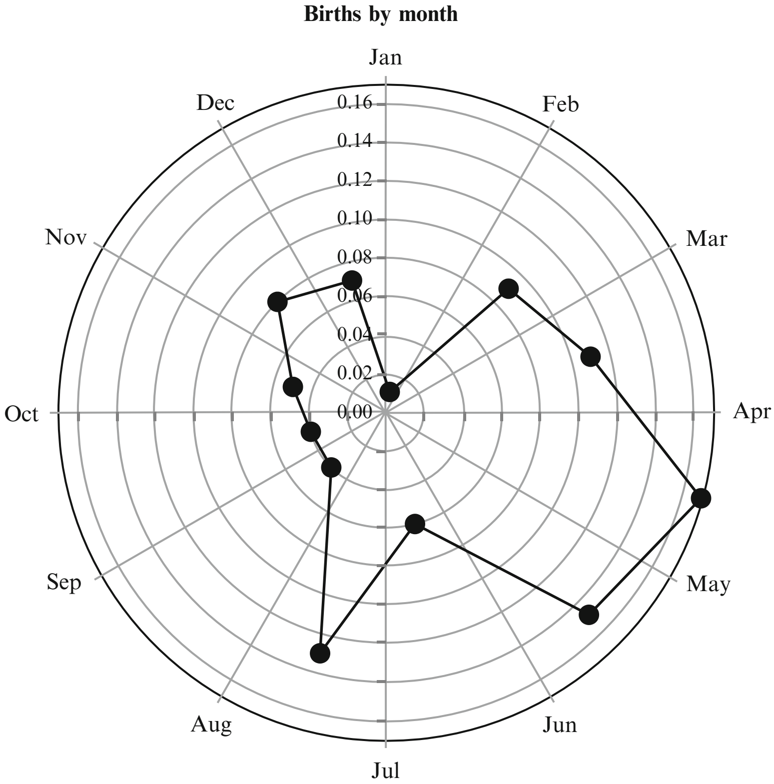

Fig. 8.3 The monthly pattern of births for 144 *Cebus capucinus* infants born in our study groups between 1986 and 2010. The dry season occurs from mid-December through mid-May

Verdolin 2005, Janson et al. 2012) they are similar to black capuchins and other more seasonal neotropical primates in that their birth peak coincides with, or slightly precedes, the seasonal peak in resource availability (Carnegie et al. 2011).

Interestingly, the white-faced capuchins studied at Lomas Barbudal (Perry et al. 2012) show even stronger reproductive seasonality than the Santa Rosa capuchins with 66.5% of all infants born between April and July. Lomas Barbudal and Santa Rosa are merely 55 km apart and are ecologically very similar so the reasons for this difference in birth seasonality are not easily explained. Variation in strength of reproductive seasonality may, perhaps, be tied to the fact that the capuchins at Lomas have year round access to fresh water, whereas the Santa Rosa capuchins drink from standing water holes, most of which have completely vanished by the end of the dry season. Indeed this single ecological difference may explain several of the demographic and life history differences that have been reported from these two nearby long-term study sites (e.g. group size, age at natal dispersal, and adult male tenure length). We plan to collaboratively address some of these inter-site differences with the Perry team of investigators over the next few years.

In some primate species, male dispersal is intimately linked to/timed with the breeding season (e.g. *Propithecus edwarsi*: Morelli et al. 2009; *Semnopithecus entellus*: Borries 2000), but the moderate seasonality displayed by our population of white-faced capuchins does not appear to directly influence male mobility. In our long-term analysis of natal and secondary dispersal, we did not find a significant relationship between the timing of male dispersal and the conception peaks (Fedigan and Jack 2004; Jack and Fedigan 2004a). Most dispersal events occur during the dry season months of January through April, a full 3–6 months prior to the conception peak. During the dry season, however, intergroup encounters are more likely to occur, usually around shared water holes, and males may use these encounters to appraise reproductive opportunities in neighboring groups and to assess the strengths of resident males in other groups. Assessment of the strength of groups targeted by would-be immigrants could be particularly important for dispersing adult males who typically fight their way into groups, although a few manage to peacefully join groups previously abandoned by resident males, a pattern we refer to as "waltz-ins". Males usually disperse in cohorts of two or more (77%, $N = 74$; Jack and Fedigan 2004a, b), and in almost all of the successful takeovers that we have observed to date ($N = 20$), coalitions of invading males outnumber those of resident males. This pattern of male dispersal leads to the complete replacement of resident males approximately every 4 years.

Over the years, we have observed 25 male replacement events in our five study groups and they are usually associated with the wounding, deaths, and disappearances of individuals from all age-sex classes (Fedigan 2003; Fedigan and Jack 2004; Jack and Fedigan 2009). Indeed male replacement events strongly influence many life history patterns. For example, the occurrence of a group takeover is the most significant factor explaining the highly variable age at which male natal dispersal occurs (Jack et al. 2010) and infant deaths are significantly more common, and females are more likely to disperse, during years with male replacements than during peaceful years (Fedigan 2003; Jack and Fedigan 2009). Given that white-faced capuchins show very high reproductive skew (Jack and Fedigan 2006; Muniz et al. 2010), with alpha males siring most infants, it is no surprise that males frequently change groups – likely in an attempt to maximize their reproductive opportunities (reviewed by Jack 2003). By changing groups, formerly subordinate males experience rank gains, which should also confer reproductive benefits (Jack and Fedigan 2004b). Even alpha males have been observed to abandon groups to join others, taking risks that seem counterintuitive at first. However, they target groups that proffer a more favorable sex ratio (i.e., more potential mates). While secondary/breeding dispersal by adult males is frequently suggested as a mechanism for the avoidance of breeding with maturing daughters (see Smith 1982), this does not appear to be the main proximate cause for the frequent dispersal of male white-faced capuchins (Jack and Fedigan 2004b). The average tenure length for an adult male in our study groups is 4 years (alphas and subordinates do not differ in this regard), which is well under the age that females first conceive and give birth (Table 8.1). Indeed in many primate species secondary dispersal by adult males is better explained by intrasexual mating competition rather than inbreeding avoidance (reviewed by Jack 2003). Genetic studies of the Lomas Barbudal population of white-faced capuchins (Perry et al. 2012), where alpha males have much longer tenures (e.g. up to 18 years) than those in Santa Rosa, have shown that there are behavioral mechanisms in place to ensure inbreeding avoidance; namely, the daughters of alpha males reproduce with subordinate males rather than with their fathers (Muniz et al. 2006).

8.3 Population Recovery in a Regenerating Tropical Dry Forest

Our demographic research began in 1983 and 1984 with extensive attempts to count all the monkeys located throughout SRNP, and since that time we have conducted 11 park-wide censuses of capuchins and howlers (Table 8.2). Except for one census conducted in August–November of 1992, these have all been carried out in April through July and mainly in May and June. For the capuchin and howler groups, we use a modified quadrat (“complete count”) technique that has proven useful in fragmented forest patches (see Fedigan et al. 1996, 1998; Fedigan and Jack 2001 for details). However, unlike capuchins and howlers, spider monkeys have fission–fusion societies and individuals range over very large areas in “parties” of frequently changing composition. Therefore, we have had to assess spider monkey densities from transect studies, which have been conducted much less frequently than our censuses of capuchin and howler populations (see Chapman et al. 1988, 1989b; Sorensen and Fedigan 2000; DeGama-Blanchet and Fedigan 2006).

We choose one area of the park at a time (usually a large forest fragment) and walk all known trails and dry stream beds there to locate monkeys. We consider any individual monkey within 100–300 m of the group and consistently traveling in the same direction as the group (even if in a peripheral position) to be part of that group. We use unique markings, known individuals and distinctive age/sex compositions to identify the same group on successive days for repeat counts. Multiple observers repeatedly count a group until achieving a stable count and composition, and plot its location on a map. After establishing a stable count on one group, we locate its nearest neighbor group. Whenever possible, with the aid of two-way radios, we use simultaneous contact with neighboring groups by different observers to establish their independence. With many years of practice, it has become increasingly easy to relocate our census groups in successive years and to determine when new groups have appeared or former groups have become extinct.

Table 8.2 shows the number of monkeys and groups we counted and the estimated population sizes of capuchins and howlers in Santa Rosa between 1972 (Freese’s original count) and 2007, a 35-year period subsequent to the establishment of the park. Whether we begin with Freese’s 1972 census or our first census in 1983, the number of capuchins in SRNP has more than doubled (e.g., from 318 in 1983 to 716 in 2007) and it gives every indication of continuing to grow (Fig. 8.4).

Howler population dynamics are different. Freese concluded that there were only ten howler groups in Santa Rosa in 1972 with a total population of only

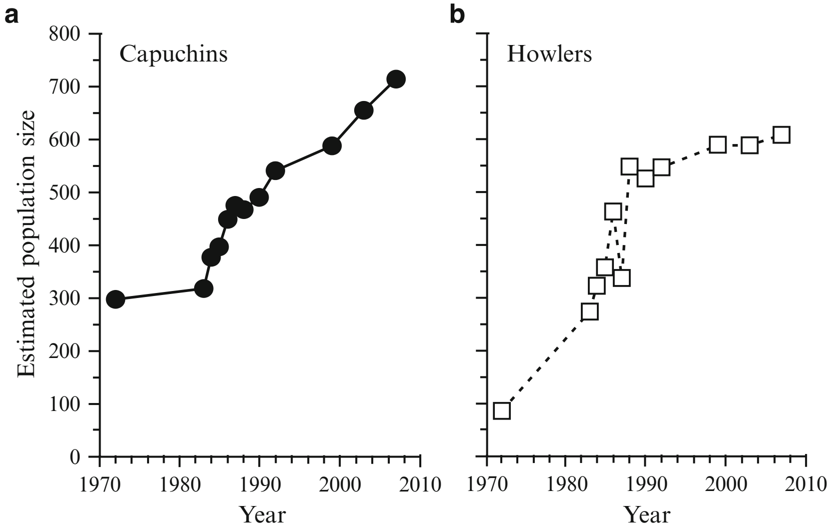

Fig. 8.4 Estimated population sizes of (**a**) capuchins and (**b**) howlers in Sector Santa Rosa, based on 12 park-wide censuses between 1972 and 2007

85 monkeys and he said that howlers were located only on the lower plateau, near the Pacific Ocean. The howler population apparently crashed shortly before the establishment of the park (see Fedigan et al. 1998; Fedigan and Jack 2001). However, at the time of our first census in 1983, we estimated there were 24 howler groups spread throughout the park, with a population of about 281 monkeys. That would indicate the howler population more than tripled in the 11-year time period between 1972 and 1983. Although howler females can first give birth at 3.5 years and can thereafter produce an infant every 20 months (Fedigan and Rose 1995), this would still be a remarkable rate of population growth. More conservatively, if we begin with our first census in 1983, the number of howlers more than doubled in a 14-year period (from 281 in 1983 to 620 in 2007). However, the Santa Rosa population of howlers began to level out in 1999 and since that time has experienced a near zero growth rate (Table 8.2).

Whether we begin our comparison of capuchins and howlers with Freese's 1972 census or our own first census in 1983, there were clearly more capuchins than howlers in Santa Rosa in the early days of the park's existence. The howler population then grew at a faster rate than the capuchins during the 1980s and 1990s, probably because howlers have a faster pace of reproduction and greater intrinsic rate of increase (earlier age at first birth, shorter interbirth intervals, Fedigan and Rose 1995). However, howlers are differentially found in the older (>60 years) evergreen forest that includes many large trees (DBH >63 cm, which is the smallest size tree in which Santa Rosa howlers rest and forage, probably to accommodate their larger body size and possibly also their folivorous diet). In the first two decades of our study, we observed several new groups of howlers colonize strips of old growth riverine forest and small patches of secondary forest that were transitioning into primary forest. But the stabilization of their population size may indicate that, at least for now, howlers have run out of suitable habitat into which they can expand as the forest fragments of Santa Rosa slowly regenerate. The smaller bodied, omnivorous capuchins, in contrast, can occupy newly regenerating forests and, as of our most recent censuses in 2003 and 2007, they once again outnumber the howlers (Table 8.2).

Figure 8.5 shows important differences in how the two populations grew in the 1980s and 1990s versus the most recent decade. Between 1983 and 1999, the capuchin population grew mainly via increases in group size (average group size went from 11 to 17) while the number of groups in the park only increased from 28 to 35. In contrast, the average howler group size fluctuated between census years, but showed no steady increase, whereas the number of howler groups doubled from 24 to 50 between 1983 and 1999 (Fig. 8.5b). During that time period, we repeatedly saw lone howler males move into unoccupied forest fragments and howl until they were joined by females and thus we surmise that the howler population initially increased by budding off small new groups. This pattern of creating new groups is feasible for howlers because both males and females regularly disperse. In contrast, the mechanism of capuchin population growth was via an increase in group size (Fig. 8.4b). Unlike the lone howler males who moved into previously unoccupied forest fragments, entire groups of capuchins began to range into new areas and because we often saw them in young forest, we infer that they accommodated their

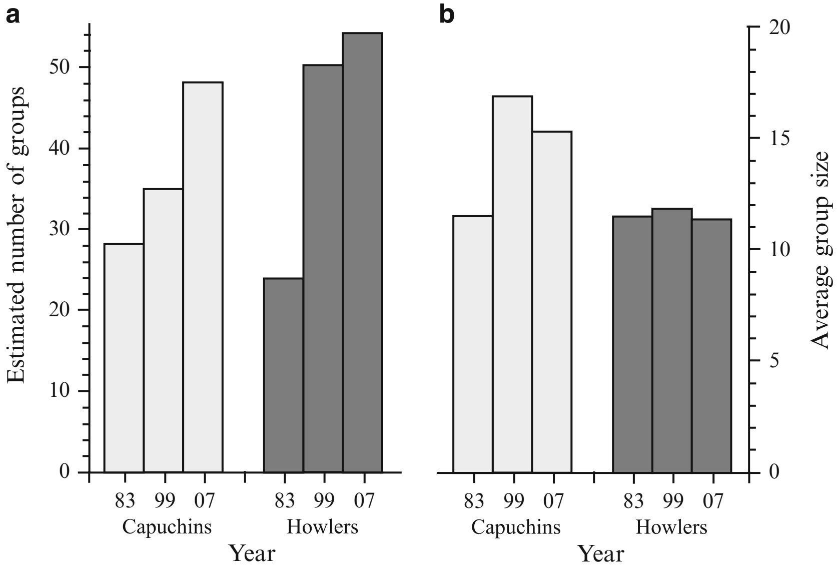

Fig. 8.5 (**a**) The estimated number of groups and (**b**) the mean group sizes of capuchin and howlers in Sector Santa Rosa in 1983, 1999 and 2007

increasing group size by expanding their home ranges into newly regenerating patches of forest.

However, beginning with our 2003 census, we started to see more new capuchin groups, their average group size stabilized and we ceased to locate new howler groups. The earlier species difference in population growth might have broken down because the howler population reached carrying capacity and because a large group size imposes reproductive costs on female capuchins – larger groups have lower female reproductive success (Fedigan and Jack 2011).

DeGama-Blanchet and Fedigan (2006) showed that the age of forest fragments significantly affects the densities of howlers and capuchins throughout ACG and that the availability of a dry season water source significantly predicts higher densities of capuchins. As pointed out by Altmann (1974) in his examination of baboon resources and home range sizes, water is the essential limiting resource for obligate drinkers living in arid regions. Sorensen and Fedigan (2000) found that capuchins can make use of forest patches as young as 25 years (Fig. 8.6), but whenever possible, they range in such a way as to have a source of dry season water within their home range from which they drink at least once daily. Capuchin densities follow a fairly linear pattern of increase from newly regenerating forest patches up to 180-year old (primary or evergreen) forest. Howlers do not usually appear in forest fragments under 60 years old and only become common in forests of 100–150 years old. Spider monkeys in Santa Rosa are only rarely seen in forest fragments less than 100–200 years old and they prefer larger patches, presumably to accommodate their trap-line pattern of foraging on fruit (Fig. 8.6). As described in Fedigan and Jack (2001), our long-term examination of the population dynamics of

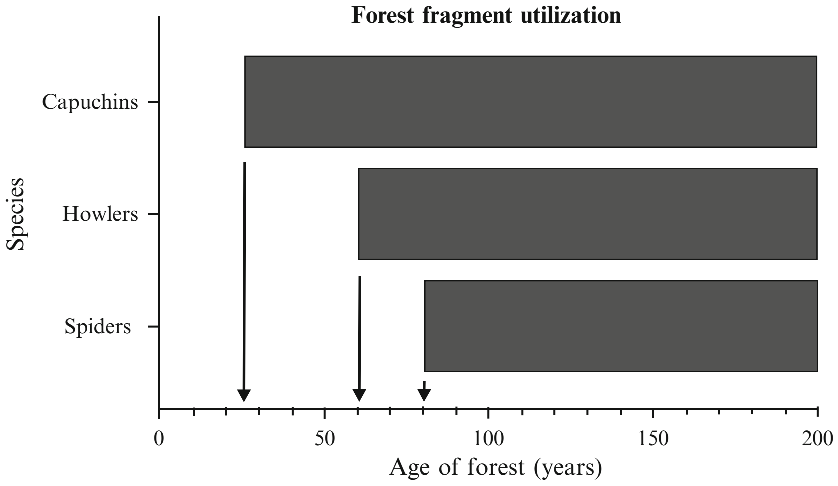

Fig. 8.6 The age of forest fragments that are utilized by capuchin, howler, and spider monkeys in Sector Santa Rosa. Capuchins can be found ranging, resting, and foraging in forest fragments ≥25 years of age, howlers in forest fragments ≥60 years and spider monkeys in forest fragments ≥80 years of age

these three species in a tropical dry forest habitat indicates that the fundamental requirement for capuchins is a year-round water source, whereas howlers (which seldom drink water) need large trees with leaves and fruit that have low levels of secondary compounds, and spider monkeys require large tracts of old growth forest to maintain their fission–fusion social system and frugivorous diet.

Another important difference in how the capuchin and howler populations have grown over the past 25 years concerns changes in age–sex compositions (Fig. 8.7). The age/sex composition of the howler population has fluctuated but not varied substantially between 1983 and 2007. However, adult males have accounted for an increasing proportion of the capuchin population. Furthermore, the ratio of adult males to females has gradually shifted from 0.47 in 1983 to 1.1 in 2007. Table 8.3 shows that while the numbers of infants, juveniles, and adult females doubled over the 25-year period, the number of adult males increased fivefold.

Why would there be a differential increase in the numbers of adult male capuchins? We offer three suggestions. First, the removal of hunters from the park has probably allowed more adult males to survive. Adult capuchin males assume a highly visible and audible protective role in their social groups and during encounters with humans they are always at the forefront of the group and are much more likely to be harmed or wounded than are other group members. Second, capuchins are a male-dispersal species and males are thus better able than are females to take advantage of protection in the park by immigrating into the more secure forests within the park boundaries. Finally, the infant sex ratios (Table 8.1) we recorded in our study groups between 1984 and 2000 were highly biased toward males in our groups and may reflect a population-wide bias toward male infants

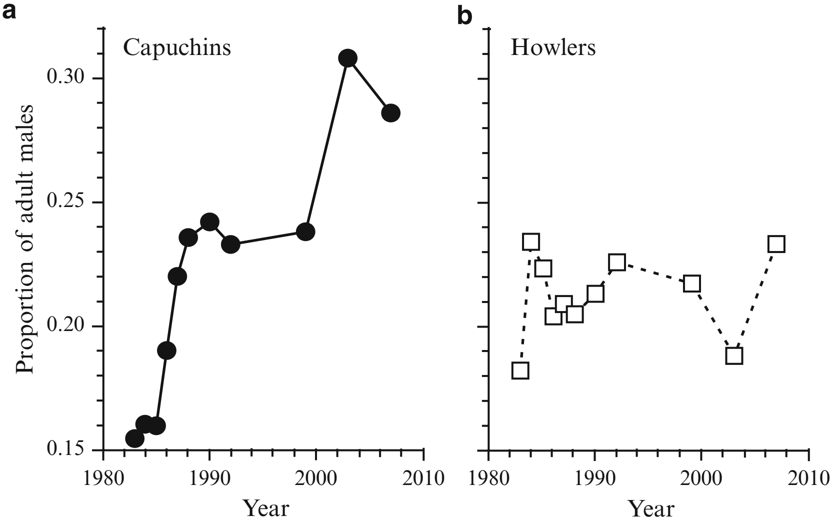

Fig. 8.7 Proportion of adult males for (**a**) capuchins and (**b**) howlers in the Santa Rosa population as counted during park-wide censuses between 1983 and 2007

Table 8.3 Age–sex composition of populations of (a) Capuchin monkeys and (b) Howler monkeys in Santa Rosa National Park, Costa Rica between 1983 and 2007

Year	# Counted	Prop. adult males	Prop. adult females	Prop. juveniles	Prop. infants	Prop. unknown	Adult males per adult female
(a) Capuchins							
1983	226	0.155	0.332	0.323	0.137	0.053	0.467
1984	338	0.160	0.337	0.349	0.109	0.044	0.474
1985	175	0.160	0.314	0.400	0.120	0.006	0.509
1986	284	0.190	0.313	0.345	0.109	0.042	0.607
1987	173	0.220	0.266	0.324	0.156	0.035	0.826
1988	123	0.236	0.276	0.382	0.098	0.008	0.853
1990	314	0.242	0.293	0.331	0.108	0.025	0.826
1992	541	0.233	0.298	0.237	0.176	0.057	0.783
1999	521	0.238	0.345	0.257	0.106	0.054	0.689
2003	655	0.308	0.276	0.342	0.072	0.002	1.116
2007	594	0.286	0.264	0.278	0.125	0.047	1.083
(b) Howlers							
1983	231	0.182	0.468	0.173	0.169	0.009	0.389
1984	299	0.234	0.425	0.217	0.124	0.000	0.551
1985	273	0.223	0.359	0.260	0.158	0.000	0.622
1986	313	0.204	0.403	0.201	0.176	0.016	0.508
1987	187	0.209	0.364	0.235	0.193	0.000	0.574
1988	220	0.205	0.382	0.205	0.209	0.000	0.536
1990	431	0.213	0.390	0.239	0.158	0.000	0.548
1992	579	0.226	0.408	0.185	0.169	0.012	0.555
1999	548	0.217	0.391	0.232	0.146	0.015	0.556
2003	538	0.188	0.411	0.227	0.169	0.006	0.457
2007	463	0.233	0.443	0.173	0.145	0.006	0.527

during this time period. If the infant sex ratios we observed in our study groups during this time period are reflective of the capuchin population as a whole, then the current population-wide male-biased adult sex ratio is not unexpected. Interestingly, the infant sex ratios in our study groups has changed to a nearly 1:1 ratio over the past decade and we are interested to see how this change will be reflected in the population-wide adult sex ratios in the years to come. Subsequent to the Trivers–Willard hypothesis (Trivers and Willard 1973), much has been published on factors affecting primate sex ratios at birth (see review and meta-analyses in Brown and Silk 2002). However, we agree with Strier (2009) that the sample sizes common in studies such as our own are too small to test whether the observed changes over time are truly adaptive or are random deviations from what will eventually prove to be a 50:50 ratio between sons and daughters at birth. Only the continuation of our already long-term study will tell.

8.4 Conclusions

Under the protection of the ACG park service, the typical tree species of a neotropical dry forest are slowly re-establishing themselves in former pasture land, creating arboreal corridors between fragments and growing into secondary forests that can be exploited by capuchins. Also, the forest fragments of Santa Rosa that were not cleared for agriculture but were selectively logged and subjected to other forms of human exploitation are now protected. Our long-term research has clearly demonstrated that monkey populations increase under these conditions. However, we can also draw the wider lesson that because the life history pattern and interaction of each species with its environment is unique, the successful restoration of primate populations is more complicated than simply removing the disturbances that humans introduced in the first place (hunters, loggers, cattle, non-native plants, anthropogenic fires).

It is essential to understand the species-specific aspects of vulnerability and potential for recovery. As pointed out by Chapman et al. (2010), a complex set of interactions govern changes in habitat composition and structure and the associated changes in animal populations. Chapman and colleagues found from repeated transect censuses in Kibale National Park between 1970 and 2006, that two of five primate species (mangabeys, black-and-white colobus) had increased in density over the study period, two (redtails, red colobus) were stable, and one (blue monkeys) had declined. In contrast, our long-term research indicates that population sizes of all three monkey species we study have increased since 1971, but differentially so. We attribute their differential patterns of population recovery to the many species-specific aspects of their biology and behavioral ecology (e.g., differences in body size, diet, life history pace, social organization and behavioral flexibility in response to change). It is encouraging that the monkey populations in the protected forests of Santa Rosa have grown substantially in the 40 years since the park was established. Although it requires great energy, optimism, and patience to work toward the regeneration of a forest, our research shows that humans have successfully created the conditions to re-grow the monkey populations of Santa Rosa.

It also takes effort, diligence and a long view to maintain a field study over a nearly 30-year period. But without a multi-year study, there is much vital information about these monkeys we could not know. We hope that this brief overview of some of the findings from our Santa Rosa project demonstrate that the rewards are well worth the effort.

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Chapter 9

The Group Life Cycle and Demography of Brown Capuchin Monkeys (*Cebus [apella] nigritus*) in Iguazú National Park, Argentina

Charles Janson, Maria Celia Baldovino, and Mario Di Bitetti

Abstract This study reports demographic and social changes across 20 years in a population of brown capuchin monkeys living in Iguazú National Park in northeastern Argentina. Three sets of results emerge that are critical to understanding the evolution of social behavior in this population. First, patterns of age-related mortality clearly highlight certain periods of increased mortality (postnatal 6 months, onset of reproduction, late senescence) and near-perfect survival (2–6-year-old juveniles, young adult females). Second, tracking the migrations and rank-related reproductive strategies of males helps to uncover the causes and consequences of long male reproductive tenures that average 5 years. Finally, observations of relatively rare male takeovers of the alpha breeding position reveal a predictable sequence of stages in a group's life cycle that tie together female fecundity, infanticide, group size, and kinship-based group fissions. These coordinated aspects of demography and kinship in different stages set the context for understanding differences between groups in social structure and organization.

9.1 Introduction

The population of *Cebus [apella] nigritus* in the Macuco trail area of Iguazú National Park, Argentina, has been studied since 1988 (Brown and Zunino 1990). This work has included censuses at least twice a year since 1991 (Di Bitetti and Janson 2001a; Ramírez-Llorens et al. 2008), and intensive behavioral and

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ecological studies spanning over 80 months (e.g., Janson 1996, 1998, 2007; Di Bitetti and Janson 2001a; Di Bitetti 2005; Baldovino and Di Bitetti 2008; Wheeler 2009; Baldovino 2010). During this period, groups have grown, split, joined, experienced male replacements, changes in matriline dominance, dispersal of subadult males, and complete replacement of the original cohort of females by their daughters. This report summarizes data on the rates of such events and on their demographic and behavioral consequences.

Both kinds of information are needed to understand the importance of a given selective force in a particular study population (Koenig et al. 2006; Kappeler and Fichtel 2012). Short-term studies can provide excellent data on the frequencies and consequences of common sources of natural selection but may miss rare albeit important sources of selection or may estimate their impact poorly. For instance, during the 30 years prior to 2004, several groups of researchers had studied various populations of *Cebus* "*apella*" superspecies (using the old taxonomy; these are now more properly referred to as species in the genus *Sapajus*: Lynch Alfaro et al. in press). Despite such effort, none had reported direct evidence of infanticide by males (although Izawa (1980) presented suggestive evidence). In 2005, we saw a male who attacked and killed an infant, and recorded two additional infant disappearances after a male takeover of our main study group (Ramírez-Llorens et al. 2008; see also Izar et al. 2007). Retrospective analysis of long-term demographic data suggests that infanticide has been the most important single source of mortality of unweaned infants in this study population, despite the rarity of male takeovers and the difficulty in documenting the behavior (Ramírez-Llorens et al. 2008). Thus, long-term studies can provide crucial context to interpret the social structure and organization of a species (e.g., Mitani et al. 2002). An important insight emerging from our analysis is that groups may show predictable "life cycles" – coordinated repetitive temporal patterns of group size, composition, and social change – that set the context for understanding rare demographic events in our study population.

9.2 Description of the Study Population

The Macuco trail area of Iguazú National Park, Argentina, is accessed from the Centro de Investigaciones Ecologicas Subtropicales (25°40′43″ S, 54°26′57″ W), just north of the main tourist attraction of Iguazú Falls. Floristically, the study area belongs to the Upper Paraná Atlantic Forest (Giraudo et al. 2003). The climate is humid and subtropical, with marked seasonality in temperature and day length, but little seasonality in rainfall. Fleshy fruits and arthropods, the most important resources for capuchin monkeys, are scarce in winter (July–August) and most abundant during spring and early summer (October–December; Placci et al. 1994; Di Bitetti and Janson 2001a; Di Bitetti 2009).

The study area contains forest in various stages of recovery from anthropogenic disturbance. First, the entire area to the north and west of the falls was a logging concession up until 1934, when the area was designated a national park by the federal government (Ministerio del Medio Ambiente 2005). Timber harvesting was highly selective but had considerable impact on the natural vegetation, removed the largest trees and created logging roads to bring the timber to the Iguazú River; two of these logging roads, Yacaratia and Macuco, remain as tourist trails within the study site. A dirt airstrip was created in 1937. It was abandoned in 1971, but signs of former human habituation are still evident near its remnants, along the southwestern part of the Macuco trail. An important legacy of this period was the introduction of several nonnative fruit species, primarily citrus varieties and *Hovenia dulcis* (Rhamnaceae), which have escaped cultivated areas and to greater or lesser degrees become naturalized in the forest.

Current protection efforts by the Argentine National Park service are largely effective at preventing illegal logging and poaching (Di Bitetti et al. 2008; Paviolo et al. 2009). The study area boasts a fairly complete set of likely and actual monkey predators: black hawk-eagles (*Spizaetus tyrannus*), ornate hawk-eagles (*Spizaetus ornatus*), jaguarundis (*Puma yagouaroundi*), oncillas (*Leopardus tigrinus*), margays (*Leopardus wiedii*), ocelots (*Leopardus pardalis*), pumas (*Puma concolor*), jaguars (*Panthera onca*), and tayras (*Eira barbara*). Two species of large raptors, crested eagles (*Morphnus guianensis*) and harpy eagles (*Harpia harpyja*), formerly bred in the area, but the removal of the large emergent trees that they favor for nesting, in addition to general habitat loss, has made them no more than occasional visitors. Most of the five pit viper species (Crotalinae) that are expected for the region are seen routinely in the summer months; the medium-sized rainbow boa (*Epicrates cenchria*) is rare. Current anthropogenic disturbances inside the study area are routine use of the Macuco trail by tourists, noise from nearby roads, and helicopter flights relatively low above the canopy. Since 2007, increasingly frequent interactions (mostly begging for or stealing food) between individuals of one of the study groups and tourists near the falls have become a source of concern.

The study animals live in multi-male, multi-female groups of between 7 and 44 individuals (Di Bitetti and Janson 2001a; Agostini and Visalberghi 2005). With rare exceptions, all individuals of both sexes can be arranged into a linear dominance hierarchy based on decided agonistic and approach-avoid interactions. As in other *apella* populations, each study group has a clear alpha male who tends to be centrally positioned within the group spread and has feeding and mating priority (Janson 1984, 1985). The Iguazú capuchins often feed on multiple food sources at a time, thereby reducing aggression and monopolization of food by dominants (cf. Janson 1996; Di Bitetti and Janson 2001b). Females are philopatric and form alliances based on kinship and reciprocal social grooming (Di Bitetti 1997).

The data for this study come from nine social groups in the vicinity of the Macuco trail, inhabiting an area of over 6 km^2 (Ramírez-Llorens et al. 2008). The early (1991–1992) groups were Macuco (MAC), Yacaratia (YAC), Barrio (BAR), Rubias (RUB), Silver (SIL), and Laboratorio (LAB). In 2005, MAC split, giving rise to two additional daughter groups, Rita (RI) and Gundolf (GUN); MAC split again in 2009, producing an additional daughter group Spot (SP). Individual animals were recognizable through a combination of relatively stable patterns of fur color, tuft shape, size, healed injuries, as well as sex and group membership; altogether, 289 distinct individuals are in the database, although not all of them survived long enough to be named or even sexed. We did not capture and permanently mark the study animals, so the displacements of emigrating animals (mostly males) were recorded only opportunistically and for at most a year after their departure from one of the main study groups. The only group for which we have consistent census information throughout the 20-year study period is MAC and its daughter groups; for these groups, it is possible to state mother–infant relationships for the 147 descendants of the initial cohort of 5 adult females in 1991. Many researchers have contributed to the demographic database over the years, but nearly all of the consistent census data come from the authors for the following periods (CHJ: 1991; MSD: 1992–1996; MCB: 1997–2010). The study groups were either the subject of intensive behavioral study or were censused thoroughly at least twice per year, once late in the year (late November or December) after the major period of births and once in May–June after the period of high infant mortality.

Like other capuchin monkeys, the study population is omnivorous, with a diet consisting mainly of ripe fruits and arthropods (Robinson and Janson 1987). Seasonal trends in diet reflect the varying abundance of these resources. In the austral winter, when neither ripe fruit nor insects are readily available, the capuchins consume large amounts of vegetation, primarily leaf bases of bamboo and bromeliads (Brown and Zunino 1990). Births are highly seasonal; nearly all occur between October and February (Di Bitetti and Janson 2001a). Because of the scarcity of ripe fruit during June through August, Janson has used this population (primarily the MAC study group) for a series of large-scale provisioning experiments using up to 27 feeding platforms to test several hypotheses about foraging cognition and feeding competition (Janson 1996, 1998, 2007; Janson and Di Bitetti 1997; Di Bitetti and Janson 2001b). Smaller-scale use of feeding platforms has enabled studies on other topics in this population (e.g., Visalberghi et al. 2003; Di Bitetti 2005; Wheeler 2009). Use of the feeding platforms has not had a detectable effect in increasing birth rates (Di Bitetti and Janson 2001a) or infant survival rates (Ramírez-Llorens et al. 2008) in MAC relative to other groups. Some nonprovisioned groups in the population experienced similar population growth during parts of this period (e.g., SIL).

9.3 Demography of the Iguazú Capuchin Study Groups, 1991–2010

Nine study groups have been followed or censused with sufficient continuity to allow tracking of life events of identified individuals. The length of study in years for each group is 1 (SP), 2.5 (BAR), 4 (RUB), 5 (RI), 5.5 (YAC, LAB, GUN), 6 (SIL), and 20 (MAC); for further details from 1991 to 2006, see Ramírez-Llorens et al. (2008). Shorter periods have provided data for demographic rates and rare events, while longer-term observations have permitted analyses of key events in the life cycle of groups (see Sect. 9.6 below). For rare events such as adult male immigration or male replacements, the sample size is the total observation years across all groups (55 group-years). In all cases, when an event happened between two censuses, the event was attributed to the date midway between the census dates, unless other information (e.g., infant size or behavior) suggested that the true date was closer to the first or second census date.

9.3.1 Fecundity

Female capuchin monkeys give birth on average every 19.4 months, without strong effects of group size or offspring sex (Di Bitetti and Janson 2001a). Birth intervals are significantly shorter if the previous infant dies before 8 months of age than if it survives its first year (14.1 versus 20.4 months; Ramírez-Llorens et al. 2008). Because births are highly seasonal, actual birth intervals cluster around 1 year or 2 years (rarely 3 or more years). If a female's prior offspring survives past 8 months, the modal birth interval is 2 or more years (52 of 80 cases), whereas if the prior infant does not survive to 8 months, the modal interval is 1 year (27 of 34 cases).

Female fecundity increases rapidly between the ages of 5 and 8, followed by a period of highest fecundity for females between 9 and 16 years of age, ending with a period of decreasing fecundity in females above 16 years of age (Fig. 9.1). There is clear statistical evidence for reproductive senescence in the declining birth rates of older females (Fig. 9.1) but not for menopause. Three of the four females estimated to have survived beyond 22 years continued to reproduce (one had an unusually long interbirth interval of 4 years); the fourth one (GU) moved with her daughter RI to form a new group in early 2005 and has had no offspring since late 2005 (ages 24–28).

The age at first birth of 27 known-age females ranged from 47.5 to 96.2 months, with a median of 71.64 months or about 6 years. Age at first birth is significantly earlier for females of alpha matrilines than for those in lower-ranking matrilines (6 of 8 first births at about 5 years of age in alpha matrilines versus 1 of 12 first births in non-alpha matrilines, Fisher exact test, two-tailed $p = 0.0044$). The likelihood that a female gave birth in a given season, after controlling for maternal age and survival of the prior infant, did not depend significantly on matriline rank measured as modal rank for foundress females during the first decade of the study and for their daughters as their mother's rank at the time of the daughter's first parturition (logistic regression, effect of rank: $p = 0.66$).

9.3.2 Survival

Survivorship is calculated based on two distinct data sets: (1) the histories of all individuals observed to be born into study groups and followed until disappearance,

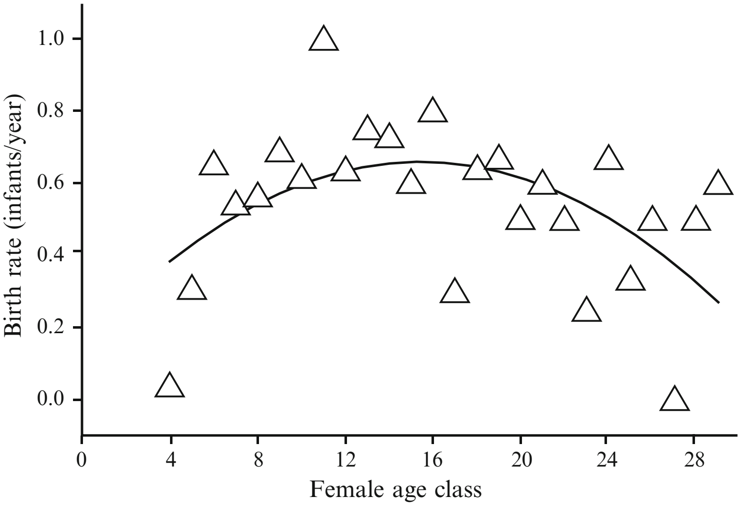

Fig. 9.1 Birth rate as a function of female age. There is a significant quadratic relationship between the fraction of females bearing offspring in a given year and the females' ages (% born = 0.73116065 – 0.0045456 × age – 0.0021112 × $(\text{age-}16)^2$; ANOVA $F_{2,23} = 4.0$, $p = 0.032$). These cross-sectional values are validated by a more appropriate longitudinal analysis. Using a logistic General Linear Mixed Model of the probability of giving birth in a given year within individual females, using female identity as a random effect, the effect of having a prior surviving infant is negative ($p < 0.0001$), and the effect of maternal age has a positive linear ($p = 0.006$) and a negative quadratic coefficient ($p = 0.006$)

death, dispersal, or the end of the present study period, and (2) individuals already present at the start of the study and similarly followed. Histories of individuals still alive at the end of the present study are right-censored, whereas histories of individuals alive for an unknown period prior to the start of observations are left-censored. However, because of predictable age-related changes in size, shape, and fur patterning from birth through early adulthood (10–15 years of age), we estimated the ages of all individuals present at the start of the study for purposes of estimating age-specific survivorship.

The survivorship curve for individuals in MAC shows several periods of distinct mortality rates (Fig. 9.2). First is a period of high postnatal mortality (48%/year) lasting until roughly 8 months of age. About 40% of this early mortality occurs within the first 2–3 weeks after birth and is likely due to infant weakness; there is some clustering of these deaths among females, as 9 of the 12 early infant deaths occurred in only 3 of the 12 females that bore at least six infants each (contingency table, G with Williams' correction = 25.8, $df = 11$, $p = 0.007$). The remaining early mortality is evenly spread across the first 6 months of life and includes infanticide, which accounts for at least 27.3% of all infant mortality (Ramírez-Llorens et al. 2008). Second is a period of lower mortality (10.1%/year) between about 8 and 18 months of age, during which weaning generally occurs. Third is a period of remarkably low mortality (2.75%/year) between 18 months and about

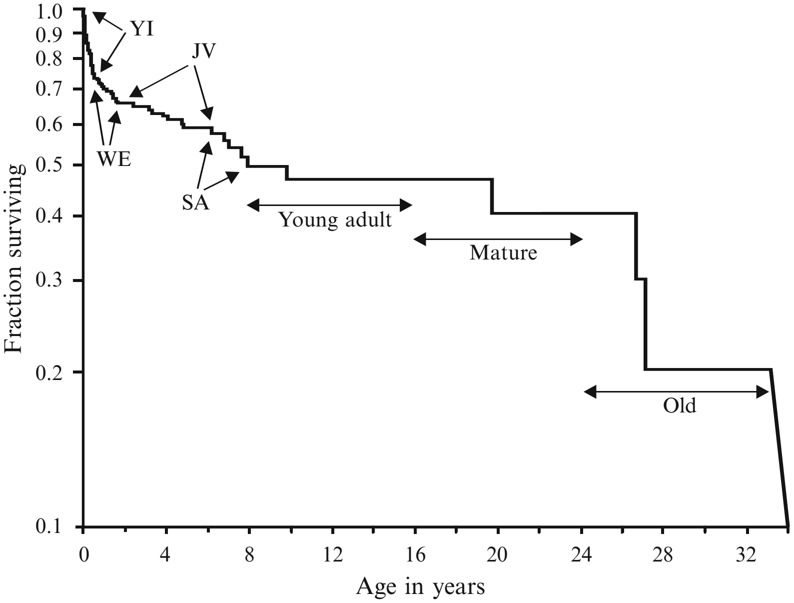

Fig. 9.2 Age-dependent survival. Survivorship graph for all individuals (male and female) born into MAC and its daughter groups in 1991–2010, combined with data on adult females categorized as young adult (YA; 8–16 years), mature (M; 16–24 years), and old (O; over 24 years) at the start of the study, for a total of 715 individual-years. Based on differences in the (log)linear slopes of contiguous regions, four periods of relatively uniform mortality can be recognized prior to adulthood (see text): YI = young infants (0–8 months old, sample size: $N = 146$), WE = weanlings (8–18 months, $N = 100$), JV = juveniles (18 months–6 years old, $N = 84$), SA = subadult (6–8 years old, $N = 37$). Sample sizes for the older female age classes are YA = 20, M = 9, O = 5. Expected lifespan at birth is 8 years, but females that survive to 8 months can expect to live another approximately 24 years on average

6 years, during which juveniles are sheltered from both competition for food (by the dominant male and their mothers) and from predation risk (by being able to occupy central positions in the group spread; Janson 1990; Di Bitetti and Janson 2001b).

Up to 6 years of age, the data include roughly equal numbers of males and females; there is no sex difference in survivorship for known-sex individuals (typically those that survive past 4 months of age; proportional hazards model, effect of individual's sex: $p = 0.50$). From 6 to 8 years, mortality increases (to about 8.6%/year) among females (most males have dispersed by the end of this age range; see below). This period includes the first birth and nursing for most females, and the higher mortality may be associated with the stresses of starting reproduction. After 8 years is a long period of negligible mortality among females (0.7%/year; Fig. 9.2). This halcyon period of near-perfect survival and high fecundity (Fig. 9.1) lasts roughly from 8 to 16 years of age, a period we refer to as "young adulthood." There follows a period of about 8 years during which "mature" females (ages 16–24) retain high fecundity but begin to experience modest mortality

(2.5%/year, Fig. 9.2). After the age of 24, “old” females experience a reduction in fecundity (Fig. 9.1) and increase in mortality (to 14.0%/year, Fig. 9.2).

Maternal rank (see Sect. 9.3.1 for definition) did not significantly affect juvenile survival for any interval of infant and juvenile ages (up to 1 month of age, 1–8 months, 8–18 months, and 18–60 months) or for cumulative survival from birth to 60 months (logistic regressions of infant survival, effects of rank: all $p > 0.34$).

9.3.3 Matriline Rank Stability and Growth Rates

Once a daughter reached adulthood, her dominance rank usually closely approximated that of her mother (Table 9.1). However, while she was still a juvenile, her rank appeared to depend more on her age and size relative to other juveniles than on her mother’s rank, although the protection and intervention of a high-ranking mother could allow a daughter preferred access to contested food sources. Juvenile females nearly always rank below any adult female in access to contested food sources, but sometimes, subadult females of high-ranking lineages could displace low-ranking adult females.

Matrilines maintained stable ranks as long as the matriarch was alive. Notable changes in matriline rank were observed only twice in the 15 study years that MAC did not divide (1991–2005), but these corresponded to the only two instances of mature or old female mortality in this period. The first case was that of OL and her presumed daughter SP (born prior to the start of the study, but associated with OL spatially and socially). OL was very old but still very aggressive, often initiating threats toward other females or soliciting coalitions to threaten other group members. Although an exact nondependent rank for OL is hard to estimate (due to the high frequency of coalitionary aggression), she was not a peripheral group member and fed in many contested food sources along with SP. Following the death of OL in 1992, SP was still a juvenile and almost immediately became one of the group’s most peripheral members, rarely seen feeding in the main group and mostly avoiding agonism in contested food trees throughout the subsequent 14 years; she split from her natal group in 2010, following a change in the dominant male, and formed a new group with one adult male and her three youngest offspring.

The second case was that of F2. She was the clear alpha female from 1991 to her disappearance and presumed death in mid-2001. During this period, both her male and female offspring benefitted from F2’s agonistic protection when entering and feeding in contested food sources. Her oldest daughter (MF) that survived to reproduce clearly ranked closely below F2 at the top of the female hierarchy but disappeared (and is presumed to have died) a few months after her mother’s disappearance. F2’s younger surviving daughter (UR) was still a juvenile when F2 disappeared; UR survived another 5 years yet never attained high rank and was among the lowest-ranked adult females at the time she first gave birth.

Table 9.1 Changes in matriline dominance across years of the study

Rank	1991–1993	1996	1998	2000	2003	2005–2006	2006–2007
1	F2	F2	F2	F2	YO(DO)	TH(DO)	TH(DO)
2	GR = OL	GR	GR	MF(F2)	TH(DO)	YO(DO)	EST(TH < DO)
3		WC(GR)	WC(GR)	GR	GU	GR	YO(DO)
4	GU = DO	GU	LU(GR)	LU(GR)	RI(GU)	CHI(GO < DO)	CHI(GO < DO)
5		DO	mf(F2)	MG(GR)	SP(OL)	SP(OL)	GR
6	sp(OL)	lu(GR)	GU	WC(GR)	CL(SP < OL)	EST(TH < DO)	CL(SP < OL)
7	wc(GR)	th(DO)	DO	GU	WC(GR)	CL(SP < OL)	OLI(SP < OL)
8		SP(OL)	TH(DO)	RI(GU)	GV(WC < GR)	OLI(SP < OL)	SP(OL)
9		ri(GU)	SP(OL)	DO	WE(WC < GR)	UR(F2)	eva(CL < SP < OL)
10		yo(DO)	ri(GU)	TH(DO)	GR	eva(CL < SP < OL)	bia(SP < OL)
11		mf(F2)	yo(DO)	YO(DO)	LU(GR)	jos(SP < OL)	jos(SP < OL)
12		mg(GR)	mg(GR)	GO(DO)	MG(GR)	bia(SP < OL)	maw(UR < F2)
13		go(DO)	go(DO)	SP(OL)	GRE(GR)		
14		cl(SP < OL)	cl(SP < OL)	CL(SP < OL)	ur(F2)		
15		we(GR)	we(WC < GR)	we(WC < GR)	est(TH < DO)		
16			gre(GR)	gre(GR)	chi(GO < DO)		
17				gv(WC < GR)			
18				mi(TH < DO)			
19				ur(F2)			

Sufficient dyadic agonistic data to produce female dominance hierarchies were obtained only by certain researchers, so sampling is not as uniform or complete as desirable. Early hierarchies were arranged by eye, but later ones were calculated using MatMan. The adult females present at the start of the study are considered the matriarchs and are given with no abbreviation in parentheses. Each offspring's abbreviation is followed by her genealogy in parentheses, with "<" meaning "daughter of." Juveniles are given in lowercase, and adults in uppercase; infants are not included. In 2004–2005, GR's matriline (except GR) fissioned from MAC to form the GUN group, and GU's matriline split off to form RI group. Unrelated females linked by '=' were not distinguishable in rank.

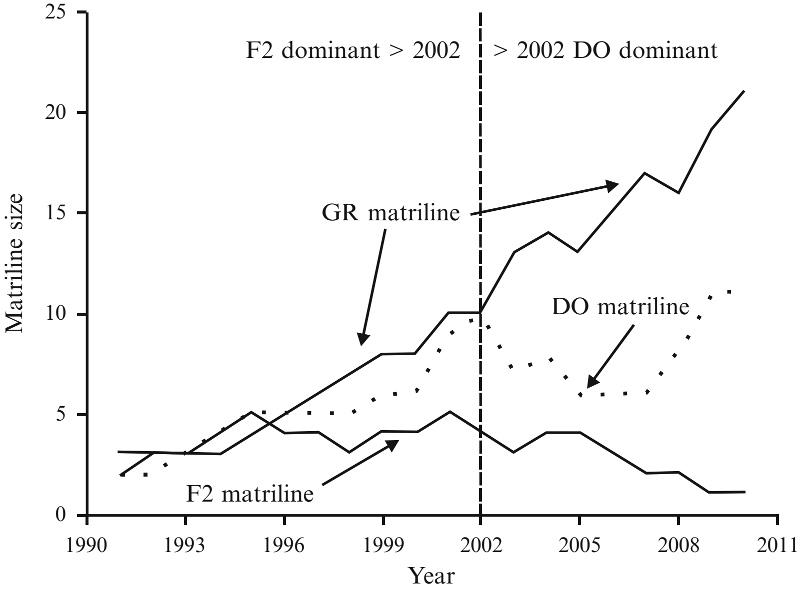

Fig. 9.3 Matriline dynamics. Growth of lineages of three of the five adult females present in the Macuco group in 1991; kinship among these females is not known. Female F2 was the alpha female during 1991–2001, GR was the beta, and DO was either delta or epsilon (depending on the year). F2 died in mid-2001, and by mid-2002, DO's matriline had moved from near the bottom of the female hierarchy to become alpha. For clarity, the growth rates of two other matrilines are not shown, but they were intermediate between GR and F2 and had net losses in only 1 of 20 observation years on average. The two dominant matrilines had losses in 4 of 20 observation years

Interestingly, after the death of the alpha female and her adult daughter, the beta female GR did not become the new alpha nor did her matriline become top-ranking, although she had three adult living daughters. Instead, the new alpha position was attained by DO's two oldest daughters of the fourth-ranking matriline (the two daughters exchanged the alpha position early in this period).

Despite the lack of significant maternal rank effects on fecundity or infant survival, the long-term success of different matrilines in MAC and its daughter groups differed markedly (Fig. 9.3). Rank effects were absent largely because alpha matrilines had the lowest recruitment of all matrilines (Fig. 9.3; F2 1991–2001, DO from 2002 onwards), whereas the beta matriline (GR) had the most consistent and highest growth rate. The low effective recruitment success of the alpha female F2's matriline was due to overproduction of male versus female offspring (ratio of 5:2 compared to 44:47 for the remaining females in MAC), along with the deaths of both of her subadult (6–8 years old) daughters. After it shifted from subordinate to alpha status in 2002, the low recruitment success of DO's matriline was due mostly to low juvenile survival (survival to age 2 of 0.4 versus 0.70 for other females). The different causes for low recruitment of these two dominant matrilines do not suggest any simple cause, but the overall pattern implies that alpha status confers no strong fecundity or survival benefits for females in this population.

9.4 Male Life Histories and Strategies

9.4.1 Natal Dispersal

We documented the emigration of 27 natal males during 55 group-years of observation. Because we do not mark individuals with permanent tags, we cannot follow the fates of dispersing males beyond about 1 year after they leave their natal or current group, and even this ability is restricted to a subset of males that we are lucky enough to find again. Thus, we cannot extend the survivorship graphs of juvenile males beyond the age of dispersal (cf. Fig. 9.3 for females), although we know the fates of a few individuals. Unlike in *Cebus capucinus* (Jack and Fedigan 2004), natal dispersals in our population were isolated events. We documented only a single clear codispersal, out of 21 natal male dispersal events in well-studied groups (MAC, GUN, RI), when two males disappeared on the same day in 2006. They were found together about 16 km from their natal group in the local town (Puerto Iguazú) a few days later. The very long dispersal distance and the unusual coincidence of their simultaneous departure gave rise to the suspicion that they had been captured by local tourists and released in the town.

Dispersal events are not clustered in time. Although in five cases, two natal males dispersed from the same group within 3 months of each other, this frequency of clustered dispersals does not differ from random (given a rate of 0.688 natal male dispersals per group-year of study, we should expect 3.32 of 21 dispersals to occur at random within 3 months of a previous dispersal, $G = 0.9$, $df = 1$, $p > 0.5$). In only one of these cases of closely spaced dispersal were the two males known to have dispersed together to the same group, which was their mother's natal group. In addition to the case of simultaneous long-distance dispersal, the fates of eight dispersing natal males were known: two were seen alone in the natal territory several weeks to months after emigration and did not appear in neighboring groups, and in six cases, the males were found in a neighboring group several months after emigration. Given that we frequently observed neighboring groups, the above data suggest that male dispersal is usually (21/27 cases, across all study groups) further than one group away.

Natal males disperse across a range of ages, but most dispersal events occur between the ages of 5 and 7 years, with a mean of 5.7 (Fig. 9.4). Both cases of infant dispersal occurred when their mothers apparently left their natal group. Three cases of male dispersal at younger than 4 years of age were all from a daughter group (RI) back to the mother's natal group (MAC); none of the mother's (known) matrilineal relatives lived in the latter. Excluding these five cases raises the mean age of dispersal to 6.5 years (median of 6.1 years). At the time of dispersal, they are clearly smaller than fully adult males of 9–10 years of age.

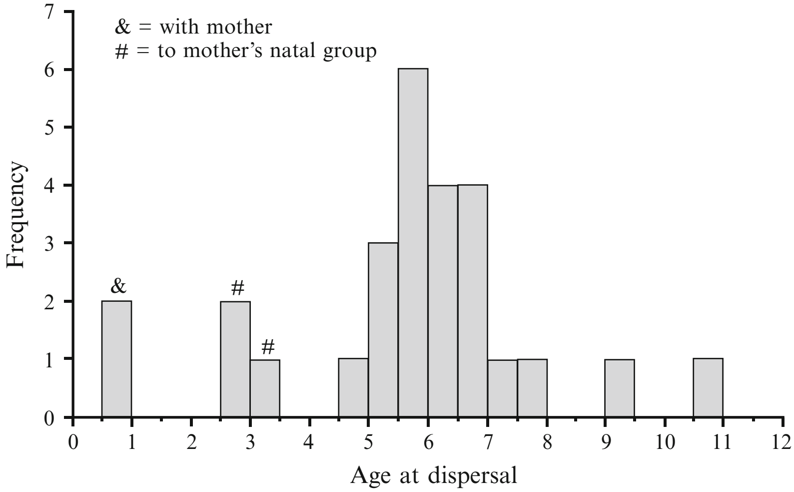

Fig. 9.4 Distribution of the ages of dispersal for natal males in all study groups 1991–2010. The two cases of dispersal at less than 1 year of age were infant males that disappeared along with the mothers and are presumed to have codispersed with them (but the possibility of coincident death cannot be excluded). The three unusual cases of dispersal between 2.5 and 3.5 years of age were from a recent fission group of Macuco (Rita) back to the Macuco group, and all occurred within 1 year

9.4.2 Immigrant Males and Their Fates

We documented the immigration of 39 subadult (5–8 years old) and young adult (9–11 years old) males into focal groups in 55 group-years; there were also 12 presumed immigrant adult males present in various study groups when we started sampling, including five that were alpha males (treated separately below). Some of the immigrant males had been seen previously alone in the home ranges of the groups that they joined, but the prior histories of most were unknown, suggesting that they did not move in from immediately neighboring study groups. Immigrant males stayed in a group until they either emigrated, challenged the dominant male for alpha status, or achieved alpha status some other way. We can assign "fates" to each of 46 non-alpha males; 17 of these were still subordinates at the end of the samples on their groups, and the remaining 29 males were involved in 35 changes in status (Table 9.2). The most striking aspect of these changes is the existence of three distinct "pathways to power": a subordinate male can become alpha by challenging the existing alpha, inheriting the alpha position if both the challenger and the alpha male are badly injured in a fight, or taking over as the alpha male of a daughter or splinter group of females that usually occurs shortly after a new male becomes established (see Sect. 9.5.1). The frequency of nonaggressive paths to power (inheritance or new group creation) is nearly as high as aggressive ones (9 versus 11 cases).

Table 9.2 "Fates" (changes in status) of 47 subordinate adult males following immigration to one of the study groups, and the mean and range (in parentheses) of values for each variable

	Challenge and replace prior alpha male	Inherit alpha role without fight	Leave as alpha male in new daughter group	Emigrate without obvious cause	Emigrate during or soon after alpha male change	Still subordinate at end of sample
N males (only complete tenures)	11 (3)	2 (1)	7 (4)	8 (3)	7 (6)	17
Mean number of years of residence prior to status change, all data	3.84 (0.02–8.49)	2.15 (1.64–2.67)	3.07 (0.41–5.0)	2.0 (0.54–5.5)	0.89 (0.22–2.36)	1.46 (0–4.64)
Mean number of years of residence prior to status change, complete tenures	3.95 (0.02–6.55)	2.67	3.92 (3.01–5.0)	2.83 (0.54–5.5)	0.85 (0.22–2.36)	NA
Mean age at status change	14.25 (10.5–21.7)	8.65 (7.6–9.6)	14.15 (10.1–18.4)	10.37 (7.8–14.5)	8.6 (6.2–12.4)	NA

Several males were assigned more than one fate, as they either changed status within a group or were tracked through more than one study group. Many of the residence durations are censored because males were already present at the start of study on each group; results are provided both for all data and only complete tenures.

Replacement of the alpha male position is associated with predictable emigration of the group's remaining non-natal males. In 6 of the 7 well-observed replacements of the alpha male in groups with three or more non-natal males, most or all of the group's non-natal males who did not obtain the alpha position left the group within days to 8 months, accounting for 10 of the 15 total individual emigrations recorded in the whole study. Even counting each bout of postreplacement emigrations as a single event, the frequency of such emigration bouts within 8 months of a male change is much higher than expected by chance (6 versus 1.33, out of 11 total bouts of emigration, $G = 11.9$, $df = 1, p < 0.001$).

Bouts of immigration are also more likely following alpha male replacements. In 13 of the 33 cases that could be scored, the arrival of new males to a group occurred within 6 months after the replacement of the group's alpha male. This frequency is much greater than the 3.6 immigration cases expected at random, given only 12 alpha male replacements in the same 55 group-years ($G = 17.97$, $df = 1$, $p < 0.001$). Thus, it appears that newly vacated "slots" for subordinate males are rapidly filled. In most (10/13) cases, the new males came into large groups with over eight adult females, suggesting a preference to join large female groups. Potential immigrants may take into account the number of males already in a group before moving: in the most closely monitored study group, the number of males lost and gained per year was well correlated (excluding the 11 years with neither losses nor gains, $N = 9$ years, $r = 0.95, p < 0.0001$).

Once a male joins a new group, his subsequent fate (Table 9.2) depends on his age and chance. Males less than 9 years old are not of full adult size and do not challenge adult males for high rank. They typically remain for shorter periods, emigrating predictably after 2–3 years of residence or when the alpha male is replaced, unless they happen to inherit the alpha status, a rare event over which they have little control. Fully adult male immigrants of at least 9 years of age take positions in the higher ranks of the male hierarchy, sometimes (three cases) challenging the alpha male within 5 months of immigrating but more commonly waiting long periods (an average of 5.2 years, $N = 8$) for successful opportunities to challenge the alpha or to become the alpha male of daughter or splinter groups of females at group fission (associated with alpha male replacement – see below). Males that took the alpha position in fission groups were of the same age on average as males that challenged the alpha (14.15 versus 14.25 years old), and spent nearly the same average time in residence before assuming an alpha role (3.92 versus 3.95 years, Table 9.2). Beta males can be very "patient" waiting for an opportunity to defeat the alpha male, which may take over 8 years to arrive (the case of GE in MAC, 1991–1999). These long waits for a beta male to take over the dominant position may provide opportunities for the beta male to reproduce, as the beta male had preferential access to females that happened to be in estrus at the same time as a more dominant female (Janson 1984) and to the daughters of the dominant male, who did not solicit their fathers as mating partners (Di Bitetti and Janson 2001a).

9.4.3 Tenure and Replacements of Alpha Males

Unlike many other primates in large multi-female groups in which the dominant male of a group may change frequently, sometimes more than once per year (e.g., Palombit et al. 2000), the alpha males in all known populations of *Cebus apella* superspecies tend to have long tenures. Figure 9.5 shows the survival plot of all tenure lengths (including censored durations) documented in the alpha males of the Iguazú population. Very short tenure lengths (less than 4 months) occurred when a male challenged the alpha successfully but the challenger was seriously injured (one case), failed to kill the former alpha male who returned to claim the alpha role (one case), returned to beta status following a group fusion (one case), or inherited alpha status and was subsequently challenged for the alpha position by an older male (one case). Tenure lengths for males that acquire alpha status by challenge versus group fission did not differ in our study (ANOVA, $F_{1,14} = 0.001, p = 0.98$). If a male retained alpha status past the first 4 months, tenure lengths were typically long, with a median duration of 5.01 years and a 0.76 chance of lasting at least 3 years. One male, Pecoso, was documented to be the alpha (in Silver group) for at least 11.6 years.

One case of failed male replacement revealed a likely cause of the relatively long tenures of dominant males in this population. Dedos, who had been the dominant male of MAC for over 6 years, was attacked and injured, but not killed, by Gendarme on about September 8, 1997. Dedos withdrew from MAC but remained

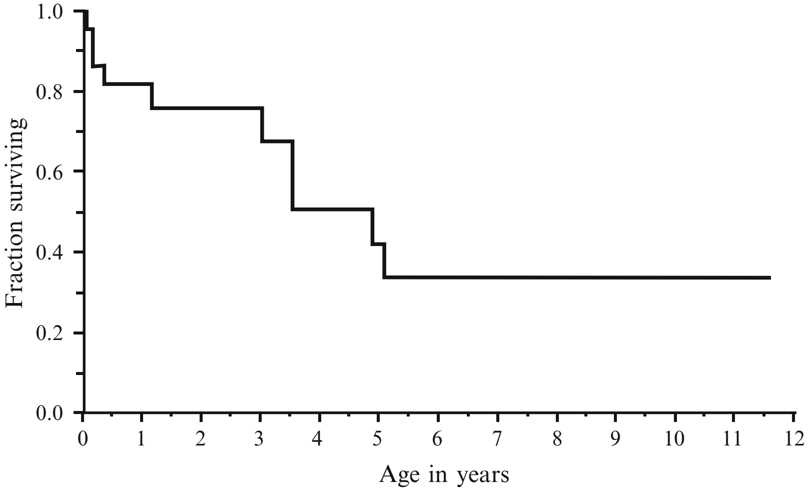

Fig. 9.5 Alpha male tenure duration across all study groups ($N = 23$ males). A tenure length was calculated as the number of days from the date of a male's first appearance as alpha to midway between his last known date as alpha and the date of the next census on his group. About 18% of alpha males held their rank for less than 4 months, but if they made it past this initial period, their expected tenure was 5 years. All four tenure lengths above 5.1 years (5.3, 5.9, 8.5, 11.6) were censored and thus represent minimal estimates of true tenure lengths

in the group's home range for over a month following his injury. Dedos then returned to MAC in late October 1997, and the two males faced off against each other. Dedos was backed up by a cohort of females, including all but one of the group's adult females, whereas Gendarme was backed up only by one female, WC, a putative daughter of Dedos. Dedos and his supporters won this encounter, whereas Gendarme suffered additional wounds during a series of fights. Dedos returned as the dominant male for another nearly 2 years until being badly injured by Gendarme in July of 1999. That the support of Dedos by other group members was more than symbolic is suggested by the fact that in the 1997 series of fights, both the dominant female, F2, and an older natal male, DF, were injured; similar injuries of natal males and adult females occurred during some other male takeover periods. Thus, the dominant male appears to enjoy support by most existing adult females and his sons in conflicts against male challengers, perhaps allowing him to maintain his breeding position in the group far longer than would be the case without this support.

9.5 Changes in Group Size, Group Fission, and Group Fusion

We have detailed data on composition, births, deaths, and migrations for all individuals in MAC and its descendant groups GUN, RI, and SP, from February 1991 through the end of 2010. During this 20-year period, numbers of individuals in these groups increased at a steady rate of about 4% per year (Fig. 9.6), regardless of alpha male changes, infanticides, and two group fissions.

Group counts from other groups span at most six continuous years and are less informative about long-term growth rates. Most groups grew in numbers over the period of observation, but four groups either went extinct or moved entirely out of the known study area and were not seen again. Two of these were small splinter groups (one from the breakup of YAC in 2009; one from the fission of MAC in 2009); in both cases, the group composition was one adult male, one adult female, and one or two juveniles. Two other groups (BAR, RUB) were not seen after 1996 and are presumed to have gone extinct or moved out of the study area; the BAR group partially occupied an area of regenerating forest that was cut down to provide new tourist facilities starting in 1998.

Temporary changes in group size occurred (see also Lynch Alfaro 2007). Very large groups (over 30 animals) tended to show signs of subgrouping behavior, which is not reflected in the total counts, but could lead to subgroups of defined composition ranging independently of other subgroups for several hours up to several days, even on occasion sleeping in different areas. Such subgrouping behavior appeared especially in the Argentine winter, the period of greatest food scarcity (Di Bitetti and Janson 2001a). When these large groups eventually split, the resulting descendant groups were not necessarily well-predicted by the composition of the previous subgroups, except that one fully adult male from the original large group tended to join each descendant group as the alpha (see Sect. 9.4).

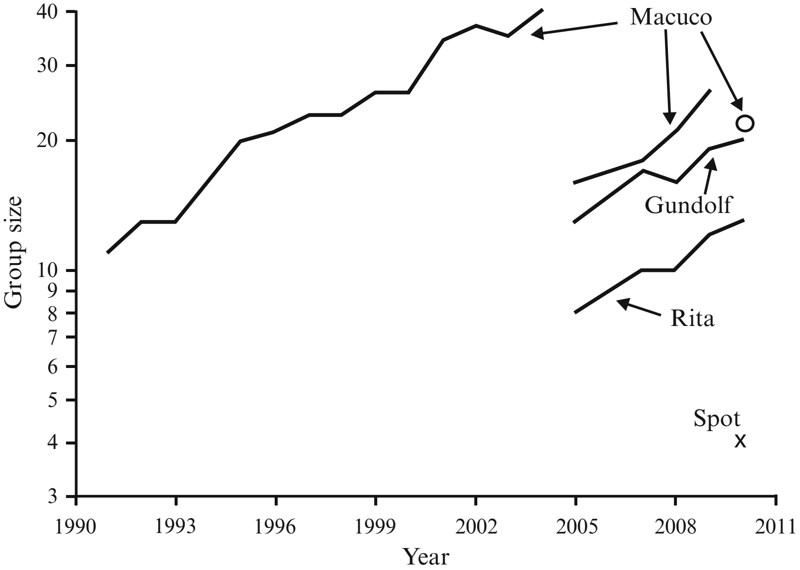

Fig. 9.6 Group sizes (excluding non-natal males) of MAC group and its daughter groups during the study period. The *y*-axis uses a log scale, so a straight line of numbers versus time represents a constant rate of growth. For the entire period, the best estimate of the growth rate is 0.04, and it does not differ before and after the group fission, nor among the daughter groups. The numbers for Rita group include the three juvenile males that emigrated back to their mother's natal group at unusually young ages (see Fig. 9.4)

9.5.1 Processes of Group Fission

We observed the detailed process of group fission in two study groups (three fission events: YAC 1991; MAC 2004–2005; MAC 2009–2010) and monitored the results of fission in a third group (SIL 1994–1995) via periodic censuses. In the first three cases, group splitting occurred in the largest groups known to us in the population at the time: YAC had 34 individuals (9 adult females) just prior to the split, and 2004–2005 MAC had 48 (14 adult females), and 2009–2010 MAC had 33 (10 adult females). In all four cases, splits occurred in association with a replacement of the dominant male in the original groups. However, not every male replacement led to group changes (see Sect. 9.4). In all of the well-observed cases, the clear establishment of the new alpha male was associated quickly with the disappearance of a majority of infants of less than 6 months of age, most likely by infanticide (Ramírez-Llorens et al. 2008). At least one group split (Rita from MAC 2004–2005) may have been the direct consequence of an adult female seeking to avoid infanticidal behavior by the new dominant male (Ramírez-Llorens et al. 2008); the same may be true of OLI's departure with her infant from MAC in late 2009, which preceded the eventual wave of infant disappearances in February–April 2010.

The fourth case of group fission occurred about 1 year following the fusion of the neighboring RUB and SIL groups, producing an enlarged SIL group in 1993. Between mid-1994 and mid-1995, the alpha male in the SIL group (LF) was replaced by a new immigrant adult male (PEC). During the same period, the two subordinate adult males in the SIL group (IN, BI) left the group with two of the three females from the original RUB group, plus one of the females formerly resident in the SIL group. One of the original RUB group females remained in the SIL group. This new RUB group remained as a separate social group, with IN as the alpha male, at least through the end of 1996. In neither SIL nor RUB did any of the infants of the 1994–1995 birth season survive to the mid-1995 census.

Group splits usually produced daughter groups of quite different sizes. In three of the four cases of group splits, the majority of the adult females remained in the original home range whereas the two new daughter groups were in each case composed of a few adult females (numbers of females for YAC 1991 = 6:2:1, MAC 2004–2005 = 8:4:2, and MAC 2009–2010 = 7:2:1) and their immature offspring. In the fourth case (Silver 1994), three females went with each daughter group.

In two well-observed group splits, smaller descendant groups were not at a demographic disadvantage compared to larger ones. There was no marked difference between the per capita growth rates of small versus large descendant groups in the 3 years following a group split, either for MAC (Fig. 9.6) or the YAC group (e.g., the Silver group increased from an initial size of about 9 animals with only two adult females in late 1991 to at least 23 individuals by 2000, an average annual increase of 10%). Because group splits were associated with a change in the dominant male and attendant infanticide, the year after a split was a year of high birth rates, as nearly all the females in a group produced offspring in the year following a male replacement.

When genealogies were known, daughter groups were found to be composed of individuals from single matrilines but did not contain complete matrilines. In the 2004–2005 MAC breakup, GUN contained all the daughters of GR and their offspring but not GR herself, who remained in MAC. Likewise, when Rita left with her offspring, her mother, GU, did not leave with her, although she joined her daughter within a couple of days. The 2009–2010 MAC split produced two splinter groups composed of portions of the matriline of SP (1 = OLI and infant; 2 = SP, BIA, DAN, FRA), yet three other adult daughters of SP (CL, EVA, JOS) stayed in MAC with their offspring, as did one of OLI's subadult daughters (OFE). Thus, the process of group fission in this population appears to produce new groups in which females are likely to be very closely related yet might well have some equally close kin in adjoining groups.

The process of group fission could take any period from 1 day to 6 months. In the case of YAC, it took about 3 months following the change in the dominant male for subgroup composition to stabilize into a close resemblance of the resulting daughter groups, during which time the group went from foraging as a single unit nearly all the time to increasing periods of 2–3 subgroups foraging separately from each other. After the fourth month, the subgroups (ST, SIL) were not seen to rejoin YAC to form the entire original group, and by the fifth month, they occupied largely distinct but adjacent core areas. In the case of MAC 2004–2005, one of the group's adult males (GUN) formed part of several spatially distinct subgroups before the alpha male (GEN) was replaced, but after GEN was removed, GUN became more independent, and within 4 months, he and a subgroup moved to a new home range adjacent to, but not overlapping with, the original range. In contrast, the second split (RI) in MAC 2004–2005 occurred over 1 day with the dispersal of Rita and her daughters to a peripheral area in MAC's home range, where she was later joined by her mother and two of MAC's former subordinate males. In the MAC 2009–2010 split, one female (OLI) and her new infant started to stay away from MAC after the first intense male–male fights in early November, and she was last seen about 1 month later in the company of one of the adult males of the group (JE). Following the death of MAC's alpha male on November 20th, 2009, continued aggression and unstable ranks among MAC males lasted until late January 2010; during December, the group showed indeterminate cohesion, some days moving as a single group and on other days dividing into at least two distinct foraging parties that sometimes even slept in different areas. After one male (ERN) assumed the alpha role starting in February, 2010, 4 of the 7 infants in the group disappeared within 2 months; by May 2010, another subgroup (SP with BIA, DAN, FRA) had left MAC.

9.5.2 Group Fusion

One case of group fusion was documented. In early 1993, RUB was composed of two adult males (NA, SO), three adult females, and several immatures. At this time, the neighboring SIL group had two adult males (LF = alpha, IN = beta), one subadult male (BI), three adult females, and several juveniles. On the 5th of June, 1993, MD discovered SO alone and with deep wounds to his hands, elbow, and shoulder. On the 14th of June, 1993, NA was also no longer with RUB, and instead, the group had only the two subordinate males from SIL, IN, and BI. These two males stayed with RUB until at least the 28th of June as the only adult males in that group. Meanwhile, on the 21st of June, SO was seen as a subordinate male in SIL, but on the 27th of August, he was back with RUB, along with IN and BI. SO had fresh wounds on his face and at the base of his tail. That same day, RUB had an intergroup encounter with SIL, during which MD saw LF (the alpha male of SIL) with deep wounds on the face. After more chases and a fight during this encounter, SO followed and gave submissive facial gestures to LF. From that date until the middle of 1994, covering seven separate censuses of the group, SIL and RUB comprised a single unit, with LF as the alpha male, IN, SO, and BI as subordinate males, and all the females and juveniles of both groups. NA, the former alpha male of RUB, was not seen again. Thus, it appears that he was displaced as the alpha male of RUB by the two subordinate males of SIL, who then rejoined SIL with the RUB females. SO and all the other known individuals of RUB stayed with SIL for about 1 year. After mid-1994, RUB and SIL fissioned (see above).

9.6 Discussion

9.6.1 Slow Life Histories

This population of *apella*-like capuchins illustrates one of the slower life histories known among monkeys. With an age at first reproduction of 6 years for females, this population would not persist without high juvenile and adult survival, which leads to a relatively high expected (at birth) lifespan of 8 years. There is some evidence that starting reproduction is stressful for females: their survival declines at age 6, and female fecundity is lower at age 5 than later (Fig. 9.1). Once a female reaches full maturity at 8 years, she has a long future life expectancy of 19 years. Although fecundity and survival begin to decline notably as a female surpasses the age of 24, there is no evidence for menopause, and even the oldest females in our study population continued to come into estrus.

Most likely because of slow infant development (Charnov and Berrigan 1993), mothers typically produce an offspring only once every other year, if the previous infant survives. This alternation of birth years sets up the conditions for sexually selected infanticide by males to be adaptive (Ramírez-Llorens et al. 2008), despite the fact that the Iguazú capuchin population is highly seasonal in its breeding (Di Bitetti and Janson 2000), which would make infanticide of little benefit to a newly dominant male in an annual breeder (van Schaik 2000). Although the great longevity and slow life history found in this population is surely assisted by the lack of large eagles preying upon adult capuchins, the reproductive parameters of Iguazú (high age at first birth, alternation of birth years) are commonly found in other capuchins (e.g., Robinson 1988; Fedigan and Rose 1995), even in areas with relatively high adult predation risk (Janson 1984). If the current notion is correct that these slow life histories are a direct result of the relatively large brain size of capuchins (Barton and Capellini 2011), then the cost of large brain size is extreme – the theoretical intrinsic rate of population growth (a rough measure of maximum fitness) in our population (from Figs. 9.1 and 9.2) is 0.1/year, a full order of magnitude less than the $r_{\max}$ of about 1 expected of mammals of equivalent body mass (Calder 1996). It is difficult to imagine what benefits of larger brains might repay such a tenfold fitness cost!

The survival of males, far more so than of females, is dictated by events related directly to their reproductive strategy, principally dispersal from their natal group and challenging an established alpha male for the dominant position in a social group. Natal dispersal is an apparent consequence of generalized incest avoidance (Di Bitetti and Janson 2001a). Prior to dispersal (typically by age 6), there is no statistical difference in survival between the sexes in natal animals in MAC. As we rarely can track dispersing males after they leave their natal group, their mortality during dispersal is not easily measured. However, we can estimate the extent of such mortality by examining group adult sex ratios, knowing the survivorship of adult females and the sources and extent of male mortality once they join established groups. Assuming the population as a whole is not growing and using the results from Fig. 9.1 and Table 9.2, the difference between the adult sex ratio expected based on postimmigration patterns of male mortality and that actually observed implies that at least 38% of dispersing males do not survive to show up in social groups. This mortality is likely spread across 2 or more years, reflecting the difference in average age between the ages of natal dispersers (6 years old; Fig. 9.4) and the estimated ages of immigrant males (typically 8 years old or older; Table 9.2). This is a high rate of mortality for capuchins in this population and may reflect the reality of risks associated with solitary living. By comparison, females from ages of 6–8 experience a total of 15.8% mortality, which itself is markedly higher than just before or after this period (Fig. 9.3). If the estimated dispersal phase male mortality of 38% is accurate, then the life expectancy of a male at birth is only about 7 years, somewhat less than that of a female; nearly 2/3 of males born will die without ever reaching dominant status, whereas only about 40% of females born will die before giving birth at least once.

After a male migrates into a social group, attaining the alpha status may entail both mortality risks and large reproductive rewards. Although a slim majority (11 of 20) of males that attain alpha status do so by challenging the group's dominant male in one or more bouts of contact aggression, nearly half of all males attain the alpha position indirectly (Table 9.2). It is not easy to calculate the real frequency of alpha challenges and their chances of success because if a challenge does not succeed, no change in the social structure occurs and both the dominant and the challenger may sustain only minor wounds. If a successful challenge occurs, the challenger is always wounded, sometimes (2 of 11 cases) severely enough that he cannot immediately assume the alpha status even if he mortally wounds the dominant. In one case (MAC, 2009), the putative challenger (HOM) appears to be have been so severely wounded that he died a few weeks later – none of the other males in the group was severely wounded and none quickly took on the alpha role after the dominant was deposed.

After achieving the dominant status, a male can expect to retain it for 5 years; once he is deposed, it appears that he usually dies (although we can absolutely confirm the death in only two cases). In two cases, the former dominant survived the challenge; in one of these (DE), he recovered from his wounds and won back the dominant position after about 6 weeks, and in the other (ST), he left with one female as a fission product of the group after his deposition, but this daughter group was last seen 3 months after the dominant was defeated. The net result of the these challenges and their attendant mortality is that male life expectancy after immigrating to a social group at age 8 is estimated to be only an additional 10.9 years (Janson et al. unpublished data), roughly half the remaining life expectancy of 19 years of an adult female that reaches 8 years of age. Based on these differences in survival rates, life history theory predicts that male capuchins from this population should show more rapid senescence than should females, even under conditions of low environmental and social stress (e.g., captive breeding colonies).

9.6.2 Female Philopatry, Matrilines, and Group Membership

Capuchin monkeys in this population conform to some but not all of the generalities about matrilineal group structure derived from Old World primates. Like baboons and macaques, capuchin females and their kin in this population tend to support each other in aggressive interactions, daughters come to rank close to (although sometimes above) their mother, and group fissions tend to follow matrilineal divisions (but one or more members of a matriline may stay behind in the natal group). However, despite clear feeding priority and central positioning of the alpha female F2 (e.g., Di Bitetti and Janson 2001a), recruitment success into her matriline was notably lower than that of lower-ranked females (Fig. 9.3); likewise, when DO's matriline became dominant in 2002, it began actually to decline in size, whereas previously, it had been increasing. In both cases, low recruitment into the matriline was seemingly due to lower survival of offspring, and in F2's case, this was compounded with a male-biased sex ratio among her offspring. The low recruitment success of the dominant matriline does not appear to occur in recently founded daughter groups, perhaps because agonistic relationships among these related females are relatively infrequent and of low intensity. Whatever the reason for the low recruitment success (and given the small sample size of matrilines for which we have long-term data, it could be coincidence), F2's small matriline was vulnerable to marked rank change when the matriarch died; a year after F2's death, the lone surviving female of that matriline (UR, Table 9.1) was the lowest-ranked adult female.

The ability of low-ranking adult females to grow their matrilines in the face of contest competition for food may be an unusual feature of this population. Low predation risk on adult capuchins because of a lack of large monkey-eating eagles means that low-ranking subordinates may have the ability to avoid contest competition by foraging at the periphery of the group on alternative resources that might yield one or a few monkeys as much food *per capita* as do the larger and more productive food sources favored (and contested) by the dominants (Di Bitetti and Janson 2001b). Although not easily amenable to an experimental test within this population, this hypothesis makes clear predictions: the relative reproductive success of subordinate females compared to dominants should be negatively correlated with the predation rate on adult females if the major predators preferentially attack animals at the periphery of a prey group.

If the lability of matriline dominance observed in MAC is a more general feature of other groups and populations of *Cebus apella*-like monkeys, this could also explain some general features of their social behavior. For instance, even though they squabble frequently at food sources, *apella*-like capuchins have been shown to be relatively socially tolerant compared to rhesus macaques (de Waal 1986; Brosnan and de Waal 2003). Second, females have not been observed to fight over rank (nearly all agonism is clearly in the context of access to food, or defense of kin or offspring against males) or to engage in the kinds of aggressive tactics expected of animals using aggression to maintain rank position (e.g., Silk 2002).

Both these features could be expected outcomes of a social system in which matrilineal support in contest competition is real, but high matrilineal rank is not easily preserved and thus not worth risking escalated contests to acquire. High matriline rank might still be worth acquiring if the breeding success of males from high-ranking matrilines is markedly higher than that of sons from low-ranking matrilines, but we have no data to test this question. A further outcome of increased mobility of matriline rank and its lack of correlation with fecundity is that females, while preferring to be "philomatric" (staying with their matriline), can take a chance to establish or join a new social group, as illustrated by the fusion and subsequent fission of the RUB group in 1993–1995 and the frequent association of group fission with male replacement.

9.6.3 Group Life Cycles

Despite some variation in details, there is an overriding pattern in group changes that profoundly affects their composition, demography, and behavior. The resulting cyclical sequence of events can be described as a group "life cycle" (cf. colony life cycles of social insects, e.g., Oster and Wilson 1978). This is summarized in a "stage" diagram (Fig. 9.7) in which each distinct configuration of group size and recency of dominant male is represented as a "stage" in the cycle, with stages connected by probabilities of moving from one stage to another. The probabilities are not shown in the diagram but could be entered into a matrix of transition probabilities based on our data. Not all the connections or possible outcomes are encompassed in this diagram, but it is a way to visualize the regularities of change in group structure that emerge from predictable individual-level behaviors. As such, it provides a way to connect natural selection on individual behaviors with their consequences at the level of group structure (cf. Hemelrijk 2002). Note that Fig. 9.7 is based on a small sample and may represent only the life cycle of MAC, which contributed most of the data; nonetheless, it provides a hypothesis against which to compare long-term demographic data from other capuchin and monkey populations.

In our study, cyclical change is driven by replacement of the group's alpha male and the attendant almost inevitable infanticide that follows (Fig. 9.7; see also Fedigan 2003). If a male attains the alpha role (by whatever means) and survives the first 6 months in that role, he is extremely likely to remain as alpha for about 5 years, although a minority can last considerably longer, even over 11 years. The lack of opportunity to replace the alpha during this period is the apparent reason that other non-natal males in the group at the time nearly always migrate away within days to months of the replacement; they are not driven out by invading males, as occurs in white-faced capuchins (Gros-Louis et al. 2003; Fedigan and Jack 2004). The lack of adult males in the group appears to attract immigration from non-natal males, especially into groups with large numbers of females. In the meantime, the alpha male will have eliminated most or all of the infants less than 8 months of age

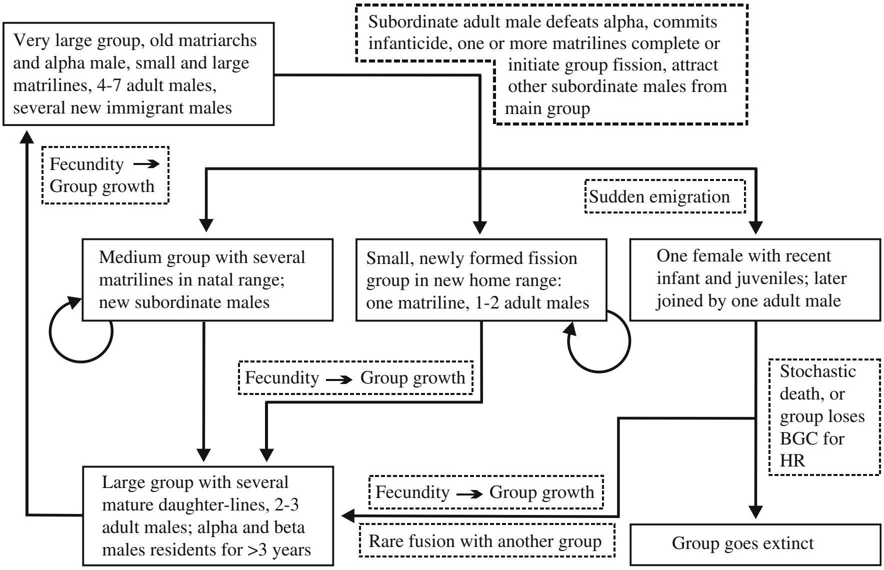

Fig. 9.7 Schematic diagram of group life cycle. Each box with a solid border is a distinct group size or composition, connected by *arrows* representing possible future outcomes of processes that are described in boxes with *dashed outlines*. These processes include net fecundity (exceeding mortality), male replacement, group fission, and risk of infanticide. *Circular arrows* pointing back to the same box represent the likelihood that a group stays in the same state from 1 year to the next. In our population, we did not observe the decline of well-established groups toward smaller sizes and extinction, but this possibility would be easy to include using *arrows* leading from larger groups to smaller ones

within 1–2 months of his having established himself as the undisputed alpha male (a process which may take up to 6 months, depending on his injuries, the presence of challengers, etc.).

Some females use the male replacement to initiate permanent group splits, either by leaving the core area of the natal group as individuals with their offspring ("splinter" groups: three cases) or by forming first temporary, then increasingly durable, foraging subgroups attended by one or two adult males from the natal group. These "daughter" groups, typically (but not always) composed of females from a single matriline, eventually move to areas that are adjacent to or slightly overlapping the natal group's home range. Splinter groups typically contain a female with her infant of the year and appear to be one way for a female to avoid infanticide by the new alpha male in her natal group. Two of the three known such splinter groups were never found again, so it may be that these females eventually join some other group far from their natal group or die as isolated individuals. The new matriarchs of fission groups experience higher birth rates in the period following the group's establishment, although the overall growth rates of fission groups are not distinguishable from that of the natal group. In typical groups where the alpha male lasts at least 5 years, group size can increase quickly, doubling within a decade, thus providing a more attractive target for new male immigration and sowing the eventual seeds of the next male replacement. If the group is still relatively small at the time of a male replacement, the group may stay together for another "round" until the following replacement. Thus, there is an overall cycle to group size and alpha male stability that is coordinated by the events that attend the replacement of a group's alpha male (Fig. 9.7).

Understanding the group life cycle not only illuminates the importance of rare sources of selection, such as infanticide, but also is necessary to place any short-term study of a particular group into a proper perspective. Given the dynamic and cyclical nature of group size and composition, observers cannot hope to study a "typical" group or even a typical set of groups. For instance, much of the variation that we observed between groups at the start of our study in 1991 was likely an effect of observing them in different stages of their life cycles. Acknowledging and documenting group life cycle should allow researchers to detect group-specific traits that reveal potentially important relationships between extrinsic traits (e.g., habitat quality) and group characteristics. Failure to understand group life cycles may lead to the false rejection of hypotheses relating within-population variation of group size to food availability, predation risk, patchiness, or other variables thought to affect sociality.

9.7 Conclusions

Long-term studies of animal populations have been important in revealing rare sources of strong natural selection, long-term demographic cycles or epidemics, and effects of slow habitat change. For slowly maturing, long-lived animals like most primates, long-term studies are also essential to document important events or phases of individual life histories that are critical to explaining variation in individual reproductive success. In our study, the rarest and most dramatic event in individual life histories is the assumption of the alpha position by males; only about 1/3 of all males survive long enough to challenge for the alpha position; the outcome of such challenges is usually fatal for one of the participants, and the consequences of a successful takeover ramify through the group via infanticide, high turnover in non-natal males, and likely group fission (Fig. 9.7). The result of these social upheavals is that male takeovers essentially "reset the clock," often producing daughter groups with all new immigrant males, females and offspring that are of a single matriline, an immediate loss of most infants followed by a year in which nearly all females have babies, and a relatively young adult alpha male that is likely to remain as alpha for 5 or more years, long enough for incest avoidance to become an important part of mating strategies. Subsequent growth of groups is associated with lower average kinship among females, greater aggressive competition between the descendants of the original adult females, larger group size, and increased attraction of immigrant males to the group, which in turn sets the stage for new male challenges to the alpha male and possible group fission. Recognizing this group life cycle places a different interpretation on differences in group size. Rather than interpreting these differences as stochastic variation around a stationary mean (e.g., Cohen 1971), or reflecting differences in habitat quality (e.g., Gillespie and Chapman 2001) or group competitiveness (Robinson 1988), various groups may simply be at distinct points in relatively predictable life cycles. The coordinated changes that accompany transition through the stages of a group's life cycle should predictably affect social behaviors (female–female agonism, existence of juvenile cohorts, female mating preferences). If predictable group life cycles emerge as a feature of other primate populations, documenting and understanding these life cycles should help to clarify the differences in social organization and structure between species, how these differences relate to ecological variables and fundamental life-history traits, and help to integrate male and female social strategies in a broader understanding of primate social systems.

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Part IV
Asia

Chapter 10
Social Organization and Male Residence Pattern in Phayre's Leaf Monkeys

Andreas Koenig and Carola Borries

Abstract The genus *Trachypithecus* (Colobinae, Presbytini) has previously been characterized by one-male groups and both male and female dispersal. Occasionally, males may mature in their natal groups, resulting in so-called age-graded multi-male groups. Our long-term observations of a population of Phayre's leaf monkeys (*Trachypithecus phayrei crepusculus*) in Thailand, while revealing values in group size and composition similar to other species, indicate a hitherto undescribed social organization, in which males mature and breed in their natal group or disperse and form new groups. Groups are not age-graded and multi-male groups are one phase of a dynamic social organization changing between multi-male and one-male constellations. The ways in which our views of the social organization of Phayre's leaf monkeys changed over a period of eight years underscore the importance of long-term studies for a full understanding of the behavioral ecology of long-lived species like primates.

10.1 Introduction

Until recently long-term studies on colobine monkeys, especially the tribe Presbytini (Asian colobines), were comparatively rare (see overview in Kirkpatrick 2007). Only two of the more than 50 species, in seven genera (Groves 2001), had been studied in detail, with multiple years of observation of identified individuals. These were Hanuman langurs (*Semnopithecus entellus*) at Jodhpur, India (e.g., Sommer and Rajpurohit 1989) and at Ramnagar, Nepal (e.g., Borries 2000), and Thomas langurs (*Presbytis thomasi*) at Ketambe, Indonesia (e.g., Steenbeek et al. 2000). This lack of long-term data is unfortunate, because the reliability of results from short-term studies is limited by default (Clutton-Brock and Sheldon 2010).

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Infrequent events will rarely be documented and life history traits and demographic data may be biased, which may lead to spurious results, especially in comparative studies (Borries et al. 2011). In addition, the two Asian colobines studied on a long-term basis have very different social systems. Hence, it is unclear what the range of social systems is among the Presbytini and whether anyone pattern predominates (for a recent classification attempt, see Grueter and van Schaik 2010). Lastly, the lack of long-term studies of Presbytini is unfortunate, because available data on group size and composition, the ecology of female social relationships, and the residence patterns appear not to fit “classic” socio-ecological explanations.

10.1.1 Asian Colobines: (Relatively) Unexplored and Enigmatic

Most genera of the Presbytini, including *Presbytis, Simias, Trachypithecus*, form comparatively small groups of 20 or fewer individuals (cf. Table 4 in Kirkpatrick 2007). Given the expectation that folivorous primates such as colobines experience little to no feeding competition and hence should face only weak constraints on group size (review in Snaith and Chapman 2007), the small groups in these taxa posed the so-called folivore paradox (Janson and Goldsmith 1995; Steenbeek and van Schaik 2001). The resolution of the paradox might be that the upper limit of group size depends not just on the trade-off between ecological costs (i.e., within-group scramble competition) and benefits (i.e., predation avoidance), but also on social constraints, particularly the risk of male takeover and infanticide (Crockett and Janson 2000). Specifically, if the rate of male takeover increases with female group size, the risk of infanticide may increase accordingly and limit maximum group size. Some evidence indeed supports this idea (Crockett and Janson 2000), but other explanations are plausible, either in addition or alternatively (Janson and Goldsmith 1995; Snaith and Chapman 2005, 2007). Thus, studies that unravel the constraints on group size in colobines, and in folivorous primates more generally, could also improve explanations of the folivore paradox.

Ecological models of female social relationships (e.g., van Schaik 1989) predict competitive regimes and female social structure reasonably well, but seem to be particularly weak in predicting dispersal patterns (Koenig 2002; Koenig and Borries 2009). Specifically, the models suggest that in female dispersal species contest competition and linear dominance hierarchies should be absent. However, in several such species females form linear dominance hierarchies and they may contest for food (e.g., mountain gorillas: Robbins et al. 2005; overview in Koenig et al. 2004). Hence, disclosing additional evidence for the links between feeding competition, social relationships, and female dispersal could improve the explanatory power of socio-ecological models.

The Presbytini also pose challenges for a comparative understanding of primate mating systems. The mating system of many nonhuman primates involves female defense polygyny, in which the number of adult males in bisexual groups is positively associated with the number of adult females and their overlap in receptivity (Emlen and Oring 1977; Nunn 1999; Kappeler 2000). In these species, males usually leave their natal groups upon reaching maturity and aggressively take over or immigrate into other bisexual groups. Among the Presbytini, specifically the genera *Presbytis* and *Trachypithecus*, the situation is slightly more complicated. The mating system has been described as female defense polygyny (van Schaik et al. 1992) and groups usually contain relatively few females, which should make them easy for single males to defend (van Schaik and Hörstermann 1994). However, surprisingly often groups contain multiple males. At least for some populations, groups can be described as age-graded (*sensu* Eisenberg et al. 1972) with male tolerance allowing maturing males to stay (Sterck and van Hooff 2000). For unknown reasons the percentage of "true" multi-male groups and age-graded multi-male groups as well as male residence vary across Presbytini, and the costs and benefits of multi-male stages are poorly understood (Sterck and van Hooff 2000).

Exploring these three aspects of primate social systems requires investigating individual social strategies, reproductive decisions, and reproductive success of known individuals over multiple groups and years; thus, it requires a long-term approach.

10.1.2 Research Goals and Expectations

These questions on the constraints of group size, female feeding competition and dispersal, and the social organization and residence pattern of Asian colobines led us to search for an appropriate study species and site in 1998. The few published reports that were available at that time indicated that the genus *Trachypithecus* in general and the species *T. phayrei* in particular might be a good fit. This and other Southeast Asian species seemed to display group sizes (13–27 on average) intermediate between those of *Semnopithecus* (ca. 26 on average) and *Presbytis* (ca. 8 on average; based on Bennett and Davies 1994); the *Trachypithecus* values are close to a proposed switch point between strong and weak risk of infanticide and, conversely, between weak and strong feeding competition (see details in Crockett and Janson 2000). At the same time it seemed likely that females would disperse (Sterck 1998) and occasional multi-male groups of *T. phayrei* had been reported (Bennett and Davies 1994).

Following explorations in Northeast India and mainland Southeast Asia in 1998 and 1999, we settled on the Phu Khieo Wildlife Sanctuary (PKWS), Thailand, as study area and began to habituate the first group of *Trachypithecus phayrei crepusculus* in October 2000 (note that there is variation in nomenclature (*T. phayrei* vs *T. holotephreus*; Groves (2001) *contra* Brandon-Jones et al. (2004)) and uncertainty in subspecies/species assignment (*T. phayrei crepusculus* vs *T. crepusculus*; Groves (2001) *contra* Roos (2004); i.e., here we follow the nomenclature provided in Groves (2001)).

In the following, we will summarize main results of our study focusing on social organization and male residence pattern reporting how, over a period of 8 years,[1] our views changed. As in other Asian colobines, we expected male Phayre's leaf monkeys to exhibit female defense polygyny (van Schaik et al. 1992) with occasional age-graded multi-male groups (Sterck and van Hooff 2000). Because groups contain relatively few females and become multi-male due to tolerance and not due to changes in monopolization potential, we expected at most a weak positive relationship between the number of males and the number of females. In a strictly age-graded system, one would further predict that males remain in their natal groups for some time following maturation and that they can be ranked according to age (Eisenberg et al. 1972). We expected both sexes to disperse, but changes in male membership to occur primarily via male immigration and takeover (Sterck and van Hooff 2000). Alternatively, one might predict a true multi-male pattern with male immigration and takeover as in Hanuman langurs (Borries 2000), or a pattern in which groups form and disband through female dispersal as in Thomas langurs (Sterck 1997). However, even in Thomas langurs male takeovers have been observed occasionally (Steenbeek et al. 2000).

10.2 Field Site: History and Methods

10.2.1 Study Area and Site

The study area, PKWS, is located in Northeast Thailand (16°5′-35′ N, 101°20′-55′ E, Chaiyaphum Province, elevation: 300–1,300 m asl) and comprises an area of 157,300 ha as part of the Western Isaan Forest Complex, a conservation area of 598,400 ha in total (Kumsuk et al. 1999). The area became a wildlife sanctuary (the highest protection status in Thailand) in 1979 and is effectively protected via ranger patrols and helicopter surveys, although illegal logging, collection of aloewood (*Aquilaria crassna*), and poaching still occur occasionally (Grassman et al. 2005). The vegetation has been classified primarily as hill and dry evergreen forest (75%) in addition to some other plant communities (Grassman et al. 2005). PKWS harbors a diverse animal community that includes Asian elephant, Asiatic black bear, Malayan sun bear, Asian forest bison (gaur), and four deer species (Kumsuk et al. 1999). With eight out of the nine felids found in Thailand (e.g., tiger, leopard, clouded leopard, golden cat), two canids (jackal and dhole), ten viverrids, five larger raptor species, and two python species, the predator community is plentiful (Grassman et al. 2005).

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[1] Systematic data collection ran from January 2001 to January 2009 when it was discontinued due to a lack of funding.

We selected a part of the dry evergreen forest at Huai Mai Sot Yai (16°27′ N, 101°38′ E; 600–800 m asl) as our study site for two reasons. First, the area is slightly hilly, but not too steep to follow arboreal primates. More importantly, cursory surveys indicated a relatively high diversity and density of primates. The primate community at Huai Mai Sot Yai consists of *T. phayrei* and *Hylobates lar*, three macaque species (*Macaca assamensis, M. leonina, M. mulatta*) and northern slow loris (*Nycticebus bengalensis*; Borries et al. 2002; Hassel-Finnegan et al. 2008).

The study site is accessible through a network of trails encompassing more than 100 km. Most of these trails were made by elephants and gaurs, with occasional connections cut between them. The trails were measured, marked, and GPS-mapped every 100 m. To put these data points on a map, we digitized the topographic maps of the area turning it into a digital elevation model.

10.2.2 Facilities

The presence of elephants did not allow maintaining a field camp close to the field site and facilities at the headquarters of the sanctuary could only be used for short periods of time. Hence, with support from the National Science Foundation we established a field station at the sanctuary's headquarters that consisted of a kitchen and lab, an office, and two residential buildings (four rooms each).

The disadvantage of this arrangement was a daily "commute" of 11 km (one way) on a small paved road to and from the headquarters located in the center of the sanctuary. However, the advantage of this arrangement was to have electricity (4 h a day via generator), which allowed running a freezer and other electrical gear (e.g., drying oven, mechanical food tester, computer, battery charging equipment, etc.). In addition, the size of the field station allowed the permanent presence of several assistants and students as well as smaller laboratory procedures and storage. Lastly, the location of the field station in the headquarters allowed researchers immediate contact with the sanctuary authorities, an important aspect for a smooth coordination of research activities. In addition, the headquarters has a helipad for emergency evacuation in case of accidents with elephants, gaurs, bears, or venomous snakes.

10.2.3 Data Collection

From the start, our project was designed as a long-term study with a multidisciplinary approach to primate behavioral ecology, particularly questions to group size constraints, the ecology of female social relationships, and female and male reproductive strategies. Accordingly, we collected data on primate community ecology along with data on the ecology, demography, life history, behavior, hormones, and genetics of Phayre's leaf monkeys. Our approaches and procedures rested on published descriptions (see below) and our past field experience in India and Nepal. In addition, we profited from material and descriptions kindly made available by colleagues (e.g., unpublished monitoring guide by J. Altmann, S. Altmann, and G. Hausfater).

10.2.3.1 Ecological Data

Weather data that included temperature, humidity, and rainfall were recorded via data loggers. Temperature and humidity were recorded directly in the forest via two loggers (2 h intervals; one logger as a back-up). To measure rainfall, a flow-through rain gauge was set up ca. 6 km away from the study site at a ranger station. A rain gauge initially installed at the field site itself was destroyed by elephants after only a few months. A second rain gauge at the headquarters served as backup.

To estimate the forest composition and to measure plant distribution, we used a stratified random approach to establish 33 botanical plots, each 50 × 50 m; this represented ca. 3% of the home ranges of our study groups (Struhsaker 1975). Within each plot we measured all trees of $\geq$10 cm in diameter and all climbers of $\geq$5 cm in diameter (total of 4,538 stems). Botanical work was done primarily by the staff of the sanctuary, because in Thailand only forest personnel are permitted to collect plant parts (we requested and received a special permit for botanical work).

From the botanical plots we selected a subsample of trees and climbers for phenology data collection. We included as many plant species as possible, because in the beginning we did not know exactly, which species were langur food. The sample consisted of 546 trees and climbers from 121 species. If possible, we included 5–10 mature individuals per common species. Rare species ($N < 5$ in botanical plots) were included if the leaf monkeys were known to use them. Data for different phytophases were collected once a month in the middle of the month using a point scale (from 0 to 3) and a semiquantitative index based on $\log_{10}$ (i.e., 0 for 1–9, 1 for 10–99 etc.; Janson and Chapman 1999). To circumvent problems with interobserver reliability, data were collected by two researchers.

10.2.3.2 Primate Community

To describe the primate community of the site, we conducted line transect sampling for four consecutive days each month on a 4-km transect. We discontinued the data collection after 480 km had been walked, when cumulative density analysis indicated no further improvement in data quality for the most common species (Borries et al. 2002; Hassel-Finnegan et al. 2008).

10.2.3.3 Habituation and Identification

We habituated four groups of Phayre's leaf monkeys. The area has experienced some hunting in the past, and all monkeys initially fled from observers. It took several months to reliably count and identify all individuals, and habituation to the point when observers were ignored took 7–12 months per group.

The federal laws and regulations for research in forested areas in Thailand make it very hard to receive permission for capturing wild animals. Thus, to identify individuals we relied on traditional methods based on physical characteristics (National Research Council 1981). All group members were identified via the shape of their crest, eye rings, white muzzle, and the shape of depigmented skin below the belly button. We established an identification sheet for each individual and a library of digital images of the markers. These tools facilitated learning the identity of the monkeys within 1–2 months. Importantly, changes in physical characteristics required an annual update of the ID charts.

10.2.3.4 Demography and Life History

In general, we followed groups from dawn to dusk for a minimum of 4 days per month (mean: 8.7 days). During every follow, we completed at least one full group count and identified all members. We also recorded births, immigrations, disappearances, emigrations, injuries, and nipple contact. Once a month we assessed immature individuals to demarcate landmarks in growth by comparing their sitting height or head-body length to adult group members (National Research Council 1981). Individuals were considered juvenile if they were smaller than adult females. Subadult males were as tall as adult females, but smaller than adult males. Both males and females became adult, when they had reached the height/length of adult males or females, respectively. Once adult, individuals were assessed for several more months to assure that they had ceased growing. The demographic data allowed for compilations of weaning ages, interbirth intervals, and rates of maturation and dispersal. Altogether the study included 277 group-contact months and 23,677 contact hours (Borries et al. 2011).

Behavioral Data

Individual behavioral data were collected via 20 min focal animal sampling (Martin and Bateson 2007), in which we combined instantaneous sampling at 1-min intervals with continuous recording. Behavioral data emphasized feeding and social behavior of adults and, sometimes, juveniles. The length of a focal sample was determined based on the median time an observer could follow an individual monkey without interruption and the median duration of certain behavioral states such as grooming (E. Larney unpublished data). Agonistic and sexual behavior was also collected *ad libitum*. Depending on the research questions, these data were supplemented with data on grooming bouts, allomaternal care, feeding rates, nutritional data, food physical properties (Lucas et al. 2003), and other variables.

At the group level, we used scan sampling (Martin and Bateson 2007) at 30-min intervals to collect data on mutually exclusive activities (feeding, traveling, resting, social) and on the height of individuals above the ground. We noted the behavior of all identified individuals except infants within 10 min. At the start and end of a group follow and on the hour and the half hour, we collected ranging data at the approximate geometric center of the group via a handheld GPS (UTM coordinates and error reading). We also collected group-level data on food patch depletion (focal tree samples; Snaith and Chapman 2005) and intergroup encounters.

10.2.3.5 Hormones and Genetics

We and our students collected fecal samples to investigate reproductive hormones (Lu 2009; Lu et al. 2010) and relatedness and paternity (Larney unpublished). Sample collection was noninvasive and followed standard procedures that either involved freezing (Lu et al. 2010) or a two-step ethanol-silica method (Nsubuga et al. 2004). As with botanical work, fecal sample collection required a special permit as well as CITES clearance for export.

10.2.3.6 Data Consistency

To ensure standardized data collection and interobserver reliability, we first established an ethogram for the species based on the behavioral repertoire for Hanuman langurs (Dolhinow 1978). The behavioral categories, including standard abbreviations and descriptions, were listed in a field manual that also explained all observational, sample collection, and data processing procedures and definitions. Such a manual is an essential tool in training and re-training of observers to ensure consistency in data collection over time. Consistency can be improved if training is conducted by the same individuals (in our study, ourselves and long-term rangers). In addition, we encouraged our assistants to specialize in certain tasks so that not everyone had to become an expert in all methods. Lastly, we conducted interobserver reliability tests (Martin and Bateson 2007) during training.

10.3 General Characteristics, Life History, and Social Organization

10.3.1 General Characteristics of Phayre's Leaf Monkeys

Phayre's leaf monkeys are midsized nonhuman primates. Adult individuals weigh about 6–8 kg with a moderate sexual size dimorphism, i.e., males weigh about 8 kg and females ca. 6–7 kg (Smith and Jungers 1997). Measurements, which we could take for one adult female (7.0 kg), confirmed the value for females.

Like many other Asian colobines, Phayre's leaf monkeys are primarily arboreal spending most of their time at heights between 5 and 50 m. During parts of the winter and spring (January–March), all groups come to the ground to eat soil and to drink. In October, they sometimes come to the ground to feed on bamboo shoots.

As members of the subfamily of Colobinae, Phayre's leaf monkeys are characterized by foregut fermentation (Bauchop and Martucci 1968) and with 46% of time feeding on leaves (data for adult individuals for three groups over 1 year; Borries et al. 2011) their diet fits the criterion for a folivorous primate (at least 40–45%; Leigh 1994). However, the amount of leaves is relatively small compared to other Asian colobines, which commonly have over 50% leaves in their diet (Kirkpatrick 2007). Conversely, Phayre's leaf monkeys devote a relatively high proportion of feeding time (35%) to fruits and seeds.

10.3.2 Life History

A recent compilation highlights similarities of life history traits of Phayre's leaf monkey with other wild Asian colobines (Lu et al. 2010; Borries et al. 2011). Female Phayre's leaf monkeys have their first infants at an average age of 5.3 years compared to 5.4 to 6.7 years for other Presbytini. The average duration of gestation is 205 days, in the middle of the range for other wild Asian colobines (198–212 days).

As in most other species of *Trachypithecus*, infants are born with a flamboyant natal coat (bright orange), which gradually changes to the adult gray coat over a period of 26 weeks (Borries et al. 2008; Larney and Koenig unpublished). Weaning (defined here as cessation of nipple contact) takes place at 19–21 months, and weaning age increases with group size (Borries et al. 2008). As in other colobines, Phayre's leaf monkey females nurse their infants almost until the next parturition (Borries et al. 2001, 2011). Thus, with an average of 22 months the interbirth interval following a surviving infant is only slightly longer than the mean weaning age (Borries et al. 2008). Interbirth intervals are significantly longer in larger groups. Because infant survival is independent of group size, these differences in reproductive rates may lead to differences across groups in mean female fitness.

These group size effects on reproductive rates stand in contrast to the absence of group size effects in folivorous mountain gorillas (Robbins et al. 2007) and are instead similar to those reported for frugivorous or omnivorous primates (van Noordwijk and van Schaik 1999; Altmann and Alberts 2003). In contrast to other folivores, increases in group size might have negative effects on reproduction in Phayre's leaf monkeys because much of their food comes from depletable patches (cf. Snaith and Chapman 2005, 2007). Alternatively or in addition, these group size effects may reflect co-variation of group size and habitat quality (Dunbar 1987; Harris and Chapman 2007).

10.3.3 Social Organization

In this population, Phayre's leaf monkeys formed bisexual groups averaging 19 individuals (Table 10.1). The mean sizes of our focal groups ranged from 12.1 to 25.7 individuals (range: 6–33), including means of 1.2–2.7 adult males (range: 1–5; Table 10.1). During one month the group PB had no adult male, because the single adult male was absent due to an injury. One-male and multi-male social organizations were about equally likely: in 48.4% ($N = 134$) of group-months, groups contained single adult males. The second (24.9%, $N = 69$) and third (15.9%, $N = 44$) most common constellations were two-male and three-male groups. Groups contained ca. 7 adult females on average; group means ranged from 4.3 to 10.4 (range: 3–12; Table 10.1). In most months (86.3%), the number of adult females ranged between four and ten. Groups typically contained close to 5 subadult or juvenile individuals and ca. 5.5 infants.

The size and composition of our focal groups varied considerably over the course of the study period (Table 10.1). Group size varied by a factor of 1.7 (PB) to a factor of 3.1 (PS) and female group size by a factor of 1.3 (PS) to a factor of 3.3 (PA). However, rather than a consistent direction of change, like the general increase in group size documented for muriquis (Strier and Mendes 2012), the changes in group size or female group size followed U, inverted U, J, or S shapes (results not shown). Only in group PA did total group size and the number of females increase overall during the study, although the increase was not steady. In addition to births and maturation, much of the variation was due to female dispersal (Borries et al. 2004). It took 16 months from the start of the study before the first female immigration could be documented; this apparently low rate was probably a habituation effect, given that we now know that female immigrations occurred at a rate of 2–3 per group-year.

These general characteristics of group size and female dispersal more or less matched our expectations: group size was indeed intermediate between *Semnopithecus* and *Presbytis* (cf. Kirkpatrick 2007), and, as in many other *Trachypithecus*

Table 10.1 Composition of the study groups until January 2009 (inclusively) arranged by group size

Group	Start	Adult males	Adult females	Subadults and juveniles	Infants	Group size
PS	Mar 2002	1.2 (1–2)	4.3 (3–7)	3.1 (0–7)	3.4 (1–5)	12.1 (6–19)
PA	Jan 2001	2.7 (1–4)	6.1 (3–10)	6.1 (3–9)	4.7 (1–9)	19.6 (14–27)
PO	Aug 2005	2.7 (1–5)	7.9 (7–9)	3.9 (1–6)	6.0 (3–8)	20.5 (15–26)
PB	Aug 2003	1.2 (0–3)[a]	10.4 (9–12)	5.6 (0–12)	8.6 (2–11)	25.7 (20–33)
Unweighted / weighted average		1.95 / 1.92	7.18 / 6.84	4.68 / 4.77	5.68 / 5.43	19.48 / 18.95

"Start" indicates the month of the first reliable demographic record. Mean values are given with ranges in parentheses. Results are based on 277 group-months totaling 2,405 contact days and 23,677 contact hours. For details on contact times see Borries et al. (2011)

[a] One month without an adult male; the only adult male had disappeared temporarily.

and *Presbytis* species (Sterck 1998), females regularly dispersed. However, compared to previous reports (Sterck and van Hooff 2000), the high frequency of multi-male groups (over 50%) was unexpected.

10.3.4 Female Group Size and the Number of Males

One-male groups were slightly smaller (17.57 ± 7.44 SD) than multi-male groups (20.22 ± 3.77 SD), but a mixed model ANOVA of group size per study year with "group identity" as random factor, hierarchically nested in social organization (fixed effect), showed no effect of the one-male *versus* the multi-male condition ($F = 0.19, p = 0.675$; Fig. 10.1a). Instead, "group identity" was the driving factor ($F = 136.58, p < 0.001$). The number of females in one-male groups was marginally higher (6.95 ± 2.98 SD) than the number in multi-male groups (6.73 ± 2.15 SD). Again, a mixed model ANOVA showed no effect of the one-male *versus* the multi-male condition ($F = 0.01$, $p = 0.937$), while the random factor "group identity" had a significant effect ($F = 150.93, p < 0.001$). Only for group PS did the number of females differ significantly between the one-male and the multi-male stage, with more females present when the group had multiple males (Fig. 10.1a).

The socio-ecological model (Emlen and Oring 1977) predicts that the number of males per group is positively related to the number of females. However, monthly data from 276 group-months (excluding one month with no adult male in PB) gave only a weak positive association between the number of females and the number of males (Pearson's $r = 0.117, p = 0.052$; Fig. 10.1b) that explained less than 2% of the variance. The number of males was much better predicted by a quadratic fit in the form of an inverted U-shape: it initially increased with the number of females,

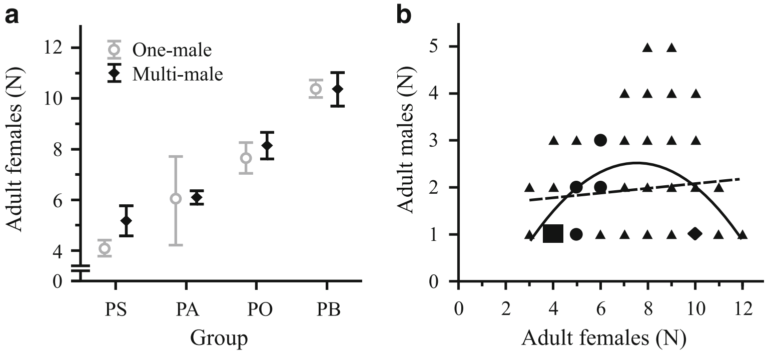

Fig. 10.1 Relationship between the number of adult females and males. (**a**) Number of adult females per group in relation to social organization (one-male *vs* multi-male) of the four focal groups. Group size increasing from left to right. Mean values and 95% confidence limits are given. (**b**) Number of males in relation to the number of females. Size and style of markers indicate the number of group-months (*triangle*: 1–10, *circle*: 11–20, diamond: 21–30, *square*: >40). Linear fit (*hatched line*): $y = 1.58 + 0.05x$; quadratic fit (*solid line*): $y = 0.41 + 0.11x + 0.01x^2$

but then decreased (similar shapes were found for fitted functions such as Lowess or Weighted Least Squares).

Overall, these results indicate that the number of males was not strongly affected by the monopolization potential of females, contrary to the socio-ecological model (Emlen and Oring 1977) and to results from Nunn's (1999) comparative analysis of data from many primate species. Instead the results were similar to other *Trachypithecus* species (Sterck and van Hooff 2000), in which multi-male groups are primarily age-graded.

10.4 Male Residence Pattern and Group Dynamics: Benefits of a Long-Term Approach

While data on group composition can answer questions on social organization and interrelationships between the number of males and females, they cannot answer questions about stability and age-gradedness of multi-male constellations. How do groups form and how are multi-male groups (or one-male groups) maintained? Do males immigrate and/or take over groups? Do they form new groups? Are males tolerated beyond maturation? Particularly questions that relate to rare events as well as to stability and maturation can only be answered with long-term data. In the following, we will therefore describe male residence patterns and group dynamics in our study population.

10.4.1 Male Residence Pattern: The First 5 Years

We started habituating the first study group (PA) in October 2000. PA's home range (bold outline; Fig. 10.2) was surrounded by those of five other bisexual groups (gray outline; Fig. 10.2). At least one of these groups (to the northeast) was a multi-male group, although its exact composition was unknown. Also, in the southeast of PA we occasionally encountered adult or nonadult males, who might have belonged to an all-male band. As of January 2001, PA itself had seven adult females with offspring. It also contained one adult and two subadult males – one bigger, one smaller – and thus had the potential to turn into an age-graded group. However, we did not know whether the oldest male was the father of the younger males and whether the males were natal. In 2002, the all-male band in the southeast of PA became a bisexual group (called R), but it was not clear, how this group had formed. Also, the group to the northeast of PA seemed to have fissioned into a small easily recognizable group with one adult male (group L) and a second group, farther to the northeast, with several males and females. During this year, male membership in PA remained stable and we habituated the second study group, PS. In the following 3 years (2003–2005) we habituated two more groups, PB and PO.

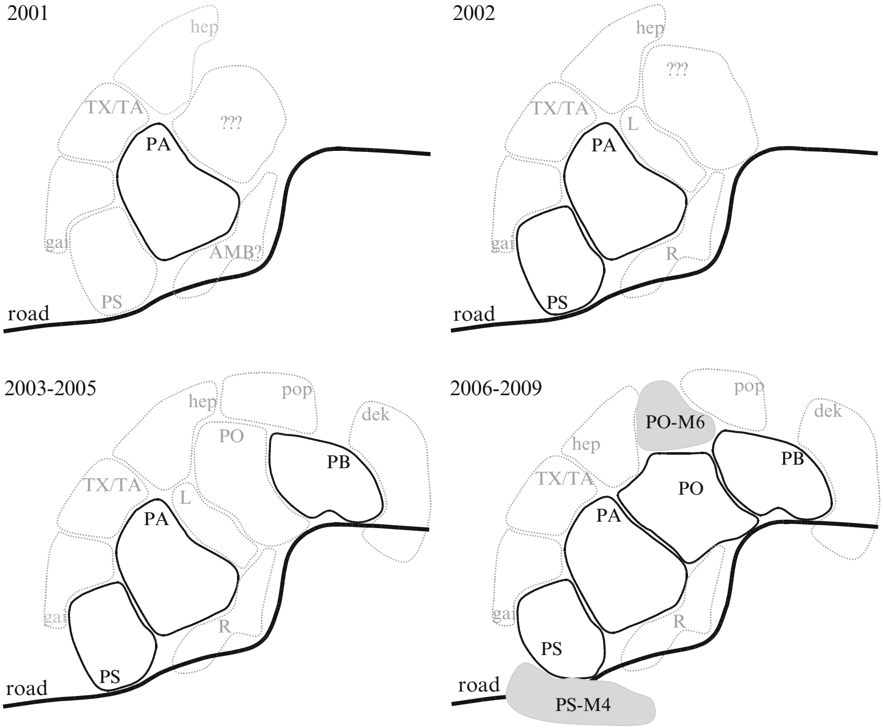

Fig. 10.2 Approximate location of home ranges of the study groups (*bold outline*) and their neighbors (*gray outline*) during the course of the study. Minor shifts of home ranges and their generally small overlap are not shown for simplicity. *Gray* areas indicate two new groups formed in 2008 by males from PO and PS (details see text)

In our four focal groups, male membership remained rather stable over the first 5 years of study. Four natal juvenile males (two in PA, two in PB) and one adult male from PA, who had matured in that group, disappeared (Table 10.2). In addition, one subadult natal male in group PA was twice temporarily absent. The absences of the subadult male were triggered by fights among the males. In the end, however, he returned to his natal group and, when adult, became the alpha male.

Thus, over the first 5 years of our study (133 group-months) not much happened with regard to male dispersal. We neither witnessed male takeover nor male immigration except as a return of a natal male. Because we had regularly witnessed female immigrations, this absence of male immigrations was presumably not caused by a lack of habituation. The question of age-gradedness was hard to answer, because only two males (one natal and one potentially natal) had matured and stayed. However, their continued residence was not a result of male tolerance as suggested for an age-graded structure. Maturing males had frequent, occasionally severe fights (Fig. 10.3) with each other or with older males (one older male lost an

Table 10.2 Disappearances and dispersal of males between January 2001 and January 2009

Years	Event	Age classes		
		Juvenile	Subadult	Adult
2001–2005	Disappearance	4		1
(133 group-months)	Temporary absence		2	
2006–2009	Disappearance	5	1	2
(144 group-months)	Temporary absence		2	4
	Emigration[a]	2	1	5
	Group fusion[b]			1

For each male all events were included, i.e., some males contributed more than once to the dataset. Emigration indicates that males had been relocated after they had left their group. Temporary absence indicates that males had been seen outside their group, but that they returned after a mean absence of 34 days (range: 2–90 days)

[a] All eight events refer to the formation of two new groups (see text for details)

[b] The small nonstudy group L (1 adult male, 1 adult female, 1 juvenile female) fused with group PO, from which it had likely fissioned several years earlier

Fig. 10.3 A subadult male from PS after a severe fight with the only adult male in the group, in which his right shoulder and neck were severely wounded. When adult, he challenged the male again and became the alpha male. Several months later the former alpha male left with three immature males and formed a new group (cf. Fig. 10.2). Photo © Andreas Koenig

eye). The timing of male rank ascendance always coincided with males reaching adulthood and was likely related to a power shift between maturing and aging males. The presence of peers seemed not to have influenced rank ascendance. If anything, fights among maturing males might have prevented or delayed ascendance. In general, contrary to our expectations and instead similar to Ugandan red colobus monkeys (*Piliocolobus tephrosceles*; Struhsaker 2010), males seemed to be philopatric. As in red colobus monkey, males occasionally emigrated from their natal groups, sometimes only temporarily, but unlike in red colobus we had not seen immigrations and group dissolution.

10.4.2 Male Residence Pattern: The Next 3 Years

In the following years (2006 to January 2009; 144 group-months), most male membership changes fitted the pattern described earlier: several juvenile, subadult, and adult males disappeared or were temporarily absent (Table 10.2). Temporary absences often occurred in connection with fights among group males. In addition, group L (1 adult male, 1 adult female, 1 juvenile female), which was sandwiched between groups PA and PO, fused with PO and its male became a member of PO (Fig. 10.2). While this event technically represented an "immigration" by an adult male, it resulted from a group fusion, during which the male returned to his original group. Given our previous observation we presume that the groups split in 2002 (or the male left and formed a new group; see below) and 4 years later the groups fused again. It seems noteworthy that none of the infants born in the small group L survived.

Events observed in the following years would change our perception of the male residence pattern further. In 2007, four of the five adult males of PO left (Table 10.2). Again this happened after severe fights. In contrast to other cases, in which males disappeared from the area, we encountered these four males occasionally at the periphery of the home range of PO. In 2008, the males had been joined by females, forming a new group north of PO (called PO-M6; Fig. 10.2). Because we did not follow this group regularly (all females were unknown to us and unhabituated), it is not entirely clear whether and how much area PO or other groups "lost" in the process of group formation. Importantly, some of the females in this new group had relatively old infants with adult coats, indicating that these infants had been born prior to group formation. Thus, females with infants must have joined the males. Some months later, an adult male (M4), plus a subadult and two juvenile males left group PS and moved south, leaving PS with a single natal adult male (Fig. 10.2; Table 10.2). These four males were joined by females with older infants, forming a new group (PS–M4). As in the case of PO, none of the females was from the males' former group.

These events, which happened after more than 7 years of study, showed clearly that some males manage to form new groups, while others emigrate but eventually return to their natal group. Thus, males have more reproductive options than breeding in their natal group. Interestingly, both mass emigrations of males seemed unrelated to male rank ascendance, but took place after the mating season and the new groups were established before the beginning of the next mating season. Since most females in their old group were pregnant and would not conceive in the next mating season, emigration and group formation might have been the result of poor reproductive prospects. Why infanticide did not occur in the context of group formation (Sterck et al. 2005) remains an open question.

Importantly, based on our initial observations one would have concluded that the adult males within a group were more or less closely related to each other (depending on group size, reproductive skew, and extra-group paternity; Lukas et al. 2005). However, during group formation, males were joined by females with infants, indicating that males co-residing in these groups may not be related at all. How extensively relatedness among group males varies is a question we hope to answer with the analysis of DNA samples. In any case, the residence pattern emerging from these observations also helped us to better understand the variable social organization of groups.

10.4.3 Group Dynamics and Group Life Cycle

One aspect of social organization, i.e., the number of adult males in our study groups, varied considerably through time (Fig. 10.4). Some of the groups had extended periods with only a single adult male, while others contained multiple males for extended periods. In all groups, this variation arose solely through male emigration or disappearance and maturation.

In PS, one adult male was present most of the time until one of the natal males matured in 2007. This natal male eventually became the alpha male, and later the only male, when in 2008 the former alpha male and 3 younger males left to form a new group (see above). Thus, the group switched from one-male to multi-male, then back to one-male. In PA, the number of adult males varied between one and four; it gradually increased during the study, and the group was multi-male 98% of the time. Changes in the number of adult males occurred through occasional

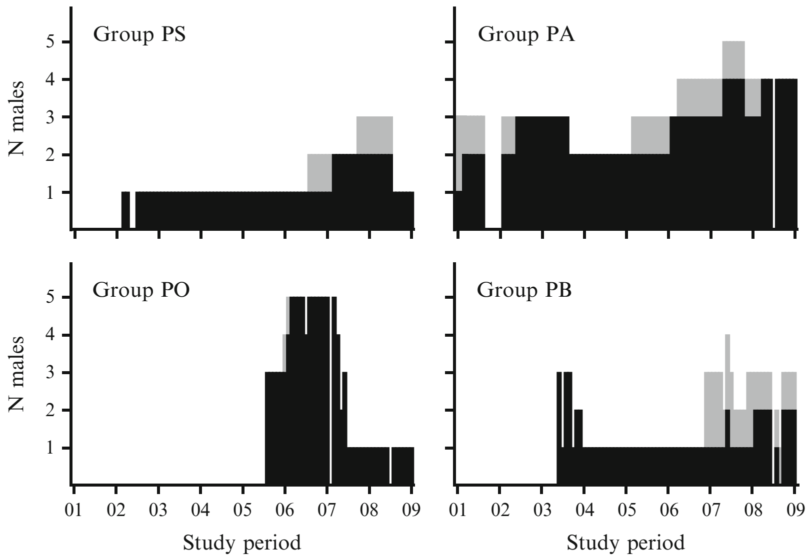

Fig. 10.4 Number of adult and subadult males of the four study groups over the study period 2001–2009. With one exception (see text) changes did not occur through immigrations but through maturation of natal males and emigrations/disappearances. *Black bars*: adult males; *gray bars*: subadult males; no column = no data available (except for group PB in September 2008 when the only adult male disappeared temporarily)

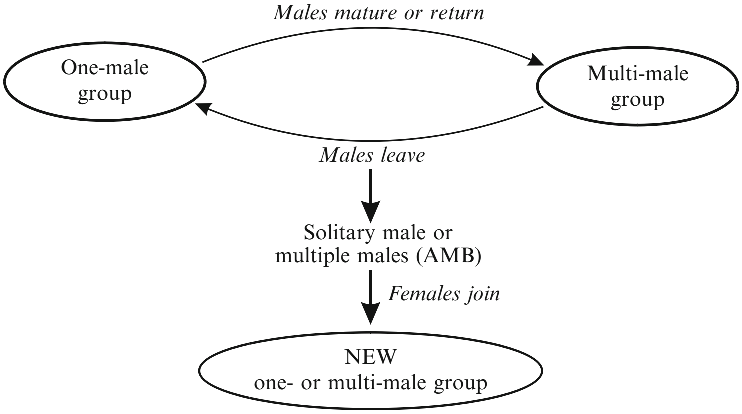

Fig. 10.5 Life cycle of Phayre's leaf monkey groups

disappearances and through maturation of natal males. When our observation of PO started, the group had multiple males. Four of these males left and formed a new group, and PO became one-male. Lastly, PB was initially a multi-male group. However, after adult males disappeared, it was one-male until natal males matured and it turned multi-male. Unfortunately, in this group the adult male died (likely due to predation by a clouded leopard or a leopard) right at the time when the first natal males matured. Thus, we do not know whether one of the maturing males would have overthrown the old male to become the new alpha male.

In essence, it seems that groups follow a rather simple "life cycle" (Fig. 10.5). Groups may change between a one-male and a multi-male stage either when males mature and breed in their natal group or when maturing natal males emigrate, either permanently or temporarily. In the latter process a group may or may not become one-male, depending on the number of males leaving a multi-male group. Dispersing males may either form new one-male or new multi-male groups. In contrast to other Asian colobines (Sterck and van Hooff 2000), we have never witnessed a takeover by a strange male or immigrations of males that were not natal (or likely natal). Similarly, in contrast to other long-term studies we have not seen groups dissolve through female dispersal (Sterck 1997). While we cannot be entirely sure that takeover, immigrations, or group dissolution will never happen, after 277 group-months we can be reasonably sure that they will be rare.

The emerging picture of the social organization of Phayre's leaf monkeys and the "life cycle" of a group is reminiscent of group dynamics in mountain gorillas (Watts 2000; Robbins 2007). Mountain gorillas are similarly characterized by natal and secondary dispersal of females and conditional male dispersal. While some groups have been found to be age-graded, in other cases natal males may become dominant over (presumed) fathers and brothers. However, unlike the nonterritorial female defense polygyny system of mountain gorillas, male Phayre's leaf monkeys actively defend areas with little overlap between groups, i.e., they defend territories (Gibson and Koenig unpublished). This pattern is more consistent with the resource defense polygyny system of chimpanzees (Williams et al. 2004). In the end, male reproductive strategies in Phayre's leaf monkeys might possibly best be described as a mixture of gorilla and chimpanzee strategies.

10.5 Conclusions

The ways in which our views have changed through time emphasize the tentative nature of short-term studies and the importance of long-term studies for a full understanding of the behavioral ecology of long-lived species like primates.

Overall, group size and composition in Phayre's leaf monkeys were similar to other species of the genus *Trachypithecus* (Sterck and van Hooff 2000). However, only our long-term results revealed a social organization differing from other Asian colobines in several aspects: unlike the "true" multi-male groups described for Hanuman langurs, variation in the number of males was not affected by the number of females and one-male groups did not turn into multi-male groups *via* immigrations (Borries 2000). But Phayre's leaf monkeys also did not resemble the one-male structure with occasional age-graded groups of Thomas langurs, in which the multi-male phase may be a transitional stage after sons have matured and before a group dissolves or is taken over (Steenbeek et al. 2000). In Phayre's leaf monkeys, males may breed in their natal groups or they may disperse and form new groups. Even adult (breeding) males may disperse to form new groups. Multi-male groups were a regular part of a dynamic system that changed back and forth between a multi-male and a one-male stage with the occasional formation of new groups. Unlike species such as Thomas langurs (Steenbeek et al. 2000), however, multi-male stages were not age-graded (Eisenberg et al. 1972). Rather, dominance rank in relation to age followed an inverted U-shape, indicating that dominance rank depends on male resource holding potential as in baboons (Packer 1979).

Grueter and van Schaik (2010) recently proposed three main categories of social organization for Presbytini: (1) one-male groups with male immigrations (with occasional age-graded multi-male groups; most *Presbytis* spp., *Trachypithecus* spp.), (2) "true" multi-male groups with male immigrations (with a variable proportion of one-male groups; *Semnopithecus* spp.), and (3) multi-level societies (most snub-nosed monkeys). This scheme must now be expanded to include a fourth form of social organization: one- and multi-male groups with male philopatry and new group formation (*T. phayrei crepusculus*). Given the fragmentary and short-term nature of data for most Asian colobines, it is possible that the social organization described here is not unique. For example, multi-male groups have consistently been found in red-shanked Douc langurs (Lippold and Vu 2008). Given that male dispersal might be conditional, depending on the costs of dispersal and breeding opportunities in multi-male groups (Watts 2000), the possibility exists that these groups resemble the pattern of Phayre's leaf monkeys. Only increased efforts to conduct more long-term studies with Asian colobines could offer an answer.

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Chapter 11
White-Handed Gibbons of Khao Yai: Social Flexibility, Complex Reproductive Strategies, and a Slow Life History

Ulrich H. Reichard, Manoch Ganpanakngan, and Claudia Barelli

Abstract Long-term field research on wild animals is essential for understanding life history and social systems of long-lived organisms like primates. Gibbons (family Hylobatidae) live surprisingly slow lives, given their relatively small body mass. Following an approximately 7-year-long juvenile period, one of the longest among all primates, Khao Yai white-handed gibbon females begin reproducing at an average age of 10.5 ± 1.2 years. This is much later than in monkeys of at least the same body mass and, remarkably, at about the same age as in mountain gorillas. Our long-term research also revealed remarkable social flexibility analogous to that seen in other apes. At Khao Yai, white-handed gibbons form pairs or small two-male/one-female reproductive units, although individuals may temporarily also live in single-male/multi-female groups, and here we report a novel, semi-solitary life stage of two older males for the first time. Mating patterns also turned out to be flexible, with males and females mating polygamously, including extra-pair copulations and regular polyandrous mating of females living in multi-male groups. We have also found that in accordance with this variability in male–female socio-sexual bonds, female gibbons at Khao Yai show cyclical sexual swellings that advertise the probability of ovulation without allowing males to exactly pinpoint the day of ovulation. After decades of research, we have come to recognize more clearly the importance of the gibbon community and feel confident that we understand the basic social and mating systems of the Khao Yai

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Khao Yai National Park, Bangkok, Thailand

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white-handed gibbon population, but we also continue to discover new details of the evolutionary forces that shape gibbons' complex social life.

11.1 Introduction

A unifying theme of early and current primate field studies is their "individual-centric" approach, which means that particular individuals and their lives become the focus of a researcher's attention and systematic data collections (e.g., Goodall 1986). Working with well-known individuals is a unique strength of long-term field studies and one that continuously draws students, volunteers, and periodically the media to our field. Hearing of the adventures of primate characters and following the fate of individuals through time often seems just as fascinating as vividly telling their stories and presenting data from the field (e.g., Perry and Manson 2008), which now sometimes even happens in "near-real-time" in the new format of primate field blogs. Beyond scientific curiosity and theoretically well-grounded questions, many primatologists, students, and professionals alike, feed off direct contact with well known, habituated individuals as their source of energy to write grant proposals, and involvement in the lives of their study subjects can bring researchers back to a field site year after year. Dedication and developing relationships with primate subjects and human communities living closest to them are emotional and intellectual reservoirs field workers use until a long-term study emerges, which is a necessary step to document life-history strategies of long-lived mammals.

11.2 History of the Khao Yai White-Handed Gibbon Study Site

Research on white-handed gibbons (*Hylobates lar*) of Khao Yai National Park (KY), Thailand began in 1977. Like other primate field projects, ours began small, but it gradually grew to become the longest ongoing gibbon study, and we have accumulated demography data on 14 habituated groups (Fig. 11.1). Like others, we believe that longitudinal research, although slow and difficult to maintain, is essential as it is often the only way to generate life history data, to decode strategies underlying complex behaviors in wild populations, like those that involve reciprocity, cooperation, conflict resolution, and to understand primate social dynamics more broadly (Wells 1991; Boesch and Boesch-Achermann 2000; Strier et al. 2002; Watts 2002). The complex social dynamics of KY white-handed gibbons would have been difficult to detect in a short-term study (see below), even if it covered several years. Lack of long-term documentation of gibbon demography, life-history strategies, and social dynamics until recently is the reason why the subtleties and complexity of their social organization remained unnoticed for a long time.

Over the years, many individuals have contributed to the ongoing demographic data collection (for a complete list, see Brockelman et al. 1998). Key people at the

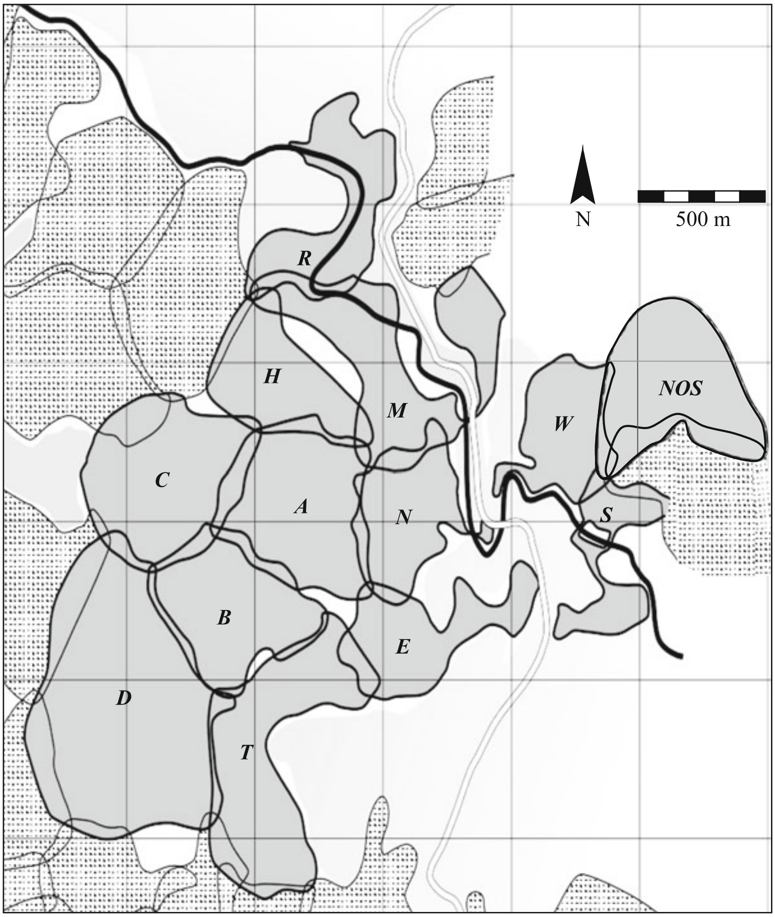

Fig. 11.1 Mo Singto study area with home range outlines of 13 habituated study groups (A-NOS). The home range of a fourteenth habituated study group is not shown on the map. *Thick solid line* = Lam Takhong river; *open line* = road; *fading areas* = tropical grasslands and low canopy regenerating forest

beginning were Treesucon (1984), Raemaekers and Raemaekers (1985) and W.Y. Brockelman, of whom only Brockelman continues to do research at the site. By the end of 1989, Reichard (1991) became involved, and in the mid 1990s, C. Barelli joined the research effort; since then, they have coordinated systematic recording of demography data. Quantitative data presented here were collected by C. Barelli and U.H. Reichard between 1989 and 2010.

Today, KY is a patch of 2,168 km^2 (Smitinand 1977) of forest surrounded by agricultural land on all sides except one. The park was established in 1962 and, in 2005, was included in Thailand's 6,199 km^2 large Dong Phayayen – Khao Yai Forest Complex (DPKY) as part of a new World Heritage site (UNESCO 2005) because it is a biodiversity hotspot in Asia (Lynam et al. 2006).

Located at latitudes 14°05′–14°15′ N and longitudes 101°05′–101°50′ E, KY is part of the Phanom Dongrak mountain range that runs north to south from the Thai–Laotian border before bending eastwards and eventually forming the Thai–Cambodian border in the region of Pang Sida and Ta Phraya National Parks. Elevation at KY ranges from ~250 to 1,351 m a.s.l., and the terrain is rugged. The climate is seasonally wet following the Asian southwest monsoon cycle (Singhrattna et al. 2005), with annual precipitation averaging 2,477 mm/year (range 2,038–3,111) (Tangtam 1992; Boonpragob et al. 1998; Kitamura et al. 2004, 2005, 2008; Bartlett 2009a; Gale et al. 2009). The wet months are March–October.

KY can be broadly classified as a tropical seasonal forest (Smitinand 1989; Kitamura et al. 2005, 2008) or moist evergreen forest (Round and Gale 2008), because this vegetation type occupies 64% of the park's land area found between 400 and 1,000 m elevation. Several gibbon study groups have established home ranges that partially include old secondary growth (i.e., groups A, H, and D). The gibbons have continuously and increasingly used these areas for travel and foraging since observations began. The park also includes areas of grassland where villagers living around the present day headquarters had cleared fields prior to the establishment of KY as a National Park; these are now maintained by annual burning and mowing.

11.2.1 Threats to Khao Yai Wildlife

Field sites vary greatly in the degree and form of threats they receive from humans. Due to its large size, systematic law enforcement is a constant challenge to park management at KY (Albers and Grinspoon 1997). Small-scale encroachment and hunting occur, although gibbons are not specifically targeted by poachers and, compared to other protected areas in Thailand, these pressures are low at KY (Lynam et al. 2006; Brodie et al. 2009). In our experience, the biggest threat to wildlife comes from selective, non-timber harvesting of *Mai hom* trees, *Aquilaria crassna* (Family Thymelaeaceae), by villagers and organized poacher groups. *Mai hom* trees produce agarwood, also known as aloewood or eaglewood, used by the perfume industry. The tree family occurs naturally in primary evergreen and semi-evergreen forests from ~600 to 1,400 m a.s.l. in many Southeast Asian countries and the commercially valuable resin is traditionally harvested by local people (Jensen and Meilby 2010).

At KY entire trees are sometimes felled, but more commonly mature trees are injured repeatedly to stimulate resin production (Zhang et al. 2008). Several months after a tree has been damaged, poachers return to chisel resin-soaked woodchips off until a tree eventually falls (Zhang et al. 2008). Large-scale harvest of *Mai hom* is obviously destructive because it involves bringing heavy machinery into the forest to fell and transport stems. But also small-scale poaching, i.e., poachers targeting specific trees and removing large quantities of woodchips, negatively affects wildlife because poachers stay in the forest for more days than they can carry food, and when their provisions are exhausted they hunt for food. Poachers often carry firearms, which makes encounters with them dangerous to park rangers, researchers, and our Thai field assistants alike. Poaching of *Aquilaria* trees also directly, although marginally affects gibbons, who feed on the tiny sprout of *Aquillaria* seeds during the trees' short fruiting period after biting off the thick husk with their long, sharp canines. Selective harvest of agarwood is not unique to KY; it also occurs at other protected sites in Thailand (Grassman et al. 2005). The market value of agarwood varies according to quality, and agarwood from KY consistently yields high market prices, which makes effective control of *Mai hom* harvest and trade difficult.

11.3 Highlights of Long-Term Gibbon Research

Identifying results and benefits of long-term research on KY white-handed gibbons is straightforward and well documented through numerous publications that span a wide variety of topics ranging from vocal communication (Raemaekers et al. 1984; Raemaekers and Raemaekers 1985) to ecology (Bartlett 2009a, b; Brockelman 2009), social behavior (Reichard 1995, 1998, 2003; Reichard and Sommer 1997; Brockelman et al. 1998; Sommer and Reichard 2000; Barelli et al. 2008a), reproduction (Barelli et al. 2007, 2008b; Barelli and Heistermann 2009), life history (Reichard and Barelli 2008), and cognition (Asensio et al. 2011).

In the following, we highlight advances in three areas of research on white-handed gibbons with which we have been particularly involved: (1) social organization, (2) reproductive strategies, and (3) life histories. Research on all of these topics substantially advances our knowledge about gibbons and helps shift understanding of gibbon social organization from a simplistic focus on monogamy to a more complex community model.

11.3.1 Flexible Social Organization

Our long-term research revealed a formerly unrecognized extent of social flexibility in white-handed gibbons. Although anecdotal reports of gibbon groups with more than one adult of one sex existed for some time (summarized in Fuentes (2000) and Reichard (2003)), systematic data allowing quantification of the frequency of social units not consisting of pairs became first available at KY (Barelli et al. 2007, 2008b; Reichard and Barelli 2008; Reichard 2009).

An important insight from our long-term observations is that white-handed gibbons are not *per se* committed to pair-living or other forms of social organization but instead respond in flexible ways to opportunities and actively pursue or passively accept changes in their social status. In the sample of 12 groups, 19 adult females and 22 adult males were residents at some point in time. Irrespective of the duration of these individuals' group membership, 42% of females and 68% of males experienced pair-living and at least one other type of group structure. Some individuals lived through multiple changes from pair-living to multi-male/single-female stages and back. For females who experienced non-pair-living periods, these times amounted to roughly 50% of the 12-year census period (range 33–100%); the corresponding value for males was ca. 60% (range 9–100%). These data illustrate that a wide spectrum from exclusive pair-living to exclusive multi-male/single-female grouping and various stages in between exist at KY and that non-pair-living is not a transitional stage, but for many adults represents a substantial portion of their prime reproductive years.

In summary, our long-term data indicate that, although a majority of gibbon groups are pair-living, breeding groups with more than two adults (excluding groups with adult offspring), particularly adult males, are no exception (Reichard 2009). In the sample of 12 well-known groups censused annually over 12 years (1999–2010, $N = 146$ units), we found an average of 25% of groups to be multi-male/single-female (Table 11.1). We believe these data are representative for the population as a whole because the values are similar to an earlier, larger census that included non-habituated groups (Reichard 2009). Importantly, some multi-male groups were always present, and in some years made up 33% or more of groups (Table 11.1). Based on long-term demographic records (Reichard 2009), most multi-male groups consisted of two adult males living with an unrelated female, i.e., a female neither one of the males had grown up with. Two groups were each composed of three adult males and one adult female and persisted for about 2 and 4 years, respectively. Group structures besides pair-living and multi-male/single-female units such as multi-female/multi-male, and multi-female/single-male have also been observed (Reichard 2009), but they are rare and, to our knowledge, have not resulted in stable breeding units.

Nevertheless, the occurrence of three multi-female/single-male groups is interesting as it illustrates the context-dependent social flexibility in this population. We twice discovered multi-female/single-male groups in which each of two females carried a nursing infant. Unfortunately in the first case, we did not know the group's social history and thus could not exclude the possibility that a daughter had conceived with the group's adult male, who had very likely replaced the female's presumed father. About 2 years and 4 months after the group had been discovered, one of the females disappeared with her offspring. In 2010, we witnessed a second group with two dependent infants. This time, we knew the social history of individuals and could confirm that a daughter gave birth a year after her mother. This was probably not the result of an incestuous mating, because the current male immigrated in 2007 and thus was unlikely to be the father of the female who had given birth recently. However, only a genetic study could confirm the kin relationships in this group. The third multi-female/single-male group formed after a young adult male and an adolescent female joined a young, unrelated adult female. The trio lived peacefully together for several years until the time of the younger female's sexual maturity, when the older female became increasingly aggressive. The younger female left before sexual behavior with the male was

Table 11.1 Group structure variation in Khao Yai white-handed gibbons, Thailand ($N = 146$ units)

		Census year[a]												Mean ± SD
		1999	2000	2001	2002	2003	2004	2005	2006	2007	2008	2009	2010	
P	(%)	83.3	75.0	83.3	75.0	70.0	63.6	66.7	66.7	75.0	75.0	71.4	53.3	71.2 ± 8.4
MM	(%)	8.3	16.7	16.7	25.0	30.0	36.4	33.3	33.3	25.0	25.0	21.4	33.3	25.3 ± 8.5
MF	(%)	8.3	8.3	0	0	0	0	0	0	0	0	0	0	1.4 ± 3.2
SS	(%)	0	0	0	0	0	0	0	0	0	0	7.1	13.3	2.1 ± 4.2
Total units (N)		12	12	12	12	10	11	12	12	12	12	14	15	

[a] Data collection period October–December

P Pairs, *MM* Multi-male/single-female groups, *MF* Multi-female/single-male groups, *SS* Semi-solitary individuals spending time alone or associated with an established group witnessed. Thus, so far we can only confirm pairs and multi-male/single-female groups as reproductive units in the KY population.

Our knowledge of the complexity of social flexibility still continues to grow. Most recently, for example, we began to recognize yet another formerly unknown status of individuals. The surprising observation is that two males sometimes associate with a group and at other times spend long periods by themselves; we have termed this "semi-solitariness". The situation is radically different from "floating" commonly used to describe a period when an unmated individual seeks a mate following natal dispersal. In contrast, the two semi-solitary males are older and come from established multi-male groups. Whether they are searching for mates is unclear. For example, Frodo is a nearly 30 year-old male who was thought to have left his multi-male group permanently in 2007, after he was absent from the group for several months. In 2008, however, he re-appeared and occasionally traveled again with his former group. At first, we speculated that he was perhaps visiting while transitioning into another group; a phenomenon we have repeatedly witnessed with young adult males during the process of natal dispersal. Over the past 2 years, however, we realized that he sometimes foraged alone in the familiar home range. His periods alone lasted from a few hours to several days. He did not attempt to immigrate into or even contact a group other than his previous group. Interestingly, he could re-join this social group peacefully and was tolerated without signs of agonism by the resident male and female. At present, Frodo lives partly with a group and partly alone and thus is semi-solitary.

The second case of semi-solitariness concerns Cassius II, who is also at least 30 years old. In early 2010, his putative son secondarily dispersed into a neighboring group and shortly thereafter Cassius II also appeared in this group. Unlike Frodo, he either spends time with his former group or the neighboring group or is by himself. He commutes between the two groups primarily during intergroup encounters and presently shows a preference for staying in the overlap area between the two adjacent home ranges. From our observations, it seems that he travels temporarily with whichever group is in the overlap area and he rarely follows either group deeper into its home range. Like Frodo, his integration into both groups seems unproblematic, with his arrival often preceded by soft hoots and loud vocalizations, but without aggression. However, both of these semi-solitary males seem subordinate to the resident males in the groups they join because they do not call during duets and also otherwise behave like secondary males in multi-male groups (Barelli et al. 2008b).

Overall, semi-solitariness seems to be rare, although we believe previous cases might have passed unnoticed because we never expected individuals of the 12-year census period to live alone almost secretively, and our data collection has always focused on individuals in identifiable groups. In the past, phases of semi-solitariness, if they occurred, were categorized as "transitional" and thus did not make it into publication, even when we were not sure about the whereabouts of "transient individuals" until they reappeared in other groups. The reasons for semi-solitariness are unclear. Perhaps it is an alternative strategy to the subordinate, secondary status in multi-male groups, because both semi-solitary males are affiliated with multi-male/

single-female groups. The presence of mature sons in the neighborhood may also importantly influence flexible group membership in this population, but further speculation must await knowledge of kin relations.

The recent observations highlight the great importance of time depth in understanding social dynamics and evolutionary forces of male–male competition and female mate choice that shape reproductive strategies in primates, perhaps particularly in apes, who express an impressive range of behavioral flexibility (van Schaik et al. 2004). Interpretations of group dynamics would have been very different had our study ceased after 5 or 10 years. We illustrate this point with an example of known transitions in and out of study group “A” (Fig. 11.2), although the argument applies to the entire study population. At each 5-year interval, the group composition of several groups involved would have looked different and consequently would have been interpreted differently with regard to the social and mating system of the population (Table 11.2).

Finally, we can ask why this flexibility (particularly in forming small multi-male units) was not recognized in earlier studies of wild gibbons. Perhaps when social histories of individuals were not known well, all too often additional adult males were considered adult sons of a breeding pair. At KY, however, longitudinal records of many groups allowed us to detect the presence of multi-male/single-female groups.

11.3.2 Female Reproductive Strategies

Our understanding of reproductive strategies of white-handed gibbon females has undergone dramatic changes during the past two decades. Although they were initially thought to be passive and monogamous recipients of males’ socio-sexual strategies, it is now clear that gibbon females actively pursue their own reproductive interests, just like other mammalian females who are pair-living or form small polyandrous groups (Griffith et al. 2002; Wolff and Macdonald 2004; Munshi-South 2007). Following a plethora of molecular studies of female reproductive strategies in pair-living birds, the classic concept of female sexual monogamy has been shattered in most pair-living species. Recent molecular genetics and endocrinology studies have changed the perception of female reproductive interests, to which white-handed gibbon females are no exception.

Primate females may generally gain from multiple mating. Polyandrous mating during fertile periods might increase the probability of conception (van Noordwijk and van Schaik 2000) or of having their offspring sired by males who produce the most competitive sperm (Small 1989; Dixson 1998). Copulating with many males may also function to confuse paternity, which is advantageous in species with a high risk of infanticide (Hrdy 1979; Nunn 1999; van Schaik et al. 2000). Moreover, if a female preferentially copulates with her social partner compared to other males, as we found for KY gibbons, she might additionally benefit from her mate’s raised paternity probability because her mate will be the most likely protector should her

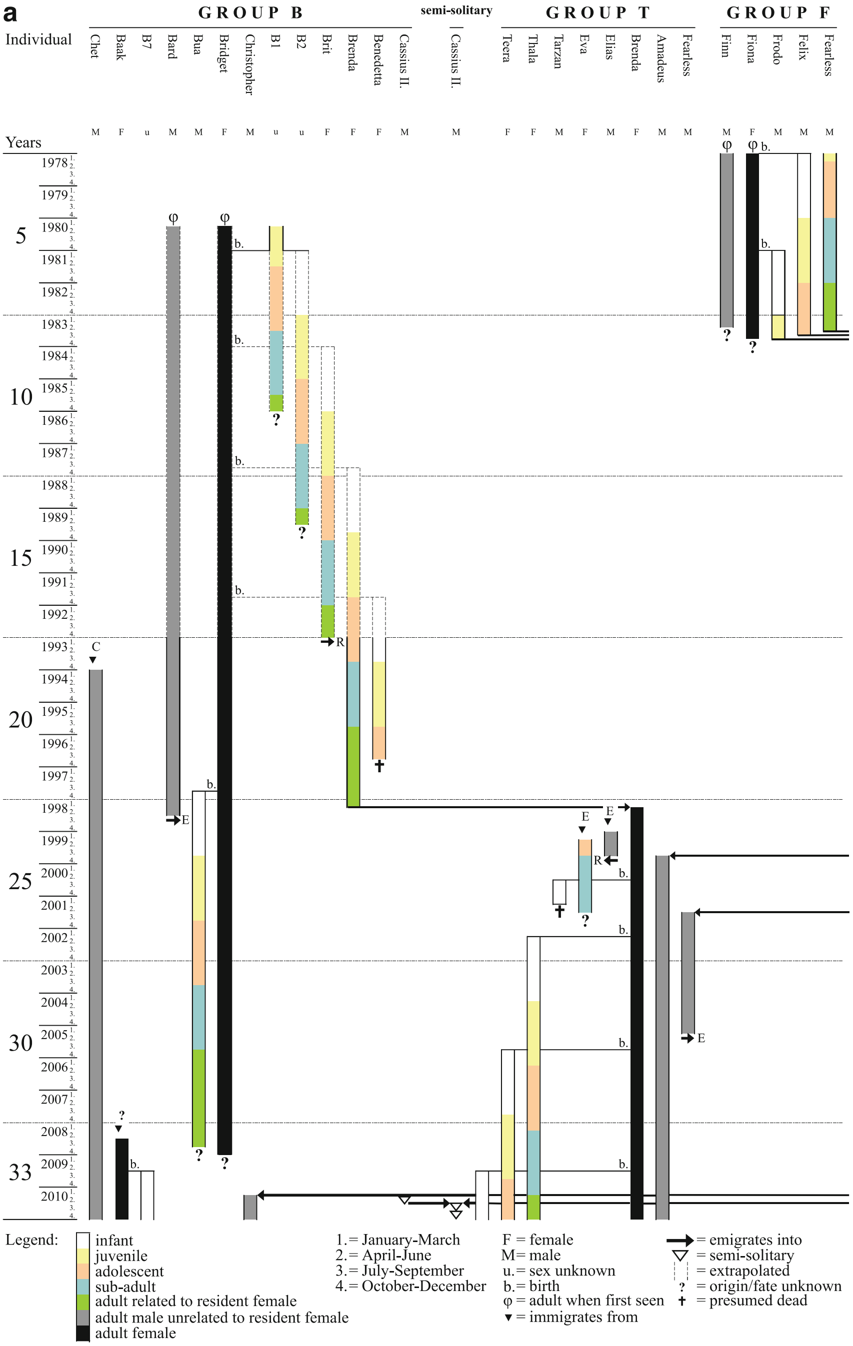

Fig. 11.2 (Continued)

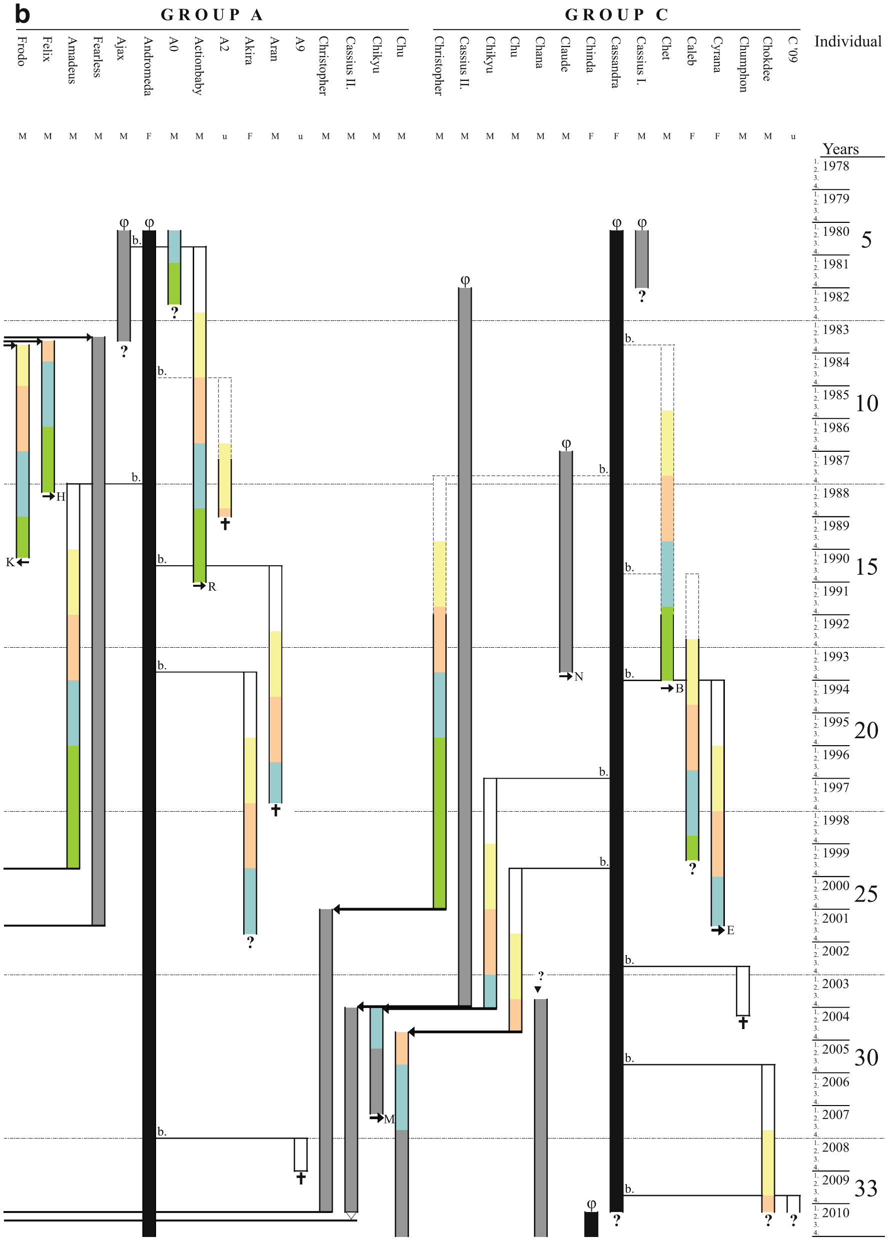

Fig. 11.2 Social histories of five white-handed gibbon groups, Khao Yai, Thailand (1978–2010)

Table 11.2 Social organization in five neighboring white-handed gibbon groups in 5-year intervals (1978–2010)

Study period	Years[a]	Group composition					Social organization		Event
		A	B	C	F	T	PL (%)	MM (%)	
1978–1982	5	PL	PL	PL	PL		100	0	Male change (group C)
1983–1987	10	MM	PL	MM	dis.		33	67	Male change (group A)
1988–1992	15	PL	PL	MM	dis.		67	33	
1993–1997	20	PL	MM	PL	dis.		67	33	
1998–2002	25	PL	PL	PL	dis.	MM	75	25	
2003–2007	30	MM	PL	PL	dis.	PL	75	25	Male change (group C)
2008–2010	33	PL/MM[b]	MM	PL	dis.	PL	50	50	Female change (groups B & C)

[a] Cumulative

[b] Occasionally joined by a semi-solitary male

PL Pair-living, *MM* Multi-male/single-female, *dis.* Dissolved

next infant be attacked by other males (van Schaik et al. 1999, 2004; Palombit et al. 2000; Buchan et al. 2003; Moscovice et al. 2009) or predators (van Schaik and Hörstermann 1994) and/or because he will defend a territory against intruders (Goldizen 2003).

Analyses of proximate aspects of reproductive strategies depend on reliable information about endocrine mechanisms and reproductive physiology that underlie interactions between hormonal and behavioral factors. Our studies have confirmed that monitoring ovarian function in wild gibbons is feasible (Barelli and Heistermann 2009), and that females exhibit behavioral and non-behavioral reproductive status cues that are displayed during both the fertile and non-fertile phase of the ovarian cycle. During a recent study (2003–2005), we found that although females' mating activity was skewed toward one preferred male (i.e., the primary male), half of the studied females ($N = 10$) lived in multi-male groups and each one also copulated with the second, subordinate male (i.e., the secondary male) in her group. Mating with a primary male increased during the fertile phase (Barelli et al. 2008b). Primary males in multi-male gibbon groups performed most copulations and had priority of access to fertile females. However, copulations by secondary males were distributed widely through female cycles, and these males had mating opportunities during periovulatory periods (Fig. 11.3). Copulating with both males even continued into non-fertile days of the menstrual cycle when conception was highly unlikely (as well as during pregnancy when conception was impossible), which contrasts strongly with the still widespread view that white-handed gibbons are socio-sexually monandrous and focused on single partners; instead, KY white-handed gibbon females are often sexually polyandrous (Barelli et al. 2008b, Reichard 2009).

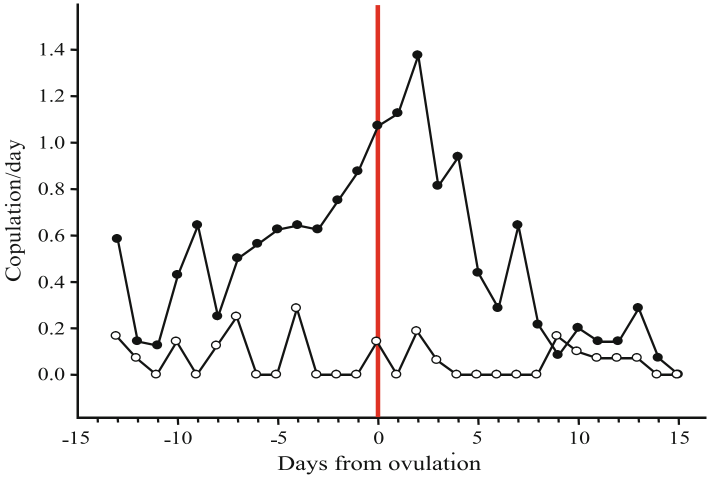

Fig. 11.3 Frequency of female copulation (number of copulations/day in which copulations occurred) with primary males (*black dots*) and secondary males (*white dots*) related to the day of ovulation (day ‘0’). Frequency of female copulation is calculated by first averaging the frequency for each female separately, and secondly across these individual values to yield a representative composite frequency that equally balanced individual contributions (see Barelli et al. 2008a, b)

Mating during pregnancy has also been suggested as a mechanism to confuse paternity and reduce the risk of infanticide in case of a male change (van Noordwijk and van Schaik 2000; van Schaik et al. 2000). It is noteworthy here that the only lactating females we have so far witnessed to become sexually active were two females who had just experienced male changes. While still carrying nursing infants, the females developed sexual swellings. In one case, the relationship with the new male was tense despite copulations. A few weeks after the male take-over, the female increasingly refused copulation attempts and stayed out of close proximity, and in the days prior to the disappearance of the female’s infant some grappling and screaming was noticed. This female’s sexual activity might have been a tactic to protect her suckling infant from harm by deceptively signaling receptivity to the new male. The anecdote is consistent with predictions of the sexual selection hypothesis for male infanticide (van Schaik et al. 2000): (1) The new male was unknown in the area and therefore can be assumed to have had a zero probability of having fathered the female’s current offspring. (2) The new male had an increased chance of fathering the female’s subsequent offspring because he remained with the female (and still is paired with her) and she mated with him during her subsequent cycle. (3) The female gave birth faster again than she would have had the infant survived. For this female, two of the three previous interbirth intervals between surviving infants were 3 years and one was 3 years and 8 months long, but the interbirth interval following the disappearance of the infant was only 2 years and 3 months.

11.3.2.1 Gibbon Sexual Swellings and Their Functional Significance

In strictly pair-living, monandrous females, sexual swellings are not expected to evolve (Nunn 1999) because male–male competition is low or absent and no selection pressure exists for females to advertise their fertile periods to a pair mate. However, gibbon females often mate polyandrously, and groups at KY frequently have two adult males that both maintain sexual relationships with the group female. It is thus not surprising that white-handed gibbons have sexual swellings (Barelli et al. 2007). These cyclical sexual swellings are admittedly small compared to the well-known, exaggerated sexual swellings of chimpanzees, baboons, and some macaques, but despite their modest size they follow the same physiological principles. Based on faecal progestogen profiles of 8 females over 15 menstrual cycles, we found that in 80% of cycles, ovulation overlapped tightly with the maximum swelling phase (duration: Ø 9.3 days; 42.8% of cycle length). In fact, the probability of ovulation peaked on average on day three of the maximum swelling period, although the timing between maximum swelling and probability of ovulation varied between days − 1 to day 13 of the swelling period and three times an ovulation fell outside the maximum swelling phase (Barelli et al. 2007). Thus, in analogy to sexual swelling patterns in primates living in multi-male social systems (Deschner et al. 2004; Engelhardt et al. 2005; Fürtbauer et al. 2010), KY gibbons also exhibit cyclical sexual swellings during their menstrual cycle that do not precisely indicate the day of ovulation.

To understand sexual swellings occurring outside the menstrual cycle better, we also tested five pregnant and six lactating females. Surprisingly, different swellings phases were noticeable also in pregnant females (and in similar proportions compared to cycling females), but not in lactating females, who were rarely swollen. We conclude that despite their smaller size, gibbons' sexual swellings probably serve functions similar to those suggested for primates with exaggerated swellings. In support of such an interpretation, female sexual activity corresponds with the size of the sexual swelling. Primary males, but not secondary males, copulate more frequently with cycling and pregnant females who are maximally swollen than with those females who are not or are only partially swollen (Barelli et al. 2008b).

Over the last 30 years, several hypotheses have been proposed to explain the evolution of conspicuous sexual swellings in species in which females mate with multiple males (reviewed in Zinner et al. 2004), whereas moderate or small sexual swellings have rarely been considered. Exaggerated swellings are hypothesized to increase paternity certainty, reliably advertise changes in female reproductive status ("obvious-ovulation hypothesis": Hamilton 1984), or provide information on female quality ("reliable-quality indicator hypothesis": Pagel 1994). They may also function to confuse paternity if ovulation does not precisely occur at peak swelling and thereby allow females to mate with multiple males when potentially fertile ("best-male hypothesis": Clutton-Brock and Harvey 1976; "many-male hypothesis": Hrdy 1981; Hrdy and Whitten 1987). Lastly, the "graded signal hypothesis" (Nunn 1999) posits that exaggerated swellings indicate the probability of ovulation, without allowing a male to precisely pinpoint the day of ovulation, thus giving a female more freedom to manipulate males' mating interests, particularly in species where males are larger than and dominant to females. Following this last hypothesis, the highest probability of ovulation should occur close to peak swelling size, but because of the prolonged duration of receptivity associated with a prolonged display of the sexual signal, females might mate with other males when ovulation is less likely but still possible (Nunn 1999). Our sexual swelling data on gibbons are in line with the graded signal hypothesis suggesting that it can also be applied to less conspicuous swellings (Barelli et al. 2008b; Reichard 2009). The occurrence of sexual swellings in gibbons (Nadler et al. 1993; Cheyne and Chivers 2006) may be related to the widespread flexibility in social organization revealed by recent research (Fuentes 2000; Lappan 2007a; Malone and White 2008; Reichard 2009).

Although "the graded signal hypothesis" offers the most comprehensive explanation for the patterns of sexual swellings, it does not explain the presence of sexual swellings during pregnancy and lactation. Developing a swelling during pregnancy may help maintain the male's sexual interest and mating activity, which can create paternity confusion and reduce the risk of infanticide (van Schaik et al. 1999; Engelhardt et al. 2005) and perhaps decrease a male's interest in EPCs and thereby allow the female to benefit from his permanent presence. Thus, flexible mating behavior and imprecise sexual swelling signals in wild gibbons are consistent with the theory of paternity confusion. Moreover, the clear association between sexual swelling size and copulation frequency supports our interpretation that the small swellings in gibbons attracts male sexual interest and are analogous to the exaggerated swellings of Old World monkeys and great apes.

11.4 White-Handed Gibbon Life History

Understanding primate life history strategies depends critically on data from wild, unprovisioned, and naturally reproducing populations (Brockman and van Schaik 2005; Cords and Chowdhury 2010; Fürtbauer et al. 2010). Our gibbon project has now reached a time-depth that allows us to begin to assess some life history variables. Perhaps knowledge of basic life history parameters should generally guide our perception of the time-depth of field studies because the number of generations contributing to a data set may be biologically more meaningful than the number of field seasons, a common proxy often used in relation to the labels "long-term" and "short-term" study. For example, a short-term study of a few years on a mouse lemur population represents a greater biological time-depth and perhaps sample size than a decade-long study of a few individuals of an orangutan population.

From a life-history perspective, our study is still in its infancy. Gibbons' adult group sizes are small and their life history is extremely slow for a primate of such small size (Ross 2004; Reichard and Barelli 2008). We still lack, for example, data on the maximum or even average lifespan. A few old individuals whom we have known for a long time have disappeared and probably died, but others who appear to be of similar age are still alive, and reliable, systematic birth records only exist for the population since the early 1990s (Reichard and Barelli 2008). To estimate a minimum age of the oldest adult females with unknown birth dates, we used long-term records of date of first appearance in the population and added to this the average years until first reproduction (see below). The data indicate that females may live to age 40 or older, although they tend to begin to "disappear" by this age, probably because they die (Table 11.3). The oldest female in our sample is alive at age 43 and some females continued to reproduce between 30 and 40 years of age, although the sample of females alive past 30 years of age is small. It is clear that wild gibbon females enjoy a long life span compared to other primates of similar mass (i.e., 5–6 kg). Unfortunately, females with known birth dates will still be nowhere near the end of their potential reproductive careers or lives at ages of 15–25 years, so our knowledge of female life histories is still incomplete (Table 11.3).

Data on age at first reproduction are available for five females, who gave birth for the first time on average at age 10.5 ± 1.2 years (range 8.4–12.8 years). We don't know the exact onset of menarche yet, but for two sub-adult females who displayed their first elongated vulva with a conspicuous mass of pink tissue at approximately 8 years of age (Hima: 8 years and 109 days; Rung: 8 years and 49 days; Barelli et al. 2007), no distinct cyclic pattern in progestogen levels (follicular and luteal components of the menstrual cycle) was detected by that

Table 11.3 Minimum age estimates of wild white-handed gibbon females at Khao Yai National Park, Thailand

Females with unknown birth date				Current status
Group	Female	Minimum age estimates (years)	Estimated age at last *or* most recent birth (years)	
A	Andromeda	43	40	Present
C	Cassandra	41	40	Disappeared
B	Bridget	39	28	Disappeared
N	Natasha	38	32	Disappeared
S	Sofi	36	35	Present
H	Hannah	32	29	Present
D	Daow	27	24	Present
R	Brit	27	22	Present
W	Wolga	25	25	Present
J	Jenna	23	18	Disappeared
NOS	Nasima	23	21	Present
Females with known birth date				
T	Brenda	25	24	Present
N	Hima	15	14	Present
M	Rung	14	12	Present

age. Two precisely known gestation periods of two females lasted 184 and 195 days respectively (Barelli et al. 2007), which is shorter than the commonly assumed 210 days gestation period for white-handed gibbons (van Tienhoven 1983). If we subtract gestation length from age at first birth we can conservatively measure sexual maturity to occur at the latest at the age of first conception, which occurred on average at the age of 10.0 ± 1.5 years (range 7.8–12.2 years, $N = 5$) in these females. An interesting difference existed among the five females because the female with the earliest onset of reproduction (8.4 years) was the only female still residing in her natal group. This group had two simultaneously breeding females for several months, because her mother had given birth a year earlier (see above), until the daughter's infant disappeared for unknown reasons. At the time of writing, the young female still resides with her natal group at age 9 years and 3 months. Pre-dispersal reproduction is exceptional in our population and most females disperse at the age of 7–8 years (Brockelman et al. 1998). Overall, white-handed gibbons at KY begin reproducing much later than monkeys of similar body mass and, remarkably, at about the same age as female mountain gorillas (Okamoto et al. 2000; Nakagawa et al. 2003; Wich et al. 2004; Hsu et al. 2006; Fürtbauer et al. 2010; Di Fiore et al. 2011).

Detailed data are also available for female interbirth intervals (IBI). The average population IBI between surviving offspring of habituated KY females ($N = 11$, 1990–2009) was 3.4 ± 0.7 years (range 34–71 months, $N = 22$ IBI). Adding one exceptional IBI of 14.4 years (173 months) increases the average IBI to 3.9 ± 0.4 years ($N = 23$ IBI). The one exceptionally long IBI was surprising because copulations were observed across most years. Prior to her most recent birth, the female was considered post-reproductive for 9.8 years according to Caro et al. (1995). The anecdote illustrates the danger of assessing female reproductive status behaviorally, which might be particularly misleading in long-lived apes. Death of a suckling infant significantly shortens birth intervals to an average 2.2 ± 0.7 years (range 11–36 months, $N = 9$ IBI; t-test: $t_{(29)} = 4.64$, $p < 0.001$), although great variation naturally exists in this measure because it depends on variables such as infant age at death or a mother's age or body condition. The shortest IBI recorded after an infant's death was 11 months, which meant that a female conceived only 3 months after she had lost an infant, and the longest was 3.1 years, which closely resembles the mean IBI in the population.

We can also calculate infant and juvenile mortality and the length of the juvenile period in our population. Infant mortality during the first year was 11.1% ($N = 54$ infants born) and until weaning it was 25.6% ($N = 43$ infants surviving from birth to weaning), which is moderate to low, compared to many other primates (Wright 1995; Boesch and Boesch-Achermann 2000; Robbins et al. 2004; Strier et al. 2006; Carter et al. 2008; Cords and Chowdhury 2010). Juvenile mortality between weaning and 5 years of age remained low at 8.8% ($N = 34$ weaned infants) but rose to 13.6% ($N = 22$ juveniles older than 5 years) if the period between weaning and dispersal is considered. Overall, the juvenile period in gibbons is very long. Considering that weaning occurs between 24 and 30 months (Treesucon 1984) and ends the latest with first conception (see above), female gibbons spend about 7 years as non-reproductive immatures.

11.5 Conclusions

The most dramatic change in our understanding of gibbons, as we see it, has been the shift from a socio-sexual monogamy model toward a dynamic community based-model in which individuals, although living in small social units and on small, group-specific home ranges, are connected to a much larger social sphere that involves permanent exchanges and interactions across core social unit's socio-spatial boundaries. Individuals call to each other in loud songs, they frequently meet in overlapping areas between group home ranges, and females visibly signal fertile periods to males in their vicinity with modest sexual swellings. Males seem to be more socially mobile than females, as predicted by sexual selection theory (Altmann 1990), given that they move more frequently between groups than females do. Females are more often the long-term occupants of home ranges and female take-overs of breeding groups usually involve younger females taking over the home range of old females whom they oust from the groups. Interestingly, so far we have not encountered an ousted female again, whereas ousted males frequently reappear in other groups and our long-term records show that some males transfer three and four times.

The dynamic community model is well suited to incorporate the recent wealth of unexpected findings that have emerged across gibbon taxa (Palombit 1994a, b; Malone and Oktavinalis 2006; Lappan 2007a, b; Lappan and Whittaker 2009). The social dynamics of gibbon communities are also in line with new findings of female reproductive strategies. Females mate polyandrously (Barelli et al. 2008b; Reichard 2009) and their moderate sexual swellings (Barelli et al. 2007) probably allow them to increase male–male competition to achieve EPCs, and more broadly to manipulate male sexual activities, all of which may benefit their own reproductive interests. However, reproductive strategies will not be fully understood until we have molecular paternity data.

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Part V
Africa

Chapter 12
The Amboseli Baboon Research Project: 40 Years of Continuity and Change

Susan C. Alberts and Jeanne Altmann

Abstract In 1963, Jeanne and Stuart Altmann traveled through Kenya and Tanzania searching for a baboon study site. They settled on the Maasai-Amboseli Game Reserve (later Amboseli National Park) and conducted a 13-month study that laid the groundwork for much future research. They returned for a short visit in 1969, and came again in July 1971 to establish a research project that has persisted for four decades. In July 1984 Susan Alberts joined the field team, later becoming a graduate student and eventually a director. Over the years, we have tackled research questions ranging from feeding ecology to behavioral endocrinology, from kin recognition to sexual selection, and from aging research to functional genetics. A number of our results have explicitly depended upon the longitudinal nature of the research. Without decades worth of individual-based data we would not have known, for instance, that the presence of fathers influenced the maturation rates of their offspring, that maternal dominance rank had pervasive effects on the physiology of sons, or that the social behavior of a female influenced her infants' survival. Here we summarize the major research themes that have characterized each of the past four decades, and our directions for the future, emphasizing the scientific insights that the longitudinal nature of the study has made possible.

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12.1 Introduction

In 1963, Jeanne and Stuart Altmann took a reconnaissance trip through Kenya and Tanzania, searching for the best site to study baboons, genus *Papio* (Altmann and Altmann 1970). They traveled in a Land Rover with their infant son, Michael, in the back, and they visited six national parks and reserves. One stood out to them as ideal: the Maasai-Amboseli Game Reserve, later Amboseli National Park, in southern Kenya immediately north and west of Mt. Kilimanjaro. The reserve had thousands of baboons, was dominated by an acacia tree woodland interspersed with areas of open grassland, and had a full complement of herbivores and predators. The fever tree woodlands were full of wildlife, visibility was very good (Fig. 12.1), and it was possible to drive through most of the terrain (often a problem in other parks and reserves because of thick vegetation or rocks). In addition, the yellow baboons, *Papio cynocephalus*, that inhabited the reserve neither approached nor fled from humans, as in other areas with high baboon populations. The Altmanns carried out a 13-month study, describing in detail the baboons' demographic structure, social system, ranging patterns, and feeding ecology (Altmann and Altmann 1970). With other studies of wild baboons that were being carried out in this decade, the groundwork was laid for baboons to become one of the best-studied nonhuman primates in the wild (e.g., Hall and DeVore 1965; Kummer 1968; Stoltz and Saayman 1970).

The Altmanns left Kenya in 1964, and stayed away for 5 years. When they returned for a visit in 1969, they encountered a vastly changed landscape in Amboseli, most strikingly characterized by a dramatic decline of the fever tree

Fig. 12.1 Baboons in Amboseli, Kenya. Visibility is very good in the ecosystem, and after four decades of research the animals are well habituated to the presence of neutral human observers. Photo © Susan Alberts

woodlands, a pattern that has continued since then. Several factors probably contributed to this woodland decline, possibly including natural aging of the woodlands, pastoralist grazing patterns and associated burning, rising water table with a concomitant rise in a salt layer in the soil and, increasingly, the impact of an growing elephant population that both kills trees and prevents woodland regeneration (Western and Sindiyo 1972; Struhsaker 1973; Western and van Praet 1973; Western and Maitumo 2004; Western 2007). The Altmanns described "walking around in shock" for the first several days of their return, confirming that the baboon population had decreased dramatically since 1964. They repeatedly re-censused the baboon population beginning in 1969, eventually confirming a drop in population size of more than 90% from the early 1960s (Altmann et al. 1985).

In spite of the changes, Amboseli remained a wonderful place to watch baboons. The baboon population was small, but was stabilizing in spite of the population decline (Altmann et al. 1985), the terrain was manageable, and the visibility was still excellent. In July 1971, the Altmanns and Ph.D. student Glenn Hausfater began observing Alto's Group, which consisted of 35 members, thus establishing a research project that has, against the odds, persisted for 4 decades.

Another study group (Hook's Group) was added to intensive study in 1980 with Michael Pereira's Ph.D. research, roughly doubling the size of the population under study. In 1984, in work led by Amy Samuels and by Phillip Muruthi, then a B.Sc. student at the University of Nairobi, we also began monitoring a social group living near a tourist lodge that subsisted partially on the lodge's refuse. Observations of Lodge Group lasted only 12 years (through 1996), but greatly enriched our understanding of the flexibility of baboon behavior and life history by demonstrating that baboons can substantially accelerate their life histories, growth rates, and reproductive rates when nutritional conditions are good, and can adapt behaviorally and ecologically to a wide range of environmental conditions (e.g., Altmann and Muruthi 1988; Muruthi et al. 1991; Altmann and Alberts 2005).

The subset of the Amboseli baboon population that is under intensive study (hereafter the "study population") currently consists of ~350 extant animals (with life history and behavioral data on an additional ~1,000 that have died) in six social groups. All six current study groups are either fission products of the two original groups (Alto's, which fissioned in 1990–1991, and Hook's, which fissioned in 1995) or are fission products of daughter groups of Alto's (Dotty's Group, which fissioned in 1999, or Nyayo's Group, where a fission is in process in 2011 at this writing; Fig. 12.2 and see also Altmann and Alberts 2003; Van Horn et al. 2007). All members of the study population subsist entirely on wild foods and experience no human management (Lodge Group is no longer a study group; instead, we monitor its demography opportunistically, as we do ~8 other non-study groups in the Amboseli basin).

The Amboseli study population is part of an extensive, continuous baboon population that occupies a large part of eastern Africa. From the perspective of baboons, the Amboseli basin is locally bounded on the west and the north by inhospitable stretches of land, but males move to and from social groups living to the south and to the east of the basin. Thus, the study population experiences gene

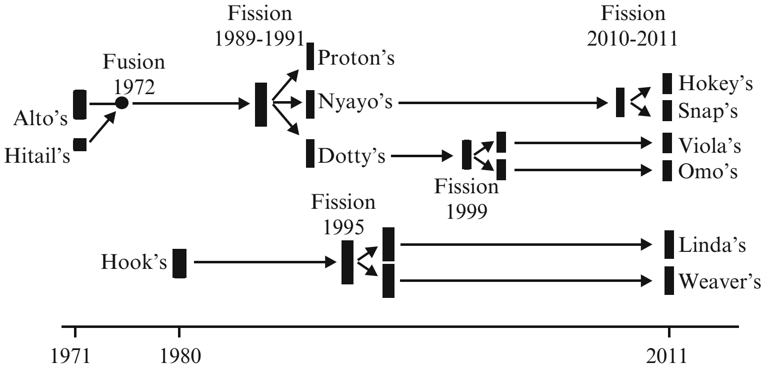

Fig.12.2 Timeline of research on wild-feeding study groups in Amboseli. Research began on Alto's Group in 1971 and on Hook's Group in 1980. Four subsequent natural group fissions produced the 2011 study groups. Proton's Group (one product of Alto's fission) was dropped from the study in 1993 for logistical reasons

flow with the surrounding local population and has a large estimated effective population size (Storz et al. 2002). The baboon population in the Amboseli basin appears to be demographically stable or moderately growing, although it still persists at a level far below that of the early 1960s (Altmann et al. 1985; Samuels and Altmann 1991).

Today the Amboseli Baboon Research Project (ABRP) is a longitudinal, coordinated series of studies of baboons in the Amboseli region with a broad range of research interests. It has supported 23 Ph.D. or M.Sc. theses, including six from Kenyan students, with another six in progress at this writing. We still rely heavily on observational techniques that have changed little since 1971, although we have also employed key technological innovations (some of which are described below) that have enriched the basic behavioral and ecological data enormously. In addition, we have invested heavily in data preservation and accessibility by developing our database, BABASE (see Sect. 12.4). This has allowed us to readily engage in multidecade and lifespan analyses as well as shorter term cross-sectional studies.

Since the mid 1990s, the longitudinal data collection (demographic, behavioral, and ecological) has depended heavily on our dedicated and highly skilled Kenyan field team. Raphael Mututua began working for the project in 1981 as a field assistant; he developed into an outstanding observer and researcher and now fills the essential role of the project's field manager. His leadership in the field is of the highest quality. Serah Sayialel (beginning in 1989) and Kinyua Warutere (beginning in 1995) fill out our senior Kenyan research team. The project would be unimaginable without them (Fig. 12.3). Several other staff members (Gideon Marinka, Benard Ochieng Oyath, and Longida Siodi) play important roles as field assistants to Mututua, Sayialel, Warutere, and visiting researchers.

Here we summarize some of the major research themes that the Amboseli Baboon Research Project has tackled since its inception. This review is by no means exhaustive; it is not possible to include all of the more than 200 publications

Fig.12.3 Raphael Mututua (*left*), field manager of the Amboseli Baboon Research Project, observing baboons with senior Kenyan team members Serah Sayialel (*center*) and Kinyua Warutere (*right*). Photo © Jeanne Altmann

on the Amboseli baboons here (see a full list of publications on the Amboseli Baboon Research Project website; http://www.princeton.edu/~baboon/). Instead, our goal is to highlight the major themes that have informed, and been informed by, the long-term and longitudinal nature of the study.

12.2 The 1970s: Foundations

Several research projects in the 1970s focused on the question of how the baboons made a living in a semi-arid environment that received only an average of ~350 mm of rain per year. The answer was: "with difficulty". These early studies showed that the baboons spent a large fraction of their time foraging – that is, moving and feeding (e.g., Altmann 1980; Post 1981). Two studies in particular suggested that the nutrition obtained by the baboons during natural foraging was minimally sufficient for growth and reproduction at a rate that would support population replacement. Specifically, Jeanne Altmann showed that mothers spent as much time feeding as they possibly could by the time their infants were 5–6 months of age, and that even when maternal feeding time was at a maximum, maintaining their own body weight would be difficult (Altmann 1980). She inferred that this constraint essentially forced the infants to begin the transition to nutritional independence at this age (Altmann 1980; see also Altmann and Samuels 1992). Further, her calculations indicated that wild baboons were subsisting on a diet that, in captivity, was considered so dangerously inadequate that experimental diets that approximated the Amboseli baboons' diet were discontinued because of health concerns for the animals (Altmann 1980). In a second, concurrent study, Stuart Altmann showed that most infants, during the transition to nutritional independence, fell well below the optimal diet that he predicted they could obtain (Altmann 1991, 1998). Decades after the infant data were collected, he was able to use the life history data that had accumulated on the female infants in his study to show that their nutritional shortfall during infancy predicted, with astonishing accuracy, their future reproductive success; such a result was only possible because of the longitudinal and long-term nature of the study (Altmann 1991, 1998). These studies of feeding ecology were important in setting the stage for future work on this population, because they framed a major component of the underlying ecological problem the baboons had to solve (the other major ecological problem, predation, provides a second, but harder to study, theme that we have not yet investigated thoroughly in Amboseli; see Alexander 1974; van Schaik 1983). Ecology provided the context in which all other aspects of behavior and life history are played out.

A second important foundation laid in the 1970s was behavioral. One of the most obvious features of baboon society, evident to any observer who spends much time watching baboons, is the agonistic interactions that regularly occur between individuals. While many less obvious features of baboon society are equally important, there is no question that the dominance relations that arise out of these agonistic interactions have a profound and pervasive influence on many aspects of baboon life. One of the first studies that the Altmanns and Hausfater carried out was a careful analysis of aggressive and submissive interactions that occurred between individuals, and the subsequent construction of dominance hierarchies based on the direction of "wins" in these interactions.

During his yearlong study, Hausfater and the Altmanns developed the system of assigning dominance ranks in Amboseli that is still used by the research project today (Hausfater 1975). With respect to male mating success, Hausfater found that higher-ranking males enjoyed greater mating success than lower ranking males, but the relationship was not perfect and the highest-ranking male in his study did not experience the highest mating success. Consequently, Hausfater's study did not provide a definitive answer to the question "what is the importance of high rank for male primates?" This question preoccupied primate researchers for several decades to come (e.g., Strum 1982; Cowlishaw and Dunbar 1991; Kutsukake and Nunn 2006; Port and Kappeler 2010; Alberts in press). However, Hausfater's study brought to the fore a model of dominance-based priority of access that Stuart Altmann had developed years before during research on rhesus monkeys (Altmann 1962). The priority-of-access model – which posits that dominance rank functions as a queue in which males wait for reproductive opportunities – still provides an important "null model" for how dominance rank works to enhance male reproductive success in multi-male social groups. It has provided measures of the relative importance of dominance rank in male reproductive success in numerous social systems (extending beyond primates), and departures from the predictions of the model have provided important insights about how factors other than dominance rank affect male reproductive success (e.g., Boesch et al. 2006; Kappeler and Port 2008; Ostner et al. 2011; Surbeck et al. 2011).

The 1970s also saw the publication of Jeanne's landmark 1974 paper on behavioral sampling methods (Altmann 1974). The paper provided methodological guidance for behavioral studies of all kinds, and was motivated by a longstanding recognition of the need for data collection methods suited to answering questions through quantitative, model-testing analyses. It was also, to a considerable extent, grounded in Jeanne's experience studying the Amboseli baboons.

By the end of the 1970s, a longitudinal, individual-based perspective had emerged among the Amboseli researchers (especially Jeanne, whose Ph.D. research on mothers and infants had impressed upon her the importance of a life history perspective on behavior). During this time period, the Altmanns and Hausfater formalized many aspects of data collection and wrote the first version of the standardized protocols used by the project, the Monitoring Guide for the Amboseli Baboon Research Project (Altmann and Alberts 2004). The intention was that participating researchers would contribute to the longitudinal data as well as collecting data for their own short-term projects and benefitting from the monitoring data gathered by others in previous years. The current version of the Monitoring Guide (Altmann and Alberts 2004) has this to say about the longitudinal data collection and the manner in which visiting researchers contribute to it:

> *Of the data sets described in this guide, some (i.e., demographic data) have been ongoing since 1971, while others extend back for somewhat shorter periods. Almost all data types that we currently collect extend back to at least 1980. Still other types of data were collected for shorter periods of time and are no longer a focus of our research efforts. Whatever the data set, the value of the data collected at the Project lies in its consistency and in its consistently high quality across time. This guidebook … is meant as a guide for the permanent staff in Amboseli, for short-term visitors to the Project, and for visiting researchers pursuing their own projects (Ph.D. students, post-docs and other collaborators that stay long enough to learn the baboon ID's and contribute to the long-term data). It is absolutely essential that everyone who contributes to the Project's data set collect the data in accordance with the guidelines laid out here. Visiting researchers will collect additional data for their own specific research questions, which will extend beyond the monitoring data described here; these visiting researchers will still contribute to the monitoring data collection that is described in these procedures.*
>
> *When you contribute to the data of the Amboseli Baboon Research Project, you are contributing to a data set that we believe is unique in its time depth, breadth and detail. It is important to us that you take this responsibility very seriously. Never be satisfied with your data collection; always strive for more data of higher quality.*

12.3 The 1980s: Females

When Jeanne Altmann began her landmark study on the ecology of motherhood and infancy in the mid-1970s, the topics of motherhood, and of female behavior in general, were not seen as a particularly important focus for the primate studies that were emerging at the time. Although infant development and maternal care were intensively studied among developmental psychologists in laboratory settings and a few initial descriptions were made in field studies, the questions posed were primarily about social and cognitive growth, with a view to understanding human development. However, change was in the air, and a number of scientists studying wild primates were beginning to pose important questions about females and their infants (e.g., Jay 1963; Hrdy 1977; Seyfarth 1977; Pusey 1978; Fossey 1979).

Jeanne's study of baboon mothers and infants in Amboseli (Altmann 1980) emphasized an evolutionary perspective on behavior and highlighted how important the evolutionary ecology of motherhood and infancy are for understanding a species' behavior and ecology. It also highlighted the importance of ecological constraints on social behavior, a topic of growing interest throughout the 1970s (e.g., Crook and Gartlan 1966; Clutton-Brock and Harvey 1977; Emlen and Oring 1977). In addition, the study was grounded in the notion, unusual at the time but now widespread in studies of evolutionary ecology, that viewing behavior in the context of life history is important, in particular for understanding how the things an animal does today are both shaped by and shape its reproductive and social trajectory.

Female dominance rank also came under scrutiny in Amboseli in the 1980s. Although the importance of female dominance rank for reproductive success was not yet fully understood, evidence of its importance for females of many primate species had begun to accumulate (reviewed in Silk 1987). Baboon females, like many cercopithecine primate females, typically attain a social dominance rank just below that of their mothers, with the help of both kin and unrelated females (Walters 1987). This phenomenon had been known for some time in cercopithecines (reviewed in Melnick and Pearl 1987); the Amboseli study revealed that its consequence was cross-generational, long-term consistency of dominance rank relationships in wild populations. Further, the Amboseli work identified this long-term consistency of female dominance ranks as the most important source of stability in baboon social structure, a phenomenon generalizable to other species with maternal rank inheritance (Hausfater et al. 1982).

Some years later, however, the accumulating longitudinal data provided an even richer picture of female dominance relationships, revealing that long periods of stability could be punctuated by short periods of rapid change when some matrilines permanently fell and other permanently rose in rank (Samuels et al. 1987). Indeed, some females, by targeting higher-ranking females, were able to raise the ranks of all their female family members, while in other cases entire matrilines fell in rank, and occasionally matrilines split, with one female maintaining a higher rank than the rest of her family (Samuels et al. 1987).

Research on female social relationships and maternal behavior has remained a major theme in Amboseli through the years (Silk et al. 2003, 2004, 2006a, b; Van Horn et al. 2007; Gesquiere et al. 2008; Nguyen et al. 2008, 2009). A major step forward in understanding the strong and complex social relationships of female baboons came in 2003, when we discovered, with collaborator Joan Silk, that strong affiliative relationships have direct adaptive value for females: infants of more socially integrated females experienced higher survival than infants of more socially isolated females (Fig. 12.4; Silk et al. 2003). The effect of social integration on infant survival was later replicated in the long-term study of a chacma baboon

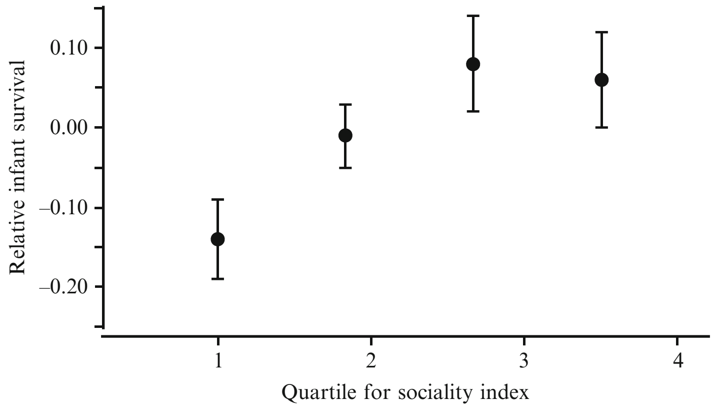

Fig.12.4 Females that were more socially integrated (females in the upper quartiles of a composite sociality index) experienced higher survival of their infants. Redrawn from Silk et al. (2003)

group in the Okavango Delta in Botswana (Silk et al. 2009), and those authors went on to demonstrate that social bonds enhanced the survival of the females themselves, not just of their infants (Silk et al. 2010). Again, without longitudinal data, these discoveries would have remained beyond our reach.

12.4 The 1990s: Males

After the first study on male dominance rank and mating behavior in the 1970s (Hausfater 1975) male social behavior took a decided back seat to female social behavior and ecological questions in the research priorities of the Amboseli team. Michael Pereira's work on the social behavior of juvenile males and females was an exception; he examined juvenile behavior in the context of the life history, and found sex differences in behavior that could be explained by the different demands made on males and females as adults (Pereira 1988a, b, 1989). Nonetheless, male social behavior was not intensively studied in Amboseli during this period, partly because of the rich vein of research on female behavior that had been tapped, and partly because some of the most interesting behavioral questions on adult males required more life history information and longitudinal data than were available in the 1970s and early 1980s.

Ronald Noë and Betty Sluijter were the first to study social behavior of adult males in Amboseli after Hausfater (Noë 1986, 1992; Noë and Sluijter 1990, 1995). They also brought a life history perspective to the study of males, in the now-growing tradition of Amboseli research, and showed that over the course of adulthood, males changed their levels of investment from an emphasis on direct male–male competition in young adulthood to a greater investment in relationships with adult females and juveniles in middle age (Noë and Sluijter 1990). These changes were associated with changes in male dominance rank, and as we amassed

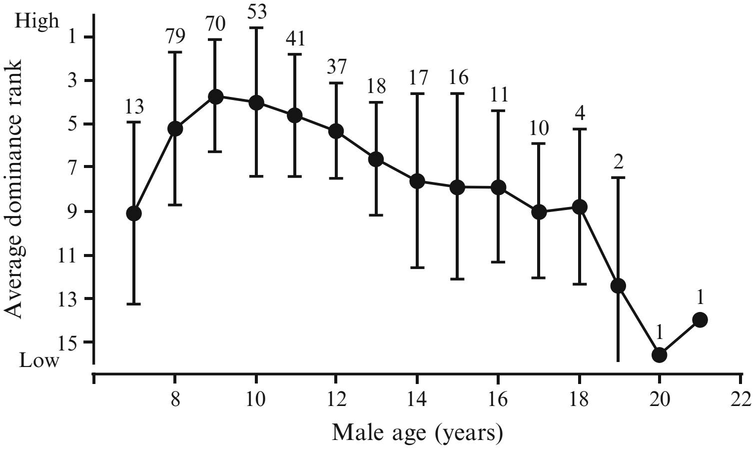

Fig.12.5 Male baboons reach their highest dominance rank in early adulthood when they are in their physical prime, and then steadily fall in rank as they age. Points show the mean (±SD) dominance rank for males in each age class, considering only males born into Amboseli study groups (i.e., males of known age); numbers above the error bars represent the number of males that contributed to the value for that age class. See also Alberts et al. (2003)

longitudinal data on known-aged individuals, it became clear how strongly age-based they were, with dominance rank peaking in young adulthood and declining steadily throughout the rest of life in a pattern very different from the relative stability of female dominance ranks (Fig. 12.5; see also Packer et al. 2000; Alberts et al. 2003).

By the late 1980s, male life history data had accumulated sufficiently for Susan Alberts to take male maturation and dispersal as the theme of her Ph.D. research. Dispersal represents an intense physical challenge at the onset of male adulthood, requiring that males leave the groups into which they were born and move into groups in which they have no prior relationships; in those groups, they must establish social relationships and obtain reproductive opportunities. Susan found that during maturation, males were subject to constraints of their mothers' dominance ranks, just as their sisters were (Alberts and Altmann 1995a). Male baboons, like most male primates, are independent of their mothers well before puberty (for an interesting primate exception to this rule see Surbeck et al. 2011); also, subadult male baboons are much larger than females and do not receive assistance from females in attaining or maintaining their dominance ranks. Indeed, analyses from another baboon population indicate that maternal dominance rank has no impact on the eventual dominance rank that sons attain (Packer et al. 2000). For these reasons, the dependence of male maturation on maternal dominance rank was surprising. However, this finding was supported by a later analysis of growth rates, which demonstrated an impact of maternal rank on growth rates for both sons and daughters (Altmann and Alberts 2005) and echoed similar findings in a few other primate species (e.g., Paul et al. 1992; Bercovitch et al. 2000; van Noordwijk and van Schaik 2001). In Amboseli, it presaged an even more profound effect of maternal dominance rank on male physiology at the onset of adulthood (Onyango et al. 2008; see Sect. 12.5).

Susan's analyses of dispersal revealed that males often spent time alone during dispersal while searching for other groups to join, and consequently both experienced elevated mortality risks (from 3 to 10 times higher than the mortality risk for males living in groups) and missed mating opportunities. However, males also appeared to experience reproductive costs if they remained in their natal group: although the sample size was small and based on observational rather than genetic estimates of paternity, the available data suggested high mortality of offspring for whom the natal males were likely fathers (Alberts and Altmann 1995b). This occurred in spite of strong evidence for close inbreeding avoidance between mothers and sons, and between maternal siblings. Finally, Susan's analysis indicated that natal males undergoing their first dispersal, and older males undergoing secondary dispersal, dispersed in response to the availability of females and to their own mating success in a given group (Alberts and Altmann 1995b; see also Altmann 2000).

By the end of the 1990s, substantial life history and behavioral data had accumulated for both males and females, and the groundwork had been laid for integrative studies of both sexes. In addition, we had begun to employ digital data loggers for collecting focal animal samples and hand-held GPS devices for collecting locational data. Among the most important advances of the 1990s was the development of BABASE, our longitudinal, individual-based database (Pinc et al. 2009). Field data are returned to the US either weekly (for digital data collected with hand-held data loggers and GPS machines) or monthly (for paper data) and are incorporated into BABASE in twice-yearly updates. BABASE is a web-based, PostgreSQL database that now houses most of our field data, including demographic, reproductive, behavioral, locational, ecological, and meteorological data. It is continually growing as we incorporate additional data sets into the original database design. These developments set the stage for the next important phase of the research, which involved getting "under the skin" with genetic and endocrine research.

12.5 The 2000s: Under the skin

In the late 1980s and early 1990s, two methodological developments occurred in genetics and physiology that had an enormous impact on primate field research, including the Amboseli baboon project. These were the development of a technique to extract DNA from feces (e.g., Höss et al. 1992; Gerloff et al. 1995) and the development of a technique to extract metabolites of steroid hormones from feces (e.g., Wasser et al. 1988). For the first time, we could study physiological responses and patterns of genetic relatedness – especially paternity – without invasive methods. This enabled us to pursue questions that were simply impossible to approach using naturalistic behavior observations alone. It would be 5–10 years after the first development of these techniques before they were perfected and applied to the Amboseli study (e.g., Khan et al. 2002; Buchan et al. 2003, 2005; Lynch et al. 2003), but once these techniques were established (with genetics analysis taking place in Susan's lab and hormonal analysis in Jeanne's), they transformed our understanding of baboon behavior and ecology (similar advances were being made in other primate field studies; e.g., Ziegler et al. 1997; Borries et al. 1999; Launhardt et al. 2001).

12.5.1 Hormones

Our hormone data have revealed several interesting surprises. In an analysis that combined endocrine data with data on male mating behavior and female reproductive states, we found that alpha males, but not males of other ranks, differentiated conceptive from non-conceptive cycles in their mate guarding (consortship) behavior, and that both the size of the sexual swelling and levels of circulating estrogen in the females provided potential cues about female fecundability (Gesquiere et al. 2007). This endocrine work nicely complemented the fecal DNA-based paternity analysis, which also revealed evidence of male mate choice (see Sect. 12.5.2 and Alberts et al. 2006).

In a study of pregnant females, we found evidence of a hormonal signature of impending fetal losses among pregnant females. This signature was evident for up to 2 months before the loss itself occurred (losses occurred in 91 of 656 pregnancies), ~14% (Beehner et al. 2006). In an additional instance of longitudinal data use, we discovered that maturing males whose mothers had been low-ranking when the males were born had higher fecal glucocorticoid levels than males whose mothers had been high-ranking, even when the glucocorticoid levels were measured 6–8 years after the males' births, years after males were independent of their mothers and in many cases years after the mothers had died (Fig. 12.6; Onyango

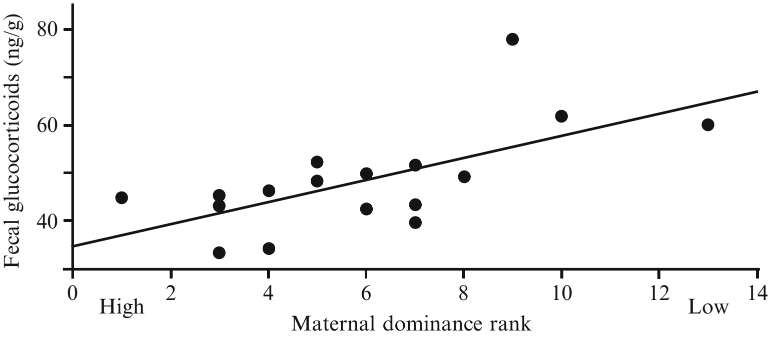

Fig.12.6 Subadult males born to higher ranking mothers had lower levels of fecal glucocorticoids than males born to lower ranking mothers, even when the fecal glucocorticoids were measured years after the period of offspring dependence on the mother. $R^2 = 0.421$, $P = 0.005$. Redrawn from Onyango et al. (2008)

et al. 2008). Glucocorticoids are products of the hypothalamic-pituitary axis (HPA) and are important in regulating the stress response and in mobilizing metabolic activity (Nelson 2005); our results indicated a long-term effect of maternal dominance rank on offspring physiology. Fecal glucocorticoid levels also predicted the peri-parturitional behavior of new mothers (specifically their responsiveness to their new infants), confirming findings that had previously only been documented in captive animals (Nguyen et al. 2008). Finally, we identified physiological effects of Amboseli's harsh dry seasons on both adult males and adult females (Gesquiere et al. 2008, 2011).

Most recently, we identified a surprising relationship between male dominance rank and endocrine profiles (Fig. 12.7; Gesquiere et al. 2011). While fecal testosterone (fT) levels declined as a function of dominance rank (with high-ranking males having the highest fT and low-ranking males the lowest), fecal glucocorticoids (fGC) presented a different and unexpected relationship with male dominance rank. Alpha males exhibited the highest fGC levels, and beta

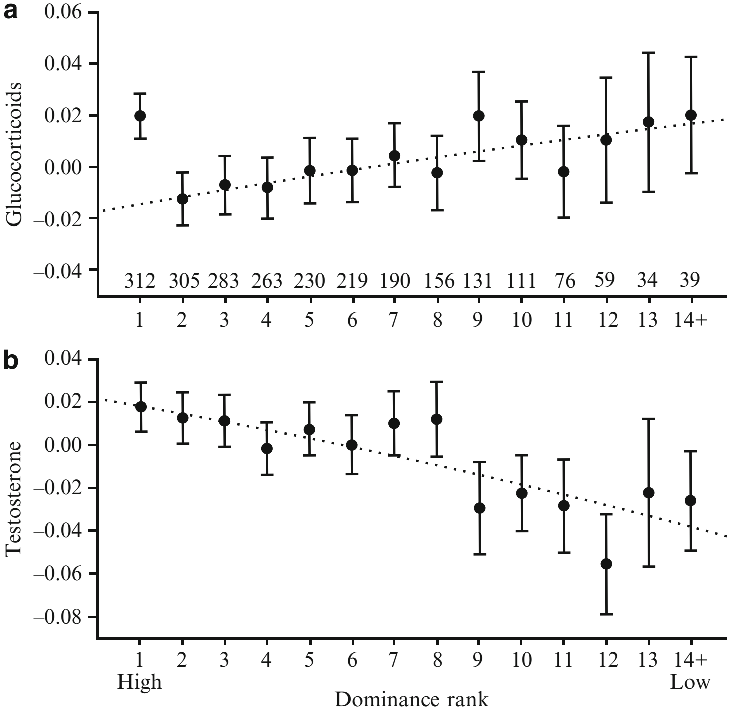

Fig.12.7 Highest ranking (alpha) males had very high glucocorticoids, much higher than second-ranking males and a striking departure from the pattern for glucocorticoids to increase (**a**) and testosterone to decrease (**b**) as dominance rank declined. Values (mean ± SE across male monthly averages) represent the residuals obtained from a statistical model of log-transformed hormone concentrations that accounted for age, environmental factors, and hierarchy stability as fixed factors, male identity as a random factor. After Gesquiere et al. (2011)

(second-ranking) males exhibited the lowest fGC levels, with a monotonic increase in fGC below rank 2. This striking difference between alpha and beta males has not been described before, possibly because researchers often group these males together as "high ranking males." Moreover, despite predictions in the literature that alpha males should experience elevated glucocorticoids only when the dominance hierarchy is unstable, we found no effect of hierarchy stability on the relative endocrine levels of alpha and beta males although overall levels of stress hormones were higher during instability. Thus, regardless of how stable male rank relationships are, being at the very top of a social hierarchy may be more stressful than being immediately below, probably because of energetic costs associated with mating and with male–male competitive interactions (Gesquiere et al. 2011).

12.5.2 Paternity

The first problem we tackled using DNA extracted from feces was the problem of paternity and its impact on social relationships. The question of whether male dominance rank mattered for male reproductive success had been a vexing one for decades; different primate studies produced different answers to this question and a resolution to the contradictions was slow to emerge (see reviews in Kutsukake and Nunn 2006; Port and Kappeler 2010; Alberts in press). Using 32 group-years of behavioral data on mating success in Amboseli, we had shown that the apparent contradictions across different studies were probably explained by real variance in the importance of male dominance rank over time for many if not most primates (Fig. 12.8; see also Strum 1982 for an early prediction of this sort). Both male

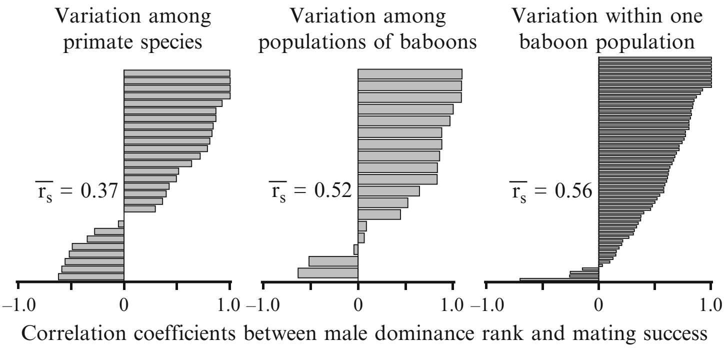

Fig.12.8 The relationship between male dominance rank and mating success shows similar variance at all levels of analysis; among primate species (*left panel*, data from Cowlishaw and Dunbar 1991), among populations of a single species, baboons (*center panel*, data from Bulger 1993), and within a single population of baboons, Amboseli (*right panel*, data from Alberts et al. 2003). Each graph shows the rank-ordered distribution of Spearman correlation coefficients for the relationship between male rank and mating success across studies (*left and center panels*) or across time periods in Amboseli (*right panel*). Redrawn from Altmann and Alberts (2003)

density and the distribution of male competitive abilities within groups affected the relationship between male dominance rank and mating success in Amboseli (Alberts et al. 2003; see also Cowlishaw and Dunbar 1991, Kutsukake and Nunn 2006; Port and Kappeler 2010).

However, an important question remained: what would the data look like if we were able to measure reproductive success using actual paternity data instead of just mating success? Our first paternity analysis, focusing on Lodge Group (the food-supplemented group that we studied from 1984 to 1996) and using DNA extracted from blood obtained during a darting project (see Sect. 12.6.4), had indicated that genetic paternity results were nicely predicted from behavioral data (Altmann et al. 1996). Would the same hold true in the wild-feeding groups? Using fecal DNA, we assigned paternity to 208 offspring conceived across a range of demographic conditions in wild-feeding groups. We found that male reproductive success, like mating success, depended on dominance rank but in a density-dependent manner and also depended on relative male competitive ability. In addition, we found little evidence for successful surreptitious mating (although subadult males occasionally produced offspring using this strategy), and no evidence for differential sperm success or sperm depletion. Most strikingly, we found clear evidence that alpha males fathered more offspring than expected based on their mating behavior, and that this excess of offspring resulted from male mate choice for female experiencing conceptive rather than non-conceptive cycles (Alberts et al. 2006). These results supported behavioral evidence of male mate choice in other baboons (Bulger 1993; Weingrill et al. 2003) and complemented our work on male mate choice based on female endocrine profiles and sexual swellings (Gesquiere et al. 2007).

The most surprising result from our paternity analyses was the discovery that male baboons differentiated their own offspring from the offspring of other males, and supported them disproportionately during agonistic interactions (Buchan et al. 2003). A number of previous researchers had hypothesized that paternal care occurred in baboons, and some had provided strong circumstantial evidence for its occurrence (Ransom and Ransom 1971; Altmann 1980; Stein 1984; Palombit et al. 1997). In addition to our confirmation of paternal care in baboons, we later discovered that offspring who resided with their fathers longer during their juvenile periods reached maturity earlier than offspring whose fathers dispersed or died earlier in their juvenile periods (Charpentier et al. 2008a). Neither of these results on paternal effects would have been discovered without longitudinal data; the implication was that paternal presence had an impact not only on the juvenile's daily interactions, but on an important life history component (see Altmann et al. 1988; Altmann and Alberts 2003 for data on the importance of age at maturity in this population). However, much remains to be done before we fully understand male–juvenile interactions in multi-male primate species. Some care by male baboons cannot be explained as paternal investment (Smuts 1985; Buchan et al. 2003; Moscovice et al. 2009; Nguyen et al. 2009), raising the possibility that males are engaged in mating effort when they care for young (incentivizing future mating with the mother; e.g., Smuts 1985; van Schaik and Paul 1996). Furthermore, the extent of paternal care in most other multi-male primate species remains an open question, with few data either refuting or confirming its occurrence (but see Paul et al. 1996; Ménard et al. 2001; Lehmann et al. 2006; Wroblewski 2010).

The paternal care that male baboons provide had an important corollary in our research; female baboons differentiated paternal sisters from non-kin, and formed preferential relationships with them (Smith et al. 2003; Silk et al. 2006a), supporting Jeanne's early predictions about paternal kin selection in primate groups (Altmann 1979). These relationships between paternal sisters were typically not as strong as relationships between maternal sisters, but were measurably stronger than relationships among non-kin, and sometimes played a role in patterns of permanent group fission (Van Horn et al. 2007). Significant relationships between paternal sisters were first documented in rhesus macaques (Widdig et al. 2001), suggesting that paternal kin networks may be a robust phenomenon in many primates (see, e.g., Watts 1997 for data on relationships among paternal siblings in gorillas, but see Langergraber et al. 2007 for different results in chimpanzees). The genesis of relationships between paternal sisters in baboons remains obscure, and fathers may well play a role in establishing them when they provide care to their offspring.

12.6 2010 Forward: New directions

At the start of this decade our energy and interest will be focused on four areas involving major new collaborations with Elizabeth Archie and Jenny Tung. These areas are aging, disease transmission, hybridization, and functional genetics and genomics. These investigations expand the multidisciplinary nature of our program in ways that explicitly allow us to capitalize on the longitudinal, long-term nature of our study.

12.6.1 Aging

With 40 years of demographic, behavioral, and ecological data accumulated, we are in a position to examine not only mortality patterns, but also behavioral and health correlates of aging that contribute to mortality; this represents a long-time goal that is finally within sight. To our knowledge, the work we have recently initiated is the first systematic study of how health and behavior change with age in a natural primate population, and of whether genetic and social predictors of these changes can explain individual differences in survival and longevity. Sex differences in health and survival during aging are major topics of interest in medicine, epidemiology, demography, and evolutionary biology. Despite this pervasive interest, and despite a wealth of data on aging in humans and a few well-studied model organisms, patterns of aging in wild animals remain largely undescribed. Not only are there large gaps in our knowledge of age-related changes in survival in wild animals, but virtually nothing is known about age-related changes in physiology, behavior, or other aspects of health and functioning for animals in the wild (Brunet-Rossinni and Austad 2006). We argue that studies of aging in wild animal populations, especially in our primate relatives, can provide a comparative perspective on human aging (Bronikowski et al. 2011), generate new questions, produce insights into the answers to old ones, and identify opportunities for alleviating the adverse consequences of aging. The longitudinal nature of our data will allow us to analyze not only declines in survival with age (demographic senescence; Bronikowski et al. 2002, 2011) but to produce a systematic description of how multiple indicators of health and functioning ability change with age in a wild primate (e.g., Altmann et al. 2010; Galbany et al. 2010, 2011).

12.6.2 Disease Transmission

Biologists currently have a poor empirical understanding of how infectious agents spread within and between social groups of wild animals, because of the logistical challenges of directly tracking the movements of infectious agents in the wild. Our parasite research, led by Elizabeth Archie, is designed to map the movements of common infectious agents onto the social landscape of the Amboseli baboons, using tools from social network analysis and population genetics.

One of our key hypotheses involves whether the transmission of nematodes or bacteria is socially structured at the level of social groups (i.e., whether baboons are most likely to be infected by group members for some or all parasites), a rarely tested but critical assumption of most research on the disease-related costs of group living (Altizer et al. 2003; Nunn and Altizer 2006). We will also test whether social networks predict the movements of infectious organisms within social group, and whether and how infection risk varies among individuals. Finally, we will examine the ecological correlates of between-group parasite transmission. This research will employ fecal samples that were collected during the past 15 years, as well as new samples, to provide a unique longitudinal perspective on parasite transmission in this population.

The result will be a picture of how different infectious agents, with a variety of transmission modes and fitness effects, move between and within social groups. This in turn will enhance our ability to understand individual differences in the risk of infection in more detail than has been possible before in natural primate populations. Socially structured disease transmission has important implications for understanding the evolution of sociality – a basic feature of our primate lineage – because exposure to disease is thought to be a major evolutionary cost of group-living (Alexander 1974; Altizer et al. 2003). Also, current models of disease transmission tend to be highly sensitive to variation in transmission patterns; hence, to predict the dynamics of an epidemic in social wildlife, biologists need accurate information on how disease spreads in natural populations of social animals.

12.6.3 Hybridization

The Amboseli baboon population comprises primarily yellow baboons (*P. cynocephalus*), specifically the "ibean" morphotype of yellow baboons. This morphotype shares some morphological similarities with anubis (olive) baboons, possibly because of anubis admixture in the ibean lineage over the course of evolutionary history (Jolly 1993). Further, Amboseli is situated on the boundary between the ranges of yellow and anubis baboons, with yellow baboons to the south and east and anubis baboons to the north and west (Jolly 1993; Kingdon 1997; Newman et al. 2004). Six anubis males have immigrated into Amboseli study groups over the course of the study, and one small (ca. 18) mixed-sex group of anubis baboons also entered the basin in the early 1980s (Samuels and Altmann 1986; Tung et al. 2008). Hybrids now occur both in study and non-study groups in Amboseli, resulting both from the anubis immigrations we have detected (and probably other, undetected anubis immigrants into non-study groups) and from the movement of hybrid males between study and non-study groups and successful reproduction by these males. In Amboseli, as in all baboon hybrid zones studied thus far, mating occurs freely and results in viable and fertile offspring; little or no evidence of hybrid dysgenesis has been found (reviewed in Tung et al. 2008).

Strikingly, in Amboseli, both males and females with a higher proportion of genetic admixture from anubis baboons (measured via a genetic "hybrid score"; see (Tung et al. 2008)) reached physical maturity earlier than animals with a yellow baboon genetic background (another result that depended on longitudinal data). Males showed a particularly pronounced effect of admixture, especially for age at natal dispersal (Fig. 12.9; Charpentier et al. 2008b). We are now poised to examine

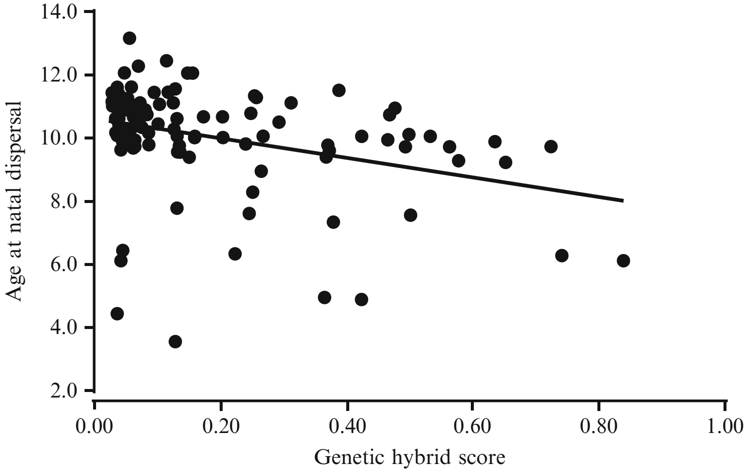

Fig.12.9 Male baboons in Amboseli with higher genetic hybrid scores (more anubis ancestry) are likely to disperse at a younger age than males with lower genetic hybrid scores (less anubis ancestry). $R^2 = 0.216$, $P < 0.0001$. After Charpentier et al. (2008a, b)

the consequences of hybridization further, considering both life history traits and behavioral traits that are associated with life history (specifically dominance, mating, and dispersal) as a function of hybridity.

12.6.4 Functional Genetics and Genomics

By combining the detailed behavioral and ecological data available for the Amboseli baboons with genetic and genomic research, we have the opportunity to place genetic inferences in the context of a well-understood natural primate system. Indeed, we have argued that as genomic resources for primate species accumulate, natural populations of primates should increasingly be targets of research on evolutionary and functional genetics and genomics because they offer the prospect of identifying functional genetic variation that influences traits of known ecological and adaptive significance (Tung et al. 2010). While work on captive populations can identify genetic systems of suspected significance, only field studies can confirm whether and how the systems in question are variable or relevant in nature (e.g., Keele et al. 2009; Tung et al. 2009); this in turn can have important implications for understanding both primate and human evolution.

In 1989, we learned from Robert Sapolsky how to temporarily anesthetize and immobilize baboons for drawing blood and taking morphometric measurements. We employed the technique at the time for both endocrine and genetic analyses, darting ~150 animals in a 3-year period (e.g., Sapolsky and Altmann 1991; Altmann et al. 1996; Sapolsky et al. 1997). We have continued to employ this technique occasionally over the years to affix radio collars to single females in each group. Beginning in 2006, we resumed a more extensive darting effort in order to obtain high quality DNA and RNA samples for as many adults as we could in the population. Because our research depends heavily on not affecting the behavior, health, survival, or reproductive success of the study animals, we have invested considerable effort in our time- and labor-intensive approach, which is focused on safety and on maintaining habituation in our study animals.

We dart individual baboons, one at a time, with an anesthetic-bearing dart, using a hand-held blowpipe. We dart no more than two animals per day, and no study group is darted more than once per week. On the day of a planned darting, the target animal (an adult male or an adult female that is not carrying a dependent infant and not past early pregnancy) is followed, often for many hours, until an appropriate opportunity arises. This occurs when the air is still, when neither the target animal nor other baboons will witness the darting, and when the animal is seated, standing still, or walking slowly. After the animal is darted and falls asleep (within 3–10 min), we wait for the other group members to move on (only rarely do other group members take any interest in the sleeping individual) and then quickly pick up the sleeping animal and move it to a shady processing site. We weigh the animal, carry out various other body measurements, and collect blood and skin samples in DNA- and RNA-preserving buffers. After the protocol is complete, the animal is allowed to recover in a holding cage in the back of our pickup truck until fully awake (after 3–4 h), when it is released at some distance from its social group but within sight. We have darted over 100 animals since 2006 in this manner, with no injuries and no untoward incidents. Blood and tissue samples remain in Amboseli for up to 48 h in an evaporatively-cooled hut before we send them to Nairobi (via air) for temporary freezing, and then transport them to the US (Tung et al. 2011).

Our functional genetics and genomics research, which uses the blood and skin samples that we collect during darting, has already begun to bear fruit even though it is in its early stages. For instance, in research led by Jenny Tung we identified variation in the *cis*-regulatory region of the baboon *FY* (Duffy) gene that was associated with variation in susceptibility to *Hepatocystis*, a malaria-like pathogen common in baboons (Tung et al. 2009). We also found evidence, in several genes involved in immunity, of allele-specific gene expression patterns (i.e., cases in which segregating genetic variants cause differences in the levels of expression of particular genes), and in one of these genes (*CCL5*) we identified an influence of maternal dominance rank on the extent to which a given *cis*-regulatory variant affected gene expression (Tung et al. 2011). Much of our effort in functional genetic analyses going forward is focused on early life effects on adult gene expression patterns.

12.7 Conclusions

The Amboseli Baboon Research Project, like the other long-term primate studies described in this volume, represents a labor of love. The researchers who have worked on the Amboseli project, particularly its directors, have made enormous personal sacrifices to keep the project going over the long term. Funding for the project has invariably come in grants of short duration, typically 2–3 years but occasionally, when we have been very lucky, 5 years. We have no NGO or endowment, and the intellectual growth of the project depends on us being able to convince grant reviewers that we really do have something new to study every few years (we have fielded questions of the sort “haven’t you studied this species enough yet? Couldn’t this be done more cheaply on captive rodents?”; other authors in this volume have surely had similar experiences). Yet, as Clutton-Brock and Sheldon (2010) have noted, long-term studies of primates and other animals offer our best opportunity for novel and innovative research on behavioral ecology. Our study provides ample evidence of this. The novel maternal and paternal effects we have described, our evidence for the functional importance of female social relationships, the patterns of continuity and change in dominance ranks that we have documented for both sexes and their implications for lifetime fitness, and a range of other results described here, have helped to shape current research in evolutionary ecology in ways that simply would not have been possible for a comparably long series of independent short-term studies. The same is true for the other longitudinal studies described in this volume. And, as we have argued elsewhere, longitudinal studies also offer our best opportunity for understanding the evolution of important traits by combining genetic, phenotypic, and environmental data on the same individuals (Tung et al. 2010). Surely, a challenge for the twenty-first century involves raising the profile of long-term primate studies and ushering in an era in which the value of such studies, as evidenced by the chapters in this volume, are more widely acknowledged.

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Chapter 13
The 30-Year Blues: What We Know and Don't Know About Life History, Group Size, and Group Fission of Blue Monkeys in the Kakamega Forest, Kenya

Marina Cords

Please note the erratum to this chapter at the end of the book.

Abstract Long-term studies uniquely allow researchers to investigate phenomena that play out over long periods, as well as rare events that accumulate slowly into a respectable sample. This chapter takes both approaches in reporting on a 30-year study of blue monkeys (*Cercopithecus mitis stuhlmanni*), reviewing life-history data mainly for females, which can live up to 33 years, and presenting data related to group fission, a rare event. Compared to close relatives, blue monkeys appear to have an exceptionally slow life history, related to low levels of mortality in forest environments. Group fissions show variable patterns, occurring at variable group sizes, and usually involving the splitting of a few family units, including mothers and young daughters. Ecological factors such as feeding competition do not appear to explain why fission occurs, and females do not seem to increase reproductive rates, improve infant survival or reduce the likelihood of male takeovers after fission.

13.1 Introduction

Long-term studies of animal populations uniquely allow two kinds of investigation. First, one can document phenomena that occur over long periods; second, one can examine patterns in rare events, which accumulate slowly. This chapter takes both perspectives in reporting on a 30-year study of blue monkeys (*Cercopithecus mitis stuhlmanni*), an African forest-dwelling guenon.

Most African guenons have not been well studied even on a short-term basis. Most likely, this reflects the practical difficulties of observation in the forested habitat that most species inhabit: dense vegetation, rather small body size, hairy faces, and the fact

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that many are hunted makes field study, and especially individual identification, a significant challenge. Long-term study offers a potential solution because it permits habituation, at least in unhunted populations. Habituation allowed me to address questions and use field methods that were unthinkable at the beginning of our study.

After describing briefly some of the conditions of the study, I first summarize what we know about the life history of this species, based on records from individually identified animals monitored over three decades. This period approaches a natural lifetime. The data allow a robust understanding of basic life-history parameters, at least for females, and contribute to a comparative view of life-history variation in the primate order. Second, I address the related topics of group fission and group size, by examining aspects of the circumstances and consequences of rare fission events. Even after 30 years, the sample is small. The data suggest some common patterns, but also present puzzles that even longer-term study may help to resolve.

13.2 Study Site, Population, and Research History

13.2.1 Study Site

The study population inhabits the Kakamega Forest, western Kenya, a rainforest at 1,765 m with a gazetted area of 238 km^2 (Mitchell et al. 2009). Annual rainfall averaged 1,973 ± 310 mm over the 1979–2009 study period (unpublished KFS and BIOTA records). Combining elements of central African lowland and Afromontane forests, Kakamega is a relatively young forest (~10–12,000 years old), more isolated than many others in the East African region from similar forest patches. This history, together with decades of human influence (Mitchell 2004), has left the forest as an island amidst densely populated farmland, and diverse in the vegetative assemblages represented. Of the total gazetted area, less than half is natural forest, with the remaining portion plantation, bush- and grassland, and even farmland.

Our ~2 km^2 study site, located around the Isecheno forest station (0°14′11″ N, 34°52′02″ E), comprises mainly near-natural and old secondary forest (Fig. 13.1). This area was selectively logged in the 1930s, with enrichment planting of some indigenous species and some exotic species (which largely failed) in the 1940s (Mitchell 2004; see Watts (2012), for a similar history in another East African forest). Trees with the highest importance values ($\geq$1.4, where IV = unitless sum of relative density, relative basal area and frequency, with 3 as a maximum value; Grieg-Smith 1983) in each monkey home range include *Antiaris toxicaria* and *Trilepisium madagascariensis* (Moraceae), *Croton megalocarpus* (Euphorbiaceae), *Funtumia africana* (Apocynaceae), *Olea capensis* (*Oleaceae*), and *Polyscias fulva* (Araliaceae; Card 2010). In the last 5 years, after several group fissions and home range shifts in the study population, we have added other forest types to the areas occupied at least sometimes by certain study groups, including mature (70 year old)

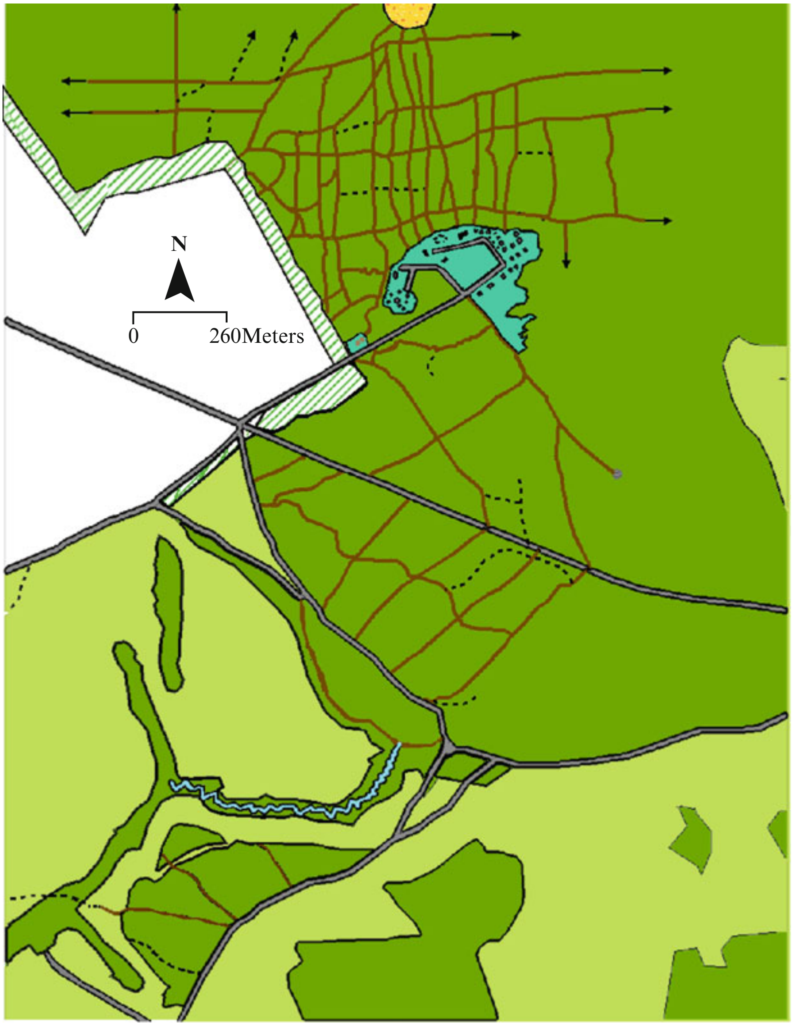

Fig. 13.1 The Isecheno study area. *Dark green* area shows forest cover (habitat used by *blue monkeys*), with footpaths used by researchers indicated in *brown*, dirt roads in *grey*. *Pale green* shows scrubland with some scattered trees, which the monkeys rarely cross; these areas of government land have varied histories, some having been plantations and/or areas of shifting cultivation. *Green striped area* represents a tea plantation ("Nyayo tea zone"), added in 1986, and white areas adjacent to tea show areas of human habitation with small-scale agriculture (private land). The forest station is indicated in turquoise. *Small yellow* area at top of the figure shows a natural grassland

"mixed plantations" (Mitchell et al. 2009) where *Prunus africana* and *Zanthoxylum gilletti* are the two most important species, and exotic plantations of *Bischofia javanica*, *Cupressus lusitanica*, *Grevillea robusta* and *Pinus patula*, all of which offer food to blue monkeys.

The Kakamega Forest as a whole has undergone significant habitat change even over the 30 years of this study, with anthropogenic increases in fragmentation and forest loss in many areas, and successional recovery in others that are better protected (Lung and Schaab 2006). The actual study area used for primate research appears to have been somewhat buffered from these forest-wide trends, probably because of its proximity to the forest station and perhaps because of the long-term presence of researchers (Fashing et al. 2004). Locally, habitat change has mainly taken the form of occasional (and illegal) tree- and liana-cutting. Two more major changes during the 30-year study include the 1986 razing of 60 m of edge forest to create the Nyayo tea zone, intended as a buffer area, and the 2008 razing of 20 m of forest along two roads passing through the study area for installation of power lines. Establishment of the tea zone decimated what was likely a considerable portion of the home range of what became one of our study groups 6 years later, but details of its effect on the monkeys are unknown as this group was not being closely monitored at the time. The 2008 cutting of forest for power lines led the three affected groups to change their ranging behavior, with each expanding into areas that were seldom or never used previously.

Natural predators of blue monkeys still occur in the forest. Alarm responses to raptors are common, typically a near daily occurrence. The African crowned eagle (*Stephanoaetus coronatus*), a confirmed predator elsewhere (Lawes et al. in press), is regularly if rarely seen, most often in aerial displays. In the first years of the study, I witnessed actual eagle attacks, but these have become much less frequent; it is possible that eagles prefer to hunt monkeys that are not as close to humans. The only witnessed predation involved a Gaboon viper (Förster 2008). We have occasionally observed humans, accompanied by dogs, hunting monkeys illegally. Circumstantial evidence suggests that a few of our study animals were killed by such hunters.

13.2.2 The Primate Community and Study Population

Common members of the Kakamega primate community include blue and redtail (*Cercopithecus ascanius*) guenons, as well as guerezas (*Colobus guereza*), which are the most commonly sighted diurnal species (Fashing and Cords 2000) and pottos (*Perodicticus potto*), which are regularly seen at night (K. Davey, W. Okeka, and E. Pimley personal communication). Rare or spatially restricted species include de Brazza's monkey (*Cercopithecus neglectus*) along particular river courses (Muriuki and Tsingalia 1990; Chism and Cords 1997/1998), olive baboons (*Papio hamadryas anubis*), and the occasional vervet (*Chlorocebus aethiops*; personal observation). Of these, deBrazza's monkeys are the only species never observed in our study area, which does not contain the riverine habitat they favor. While the more common species have been the subject of detailed study (Cords 1987; Wahome et al. 1993; Fashing 2001a, b, c, 2002; Chapman et al. 2002; Fashing et al. 2007), long-term individual-based records are available only for blue monkeys (Cords and Chowdhury 2010). The study population, at 198–242 individuals per km^2, is relatively dense (Fashing and Cords 2000), and it has been holding steady, or possibly increasing slightly, over the study period (Fashing et al. in press).

13.2.3 History of the Study

Blue monkeys at Kakamega live in groups of 7–65 members, with a single adult male most of the time (although other adult males may join during the breeding season, Cords 2002a). When I began research in July 1979, I studied just one group (T) of ~45 individuals (as well as one group of redtail monkeys). The T group fissioned in 1984 (Cords and Rowell 1986), but one daughter group moved into inaccessible habitat by 1989, forcing us to truncate records for these animals. In 1992 we began working with a neighboring group (G), which fissioned in 1999. Three subsequent fissions (2005–2009), described in more detail below (Table 13.1), left us with six groups in the study population in 2009.

Several aspects of the study conditions changed gradually over the three decades. First, the animals became more habituated to human observers, with particularly noticeable changes during the first 15–20 years. Although blue monkeys are primarily arboreal, I sometimes found them in low vegetation and even on the ground during my first 12 months, but they were skittish and retreated into the canopy when I came close. After 20 years, by contrast, the presence of observers seldom had any noticeable effect on their movements or location. Second, increasing habituation facilitated individual recognition, as it allowed the close-up inspections needed to distinguish individuals based on minutiae of their physical appearance. Our study never included any kind of capture or marking for this purpose; instead, we used features such as the shape of the tail end, nose and ears, hairiness of ears, and subtle differences in skin or hair color. For adult females,

Table 13.1 Group fissions in the Kakamega blue monkeys from July 1979 to July 2010

Size of parent group (name)[a]	Date of fission	Size of larger daughter group (name)[a]	Size of smaller daughter group (name)[a]	Fraction of matrilineal family units that broke apart[b]	Ranks of matrilineal units in the smaller group[c]
46 (T)	1984	33 (Tw)	13 (Te)	–	–
49 (G)	Oct 1999	28 (Gs)	21 (Gn)	–	–
61 (Tw)	Apr 2005	44 (Tws)	17 (Twn)	2/12	1, 2*, 3*
37 (Gs)	Oct 2008	30 (Gsa)	7 (Gsb)	2/8	4*, 5*, 6, 8
31 (Gsa)	Nov 2009	22 (Gsaa)	9 (Gsc)	2/5	2*, 4, 5*

[a] Group sizes exclude the resident adult male

[b] See Fig. 13.2 for details

[c] Highest-ranking matriline = 1; asterisks indicate matrilines whose members ended up in different daughter groups

nipple length and coloration, and for males, scars and stiff fingers, were also useful features, documented in recent years with digital photographs. Third, habituation allowed close following of individual animals and more continuous monitoring of their movement and activity patterns. Focal samples would have been unthinkable early on, but were possible by the late 1990s (Pazol and Cords 2005). Some of the results presented below derive from focal animal samples taken in recent years. Fourth, the observation schedule changed: after 2 years (1979–1981) of observations averaging 12 days per month, there followed 16 years in which observer presence was more intermittent, typically 2–5 months of near daily records per year. Beginning in mid-1997, however, observations occurred continually on a near daily basis (Cords and Chowdhury 2010 present further details). Fifth, the research focus shifted, reflecting what was possible logistically. Initially I studied interspecific sociality, examining associations of blue monkeys with redtails (Cords 1987, 1990a, b), and aspects of the mating behavior of adults (Cords 1988, 2002a; Cords et al. 1986). Only after 20–25 years was it possible to conduct detailed studies of social behavior of younger animals (Förster and Cords 2002, 2005; Ekernas and Cords 2007; Cords et al. 2010) and to amass rare events into an informative sample (Cords 2007; Cords and Fuller 2010). Lastly, the number of monitored groups increased throughout the study, from one in 1979 to six in 2009. This increase reflects the facts that greater habituation facilitated observational study generally and that we were motivated to continue monitoring long-studied individuals after natural group fission events.

13.3 Long-Term Data: Life History

13.3.1 *Summary of Life-History Patterns*

Beginning in late-1979, we collected data on births, disappearances and deaths, immigrations and emigrations of individually recognized animals. These data allowed derivation of basic life-history variables for this population (Cords and Chowdhury 2010), especially for females, the philopatric sex. Males emigrate from their natal groups at puberty (7 years; Ekernas and Cords 2007), and thereafter live for several years either alone or in loose associations with other males away from groups with females. After emigration, they therefore become difficult to monitor longitudinally. Here, I summarize the main findings of our study (details in Cords and Chowdhury 2010).

Blue monkeys have an extremely slow life history in the context of other cercopithecines (Cords and Chowdhury 2010). The mean, median, and modal age of first birth for females is 7 years. Most interbirth intervals lasted 24–36 months, averaging 25 months during the later years when observations were not intermittent; in these years, observers were not likely to miss births followed by neonatal death. This figure masks the usual strong effect of the first infant's fate on the interbirth interval, however. The mean interval increased from 18 months ($N = 53$) when the first infant died within 12 months to 31 months ($N = 193$) when it survived the first year (Cords and Chowdhury 2010). Given moderately strong seasonality in births (Cords and Chowdhury 2010), this means that most females produce a new infant after 2–3 years when the first one survives its first year.

Age-specific survivorship showed patterns common to many primates (Fig. 13.2), with higher mortality for infants (23% died, 5% were right-censored, i.e. had unknown fates) and a fairly constant rate of mortality from young adulthood onward. Annual mortality rates for juveniles (aged 2–4 years, all prereproductive) averaged 5 ± 8% ($N = 29$ years), an identical value for annual mortality of adults (aged 5 years or older, 5 ± 5%, $N = 29$ years). The oldest female of known age lived to at least 33.5 years; several others that apparently died of natural causes (as opposed to a few cases in which human intervention was suspected) lived into their late 20s, and several females of this age are alive at the time of writing.

For animals with such long lifetimes, even 30 years is insufficient to document maximal lifespan with a large sample, and an estimate of average lifespan would be biased toward animals that died young. Despite sparse information on old females, our data suggest that female blue monkeys that live into their 20s and beyond may have postreproductive lifespans of several years. The female with the longest known lifespan did not give birth during the last 11 years of her life. Observations were not intermittent, so the long nonreproductive period cannot be attributed to undetected births followed by neonatal death. Other females also had long periods (8.0, 6.4, and 3.7 years) between the birth of their last offspring and their own deaths but intermittent observations, at least in the first two cases, make it impossible to ascertain that intervening births (followed by neonatal death) did not occur. Some other individuals, however, showed no evidence of reduced reproductive

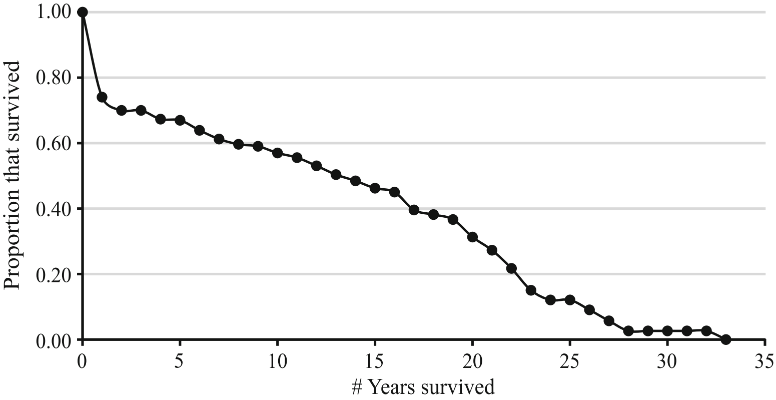

Fig. 13.2 Age-specific survivorship curve, based on minimum survival data from 418 individuals. Age class 0 refers to newborns, 1–0–1 year olds, and so forth. For further details, see Cords and Chowdhury (2010). Reprinted with kind permission from Springer Science + Business Media, Cords and Chowdhury (2010; Fig. 2)

rates even though they lived into their late 20s. Two females lived to ≥27 years and each gave birth for the last time within 2 years of her death.

We evaluated reproductive termination using Caro et al.'s (1995) criterion, by which a female is considered to have terminated reproduction if the difference between age at death and age at last birth exceeds the mean of her interbirth intervals by ≥2 standard deviations. Only 14 females with known or estimated ages died after giving birth at least three times, allowing calculation of mean birth intervals and standard deviation. Two of the 14 terminated reproduction, according to Caro et al.'s criterion. One of these females had the longest recorded lifespan at Kakamega and the other died at about 21 years. However, included in this analysis were four females who we suspected were victims of poaching; if their deaths were thus untimely, they may inflate the number of females that did not show slowdowns at the end of their lives.

Age-specific fecundity rose fairly steeply during years 5–8, and appeared to decrease gradually from about age 13 years (Fig. 13.3). The most advanced age at which a female gave birth was 26 years when we included only females whose ages were known to the nearest year. The fecundity curve shows nonzero values at ages 27 and 28 because there was some probability of a female being 27–28 years old at the birth of an offspring in cases where maternal age was estimated with greater uncertainty (see Cords and Chowdhury 2010 for further details on age estimation). Even though our data spanned a 29-year period, sample sizes for these old females were small.

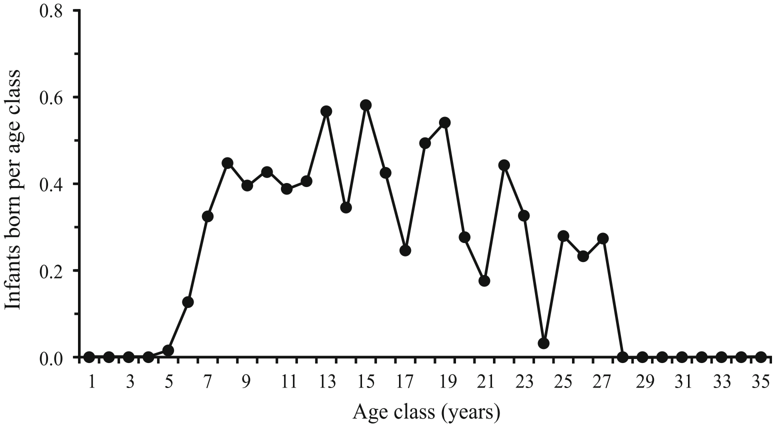

Fig. 13.3 Age-specific fecundity. Data include male and female infants born to 65 females. Greater fluctuations at later ages likely reflect reduced sample sizes. Reprinted with kind permission from Springer Science + Business Media, Cords and Chowdhury (2010; Fig. 3)

13.3.2 Blue Monkey Life History in a Comparative Context

The extreme slowness of the blue monkey life history is apparent when one compares these data with reports from other taxa. Ross (1992a) compiled data from multiple primate species on age at first reproduction, birth rate (interbirth interval), and maximal longevity to estimate $r_{\max}$, the maximum potential rate of population increase. Data came from both captive and wild animals, but it is noteworthy that she identified blue monkeys as the second slowest breeding cercopithecid, after the closely related *C. ascanius*. Only apes had $r_{\max}$ values lower than these two forest-dwelling guenons.

Isbell et al. (2009, 2011) examined Ross' values in the context of body size variation to emphasize the extremely fast life history of patas monkeys relative to their body size. I repeated their analysis, using my data to calculate $r_{\max}$ for blue monkeys ($r_{\max} = 0.11$). As Fig. 13.4 shows, among guenons some species breed considerably faster than expected for their body sizes, and others breed slower. Isbell et al.'s (2009) conclusion about the extraordinarily fast patas monkey is robust: among haplorrhines, only callitrichines have even higher $r_{\max}$ values relative to body size. Blue monkeys join *C. ascanius* and *Miopithecus talapoin* in having $r_{\max}$ values that deviate most negatively from the haplorrhine regression line, i.e. that are the lowest relative to expectations (Fig. 13.4). Thus the guenon tribe of cercopithecines includes both the fastest- and slowest-breeding Old World monkeys in this sample.

Cords and Chowdhury (2010) examined comparative data as well, but limited their consideration to *wild* cercopithecines. Even uncorrected for body mass (and *C. mitis* are among the smaller animals in this clade), blue monkeys had the latest age at first reproduction and were among three species with the longest mean

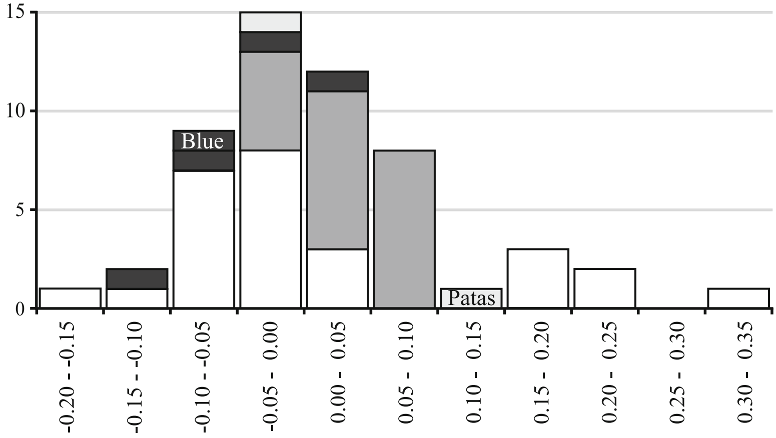

Fig. 13.4 Histogram of residuals of regression between ln body mass and ln $r_{\max}$ for haplorhine primates, using data from Ross (1992a). Forest guenons shown in *black*, open-country guenons in light *grey*. *Dark grey* represents other cercopithecoids, *white* shows noncercopithecoids, i.e., platyrrhines and apes

interbirth interval. Data on mortality after infancy require long-term study and are therefore scarce for wild populations, preventing a thorough analysis. However, a smaller-scale comparison within the guenon (Cercopithecini) tribe, which is thus more phylogenetically controlled, supports theoretical predictions (Promislow and Harvey 1990; Reznick et al. 2002) in relating life-history "speed" to levels of juvenile and adult mortality (Cords and Chowdhury 2010). When adult mortality is relatively high, selection should favor individuals breeding relatively early and often. Savanna-woodland guenons (vervets and patas monkeys) have annual juvenile and adult mortality rates three to six times higher than those of forest-dwelling blue monkeys: for example, Isbell et al. (2009) reported average annual adult mortality of 15% for vervets and 22–33% for patas, while the equivalent figure for Kakamega blue monkeys is only 5%. Similarly, maximal lifespans are very different, with vervets and patas living only into their teens (Isbell et al. 2009), while blue monkeys live into their 20s and sometimes into their 30s. Vervet and patas females first give birth much younger than blue monkeys (3 years patas, 4.5–5.7 years vervets), and interbirth intervals are considerably shorter (13–14 months). Finally, it is worth noting that these differences in life-history characters appear to be evolved ones: Rowell and Richards (1979) compared the same three guenons held in a single captive location and found the same relative patterns of age at first reproduction, interbirth interval and longevity as data from the wild provide.

Environmental variables are expected to affect life-history speed through their effects on mortality rates, but analyses of primate life histories in the context of environmental variation have been somewhat contradictory, perhaps reflecting limitations on both the data (both on the animals and their habitats) and the analytical methods (Ross and Jones 1999). The guenons are an excellent primate group in which to consider how habitat-related variation in mortality drives life-history speed, as this group includes both obligate forest dwellers, such as blue monkeys, and species that inhabit more open savanna-woodland environments. Mortality levels appear to be very different in these environments, even though very little information is available on causes of mortality in forests (Cords and Chowdhury 2010). It would be valuable to corroborate the preliminary cross-species comparisons with data from additional forest-dwelling guenons, but to my knowledge, there are no ongoing long-term studies that include individual-based life-history records. Replicating such analyses with data from wild populations of other primates may occur sooner: the macaques, a similarly species-rich group whose members inhabit a wide variety of habitats, would be good candidates. Indeed, Ross (1992b, but see Ross and Jones 1999), using data largely from captive macaques, found interspecific variation in life-history speed consistent with expectations from variation in the habitats characterizing wild populations. Long-term data from multiple wild populations are not yet available, but should provide an informative comparison.

13.4 Rare Events: Group Fission and Group Size

For social animals that spend their entire lifetimes in single groups, studying the adaptive benefits of group-living is difficult: one cannot experimentally manipulate the variable of interest, and even natural variation may be nonexistent. In blue monkeys, for example, females remain in their natal groups for life, never spending time alone or transferring to new groups. A female's group identity changes only during group fissions and fusions. These events offer a potentially revealing window through which to consider the costs and benefits of group-living (Dittus 1988; Van Horn et al. 2007), as both the circumstances surrounding the fission or fusion, and the way in which individuals realign themselves in new groups, may indicate what makes a group successful or not for its members. Such events are typically uncommon, however, and gathering even a modest sample of occurrences from which to generalize patterns can be a challenge. In 30 years, only five fissions occurred in our study groups, and the first example of a fusion occurred in the 30th year. Here I report on the fission events, and how they may inform an understanding of blue monkey society.

13.4.1 Basic Features of Blue Monkey Fissions

Group fissions occurred episodically over the 30-year period (Table 13.1). The rate of fission would be entirely different if one compared the first vs. last few years of the study. In addition, the critical group size at which fission occurs appeared to be 45–50 animals after the first two fissions (agreeing with reports from another wild guenon, *C. ascanius*; Struhsaker and Leland 1988; Windfelder and Lwanga 2002), but then group Tw grew to 61 animals before it split in 2005. By contrast, the two most recent fissions occurred in groups that were considerably smaller than in previous cases (Table 13.1), suggesting that the processes driving fission are not simple consequences of group size.

A common feature of all group fissions was that the parent group split unequally (see also Perry et al. 2012). The larger daughter group averaged 70% of original group members (Table 13.1). In all cases, the larger daughter group claimed the larger portion of the original group's territory. Another common characteristic of fissions was that one of the daughter groups expanded its territory within a year after the fission, engaging in a series of aggressive intergroup encounters with neighboring groups that had previously occupied the new area. In four of five cases, it was the smaller daughter group, relegated to the smaller portion of the original range, that did this, suggesting that an insufficient supplying area for food drove the territorial expansion. Territory boundaries remained remarkably stable except after fissions: indeed, some boundaries between groups have involved the very same trees over 30 years (Cords 2007). Similar range changes have been reported for redtail monkeys, with range expansion sometimes involving the larger and sometimes the smaller fission product (Struhsaker and Leland 1988; Windfelder and Lwanga 2002).

Unfortunately we had little background knowledge of neighboring nonstudy groups, which would assist a more detailed understanding of how these range expansions come about. A new group that is too small may face particular challenges. For example, 6 months after the most recent fission (2009), the ten-member Gsc group had managed to secure only a very small area of forest (approximately 3 ha) where it had priority over its neighbors. In contrast, other groups typically have areas of exclusive use that are five to ten times larger. The addition of nine new group members to Gsc (two adult females, seven mixed-sex juveniles), in the first fusion ever witnessed in blue monkeys, had not changed this situation 14 months later. Gsc seemed to move through the forest at the mercy of other groups, usually retreating from any they encountered. Struhsaker and Leland (1988) reported a similar consequence for an unusually small (~15 member) group formed after a redtail monkey group fission.

Females appeared to engineer the process of group fission in every case: over a period of days to months, they formed temporary subgroups with unstable membership, with no noticeable increase in aggression (see also Perry et al. 2012). Eventually, they settled into parties that remained apart from one another and aggressively defended their portion of the original group's territory against the new sister group. We have taken the date of the first aggressive territorial encounter between new sister groups as the date of fission in our study. Females also sometimes appeared to take an active role in deciding how the original groups divide. This was most obvious when they directed aggression at one another, seemingly trying to deter a former group-mate from joining their new sub-party. In contrast, no aspect of male behavior suggested that males attempted to influence the process of fission. The adult male resident in the original group joined the larger daughter group twice, and the smaller group three times.

Female cercopithecine monkeys typically remain with their female kin for life. One would thus expect fission to occur along kinship lines, as reported for baboons and several macaques (Dittus 1988; Oi 1988; Ménard and Vallet 1993; Okamoto and Matsumura 2001; Widdig et al. 2006; Van Horn et al. 2007). The three most recent fissions in our study population occurred when we had sufficiently deep pedigree records to evaluate whether close maternal kin (grandmother–granddoffspring, mother–offspring and sibling pairs) remained together after fission. While matrilines generally did stay together, each fission included 2–3 matrilineal units that broke apart (Table 13.1; Fig. 13.5). In six of these seven cases, mothers ended up in different groups than some or all of their daughters, and all six involved the separation of a mother and at least one *juvenile* daughter, even though juveniles are socially close to their mothers as indicated by frequent grooming (Cords 2000a; Cords et al. 2010). The seventh case involved three sisters whose mother was no longer alive at the time of group fission: the youngest (aged 4) did not join her older sisters after the split. A particularly puzzling observation was that one adult female (indicated by an asterisk in Fig. 13.5), abandoned her mother, sisters and 2.4 year old daughter (who was occasionally seen to suckle just weeks

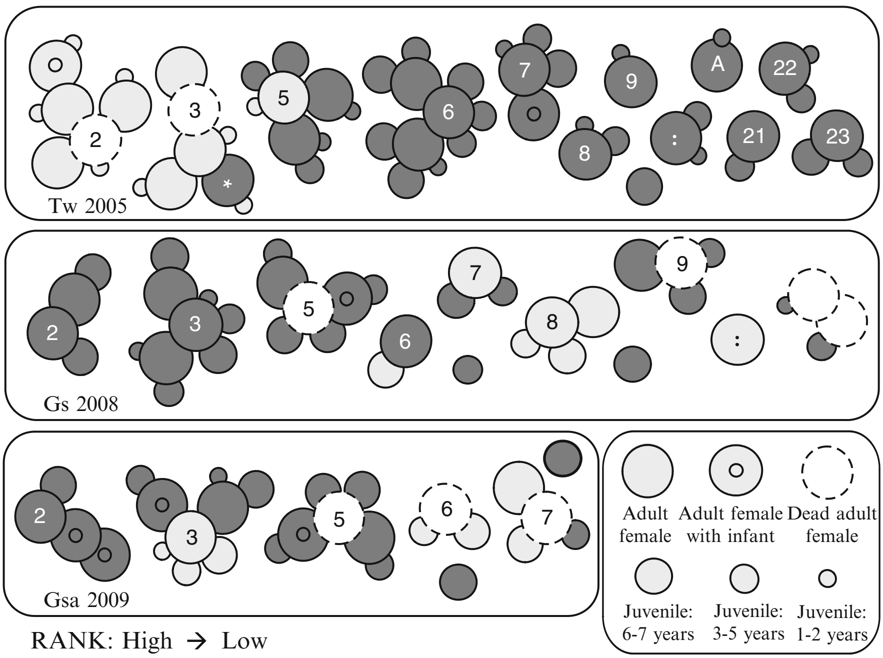

Fig. 13.5 Maternal kinship, rank, and group fission. For each of three fissions, individuals are represented as *circles*, with *shading* (*light vs. dark grey*) indicating group membership after fission, and size proportional to age (see legend). To indicate maternal relatedness, a large circle (mother) overlaps the circles representing her offspring. Matriline rank decreases from left to right, indicated by integer values (1 = highest). Matriline rank was derived from dyadic agonistic interactions among adult females, 9–12 months before fission; matrilines represented only by juveniles therefore have no rank and are randomly placed. Individual marked by *asterisk* is discussed in text

before the split) to become the sole member of her matriline in her new group. Although her family was second-ranking in the original group, and retained this position in their new daughter group, this female sunk to the bottom of the hierarchy in her new group, where she was regularly harassed. She seemed highly motivated to join this group, despite social obstacles and disadvantages. Most oddly, as the two daughter groups engaged in aggressive territorial fights, thus dividing up their former joint territory, this female crossed back on six occasions to fight with her family against the group in which she now lived.

Exceptions to the rule of kin remaining together after fission have been noted in rhesus and Japanese macaques (also capuchins, Perry et al. 2012), and attributed to paternal kinship and social bonds (Van Horn et al. 2007). Analyses now in progress may allow us to evaluate these factors as explanations for the severing of bonds with close kin in our study population.

13.4.2 Group Fission and the Costs of Feeding Competition

Primatologists often interpret group fission as an ecological necessity, inevitable when a group is too large for its individual members to move and forage efficiently because competition for food is too high (Koenig 2002; Sussman and Garber 2007). To see whether data from Kakamega support this interpretation of group fission, I compared movement and time budgets of adult females in groups of different size, and rates of aggression and reproductive output for the same females before and after fission.

As more animals in one place are likely to exhaust the food supply more quickly, larger groups should move farther and faster than smaller ones, or cover larger areas to meet their resource demands, assuming equal food density and abundance (Snaith and Chapman 2007). We examined these predictions using data on group travel, in which an hourly "center of mass" was plotted on a map of the study area, and all $50 \times 50 \text{ m}^2$ quadrats used on a given day were noted. We found no difference in the area occupied per day among groups whose sizes differed up to twofold (Table 13.2a). Furthermore, while the group's daily travel distance varied significantly among three groups, the pattern was opposite the expectation, with the smallest group moving farthest. This pattern was not caused by variation in habitat quality, estimated as the basal area of food trees (m^2/ha), which would lead one to predict even longer routes in larger groups (Table 13.2a).

I also examined travel distances of individual females, as opposed to a center of mass of the entire group, to provide a higher-resolution analysis of foraging effort. Contrary to expectation, however, females in larger groups did not cover longer distances (Table 13.2b). Feeding activity – along with associated movement – has a diurnal rhythm, with peaks in the morning and afternoon hours (Cords 1987). When I analyzed the travel data separately for the morning, midday and afternoon hours, weak group effects emerged for morning and afternoon, but these were opposite those expected, with smaller groups moving farther than larger ones (Table 13.2b). Differences in habitat quality (measured as basal area of major food trees, Table 13.2b) could not explain these results: for example, females in larger groups might in principle reduce travel if they occupied better-quality habitat, but this was not the case. A possible explanation for greater travel in the two smaller groups (TWN, GN) relates to the attractiveness of particular resources at the edges of their home ranges: GN ate soil at a particular spot while TWN used exotic fruiting trees in the forest station.

To examine changes in time budgets, I compared females present both before and after two fissions (Gs group fission in October 2008, $N = 13$ females and Gsa group fission in October 2009, $N = 9$ females). We conducted focal samples (averaging 32 h per female in the 4 months before and in the 4 months after the 2008 fission, and 34 h per female in the 4 months before, 24 h per female in the 4 months after the 2009 fission) in which activity (moving, feeding, resting, social) was noted at 1-min intervals. I conducted before-vs.-after comparisons and present results separately for females in the two daughter groups, since fission might benefit

Table 13.2 Ranging variables and habitat quality for groups of different size

(a)	Gn: 23	Gs: 33	Tw: 46	Comparison
Area used by group (ha/day)	4.12 (2.75–5.73, 35)	4.25 (3.61–5.02, 29)	3.47 (2.62–4.88, 18)	Kruskal–Wallis, $p = 0.302$
Daily travel path of group (m)	733 (590–853, 39)	639 (536–761, 31)	583 (495–646, 17)	Kruskal–Wallis $H = 8.15$ $p = 0.017$
Habitat quality: basal area of food trees[a] (m^2/ha)	49.0	48.4	43.2	–

(b)	Twn: 16.5	Gn: 30.5	Tws: 43	Gs: 47	Comparison
Individual travel: estimated marginal means ± SEM	20.0 ± 1.2	18.8 ± 1.1	17.3 ± 2.5	19.1 ± 2.3	GLMM[b] Group: $F = 0.36$, $p = 0.75$; Period: $F = 6.28$, $p = 0.002$; Month: $F = 14.35$, $p < 0.001$
Individual travel AM (m per 10 min)	20.4 ± 2.2 (98)	23.8 ± 3.9 (130)	11.4 ± 1.7 (55)	16.8 ± 1.9 (23)	GLMM[c] Group: $F = 2.26$, $p = 0.093$
Individual travel MD (m per 10 min)	18.5 ± 2.3 (86)	16.6 ± 1.2 (119)	14.9 ± 3.6 (21)	14.0 ± 3.1 (29)	GLMM[c] Group: $F = 1.02$, $p = 0.383$
Individual travel PM (m per 10 min)	23.3 ± 1.9 (112)	23.1 ± 2.8 (117)	16.3 ± 5.2 (19)	10.7 ± 1.8 (13)	GLMM[c] Group: $F = 2.20$, $p = 0.090$
Habitat quality: basal area of food trees[d] (m^2/ha)	44.0	57.0	54.5	34.3	–

Each group indicated by name and total membership at time of data collection. (a) Area used and travel distance by group on days with ≥10.5 h observations, March–August 2001. Values reported are medians, with inter-quartile range and *N* of days in brackets. (b) Travel distance of individual females in 10 min samples (means ± SEM for each of *N* (in brackets) females). Row 1 shows estimated marginal means for each group as derived from full dataset; rows 2–4 show observed values from each of three periods, morning (AM: 0700–1030), midday (MD: 1030–1430) and afternoon (PM: 1430–1800)

[a] Trees included were the top 30, according to plant feeding records made over an annual period (Cords 1987), and including *Maesopsis eminii* which was identified later as a major feeding tree. These species accounted for 89% of all feeding records

[b] Data from 822 10-min focal samples collected from 54 females in four groups over 8 months (July 2005–May 2006). GLMM included group ($N = 4$) and period of day ($N = 3$) as fixed factors, month as covariate, and individual as random effect

[c] GLMM with auto-regressive covariance structure included group as fixed effect, date as repeated effect, and individual as random effect. Pairwise comparisons distinguished TWS from TWN and GN groups in the morning ($p \leq 0.024$), and GS from TWN and GN groups in the afternoon ($p \leq 0.02$), although these differences became insignificant with Bonferroni correction

[d] Trees included each accounted for ≥0.1% of annual plant feeding records, as per Cords (1987). Together, they constituted 92% of all feeding records

one new group but not the other. In 2008, the five females that ended up in the smaller group showed no significant change in time budgets; for the eight that joined the larger group, moving time increased after fission from 18 ± 6% to 22 ± 8% of point samples (Wilcoxon matched-pairs signed-ranks test, $W = -34$, two-tailed $p < 0.02$), while other activities showed no significant changes. To the extent that moving time varies positively with energetic costs, an increase in smaller groups is just opposite to expectations. In 2009, the smaller group contained only two females, whose shifts in activity did not coincide. The seven females in the larger group increased feeding time (from 44 ± 2% to 48 ± 2%, $W = -24$, two-tailed $p < 0.05$) and decreased resting time (from 26 ± 2% to 23 ± 3%, $W = 28$, two-tailed $p < 0.02$) after fission. If food is harder to find in larger groups, and thus requires greater foraging effort, these changes are also opposite to expectations.

The relationship of contest competition to group fission can be evaluated by mapping dominance ranks onto fission dynamics and by comparing rates of aggression before and after fission. Neither approach suggests a clear relationship between fission and direct competition. We could evaluate dominance relationships for adult females for the four most recent fissions. In two cases (2005, 2008), fission separated higher-ranking from lower-ranking females (Fig. 13.5), although high-ranking matrilines formed the smaller daughter group in 2005 and the larger one in 2008. In the 1999 and 2009 fissions, high- and low-ranking females in the original group did not separate cleanly from one another: daughter groups included both high- and low-rankers, who generally maintained their relative positions in the new groups (Klass 2010; Fig. 13.5; n.b. the 1999 fission is not shown because kinship was not well known).

The lack of a consistent rank-related fission pattern agrees with the observation that the behavioral process of fission did not seem to involve one subgroup (presumably of low-ranking individuals) *seceding* from the main group, as has been reported in other cercopithecines where dominance rank is generally a more important predictor of social behavior (Malik et al. 1985; Dittus 1988). In blue monkeys, high- and low-ranking individuals seem to differ little socially, ecologically and reproductively (Cords 2000b; Pazol and Cords 2005, but see Förster et al. 2011); the lack of clear rank-stratification in group fissions is consistent with this general pattern, and agrees with the report of a single fission in relatively tolerant moor macaques (Okamoto and Matsumura 2001).

Blue monkeys generally exhibit low rates of aggression, but most aggressive acts – more than expected by chance – occur in a feeding context (Cords 2000b; Pazol and Cords 2005), suggesting that females compete directly for food. Therefore we also checked whether rates of aggression received decreased after fission for individuals in our study groups; such a pattern would suggest that fission reduces contest competition. Again we used focal animal data for 4 months before and after two group fissions, in which all aggressive interactions of focal subjects were noted. In one case (Gs fission in 2008), rates of aggression received did not change significantly (Wilcoxon matched-pairs signed-ranks test, two-tailed $p > 0.05$). For the eight females in the larger group, the average rate (±SEM) actually increased from 0.084 (±0.033) to 0.165 (±0.037) acts per hour, but this difference was not significant. Females that ended up in the smaller group received aggression at higher rates than those in the larger group, but the rate did not decrease significantly for them after fission either (before: 0.334 (±0.079), after: 0.309 (±0.092) acts per hour, $N = 5$). Altogether, 9 of 13 females received aggression at higher rates after fission. The results did not change if we considered all aggression, both received and given (data not shown).

In the second case (Gsa fission in 2009), the females that ended up in the larger group received aggression at lower rates after fission (before: 0.100 (±0.032) vs. after: 0.039 (±0.021) acts per hour; $W = 21$, $N = 7$, $p \leq 0.031$), suggesting that contest competition was reduced. Six of seven individuals received less aggression. The two females in the smaller group showed an inconsistent pattern, with one receiving aggression at a higher rate, and one at a lower rate, after fission. For all individuals, results were very similar if we considered all aggression, both received and given (data not shown).

The decrease in rates of received aggression that occurred in one new group after the second fission likely reflected changes in the monkeys' feeding behavior from the pre- to postfission periods. In 2009 only, the proportion of time spent feeding on fruits was lower after fission (median: 7% of observation time) than before fission (11% of observation time; Wilcoxon matched-pairs signed ranks test, $N = 9$, $W = 41$, $p \leq 0.027$); no such decrease occurred in 2008. Aggression occurs disproportionately when blue monkeys feed on fruit (Cords 2000b), so this change in diet might have driven changes in aggression rates. Indeed, rates of aggression relative to time spent feeding on fruit were not different before vs. after fission in either 2008 ($W = 44$, $N = 13$, $p \leq 0.946$) or 2009 ($W = 21$, $N = 9$, $p \leq 0.910$). Overall, then, analyses of aggressive rates did not support the hypothesis that rates of contest competition decreased after fission.

13.4.3 Group Fission and Female Reproduction

Ultimately, behavioral costs and benefits should be reflected in measures of reproductive output. In some cercopithecine monkeys (e.g., redtails: Windfelder and Lwanga 2002; baboons: Altmann and Alberts 2003), but not all, females have shown higher reproductive rates after fission. For three of the later fissions we observed, life-history data allowed us to examine whether reproductive success improved for individual adult females after fission. Figure 13.6 shows the birth rate for females that were monitored 4–6 years before and after three group fissions (1984, 1999, 2005). We deliberately chose a fairly long multi-year window before and after the fission to dampen effects of random variation in a species with interbirth intervals of 2–3 years. None of these comparisons revealed a significant difference (Wilcoxon test, all $p > 0.05$). We also compared rates of infant survival before vs. after fission (2005, 2008), but there were also no differences (Fig. 13.7). Overall, the results from these measures of reproductive success agreed with our behavioral measures in showing no advantage to females living in smaller groups after fission.

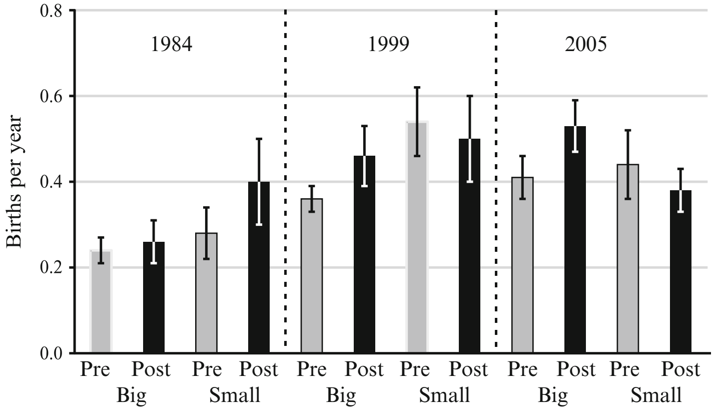

Fig. 13.6 Birth rate of females in big and small daughter groups before and after three group fissions. Females were included only if present both before and after fission for 4–6 years. No differences were statistically significant (see text)

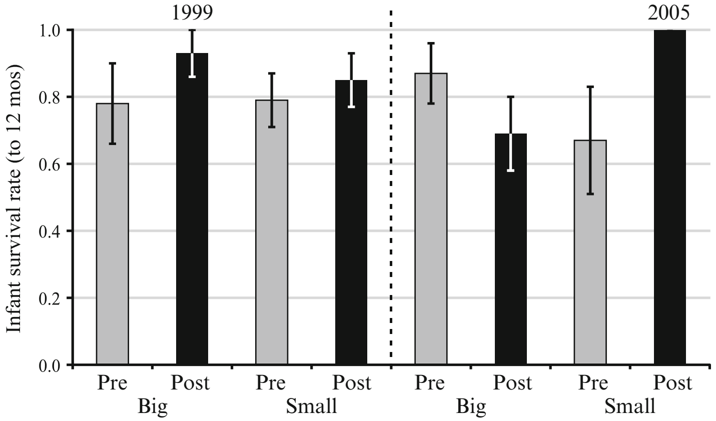

Fig. 13.7 Infant survival (to 12 months) for females in big and small daughter groups before and after two group fissions. Females were included only if they gave birth to at least one offspring within 4–6 years both before and after fission. No differences were statistically significant (see text)

13.4.4 Group Fission and Male Group Membership Changes

However, group size may affect reproductive success in other ways. In some primates, for example, infanticide risk is greater in larger groups (Crockett and Janson 2000). Blue monkey males in this population and others sometimes kill infants when they take over groups (Butynski 1982; Fairgrieve 1995; Cords and Fuller 2010). If group fission reduces the risk of infanticide, male takeovers should occur less often after fission than before. To date, however, there is no evidence that

Table 13.3 Dynamics of adult male group membership before and after group fission

Group and fission date	Parent group	Larger daughter group	Smaller daughter group	Years of observation
(a) Rate of male replacement (# singular resident males per year)[a]				
T 1984	0.2	0.2	0.25	5
G 1999	0.6	0.6	0.6	5
Tw 2005	0.2	0.2	0.4	4.5
(b) Number of breeding season male influxes per breeding season				
T 1984	0.4	0	0	5
G 1999	0.6	0	0	5
Tw 2005	0.8	0.2	0.6	5

[a] Singular male residents lived in the group for some period with no other adult males present, in contrast to some male influx participants who were never the *only* male present

the rate of male takeovers or the occurrence of male influxes during the breeding season (which also introduce unfamiliar males to the group) declines after fission (Table 13.3). Reports of fission in other (redtailed) guenons actually showed increased rates of male membership changes after fission (Struhsaker and Leland 1988; Windfelder and Lwanga 2002).

13.5 Conclusions

Clearly 30 years is not enough to understand fully the group dynamics in a study population like ours. Five fissions is still a small sample. Furthermore, making inferences about the effects of group size based on comparisons of groups that vary in size can be difficult when groups are large and animals are hard to see and habituate. In such cases, the number of groups that researchers can monitor at once is limited. When our study began, we were also unaware that group size varied extensively, given that occasional counts of neighboring groups suggested numbers like those in our single study group. The process of fission, along with background demographic processes influencing age and sex composition, has actually expanded the range of variation in a small cluster of neighboring groups, and raised questions that were not even apparent early on. It took 30 years for us to detect a group with only ten members.

Further research should resolve some of the unanswered questions. While current evidence does not seem to support within-group competition for food as a factor stimulating fission or regulating group size, the advantages of smaller group size might be apparent only episodically or when evaluated over a longer period. The immediate stimulus for group fission may not be ecological disadvantage, but the disorganized and uncoordinated movement that typifies the largest groups (also Perry et al. 2012), or less connected social networks within groups that fission. Also, we have not thoroughly documented the extent of between-group competition, and its relationship to group size. Frequent aggressive intergroup encounters over feeding trees or feeding areas suggest an important role for between-group contest competition. We know already, however, that success in individual inter-group encounters depends primarily on where the encounter occurs rather than on relative group size, with even a single animal from the "home" group able to evict a larger party of intruders from its territory (Cords 2002b). This pattern raises a different question: how are territorial boundaries established, and when do they change? For blue monkeys, group fission is apparently an important part of the answer. Relative group sizes are set at the moment of fission, and group sizes in turn seem to determine territory sizes of the new groups; thus fission provides an opportunity for individuals to reconfigure their distribution – as groups – on the landscape.

Our ongoing study will address such possibilities, as well as the ways in which life-history variables respond to variation in group size. Ultimately, some signal in life history is expected to reflect the benefits that females gain from living in relatively small groups, hence to explain the propensity of groups to fission when they become large. Only long-term data offer the possibility to detect group size effects on fitness in a species with a life history as slow as that of blue monkeys.

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Chapter 14
Long-Term Research on Chimpanzee Behavioral Ecology in Kibale National Park, Uganda

David P. Watts

Abstract Long-term data are crucial for addressing questions about the behavior and ecology of chimpanzees because of their slow life histories. Despite the long history of field research on chimpanzees, the number of sites that have provided long-term data on multiple communities in the same population is still small. Long-term data on two habituated chimpanzee communities in Kibale National Park, Uganda, have provided important insights into variation in chimpanzee behavioral ecology and life-history strategies. Long-term data on diet, phenology, and forest composition indicate that Ngogo is better habitat for chimpanzees; this helps explain why chimpanzee population density is three times higher there than at Kanyawara, why the Ngogo community is three times as large as that at Kanyawara, and why female gregariousness is higher at Ngogo. Both sites have provided important data on sex differences in gregariousness and in space use, on long-term social bonds, on hunting, on intergroup aggression, and on other important topics in behavioral ecology. The large size of the Ngogo community offers valuable insights into demographic influences on behavior and on male reproductive success and into chimpanzee-red colobus predator–prey dynamics. In this chapter, I summarize some of the major findings of this research and compare Kibale data to those from other long-term chimpanzee research sites.

14.1 Introduction

Chimpanzees (*Pan troglodytes*) are well-studied compared to most other primates, as evidenced by other chapters in this volume (Gombe: Wilson 2011; Mahale: Nakamura and Nishida 2011) and by ongoing long-term studies at Taï (Boesch and Boesch-Achermann 2000; Boesch 2009), Budongo (Reynolds 2005), and Bossou

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(Matsuzawa 2002), younger ongoing projects elsewhere (e.g., Kalinzu: Hashimoto et al. 2001; Furuichi et al. 2011; Goualougo: Morgan and Sanz 2006), and multiple shorter studies (reviewed in Stumpf 2007). Phylogenetic closeness to humans makes chimpanzees a favored "referential model" (Moore 1996) for early hominins and partly explains the relatively large number of field studies. Detailed demographic, behavioral and ecological data exist for several chimpanzee populations, sometimes supplemented by noninvasively collected hormonal and genetic data used to address questions about reproductive ecology (e.g., Emery Thompson et al. 2007a), physiological costs of male–male competition (e.g., Muller and Wrangham 2005; Muehlenbein et al. 2004), male reproductive skew (e.g., Wroblewski et al. 2009), and other topics.

Paradoxically, chimpanzees are still poorly understood in many important respects. They are difficult to habituate, partly because fission–fusion sociality makes contacting individuals (especially females) repeatedly and reliably difficult. Like most other primates, chimpanzees have slow life histories; interbirth intervals and maximum lifespan are particularly long (Bronikowski et al. 2011). Thus many years are required to collect adequate data on survival, reproductive success, and other variables for direct tests of evolutionary hypotheses. For example, males compete and cooperate in complex ways within communities, and questions about the fitness consequences of alliance formation, grooming tactics, maneuvering for rank acquisition, and other aspects of male social strategies remain open despite years of study (Muller and Mitani 2005; Mitani 2009a; Fig. 14.1).

Ecological complexity compounds the challenges that social complexity poses for understanding chimpanzee behavior. Chimpanzees eat varied diets, and ecological flexibility allows them to occupy a wide range of habitats (Caldecott and Miles 2005). Variation in food abundance and distribution, predation risk, and socially transmitted extractive foraging techniques contribute to differences in socioecology among and within populations (e.g., greater female gregariousness at Taï than at Gombe or Mahale; Lehmann and Boesch 2009; Boesch 2009). But the number of

Fig. 14.1 Adult male chimpanzees at Ngogo, Kibale National Park, Uganda (Photo © David Watts)

sites with habituated communities is small and most long-term data come from single communities at each, which limits knowledge of within-population variation and hampers assessment and explanation of between-population variation. Researchers at Taï (Herbinger et al. 2001) habituated three adjacent communities, but subsequent population declines due to disease and poaching unfortunately limited comparative study. Mahale researchers habituated two communities, but have followed only one since the demise of K Group early in the study (Nakamura and Nishida 2012). All three communities at Gombe are now under study, but only two are subject to direct observations (Wilson 2012).

In this chapter, I review some highlights of two long-term chimpanzee research projects in Kibale National Park, Uganda. Kibale is the second largest remaining forest in Uganda and has the largest Ugandan population of chimpanzees. It has a long and distinguished history of research on primate behavioral ecology and African rainforest ecology (Struhsaker 1997; Chapman et al. 2005). Chimpanzee research there is now in its third decade at Kanyawara and well into its second at Ngogo. These two study areas are separated by only 10–12 km, but the resident chimpanzee communities differ vastly in size (see Sect. 14.3.1). Long-term comparative data on demography, diet, and the phenology of important food species at both sites thus provide important insights into socioecological variation. Kanyawara–Ngogo comparisons also raise intriguing questions about variation in chimpanzee life-history strategies. Moreover, results of Kibale chimpanzee research are relevant to many issues in behavioral ecology that can only be addressed with long-term data. These include the question of whether members of primate groups maintain consistent, long-term social relationships. Other questions concern hunting and meat eating: chimpanzees engage in group hunts of a variety of prey species, but determining whether hunting and meat transfers are cooperative and investigating predator–prey dynamics requires long-term data. A third set of issues concerns intergroup aggression, which involves within-group cooperation in chimpanzees: inter-group hostility seems universal in chimpanzees and can involve cooperative “patrolling” of territory boundaries and incursions into neighboring territories that sometimes lead to lethal attacks on members of other groups (Wrangham 1999). Patrols and incursions are infrequent events and observations of lethal attacks are rare (Wilson and Wrangham 2003; Mitani et al. 2010; below); thus long-term observations are necessary to assess their functions. Finally, as for most primates, measuring and explaining variation in reproductive success requires long-term data.

14.2 The Study Site: Kibale National Park

Kibale has had protected status since 1932, first as a Forest Reserve and eventually as a National Park. Research is conducted under the auspices of the Makerere University Biological Field Station (MUBFS), which maintains two principle research camps. In this section, I briefly describe research infrastructure, describe the habitat, and summarize the history of research, focusing on chimpanzees.

14.2.1 Research Infrastructure

Researchers require permission from the Makerere University Institute for the Environment and Natural Resources, which operates MUBFS; the Uganda Wildlife Authority, which manages the park; and the Ugandan National Council on Science and Technology. MUBFS maintains research facilities (including extensive trail grid systems) at Kanyawara and Ngogo. Facilities at Kanyawara include concrete houses for researchers, offices, a small library, dormitories used to host students enrolled in Tropical Biology Association field courses and participants in occasional conferences, and power from the main electricity grid. Individual researchers make their own arrangements for lab facilities, sample storage, computer use, etc. Ngogo camp is smaller; researchers stay in wooden houses or tents, have additional open-air work and eating space, and rely on solar panels for electricity and on propane for refrigeration and for freezing biological samples (e.g., chimpanzee urine).

14.2.2 Ecology of Kibale Forest

Kibale is in southwestern Uganda just north of the equator, between 0°13′–0°41′ N and 30°19′–30°32′ E (Fig. 14.2). The habitat follows decreasing north–south gradients in altitude (from 1,590 m to 1,110 m) and rainfall. Data on rainfall and minimum/maximum temperatures are collected daily at both sites by chimpanzee research project personnel and those of other projects; data from earlier research and historic records from nearby Fort Portal are also available (Struhsaker 1975, 1997; Chapman et al. 2010). A typical year includes two rainy seasons (September–November, March–May) and two dry seasons (December–February, June–August), although the amount and timing of rainfall varies considerably among years (Struhsaker 1997; Chapman et al. 2010). Mean annual rainfall at Kanyawara was 1,475 mm between 1970 and 1991 (Struhsaker 1997), but 1,749 mm between 1990 and 2001 (Chapman et al. 2010). Annual rainfall at Ngogo was 1,393 ± 200 mm from 1998 to 2009 (Mitani and Watts, unpublished data).

Kibale is a mid-altitude, moist semi-deciduous forest, with plant species composition and diversity intermediate between lowland and montane African moist evergreen forests (Struhsaker 1975, 1997; Butynski 1990; Chapman and Lambert 2000). The vegetation comprises a mix of old growth forest (about 57% of total surface area; Chapman et al. 2010); anthropogenic grassland; woodland; swamp forest; *Papyrus* swamp; and young forest at various stages of regeneration from human disturbance (Struhsaker 1975, 1997; Butynski 1990; Lwanga 2003; Chapman et al. 2010). Commercial logging occurred in some of the Kanyawara study area from the 1930s until the early 1990s (below); the Ngogo study area was never subjected to commercial logging (Struhsaker 1997) and consequently contains proportionately more old growth forest. However, even old growth forest at Ngogo shows signs of human disturbance (e.g., grindstones on the forest floor),

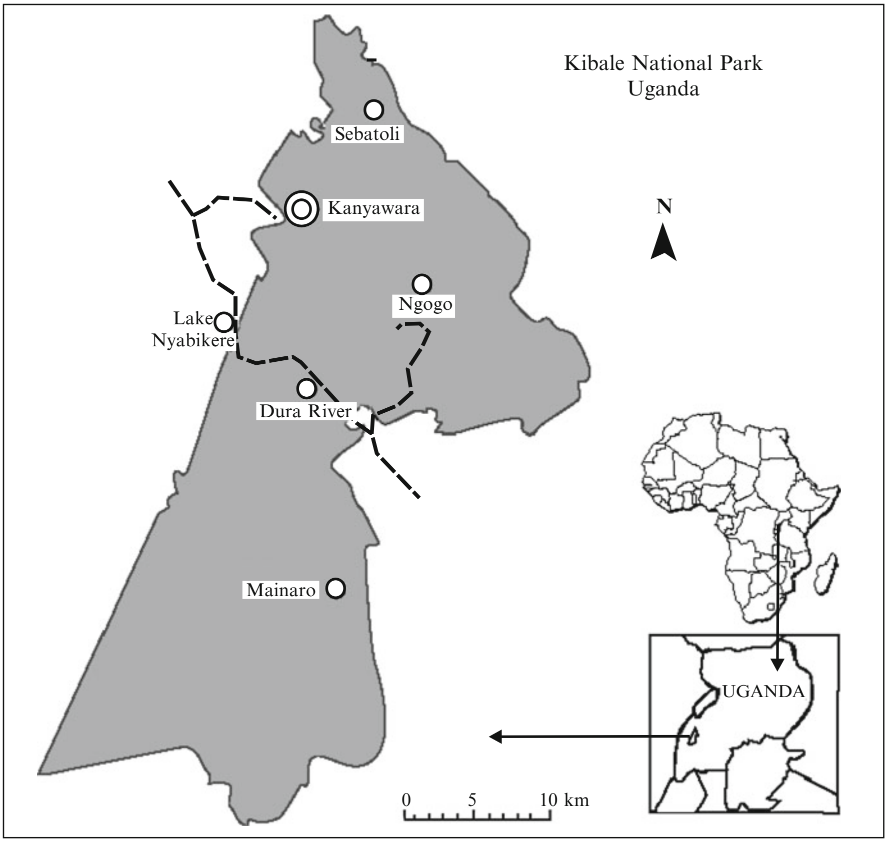

Fig. 14.2 Location of Kibale National Park and of Kanyawara and Ngogo

and Kibale provides a case study of potential forest recovery from anthropogenic disturbance that belies the mythology of "pristine" tropical forests (Struhsaker 1997; Lwanga 2003; Chapman et al. 2010).

Field assistants at both sites collect monthly data on the phenology of important chimpanzee food species. Comparative data on other common tree species, including those important in the diets of monkeys, are available from previous research (e.g., Struhsaker 1997) and other ongoing projects (e.g., Chapman et al. 2005). At Ngogo, the phenology sample includes 20 stems each of 20 tree species from which the chimpanzees eat fruit. These data serve to calculate a monthly ripe fruit score (RFS), given by (Mitani et al. 2002a):

$$\mathrm{RFS} = \sum_{i=1}^{20} p_i \cdot d_i \cdot s_i,$$

where p_i = percentage of the ith tree species possessing ripe fruit, d_i = density of the ith tree species (stems per ha), and s_i = mean DBH (cm) of the ith tree species. The sample includes six fig species, and thus also provides phenology scores for figs and for nonfig-fruit separately.

Phenology data show complex patterns of variation in fruit abundance. For example, on average, 1.17–6.67% of stems of the 20 most common tree species at four Kibale sites fruited per month in each of the 12 years from 1990 to 2001 (Chapman et al. 2005), with no significant difference in the proportion of trees fruiting in wet- versus dry-season months. Inter-monthly variation in the availability of ripe fruit from species important in the Ngogo chimpanzee diet is bimodally distributed, with a moderate peak in May to July and a higher peak in September through December, but inter-annual variation in monthly and total annual fruit availability is pronounced (Mitani et al. 2002a; Watts et al. in press a, b; Fig. 14.3). Fruit production varies more at Kanyawara than Ngogo (Chapman et al. 1999) and many important chimpanzee food species are more abundant at Ngogo (Potts et al. 2009), which helps explain differences in chimpanzee population density between the sites (see Sect. 14.3.1). Some important chimpanzee food species fruit predictably in certain months, although not necessarily annually; for example, *Uvaropsis congensis* has a major fruiting peak around April–June in most years at Ngogo and a secondary peak around November–December in some years (Watts et al. in press b). Fruiting seasonality is less evident or absent in other cases (Struhsaker 1997; Chapman et al. 2005). *Chrysophyllum albidum*, an important chimpanzee food species at Ngogo, is a mast fruiting species; masting events have occurred in 2000, 2005, 2010, whereas in other years since 1995 this species has produced little

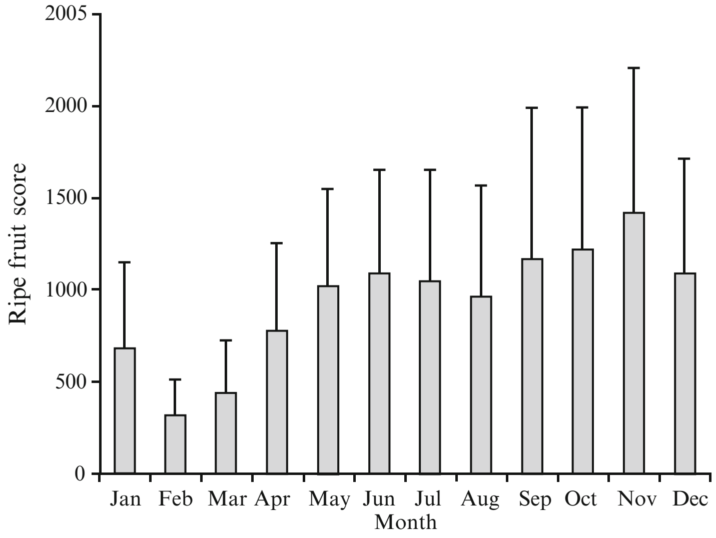

Fig. 14.3 Inter-monthly and inter-annual variation in ripe fruit availability at Ngogo, 1998–2009. Values are monthly mean ripe fruit index scores; error bars show one standard deviation

fruit. Neither the remarkable inter-annual variation in fruit availability nor the gradual changes in tree communities associated with regeneration from human disturbance, the aging of mature forest, and climate change would be evident without long-term phenology data and the rich history of work on vegetation dynamics (e.g., Chapman et al. 1999, 2005, 2010; Struhsaker 1997; Lwanga et al. 2000; Lwanga 2003; Omeja et al. 2009).

Seven diurnal primate species besides chimpanzees occur in Kibale: three guenons (redtailed monkeys, *Cercopithecus ascanius schmidti*; blue monkeys, *Cercopithecus mitis stuhlmanii*; L'hoest's monkey, *Cercopithecus l'hoesti*), two colobines (red colobus, *Procolobus rufomitratus tephrosceles*; black and white colobus, *Colobus guereza*), baboons (*Papio anubis*), and grey-cheeked mangabeys (*Lophocebus albigena*). Vervets (*Cholorocebus aethiops*) occur along the forest margin and in grasslands in some areas. Nocturnal primates include pottos (*Perodicticus potto*), Demidov's dwarf galago (*Galagoides demidovii*), and the eastern needle-clawed bushbaby (*Galago inustus*). Leopards might have preyed on chimpanzees historically, but are now absent. Kibale is home to a variety of forest ungulates, including several on which chimpanzee prey (blue duiker, *Cephalophus monticola*; red duiker, *Cephalophus callipygus*; bushbuck, *Tragelaphus scriptus*; bushpig: *Potomochoerus porcus*; Watts and Mitani 2001), and to diverse rodent, avian, and invertebrate faunas (reviewed in Struhsaker 1997). Elephants are abundant; their feeding on saplings and pole-sized stems and trampling of seedlings influences forest structure and, combined with rodent and insect predation on seeds and seedlings, can prevent forest regeneration in large gaps (Struhsaker et al. 1996).

14.2.3 A Brief History of Kibale

The Government of the Uganda Protectorate gazetted Kibale as a Crown Forest, to be managed for timber production by the Uganda Forest Department, in 1932 (Struhsaker 1997). Management included various intensities of selective commercial logging in some forest compartments and clear-cutting and replacement of native species with plantations of exotic pine and cypress in some others, while other areas were left intact or subjected to only small-scale pit sawing for local use. The Kanyawara area experienced a mix of all these options. In contrast, the Ngogo area was not subject to commercial logging, although it shows other effects of human disturbance (e.g., anthropogenic grasslands). Struhsaker (*ibid.*; cf. Omeja et al. 2009) provides a detailed history of how logging affected vegetation composition and populations of arboreal cercopithecoid primates, ungulates, and rodents, and summarizes the conflicts between wildlife conservation and management for timber extraction.

Conflict heightened in 1964 with the establishment of a wildlife corridor between Kibale and Queen Elizabeth National Park to the southwest, but was resolved in 1993, when Kibale was declared a National Park. This brought it under the administrative control of the Uganda Wildlife Authority, ended all legal timber extraction once remaining plantation forest had been clear-cut, and shifted management priority to wildlife and habitat protection and ecotourism development. Recent research by Omeja et al. (2009) has shown that the forest is regenerating naturally in previously clear-cut areas at Kanyawara, and that enrichment planting of indigenous trees does not improve regeneration success. Likewise, Jeremiah Lwanga's (2003) work at Ngogo shows that forest can regenerate from grassland naturally so long as animal seed dispersers are still present and the young forest/grassland mosaic is protected from fire.

In 1970, Thomas Struhsaker initiated the Kibale Forest Project at Kanyawara; in 1972, he established a second research area at Ngogo, in the forest interior (Struhsaker 1975, 1997; Fig. 14.2). His primary focus was forest ecology and the behavioral ecology of red colobus monkeys (Struhsaker 1975, 2010), but he also studied the behavior ecology of redtailed monkeys and grey-cheeked mangabeys and the effects of logging. Since 1971, many expatriate and Ugandan students, often mentored by Struhsaker, and many independent researchers have studied primate behavioral ecology, forest dynamics, rodent population biology, elephant ecology, and other topics (Struhsaker et al. 1996; Chapman and Chapman 2000).

Notable among the numerous long-term research efforts besides Struhsaker's is work on primate ecology, complemented by regular primate censuses, by Colin Chapman and his students. This has mainly focused on Kanyawara, but covers multiple sites, including forest fragments outside the park (e.g., Chapman et al. 2002). Among its important results has been demonstration of unexpectedly high within-habitat variation in red colobus diet composition and food nutritional quality (Chapman et al. 2002, 2010). To summarize this rich body of research and the many other long-term Kibale projects is beyond the scope of this chapter, but it is clearly important for understanding chimpanzee behavioral ecology and for conservation.

14.2.4 Chimpanzee Research

Michael Ghiglieri conducted the first Kibale chimpanzee research, at Ngogo, in 1976–1978 (Ghiglieri 1984, 1986). He collected valuable information on diet opportunistically and by watching large trees that had attractive fruit crops, especially figs. He confirmed that chimpanzees at Ngogo had a fission–fusion social system and that males were relatively highly gregarious, and he noted that males associated and groomed more with each other than with females (Ghiglieri 1984). However, limited habituation prevented him from following the chimpanzees consistently or from obtaining accurate information on community size and composition. He did not see chimpanzee hunts, nor did he see boundary patrols or interactions with neighboring communities (*ibid.*). This was ironic given later documentation of extremely high predation on red colobus and of high rates of patrolling and lethal inter-community aggression at Ngogo (see Sects. 14.3.4 and 14.3.5), especially because Power (1990), citing Ghiglieri, argued that the supposed absence of hunting and lethal intergroup aggression at Ngogo showed that such behaviors at Gombe and Mahale were artifacts of disturbance by humans.

A hiatus on chimpanzee research at Ngogo followed Ghiglieri's fieldwork. Meanwhile, Gilbert Isibirye-Basuta initiated research on chimpanzee behavioral ecology at Kanyawara in 1985. He habituated the chimpanzees sufficiently to gather quantitative data on diet, on the relationship of party size to food patch size, and on how gregariousness varied in relation to variation in fruit abundance (Isibirye-Basuta 1989). Subsequently, Richard Wrangham started the Kibale Chimpanzee Project at Kanaywara in 1987. The Kanyawara chimpanzee community has been observed continuously since then and its members have been well habituated for most of that time. Under Wrangham's direction and, since 2008, the co-direction of Martin Muller, researchers affiliated with the project have studied many aspects of behavior and ecology (e.g., male behavioral endocrinology: Muller and Wrangham 2004a, b; competition between resident and immigrant females: Kahlenberg et al. 2008a, b) and compiled a long-term demographic and life-history data base that substantially adds to comparative data from other long-term chimpanzee research sites (Emery Thompson et al. 2007b; Hawkes 2010).

Chimpanzee research resumed at Ngogo in 1991 when Bettina Grieser-Johns, helped by expatriate research assistants and a Ugandan field assistant, started habituation efforts (Grieser Johns 1996). Simultaneously, R. Wrangham and C. Chapman employed four other Ugandan field assistants to work on habituation and to conduct comparative research on chimpanzee and baboon feeding ecology that combined direct observational with collection of fecal samples (Wrangham et al. 1991). David Watts spent 2 months at Ngogo in 1993 to investigate prospects for a long-term study; he returned with John Mitani in 1995 to initiate the Ngogo Chimpanzee Project. In collaboration with Jeremiah Lwanga (since 1997) and with the help of doctoral and postdoctoral researchers and Ugandan field assistants, they have since maintained a continuous research presence. Steady progress with habituation led to the identification of all community members; to extensive databases on hunting, meat eating, and inter-community aggression; and to detailed studies of feeding ecology, mating strategies, and many aspects of social relationships. At 16 years, the Ngogo demographic and life-history database is still shallow, but it allows preliminary comparisons with data from other chimpanzee research sites (see Sect. 14.3.2).

Both chimpanzee research projects have provided extensive research and training opportunities for Ugandan scientists. For example, Emily Otali received her doctorate from Makerere University for research on chimpanzee social behavior at Kanaywara and is currently (2010) Project Manager for the Kibale Chimpanzee Project. Jeremiah Lwanga, who had earlier done Master's research (Makerere University) on blue monkey behavioral ecology and doctoral research (University of Florida) on forest ecology in Kibale, became Project Manager for the Ngogo Chimpanzee Project in 1997; he is currently (2010) Interim Director of MUBFS. Both projects have sponsored Master's research by Makerere students. Researchers and Project Managers at both sites work with UWA officials and park rangers to help coordinate anti-poaching efforts, and the research projects have contributed formally and informally to financing these efforts and to maintenance of park infrastructure. Researchers provided information and advice that facilitated successful habituation of chimpanzees for tourism at Kanyanchu, a Kibale site reserved for that purpose, and they participate in planning of park management strategy and of chimpanzee and forest conservation efforts in Uganda. As at other African research sites where great apes are habituated, research and tourism bring risks of disease transmission from humans, but also help to protect the animals and their habitats (Köndgen et al. 2008).

Some individual research projects have focused on feeding ecology (e.g., Wrangham et al. 1998; Potts 2008), and Ugandan field assistants at both sites routinely collect data on diet via scan sampling; these data plus phenology records allow long-term assessment of dietary variation. Field assistants systematically collect data on party size and composition, home range use, and aspects of social behavior on a near-daily basis and collect data specific to particular research questions on an as-needed basis. All researchers and field assistants contribute to long-term demography and life-history data bases and provide data on uncommon, but important events such as hunts and meat eating, boundary patrols, and inter-community interactions. Kanyawara researchers have established a relational database that covers many aspects of behavior and ecology (e.g., diet; Gilby et al. 2010b) and a website with information about research and conservation (http://www.fas.harvard.edu/~kibale/index.html). Ngogo researchers have not yet developed such resources, nor have all aspects of data collection been standardized between Kanyawara and Ngogo; collaboration in data collection and management should be a priority for the future.

14.3 Important Results of Long-Term Research

14.3.1 Feeding Ecology, Community Size, and Population Density

Gaining accurate information on community size and composition and on the size of the respective home ranges required years of effort. Since the late 1980s, the Kanyawara chimpanzee community has numbered about 40–55, including 8–12 adult males. In contrast, the Ngogo community has had from about 142–165 members, with between 22 and 32 adult males; these numbers are unprecedented in chimpanzee research. The home range of the Ngogo community was about 29 km^2 between 1998 and 2009 (Mitani et al. 2010). The Kanyawara community has a home range of about 35 km^2 (Emery Thompson and Wrangham 2008); thus, chimpanzee population density is three times higher at Ngogo. Such large differences in community size and population density are startling given the proximity of the sites and caution against assuming that data on the behavioral ecology of a single community represent its population. They would not have been evident had research lasted only a few years, nor would the large extent of the contrasts in forest ecology and chimpanzee feeding behavior over this small geographic scale that help to explain them.

Studies of primate feeding ecology typically span a single annual cycle, but even several years may be inadequate to document the full range of dietary flexibility in species that have diverse diets and in whose habitats food availability does not follow predictable annual cycles. Long-term Kibale data are consistent with those from other sites indicating that chimpanzees are highly frugivorous, but also highlight the absence of universal constraints on their foraging strategies. Fruit, including figs, accounts for most chimpanzee feeding time at both sites (Fig. 14.4; Conklin-Brittain et al. 1998; Wrangham et al. 1996, 1998; Potts et al. 2009; Watts et al. in press a).

At Kanyawara, data from one annual cycle showed that feeding time devoted to nonfig fruit was positively related to its abundance, consistent with the argument that chimpanzees are ripe fruit specialists (Wrangham et al. 1998). Long-term data from Ngogo substantiate this finding: the percentage of feeding time devoted to nonfig fruit was positively related to its abundance over a 125-month period (Watts et al. in press a). Figs also have great importance and account for the second highest percentage of chimpanzee feeding time at both sites (Wrangham et al. 1993; Watts et al. in press a). More detailed consideration of fig use shows a crucial difference between the sites, however: figs from *Ficus mucuso* are quantitatively the most important food at Ngogo, whereas this species is absent at Kanyawara. Availability

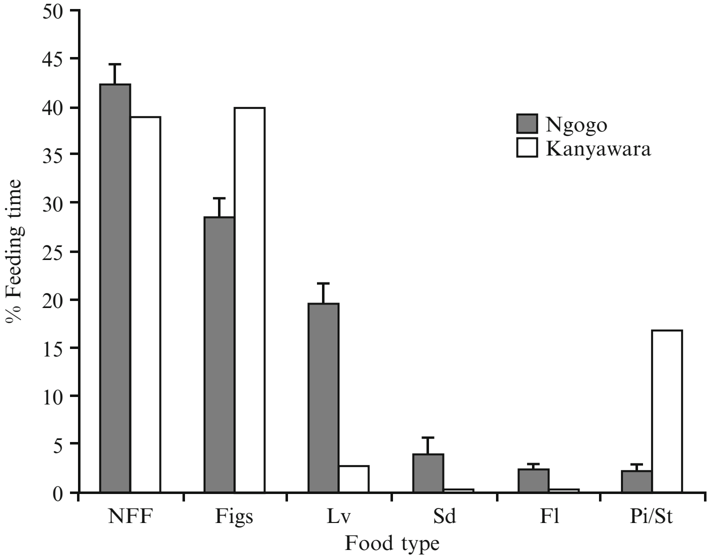

Fig. 14.4 Percent of annual feeding time devoted to major plant food categories at Ngogo and Kanyawara. Ngogo data cover eight consecutive years; data from Kanaywara cover four consecutive years (Wrangham et al. 1996). Column height shows annual mean; error bars give 1 sd for Ngogo data. *NFF* non-fig fruit; *Figs* all fig species; *Lv* leaves; *Sd* seeds; *Fl* flowers; *Pi/St* pith and stems. Minor items (e.g., rotting wood) and meat not included

of figs from *F. mucuso*, which fruits nonseasonally, is independent of the availability of nonfig fruit, and the proportion of feeding time devoted to *F. mucuso* varies inversely with time feeding on nonfig fruit. It is thus a "filler" fallback food, *sensu* Marshall et al. (2009). Kanyawara chimpanzees also use figs as fallbacks (Wrangham et al. 1993), but no species there provide the enormous fruit crops of *F. mucuso*, which has a relatively high stem density in the Ngogo study area and produces some fruit during all months of an average year. Terrestrial piths and stems are also fallbacks at Kanyawara (Wrangham et al. 1993), but not at Ngogo, where leaves supplement figs as fallbacks (Watts et al. in press b). Leaves of *Pterygota mildbraedii* saplings, which are highly abundant at Ngogo, are among the most important foods there, and seeds from the fruit of mature *P. mildbraedii* are also important; this species is virtually absent at Kanyawara. In all, chimpanzees at Ngogo devote most of their feeding time to foods that, for reasons that are not well understood, are common there but rare or absent at Kanyawara (Potts et al. 2011; Watts et al. in press a).

Observational data on diet composition are also available from studies at six other chimpanzee research sites, most covering much shorter periods than studies of feeding ecology in Kibale (summarized in Morgan and Sanz 2006). Considerable cross-site variation exists, but inter-annual variation in Kibale nearly encompasses the total range. For example, the proportion of annual feeding time devoted to fruit (including figs) varies from 59% (Gombe: Wrangham 1977) to 87% (Ngogo, females only: Wakefield 2010); data collected independently of Wakefield's (*ibid.*) at Ngogo gave a community-wide range of 63.4–76.2% over eight consecutive years (Watts et al. in press a), and Kanyawara values over four consecutive years varied from 74.5% to 84.5% (Wrangham et al. 1996). Such extensive variation in one population highlights chimpanzee ecological flexibility.

14.3.2 Female Reproductive Ecology and Life-History Strategies

Emery Thompson and Wrangham (2008) used 12 years of data on ovarian steroid hormones, female reproductive parameters, fruit availability, and diet to show that ovarian functioning of "central" females at Kanyawara varied with their intake of drupaceous fruit and that they were more likely to cycle and to conceive when drupe intake, and thus relative energy intake, was high. Long-term Kanywara data also show inter-individual variation in ovarian function and reproductive rates associated with variation in female core area quality (Emery Thompson et al. 2007a) and dominance ranks (Kahlenberg et al. 2008b), presumably due to variation in net energy intake mediated by differential access to good feeding areas and to individual feeding sites. Given lower variation in fruit availability at Ngogo (Chapman et al. 1999), questions arise concerning whether Ngogo female reproductive rates are higher than those of Kanyawara central females, mirroring the faster central vs. slower "northern" Kanyawara female contrast (Emery Thompson et al. 2007a), and whether survivorship is higher at Ngogo. These are important with regard to reconstructions of human life-history evolution that compare pooled chimpanzee data from Gombe, Mahale, Tai, Bossou, and Kibale-Kanyawara to data on recent hunter–gatherers (e.g., Kaplan et al. 2000; Hawkes 2010). The chimpanzee data show a population in decline, a condition that cannot have held over evolutionary time (Hill et al. 2001).

Preliminary Ngogo data indicate that reproductive rates may indeed be high. Ngogo records now include 20 completed intervals between the birth of a surviving infant and the birth of the female's subsequent infant. Mean interbirth interval length is 62.9 months ($sd = 8.31$, $median = 63$ months). This is significantly shorter than the mean of 69.1 months ($sd = 8.58$, $median = 68$ months) for 31 intervals at Mahale (Nishida et al. 1985; unpaired t-test, $t = 2.52$, $df = 49$, $p = 0.015$), and shorter, although not significantly so, than the mean of 69.1 months ($sd = 17.4$, $median = 65$ months) for 33 intervals at Taï (Boesch and Boesch-Achermann 2000; unpaired t-test, $t = 1.75$, $p = 0.087$). The Ngogo mean is substantially lower than the mean of 73 months ($sd = 13.5$) for central females at Kanyawara (Emery Thompson et al. 2007a), although the Kanyawara values include incomplete intervals and are thus not directly comparable. The mean length of completed intervals following surviving births at Gombe is around 6 years (Fig. 1 in Jones et al. 2010). Excluding censored intervals tends to decrease estimates of interval length (*ibid.*). Still, a Kaplan–Meier survival analysis of Ngogo data that includes incomplete intervals of at least 24 months ($N = 48$) yields a median interval of 62.5 months, considerably shorter than the means for Kanyawara and Gombe. Restricting the analysis to incomplete intervals of at least 48 months, as Emery Thompson et al. (2007a) did for Kanyawara, also gives a median of 62.5 months.

Infant survival to 1 year is not unusually high at Ngogo (77.6% of 98 births, including three within-community infanticides), nor is survival to 5 years (71.8% of 75 births) high compared to Kanyawara (c. 85% survival to 5 years; Emery Thompson et al. 2007b) or to Taï before predation and disease epidemics greatly increased mortality (88% survival to 5 years; Boesch and Boesch-Achermann 2000). However, mortality at Ngogo has been concentrated among known first offspring (9/15 births, including one infanticide) and has been lower for infants of multiparous females. Perhaps females respond to favorable ecological conditions by starting their reproductive careers before they are fully grown, then face tradeoffs between investing in offspring growth or in their own growth and survival, as Altmann (1980) described for baboons. In contrast, adult female survival seems relatively high at Ngogo. Assigning females to 5-year age categories based on known or estimated ages and calculating deaths per female per year gives an approximate value of 69.9% survival to age 30, considerably higher than the value of 46% that Emery Thompson et al. (2007b) calculated using data from five other sites. However, this tentative result awaits confirmation with longer-term data and proper comparative analysis.

14.3.3 Social Relationships

Long-term research confirms Ghiglieri's (1984) inference that on average, males are more gregarious than females in Kibale (Mitani et al. 2000; Gilby et al. 2008; Langergraber et al. 2009). However, habituation led to the realization that Ngogo females are generally more gregarious than those at Mahale and Gombe and as gregarious as those at Taï, which shows that no east/west dichotomy of female chimpanzee gregariousness exists. Also, variance in "pairwise dyadic affinity" indices is higher for males than females, with both the lowest and the highest values belonging to female dyads (Langergraber et al. 2009).

Males invest considerable effort in competing for status and form dominance hierarchies (Watts 1998; Watts and Mitani 2001; Muller and Wrangham 2004a, b, 2005; Mitani 2009a). Male rank is positively related to reproductive success at Ngogo, but reproductive skew is low, as expected given the large number of males (Langergraber et al. 2010; cf. Wroblewski et al. 2009). Male–male social relationships are differentiated, with some dyads associating in parties, remaining in close proximity, grooming, and forming coalitions more than others (Watts 2000a, b; Mitani et al. 2002b; Langergraber et al. 2007; Gilby et al. 2008; Mitani 2009a, b). Ngogo has provided some of the most extensive data on social exchange among male chimpanzees: males show reciprocity in grooming, coalition formation, and meat sharing and interchange between grooming and coalitionary support, grooming and meat sharing, and coalitionary support and meat sharing (Watts 2000b, 2002; Mitani and Watts 2001; Mitani 2009a). Males also engage in boundary patrols most often with others who are their main grooming and coalition partners and with whom they most often participate in hunts (Watts and Mitani 2001).

Langergraber et al. (2007) used noninvasive genetics sampling at Ngogo to help resolve long-standing questions about the influence of kinship on male–male social relationship. Compared to chance expectations, maternal brothers associated in the same parties more, spent more time in close proximity, groomed more, and formed coalitions, shared meat, and jointly participated in boundary patrols more often. However, most dyads with high scores on these measures were nonrelatives. No evidence of paternal kinship effects exists yet, although this is a subject of ongoing research.

Long-term data on male social relationships support the argument that nonhuman primates establish and maintain social bonds – i.e., invest differentially in social relationships with particular individuals (Silk 2007; Silk et al. 2010) – rather than merely interacting in biological markets in which individuals seek to maximize net gains from competitive and cooperative interactions, and differentiation of social networks reflects variation in partner availability and value (Henzi and Barrett 2007). Social exchange and alliance formation between male chimpanzees is consistent with biological markets theory, but males at Ngogo also show long-term consistency in association and grooming and considerable consistency in coalition formation (Mitani 2009b), although alliances form and dissolve tactically (Watts and Mitani unpublished data). Male dyads also show long-term consistency in party association and time spent in close proximity at Kanyawara, although association patterns underwent considerable realignment following a change of alpha males (Gilby and Wrangham 2008). Data on long-term consistency in grooming and coalition formation at Kanyawara are not yet available.

Female dyads at Kanyawara also show long-term consistency in association (*ibid.*), a finding at odds with the standard idea that female–female social bonds are unimportant in eastern chimpanzees. Frequent and consistent association between some female dyads may help them to maintain relatively high quality core areas and to resist attempts by immigrants to establish core areas: residents are often aggressive to new immigrants and males often intervene in such female–female conflicts to protect recent immigrants (Kahlenberg et al. 2008b). Data on fertility and infant survival at Kanyawara indicate that female lifetime reproductive success should vary positively with core area quality (Emery Thompson et al. 2007a). Joint harassment of immigrants may represent mutualism: females who often associate for other reasons are acting in self-interest, but their interests are similar.

Females at both Kibale sites form spatial “neighborhoods” (Emery Thompson et al. 2007a; Wakefield 2008; Langergraber et al. 2009). At least at Ngogo, social cliques form; these comprise females who associate more often than expected by chance, independently of core area overlap, and who often groom each other (Wakefield 2008). Thus females have differentiated social relationships similar to those at Taï (Boesch and Boesch-Achermann 2000; Lehmann and Boesch 2008, 2009). We do not have long-term quantitative data on Ngogo females to rival those on males, but some female cliques apparently can persist for over a decade (although not necessarily with constant membership) and some preferred partnerships last for many years.

Long-term data on habitat use and demography at Ngogo, combined with paternity sampling, have revealed unexpected complexity in male socio-spatial and reproductive strategies. As at other eastern chimpanzee research sites (e.g., Mahale), males range more widely than parous females and use all of the territory. However, individuals tend to use the territory unevenly and to form spatial subgroups, and grooming and coalition formation is more common within than between subgroups (Mitani and Amsler 2003). Such socio-spatial substructuring has not been reported from other sites and may result from a tendency of adult males to concentrate their activities near where their mothers had core areas when the males were young (as documented at Gombe; Murray et al. 2008) combined with the unusual demography of Ngogo. Substructuring enters into male mating strategies: the probability that a male sires a female’s offspring varies positively with the extent to which he associates with her when she is not in estrus, independently of the positive effects of dominance rank on paternity probabilities (Langergraber et al. 2010).

14.3.4 Hunting and Meat Sharing

Both Kibale sites have produced extensive data on hunting and meat sharing. Ngogo researchers have documented predation on 12 species, including all seven other diurnal primates, but over 80% of hunts have been of red colobus. The chimpanzees succeed in over 80% of red colobus hunts and average about four kills per successful hunt (maximum = 13); thus red colobus have accounted for close to 90% of all kills (Mitani and Watts 1999, 2001; Watts and Mitani 2002a, b; unpublished Ngogo data). At Kanyawara, 49% of 152 red colobus hunts between 1990 and 2003 were successful; most led to single kills, with a maximum of seven (Gilby and Wrangham 2007). Kanyawara values are similar to those for Mahale, Gombe, and Taï; the high Ngogo values reflect the large size of typical hunting parties there (Mitani and Watts 1999; Watts and Mitani 2002a, b).

Long-term data from both sites have provided new insights into hunting decisions and the function of meat transfers. At Kanyawara, hunts are more likely to follow red colobus encounters when drupaceous fruit is abundant than when it is scarce, independently of the number of male chimpanzees present per encounter. This supports the hypothesis that chimpanzees engage in this risky and energetically costly behavior more when they can easily gain energy from other food sources (Gilby and Wrangham 2007). At Ngogo, the frequency of red colobus hunts also varies positively with ripe fruit availability (Watts and Mitani 2002a). This relationship seems to be driven by a positive relationship between fruit availability and the number of males per party; both hunting success and meat offtake increase with the number of males present (Mitani and Watts 1999; Watts and Mitani 2002b), which is the best predictor of whether chimpanzees hunt red colobus on encounter (Mitani and Watts 2001). In contrast, the presence of particular males who were most highly motivated to pursue monkeys was the best predictor of whether Kanyawara chimpanzees hunted on encounter; the absolute number of males present had no significant effect (Gilby et al. 2008).

At both Ngogo (Watts and Mitani 2002b) and Kanyawara (Gilby et al. 2008), the number of males who receive meat increases with the number of males present after successful hunts, but per capita meat availability does not increase with male party size at Ngogo (Watts and Mitani 2002a, b). Individuals not present at hunts and who thus did not contribute to prey captures nevertheless sometimes receive meat. Also, successful beggars often receive only small amounts, a finding consistent with the hypothesis that the main nutritional importance of meat eating is to provide micronutrients (the “meat scrap hypothesis”; Tennie et al. 2009). Data on hunting decisions and meat transfers provide evidence against the hypothesis that males exchange meat for mating opportunities: males are less likely to hunt on encounter when sexually receptive females are present (Mitani and Watts 2001; Watts and Mitani 2002a; Gilby et al. 2010a); they do not preferentially share meat with sexually swollen females, and copulations associated with meat transfers are uncommon (Mitani and Watts 2001; Gilby et al. 2010a). Moreover, meat transfers to swollen females at Ngogo do not influence the probability of mating in subsequent cycles (Mitani and Watts 2001). Meat transfers at Ngogo occur preferentially between maternal brothers and between males who are important grooming and/or coalition partners, consistent with the "male politics" hypothesis (Mitani and Watts 2001). Meat transfers sometimes involve aggression or persistent begging that interrupts consumption; over 60% of bouts at which multiple individuals consume meat include active (voluntary) meat transfers (Watts and Mitani unpublished data). Given that transfers mostly occur between closely bonded social partners, they probably do not function simply to reduce harassment, contrary to Gilby's (2006) "harassment" hypothesis.

The availability of long-term primate census data at Ngogo has allowed assessment of the impact of predation by chimpanzees on the local red colobus population. Red colobus population density declined steeply between 1975 and 2007, whereas the densities of redtails and mangabeys remained stable (Teelen 2007; Lwanga et al. 2011; Fig. 14.5). Teelen used data on red colobus diet, tree species stem densities, and long-term data on tree mortality (Lwanga et al. 2000) to argue that changes in forest composition could not explain the red colobus decline and that predation by chimpanzees was probably the explanation (cf. Lwanga et al. 2011). She substantiated this with simulation models, based on red colobus group composition and life-history data, that predicted the likelihood of population persistence for 100 years given predation that varied from zero to the extreme levels documented in 2002 (Teelen 2008). The model with zero predation showed a healthy population with extremely low probability of extinction. Low levels of predation were sustainable, especially if few adult males were killed. However, actual predation rates – even moderate ones – led to extremely low probabilities of persistence, and continued predation at the extreme 2002 rate led rapidly to extinction.

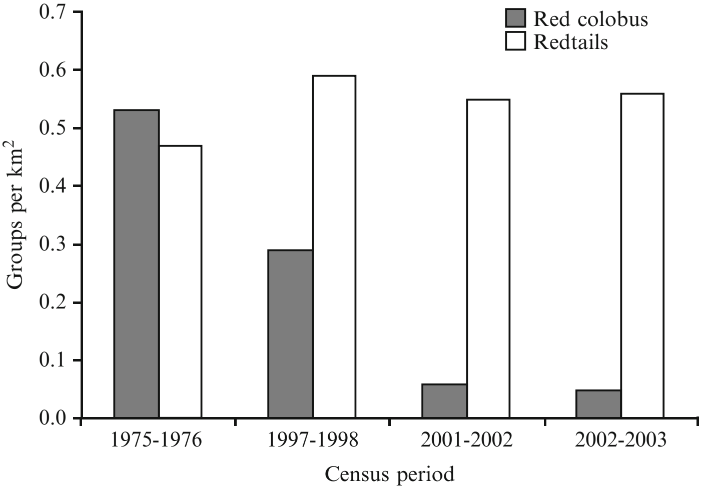

Fig. 14.5 Density of red colobus and redtail groups in the Ngogo study area, 1975–2003. Data from Teelen (2007)

Chimpanzees are not obligate carnivores, and hunting rates should decline as prey encounter rates decline and the chimpanzees must expend increasingly more time and energy to find situations where success is highly likely, especially given that most hunts occur during hunting "patrols" that can last up to several hours (Watts and Mitani 2002b). Indeed, both encounters between chimpanzees and red colobus and the frequency of red colobus hunts have decreased in recent years; such hunts account for a declining proportion of all hunts, and predation intensity has correspondingly declined. This may eventually allow the red colobus population to recover, but ongoing censuses show no evidence of recovery yet (J. Lwanga personal communication 2010).

14.3.5 Territoriality and Intergroup Aggression

Relations between neighboring chimpanzee communities are hostile, and chimpanzees are among the few mammals that regularly engage in lethal coalitionary intergroup aggression (Manson and Wrangham 1991; Wrangham 1999; Wilson and Wrangham 2003; Muller and Mitani 2005). Males perpetrate most between-community aggression, and all the males of one community are allies in competition with outside males regardless of within-community competition. Long-term data on intergroup aggression from Kibale, especially from Ngogo, have been important in dispelling the argument that such aggression is a nonfunctional response to disturbance by humans. Neither chimpanzee community was provisioned, and the Ngogo chimpanzees never reach the forest edge, but chimpanzees at both sites regularly engage in boundary patrols and respond fearfully and/or aggressively to neighbors encountered during patrols or in other situations (Watts and Mitani 2001; Mitani and Watts 2005; Wilson et al. 2001; Wilson and Wrangham 2003). Lethal attacks during inter-community encounters have been documented at both sites (Wilson and Wrangham 2003; Watts et al. 2006; Muller and Mitani 2005; Mitani et al. 2010). Playback experiments at Kanyawara confirmed that males use auditory information to make numerical assessments in deciding how to respond to the proximity of neighbors (Wilson et al. 2001). This supports the "imbalance of power hypothesis" (Manson and Wrangham 1991), which holds that males are unlikely to attack neighbors without overwhelming numerical superiority that greatly reduces their own risks; the hypothesis is difficult to test otherwise unless observers follow habituated chimpanzees in neighboring communities simultaneously (Herbinger et al. 2001).

But the possibility of making low-risk attacks does not explain why they occur, nor is the "rival reduction hypothesis" (Wrangham 1999), which holds that lethal attacks on males reduce the strength of neighboring male "coalitions," an ultimate explanation for cooperative male aggression against neighbors. Coalitionary aggression is not risk free and patrolling has time and energy costs (Watts and Mitani 2001; Amsler 2010). Long-term Ngogo data have helped to clarify the function of such cooperation. At Gombe, reproductive rates of Kasakela females were higher when the community's territory was relatively large (because of expansion into areas previously used by the Kahama community) than when it was smaller; the expansion followed a series of lethal attacks on Kahama males (Williams et al. 2004; Wilson 2012). This finding supports the hypothesis that the main function of coalitionary intergroup aggression is to defend access to food that females need for successful reproduction and, if possible, to increase food availability.

Over a 10-year period at Ngogo, researchers documented 114 boundary patrols and recorded the location and outcome of all inter-community encounters during patrols and in other contexts; they also documented 21 lethal attacks by Ngogo males on outsiders (Mitani et al. 2010). Most patrols and encounters were concentrated in the northeast and the southwest of the Ngogo territory. Lethal attacks were concentrated in the northeast; if all targeted a single community, they constituted a major source of mortality. 2009 saw a major expansion of the Ngogo territory to the northeast, with many chimpanzees routinely traveling and feeding in a large area that they previously rarely entered except on boundary patrols or hunting patrols. This provides strong circumstantial support for the "food defense" hypothesis, although evaluating the reproductive payoffs of the territory expansion will require many more years of life-history data. Meanwhile, most encounters in the southwest have happened while chimpanzees from both communities were feeding near each other during major fruiting events by *C. albidum*, *U. congensis*, or *Aningeria altissima*, three of the most important food species at Ngogo (Potts et al. 2009; Watts et al. in press a). The high frequency of such intergroup feeding contests is also consistent with the food defense hypothesis. Feeding parties on both sides are typically large, so power imbalances are slight at most encounters. Despite frequent patrols and multiple lethal attacks in the southwest, the Ngogo territory has not obviously expanded in this high quality area (Mitani et al. 2010). Unfortunately, the size and composition of neighboring community is unknown, but it is clearly large and its males have killed at least three adult males from Ngogo (unpublished Ngogo data); its strength presumably makes expansion difficult.

14.4 Discussion

Chimpanzee research in Kibale is still young compared to projects at Gombe (Wilson 2012) and Mahale (Nakamura and Nishida 2012). Nevertheless, it has contributed important comparative data on many aspects of behavioral ecology, notably long-term data sets on feeding ecology, hunting and meat transfers, intergroup aggression, social relationships, and female reproductive competition and life-history strategies. Data on female reproductive success from Kanyawara are consistent with Gombe data (Pusey et al. 1997) in showing that competition for status can influence female reproductive success, presumably because high status helps females to establish high quality core areas in heterogeneous habitats and thereby gain nutritional benefits. Given that female chimpanzees can live more than 50 years and that intervals between surviving births are around 6 years (Emery

Thompson et al. 2007a, b; Bronikowski et al. 2011), measurement of female chimpanzee reproductive success clearly requires long-term research. Likewise, Ngogo data, obtainable only after a multi-year habituation effort, show that eastern chimpanzee females sometimes establish strong social bonds with each other and that no strict eastern vs. western chimpanzee dichotomy in female gregariousness and social bonding exists. Continued long-term research will show whether these strong bonds endure as long, or even longer, than those between certain male dyads (Langergraber et al. 2009; Mitani 2009b) and will also explore the fitness consequences of individual variation in sociality.

The extreme difference in community size between Ngogo and Kanyawara is one of the most remarkable findings of Kibale research. While similar size disparities have been documented elsewhere, this has been in the context of community declines due to human disturbance and/or disease (e.g., Tai: Boesch and Boesch-Achermann 2000) or to community dissolutions apparently associated with intergroup aggression (e.g., Mahale: Nishida et al. 1985). Kibale stands out because the communities at Ngogo and Kanyawara have been stable throughout the course of research. Findings from Ngogo extend the known range of viable community size for chimpanzees, and Ngogo-Kanyawara comparisons, combined with long-term Kibale data on forest composition and phenology, provide strong evidence that ecological variation both within and among habitats can influence community size and imply that this can translate into life-history variation.

These comparisons, and much of the research at Ngogo, repeatedly invoke the theme of demographic variation on chimpanzee behavior (Mitani and Watts 1999; Mitani 2006). High rates of boundary patrolling (Watts and Mitani 2001), high hunting success and prey offtake (Mitani and Watts 1999; Watts and Mitani 2002b), low male reproductive skew (Langergraber et al. 2010), substructuring among males in space use and social relationships (Mitani and Amsler 2003) and its effect on male mating strategies (Langergraber et al. 2010), and strong differentiation of female–female social relationships (Wakefield 2008, 2010; Langergraber et al. 2009) all point to ways in which variation in community size, thus in the number of social partners and competitors, can lead to variation in aspects of ecology and social behavior that can have important impacts on fitness. How great these impacts are is unclear, but is a crucial question for future research and a powerful justification for continuing research at both sites.

Kanyawara has already contributed importantly to understanding of female chimpanzee life-history strategies and to comparative understanding of human life-history evolution. Ngogo data offer the tantalizing possibility that this understanding requires substantial revision, especially because they come from a site that is ecologically highly favorable to chimpanzees and arguably the least disturbed of current long-term chimpanzee research sites (no history of provisioning or commercial logging, no crop raiding or direct contact with humans other than researchers and field assistants, no human-introduced disease epidemics). We can only hope that political and economic realities allow the research to continue long enough that we can determine how extensive any revision should be and allow the chimpanzees themselves to have a viable future.

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Chapter 15
Long-Term Field Studies of Chimpanzees at Mahale Mountains National Park, Tanzania

Michio Nakamura and Toshisada Nishida

Abstract Chimpanzee research in the Mahale Mountains, on the eastern shore of Lake Tanganyika, Tanzania, began in 1965. Although the Mahale Mountains did not initially have official protected status, researchers' conservation efforts and the financial support of the Japanese government led to the designation of Mahale as a national park in 1985. The Mahale project is the second-longest continuous field study of chimpanzees. Long-term demographic data show that the habituated chimpanzee group has decreased in size, largely due to disease outbreaks. Recent research has focused on variation in the behavioral repertoire of chimpanzees, producing a detailed audio-visual ethogram as well as evidence of social customs, some of which are candidates for cultural variation. Many primatologists are beginning to accept the notion that some behavioral elements of nonhuman animals are socially shaped. Our long-term studies of chimpanzee behavioral variation will hopefully contribute to a better understanding of the ways in which human and nonhuman primate behavior is shaped by the interaction between genes and culture.

15.1 History and Infrastructure of Mahale

15.1.1 Study Area

Mahale Mountains National Park is the largest protected area for wild chimpanzees (*Pan troglodytes*) in Tanzania and the world's second-oldest chimpanzee study site (Nishida 1990). It is located at 6°15′ S, 29°55′ E about 120 km south of Kigoma

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Town on the eastern shore of Lake Tanganyika. The national park protects 1,613 km^2 of semi-evergreen medium-altitude forest, montane forest, montane savanna, miombo woodland, and *Oxytenanthera* bamboo woodland (Nishida and Uehara 1981). The biological diversity of this area is characterized by the coexistence of fauna and flora of eastern and western Africa (Anonymous 1980). The terrain is mostly rugged and hilly, dominated by the Mahale mountain chain that runs from northwest to southeast across the western part of the park. The highest peak is Nkungwe (2,462 m a.s.l.).

The main area of long-term chimpanzee research (the Kasoje area) is relatively flat, and because the mountain chain blocks moisture from the lake, the area is dominated by continuous evergreen forest (Kasoje Forest). Chimpanzees and other animals also regularly frequent the well-developed riverine forests in steep areas at higher altitudes. *Isoberlinia* woodland dominates *Brachystegia* woodland in the eastern part of the park, and *Oxytenanthera* or *Oxytenanthera*/miombo mixed woodland is dominant in the central and eastern parts.

15.1.2 Access and Logistics

Mahale is more difficult to access than other chimpanzee research sites. It can be reached from Kigoma, the nearest town to the Gombe and Mahale sites and the capital of the Kigoma region. All research supplies must be brought in from Kigoma by boat via Lake Tanganyika, which takes at least 12 h. Most tourists fly directly into Mahale Mountains National Park on chartered flights from Arusha.

15.1.3 Brief History of Research at Mahale

Chimpanzee research by the Kyoto University team began in 1961, when Kinji Imanishi organized the Kyoto University Africa Primatological Expedition (KUAPE) and established a research camp at Kabogo Point on the shore of Lake Tanganyika (Azuma and Toyoshima 1961). Jun'ichiro Itani led the team from the fourth KUAPE expedition onward. These researchers carried out extensive surveys throughout western Tanzania, including in the Masito Escarpment and Ugalla areas (Suzuki 1969; Izawa 1970; Kano 1972; Itani 1979).

The Mahale Mountains Chimpanzee Research Project (MMCRP) was initiated in 1965, when Toshisada Nishida, then a graduate student at Kyoto University, first visited Mahale as a part of the fourth KUAPE expedition. Mahale was selected as a long-term research site after successful habituation of the chimpanzees by provisioning in 1966 (Nishida 1968, 1990). Figure 15.1 shows the number of researchers that have visited Mahale each year. In recent years, seven to ten researchers per year have visited Mahale; a total of 70 researchers had visited Mahale by 2009.

The researchers' activities have included efforts to conserve Mahale. Nishida had developed a proposal for a protected area as early as 1967. This vision gained

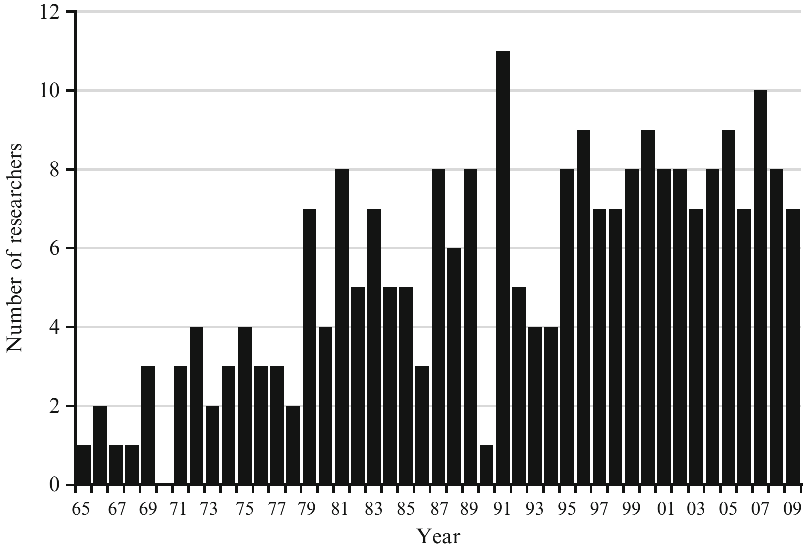

Fig. 15.1 The number of researchers who have visited Mahale each year between 1965 and 2009. Those who stayed over the new year were counted in both years

momentum in 1974, when the Japanese government provided financial support to the Japan International Cooperation Agency (JICA) for the surveys required to establish a protected area. Dr. Derek Bryceson, then Director of Tanzania National Parks (TANAPA), and Mr. Nobuyuki Nakashima, then Japanese ambassador to Tanzania, were earnest supporters of this project. During the JICA project (1975–1987), Mr. Raphael Jingu, then Director of the Game Division, established the Mahale Mountains Wildlife Research Centre (MMWRC) under the auspices of the Serengeti Wildlife Research Institute (now Tanzania Wildlife Research Institute). This center provided a base camp for patrolling the future park area and secured logistical support for the research project. When Mr. Eramus Tarimo became the Acting Director of MMWRC in 1979, practical preparations for the national park, including boundary demarcation, moved forward and Mahale was finally declared a national park in 1985 (Nishida and Nakamura 2008). In 1994, Tanzanian and Japanese researchers established a nongovernmental organization, the Mahale Wildlife Conservation Society (MWCS), with the goal of protecting wildlife at Mahale, mainly through local environmental education efforts.

15.1.4 Facilities and Basic Data Collection

The research camp at Mahale (Kansyana Camp) is situated in the Kasoje area, about 1 km from the lakeshore. It currently consists of two simple buildings with five bedrooms, a library, and storage rooms. Water is manually carried to a storage drum in the dry season and cooking is done using kerosene stoves and dead firewood collected from the forest. A limited solar-power system is available to charge computers and batteries, and a small weather station monitors daily temperatures and precipitation (Itoh et al. in press). We also collect monthly plant phenological data with the help of research assistants (Itoh and Nishida 2007; Itoh et al. in press) and keep daily records of chimpanzee sightings and demographic changes (see below).

15.2 Demography, Group Dynamics, and Life Histories

15.2.1 Study Groups

The chimpanzees were provisioned from the onset of research to facilitate habituation, until this practice was stopped in 1987. Following habituation of the chimpanzees in 1966, the initial study unit-group (or community) was called the Kajbara group (K group). A second group (Mimikire or M group) was habituated in 1968. Observation of these two adjacent habituated groups led to the identification of the natural fission–fusion social unit (Nishida 1968), description of antagonistic relationships between adjacent unit-groups, documentation of female transfer between groups (Nishida and Kawanaka 1972), and collection of detailed data on social behavior in K group (e.g., Nishida 1970, 1979). Following the extinction of K group in 1982 (Nishida et al. 1985), research efforts focused on M group. In the late 1990s, we noticed that an unidentified unit-group was utilizing the area made vacant by extinction of K group. In 2005, we began studying this new group (Miyako or Y group) living north of M group (Sakamaki and Nakamura 2007), but habituation had not yet been achieved by 2010.

15.2.2 Demographic Changes in M Group

One obvious benefit of long-term research is the collection of demographic data in combination with individual life histories. We have published demographic data through 1988 (Nishida et al. 1990) and 1999 (Nishida et al. 2003), respectively. In this section, we add data from 2000 to 2009 to provide updated information on changes in group size.

Figure 15.2 shows the demographic changes in M group between 1980 and 2009. Our study of M group began in 1965, but 50% of its members were not individually identified until 1980 (Hiraiwa-Hasegawa et al. 1984). The rapid increase in group size in the early 1980s was partially due to the immigration of K group females (with some immature offspring) in the course of that group’s extinction. As a result, M group once contained more than 100 individuals. However, the size of M group

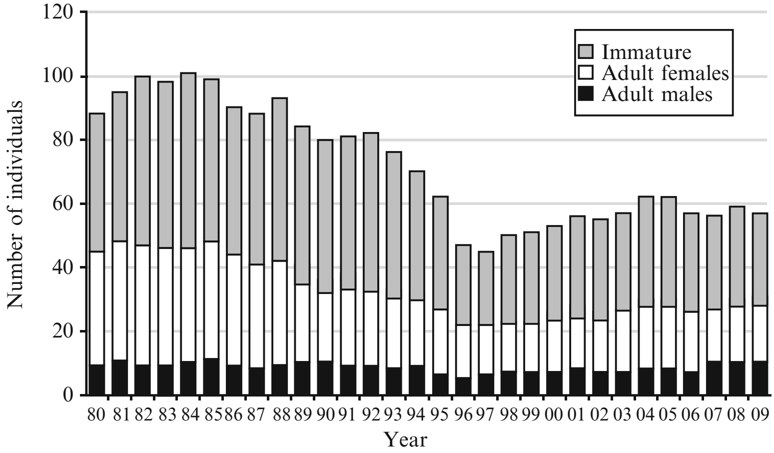

Fig. 15.2 The number of chimpanzees in the Mahale M group between 1980 and 2009. Numbers at the end of the year (31 December) represent those in the previous year. Adult males were defined as 16 years or older and adult females were defined as 13 years or older

decreased considerably between the late 1980s and 1997. Following this decline, M group gradually recovered until 2004 and remained nearly stable thereafter, except for a decrease in 2006. In 2009, the group had 57 members. Despite these fluctuations, the number of adult males (7–11) has remained relatively stable, except during 1995–1997, when it varied between 5 and 6. In contrast, the number of adult females has decreased by about two-thirds over the past 30 years. As a result, the socionomic sex ratio changed from 0.25 in 1980 to 0.48 in 2009. Such dynamics can only be documented by long-term studies spanning several decades.

Figure 15.3 shows the number of female immigrations into M group, excluding those of parous females from K group during that group's extinction. An average of 0.57 ± 0.73 females per year visited and eventually immigrated into M group. The number of immigrations has not declined in recent years; thus, the decrease in females in M group cannot be attributed to a reduction in female immigration. Although most females born into M group have emigrated to other groups during adolescence, four females born in the 1980s did not emigrate and subsequently gave birth in their natal group. These females were adolescents during the mid- to late-1990s, when M group was at its smallest. Thus, group size and composition may affect female transfer decisions. The ratio of females who emigrate from their natal group varies considerably among chimpanzee research sites (summarized by Nishida et al. 2003). Although costs for females are reportedly high in a new group (Nishida 1989; Williams et al. 2002; Kahlenberg et al. 2008; Pusey et al. 2008), they are only realized after immigration (or attempted immigration). The factors affecting female emigration or continuation in the natal group have not been fully investigated to date.

Figure 15.4 shows the number of male and female births in M group. Although the average number of male births (1.40 ± 1.25 per year) is smaller than that of

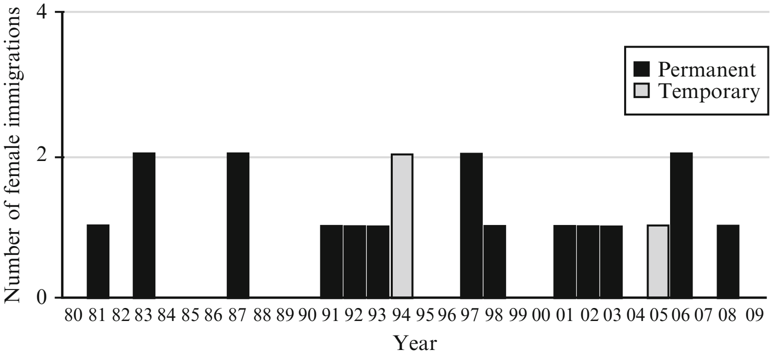

Fig. 15.3 The number of females immigrating into the Mahale M group between 1980 and 2009. Unknown adolescent females observed with M group members were identified as either temporary visitors or permanent immigrants. Temporary visitors were defined as those who stayed as long as several months, but disappeared before giving birth without apparent health problems or injury. Permanent immigrants were defined as those who stayed longer and usually gave birth within a few years

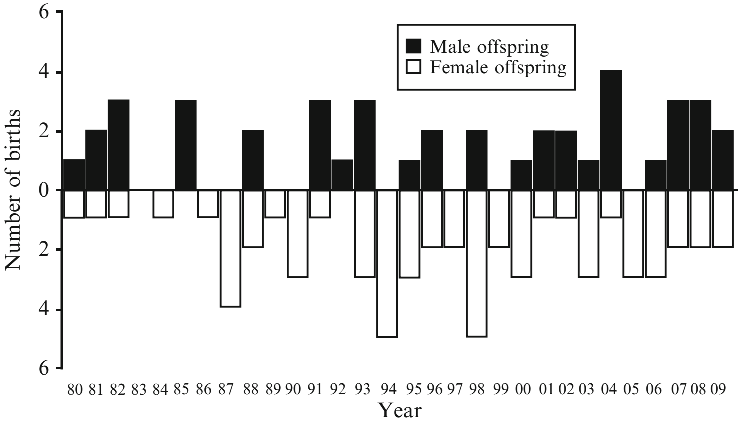

Fig. 15.4 The number of births into the Mahale M group between 1980 and 2009

female births (1.97 ± 1.33), this difference is not significant and has not changed over time. The overall trend of birth sex ratios that do not differ significantly from 1:1 but favor females slightly is similar to those reported for other chimpanzee study sites (Gombe: Goodall 1986; Taï: Boesch 1997).

The decrease in the size of M group thus cannot be explained by these factors. Most of the larger declines have been caused by disease outbreaks. In 1986, an epizootic that research assistants called an "AIDS-like disease" killed several chimpanzees in M group (Nishida 1990), and in 1993, a flu-like epizootic (severe coughing and sneezing) killed at least 11 chimpanzees (Hosaka 1995; Hosaka et al. 2000). From June to July 2006, a flu-like disease broke out in M group and likely killed 12 individuals (Hanamura et al. 2008). Nishida et al. (2003) estimated that about 48% of all Mahale chimpanzee deaths to 1999 were caused by disease. An additional large decline in group size was caused by lion predation in 1989 (Tsukahara 1993).

Unfortunately, we do not know the cause for the largest decline in group size between 1995 and 1997, when as many as 20 individuals disappeared and only three bodies were recovered. Since there were no signs of disease outbreak and many mature males and females disappeared during this period, researchers hypothesized that M group had fissioned. Surveys around the periphery of M group's home range, however, located no "branch" or "splinter" group. The sources of this dramatic population loss remain unknown.

15.2.3 Life History of the Oldest Female

Studies of individual life histories can inform analyses of social and demographic data. Here, we present the life history of the current oldest female at Mahale, called Calliope. She was first identified in 1973 as a young adult. She was estimated to have been born in 1960, based on the age of her accompanying juvenile daughter. She gave birth to five infants (three females, two males) through the age of 37 years (Table 15.1). Her reproductive cycle resumed after her last offspring was weaned, but she did not give birth again. She stopped cycling in her 48th year. Although she has not given birth in the last 12 years, including 5 years during which she was nursing her last offspring, she remains alive and well. Another old female (Wakusi; ~49 years old in 2010) also stopped reproducing in 2005, indicating that Calliope's case is not exceptional. Although menopause may not be part of the typical life cycle of female chimpanzees (Nishida et al. 2003; Emery Thompson et al. 2007), some females experience several years of postreproductive life. Because it is often difficult to estimate the ages of older individuals and because older females are often shy toward human observers, insufficient data have been compiled on old females despite decades of research. We therefore need additional continuous

Table 15.1 Calliope's reproductive profile: an individual chimpanzee life history

Year	Event	Estimated age (years)
1976?	Gave birth to CB (f)	16
1981	Gave birth to CC (f)	21
1985	Gave birth to CT (m)	25
1991 Dec	Gave birth to CD (m)	31
1997 Sep	Gave birth to CR (f)	37
2001 Dec	Resumed reproductive cycle	41
2008 Mar	Final estrus	48
2010 Jul	Remains alive and well	50

observation to understand the entire chimpanzee life cycle and to document the extent and causes of inter-individual variation in life histories, including variation in female reproductive profiles.

15.3 Highlights of Studies Made Possible by Long-Term Research

15.3.1 Ethogram and Ethnography of Chimpanzees

One of the benefits of long-term research is the continuous accumulation of behavioral repertoire details through ongoing observation. The compilation of a detailed ethogram is a starting point for description of a species' behavioral diversity. The understanding of such behavioral diversity, in combination with socioecology, social relations, and the mind of the target species, may lead to the study of nonhuman "ethnography" (Wrangham et al. 1994; McGrew 2004). Although the use of the term "ethnographic" by researchers of animal behavior (e.g., Rendell and Whitehead 2001; Laland and Janik 2006) may be considered inappropriate by some cultural anthropologists (Ingold 2001), there is no reason to believe that researchers cannot conduct ethnography on nonhuman animals unless we define the term narrowly to exclude them.

Our 1999 ethogram of the Mahale chimpanzees (Nishida et al. 1999) listed 515 behavioral patterns. The new videographic version of the ethogram (Nishida et al. 2010) lists 891 behavioral patterns, constituting the largest ethogram of chimpanzees or any other primates. Such detailed data can form the basis for comparison of chimpanzee cultures (see Sect. 15.3.2) and for behavioral reconstructions of the common ancestor of *Pan* and *Homo*. Although not an originally intended application, the ethogram can also be used to assess behavioral enrichment in captivity by providing a reference for comparison of captive and wild behavioral repertories.

We have also published brief notes on rare behaviors by Mahale chimpanzees (see Nishida et al. 2009 for a detailed review). Single-case observations include colobus skin washing by an adult male (Nishida 1994), algae-feeding by a female (Sakamaki 1998), deception by an adult male to snatch a dead infant from its mother (Nishida 1998), knotted colobus skin "necklace" wearing (McGrew and Marchant 1998), self-medication in an attempt to remove sand fleas from a toe with a stick (Nishida 2002), playing with a squirrel (Zamma 2002a), exploratory/threatening behaviors toward a porcupine (Matsusaka 2007), use of wet hair to capture swarming termites (Kiyono-Fuse 2008), and collection and carrying of guinea-fowl feathers (Nakamura 2009). Although each of these observations may not be considered important on its own, the accumulation of such published cases allows us to grasp the full behavioral flexibility and variation of chimpanzees. After more than 40 years of research, we continue to observe new behavioral patterns.

Some initially anecdotal behaviors later became more common, suggesting behavioral innovation or the acquisition of a new habit (see also Perry et al. 2012). One example is chimpanzee predation on yellow baboons. Although chimpanzees at Gombe are known to occasionally hunt olive baboons (e.g., Teleki 1981), Mahale chimpanzees were first observed hunting and eating yellow baboons in 1996 (Nakamura 1997). Subsequent research documented several more incidents of predation on baboons, although this behavior was infrequent (Nishie 2004). The use of tools during hunting is another example of initially anecdotal behaviors that later became more commonly observed. Huffman and Kalunde (1993) reported tool-assisted squirrel hunting, but this was the only report of its kind until Pruetz and Bertolani (2007) documented 12 cases of hunting with tools by Fongoli chimpanzees. The Mahale case was assumed to be anecdotal and such habitual behavior was believed to be limited to Fongoli. However, several other cases at Mahale (Nakamura and Itoh 2008) suggested that the Mahale chimpanzees also habitually hunt with tools; this behavior is rarely observed because of difficult observation conditions. Similar explanations can be applied to a few observations of wild fruit sharing among adult males (Nakamura and Itoh 2001), genito-genital rubbing among females (Zamma and Fujita 2004), and nasal probing and nipple pressing (Marchant and McGrew 1999).

It is also important to record rare events, such as an unknown group's incursion into the center of M group's territory (Itoh et al. 1999) and the chimpanzees' attitudes toward a seriously weakened adolescent female. In the latter case, several adult females harassed the adolescent but other individuals intervened (Shimada and Matumula 2004). Finally, it is also important to accumulate observations of common but difficult to observe events, such as the behavior of a newly immigrated female. Although female immigrations are not rare, it is usually difficult to observe the behavior of such females because they are often very shy toward human observers. However, one immigrant female was continuously observed on the first and the second days of immigration (Nakamura and Itoh 2005). M group members, especially males, seemed to be excited to see the newcomer, which was groomed by three females and three males. Only one case of threatening by an adult female was observed during these 2 days. Although researchers have often emphasized the higher rates of aggression directed toward immigrant females by resident females (Nishida 1989; Kahlenberg et al. 2008), most resident females were not hostile to the newcomer in this case. Instead, resident males and females received the newcomer with "curiosity" and showed affiliative behaviors to her. Even a female who threatened the newcomer subsequently groomed her.

15.3.2 Cultural Behaviors

The formation of traditions and the genesis of fashions (seemingly new behaviors that may or may not become traditions) can only be identified through long-term study. The detailed ethogram allows us to detect cultural differences in behavior among chimpanzee populations. Although the use of various tools to obtain otherwise unreachable food resources have been a central topic of chimpanzee cultural studies (e.g., McGrew 1992), cultural variations also exist beyond the context of tool use. Comparison of our Mahale chimpanzee data with information from other chimpanzee study populations has revealed behavioral variation in several social domains, such as grooming and courtship displays (see Nishida et al. 2009 for a recent review).

15.3.2.1 Grooming

Hand-clasp grooming (McGrew and Tutin 1978; Nakamura 2002) is the classic example of cultural variation beyond the context of feeding technology. In this form of grooming, two chimpanzees sit face to face and clasp their right or left hands or wrists overhead to form an A frame; they then groom each other's lower arms. This behavioral pattern has been customarily performed in Mahale (M and K groups), Kibale (Kanyawara and Ngogo groups), Kalinzu, and Lopé, whereas only a few individuals have performed it in Taï and it has never been reported from Gombe, Budongo, or Bossou (Nakamura 2002). The pattern has also been observed in the captive colony of the Yerkes Primate Research Center (de Waal and Seres 1997; Bonnie and de Waal 2006).

McGrew et al. (2001) reported two grooming hand-clasp patterns: palm-to-palm and non-palm-to-palm. In the former pattern, the groomers clasp each other's palms, whereas in the latter pattern their wrists are often flexed and one hand rests on the other. The researchers argued that the palm-to-palm pattern was dominant in the Mahale K group but absent in M group. However, after reexamination with a larger data set, Nakamura and Uehara (2004) found that the palm-to-palm pattern was infrequently performed in M group.

Social scratching (Nakamura et al. 2000) is another common cultural behavior at Mahale. This simple behavior consists of one individual scratching another while grooming him/her. Adults most frequently scratch each others' backs, and mothers scratch various body parts while grooming their infants. Social scratching also occurs at Ngogo, but differs from that at Mahale (Nishida et al. 2004). A Mahale researcher who visited Gombe for a short time observed that three chimpanzees there scratched socially (Shimada 2002). However, there are no other reports of this simple behavior from other study sites.

Sounds produced during grooming are also known to differ among sites. When Nishida visited Ngogo, he noticed that chimpanzees there "sputtered" as though forcing air through their lips; Mahale chimpanzees do not (Nishida et al. 2004). Nakamura also observed this behavior among a few individuals at Bossou, although it was practiced primarily by a single juvenile male (Nakamura and Nishida 2006) and may not have reached the group level.

15.3.2.2 Courtship Display

Courtship displays (Nishida 1997) also vary among populations. Because the sexual context is usually obvious from the penile erection of the male and the sexual swelling of the female, any attention-getting courtship displays by males or females easily convey their intention to copulate. However, the frequent convergence of courtship displays within groups and variation among groups suggest underlying cultural processes. Leaf-clipping, in which a leaf (or leaves) is clipped to produce an audible sound, is a classic example of such a courtship display at Mahale (Nishida 1980). Bossou chimpanzees also exhibit this behavior, but Sugiyama (1981) argued that it is used there to express frustration. Taï chimpanzees also clip leaves, but only before they perform buttress drumming (Boesch 1996). The majority of leaf-clipping by Ngogo males is performed when soliciting estrous females, but it is also used before buttress drumming (Watts 2008). Thus, this pattern may not have been completely ritualized to a single context.

When Nakamura visited Bossou, he noticed that mature males often performed heel-tapping in the context of courtship (Nakamura and Nishida 2006). In this behavior, a tree bough, a rock, or the ground is rhythmically tapped with the heel to produce a conspicuous sound. Heel-tapping differs from stamping because the sole makes no contact with the substrate, but instead is held upright and facing forward; only the heel makes contact. Stamping is a common element of male courtship displays at Mahale (Nishida 1997), but heel-tapping has never been observed. Sugiyama (1989) observed heel-tapping among immature individuals at Bossou to invite play. Other courtship displays, such as shrub-bending (Nishida 1997) and knuckle-knocking (Boesch 1996), may be candidates for cultural variation.

15.3.2.3 Hygienic Behaviors

Grooming serves a social function in chimpanzees but also functions hygienically to remove ectoparasites and debris from the body. After removing an ectoparasite, chimpanzees often inspect and squash it. Behaviors associated with ectoparasite removal also vary among populations. Chimpanzees at Mahale perform leaf-grooming, in which they pick up ectoparasites with their lips during grooming, place them on leaves, and then squash them with their thumbs (Zamma 2002b). Chimpanzees in Gombe (Goodall 1965), Budongo (Assersohn et al. 2004), and Ngogo (Watts 2008) also leaf-groom. Chimpanzees at Bossou perform a similar behavior, but they place the parasites in the palm of one hand and smash them with the opposite index finger (Nakamura and Nishida 2006). Similarly, chimpanzees in Taï smash the parasites against a forearm with the index finger of the free hand (Boesch 1995).

These behaviors may have social functions, such as offering an opportunity for joint attention. Leaf-grooming at Mahale and index-to-palm squashing at Bossou sometimes attract the interest of other individuals, who gather around and watch. Moreover, leaf-grooming at Mahale sometimes occurs outside of the grooming context (Nakamura personal observation); this behavior may thus be performed without actual ectoparasite smashing.

15.3.2.4 Play

Variation in play is not well documented at most study sites, perhaps because the function of play is often difficult to define and young individuals are rarely the focus of study. However, leaf-pile pulling (Nishida and Wallauer 2003) at Mahale and Gombe may be an example of cultural variation in play behavior. In leaf-pile pulling, young chimpanzees walk backward while raking a pile of dry leaves with both hands down a slope, producing copious noise. Although this may be interpreted as solitary play, the performer often faces an individual immediately following him or her and attracts social attention.

Another local variant of play is the use of tools for drinking, whereby a chimpanzee uses leaves or sticks to obtain water. This tool use is usually not considered to be play at other study sites, but to function solely to obtain water (e.g., Tonooka 2001). This behavior had been only rarely observed at Mahale (Nishida 1990) until the early 1990s, but has since become more frequent among immature chimpanzees (Matsusaka et al. 2006). Most such behavior occurs during the rainy season, when running water is plentiful and tools are not necessary to obtain water. This tool use is often conducted in apparently playful contexts. The current form of drinking tool use at Mahale thus likely occurs as part of play, rather than out of necessity. It may lead in the future to more purposeful and efficient use of tools when obtaining water is difficult, in which case the playing would retrospectively be called an exploratory behavior leading to innovation.

15.3.2.5 Feeding

Differences in feeding behaviors were studied at Gombe and Mahale in the early period of research (Nishida et al. 1983) but have not been systematically analyzed. Mahale chimpanzees never utilize oil palms, but began to utilize other species introduced by humans as food sources (e.g., mangoes, lemons, guavas; Takasaki 1983; Takahata et al. 1986; Nishida et al. 2009). If learning about new food items occurred at the individual level, some individuals would eat oil palms and some would not eat lemons. However, none of the Mahale chimpanzees eats oil palms and all eat lemons, suggesting that some form of social learning may play a role in the modification of food repertoires. Such factors are rarely considered in current studies of chimpanzee culture, perhaps because variation in feeding behavior is more parsimoniously explained by ecological differences (Byrne 2007). In contrast, Boesch et al. (2006) compared three groups at Taï and suggested that variation in feeding time relative to fruit availability may reflect cultural differences. Similarly, Sakamaki et al. (2007) reported that two adjacent groups at Mahale used different food items, despite the availability and common occurrence of all items in both areas. Of course, unknown environmental factors may also explain such differences.

Behavioral variation outside tool-use contexts is infrequently described. For example, although hand-clasp grooming at Mahale was reported decades ago, it was not properly described using data from other sites where this behavioral pattern was known to exist. This omission forms a striking contrast to the detailed and repeated reports of the same type of tool use from different study sites. In addition, subtle behavioral patterns such as social scratching are seldom described separately. Such biases of behavioral description should be corrected to facilitate our understanding of the full range of behavioral and cultural variation in nonhuman primates.

15.4 Conclusions and Future Perspectives

Chimpanzee research at Mahale, on the eastern shore of Lake Tanganyika, has been ongoing since 1965. Long-term demographic monitoring has identified a decline in chimpanzee numbers, largely due to disease outbreaks. We must take the strongest precautions to prevent the introduction of human diseases into wild chimpanzee populations (Hanamura et al. 2008; Kaur et al. 2008). In 2006, we thus began requiring that all people visiting the chimpanzees wear masks (Hanamura et al. 2006), and we restricted the number of researchers and introduced quarantine periods for new researchers. With the assistance of the Frankfurt Zoological Society, TANAPA (2006) has finalized a general management plan that includes regulations for tourists intended to minimize the risk of disease introduction. Regrettably, some regulations are presently not well followed (Nakamura and Nishida 2009).

Long-term study allowed us to accumulate demographic, life history, and basic behavioral data on a long-lived species. These data are important not only within the context of academic knowledge, but also for the conservation of primate species, many of which face extinction. Long-term research is also personally rewarding to field workers; the term “nature smiles” appeared in an essay by the late Dr. Jun’ichiro Itani, the pioneer of Japanese primate field studies:

> “*After half a century of field research, I often recall a few moments that I can never forget. They are the moments when almost all the important ideas came to me. . . . They are the jewels that we, field workers, dig out from the field with painstaking effort. We may say that they are the moments when nature smiles on the observer after bewilderingly long, long field work.*” (Itani 1993, our translation)

Our research projects have recently focused on the accumulation of comparative data on chimpanzee behavioral repertoires, especially on types of behavior that are candidates for cultural variation. Such work has produced a detailed chimpanzee ethogram and allowed us to gain insights into social customs. Although researchers have been studying chimpanzees for half a century, we still do not fully understand the variety of behaviors and the richness of chimpanzee societies. Encouraged by occasional smiles from nature, we continue to accumulate behavioral observations and to document the historical changes in chimpanzee society.

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Chapter 16
Long-Term Studies of the Chimpanzees of Gombe National Park, Tanzania

Michael L. Wilson

Abstract The study of chimpanzees at Gombe National Park, which has continued for over 50 years, has yielded many discoveries that would have been impossible without long-term data. The basic data collection procedure has remained constant since the early 1970s, with a team of Tanzanian field assistants conducting all-day focal follows of individual chimpanzees in the Kasekela (1974–present) and Mitumba (1994–present) communities. Field assistants record map location and party composition at 15-min intervals and keep a continuous record of the focal subject's feeding behavior and narrative notes on behavior, including mating, agonistic interactions, tool use, hunting, boundary patrols, and intergroup interactions. Field assistants have also monitored the unhabituated Kalande community since 1999. A relational database developed from these data provides a powerful tool for analyzing long-term patterns. Studies using this database in combination with new technologies have deepened our understanding of chimpanzee pathogens, genetics, hormones, tool use, hunting, meat sharing, social relationships, habitat use, dispersal, life histories, and demography. This chapter focuses on life histories and demography, followed by a section that highlights findings on two topics for which long-term data have proven especially informative: intergroup aggression and disease ecology.

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16.1 History and Infrastructure of Gombe Stream Research Centre

Long-term field studies are essential for understanding the lives of our closest relatives, including chimpanzees (*Pan troglodytes*). Jane Goodall began the first such study of chimpanzees at what was then Gombe Stream Game Reserve in 1960. Studies of captive chimpanzees by Wolfgang Köhler (1925) and Robert Yerkes (Yerkes and Yerkes 1929) had provided intriguing insights into chimpanzee cognition, but very little was known about chimpanzees in the wild. Nissen's short study of chimpanzees in French Guinea provided some of the first observations of feeding and social behavior (Nissen 1931). By 1960, technological advances such as jet travel and antimalarial drugs had made tropical field sites more accessible and medically safer for researchers from temperate zone countries, who had begun studying various primate species (e.g., Hanuman langurs (Jay 1962), savannah baboons (DeVore and Hall 1965), and mountain gorillas (Schaller 1963)), including chimpanzees (Kortlandt 1962).

16.1.1 Study Area

Gombe Stream Game Reserve was established in January 1943 (Thomas 1961) and upgraded to national park status in 1968 (Goodall 1986). Gombe National Park constitutes a 2–3.5-km-wide wedge-shaped strip of mountainous terrain rising from an elevation of 766 m along the shore of Lake Tanganyika to peaks ranging from 1,300 to 1,623 m along the crest of the rift escarpment in the east (Pintea et al. 2010; Fig. 16.1). Gombe's southern border is 15 km north of the town of Kigoma. The park extends roughly 14 km along the lake, with villages at its northern and southern ends and less densely settled land to the east (Fig. 16.2).

The park's area of 35.4 km^2 (13.7 square miles) consists of a series of steep ridges and valleys that descend westward to the lake. Roughly half of the 15 major valleys contain year-round streams; other streams flow seasonally. The vegetation varies from evergreen forest in valley bottoms, to thicket, vine tangle and semi-deciduous forest on the lower slopes; open woodland on the upper slopes; and grassland on the highest slopes (Clutton-Brock and Gillett 1979). Moist air from the lake combined with a north–south gradient of decreasing altitude creates a north–south gradient of decreasing rainfall. The north is thus more heavily forested, while the south is drier, with more woodland, and the density of chimpanzee food plants is substantially higher in the northern half of the park (Rudicell et al. 2010). In the 1960s, much of the park burned each year, creating an open habitat with little undergrowth. Fire has been suppressed since 1968, resulting in an increase in shrubs and vines and in overall greenness, especially in the north (Pintea et al. 2010). The increased undergrowth has not only likely improved the amount of food available to chimpanzees (Pintea et al. 2010), but has also reduced visibility and made following chimpanzees more difficult.

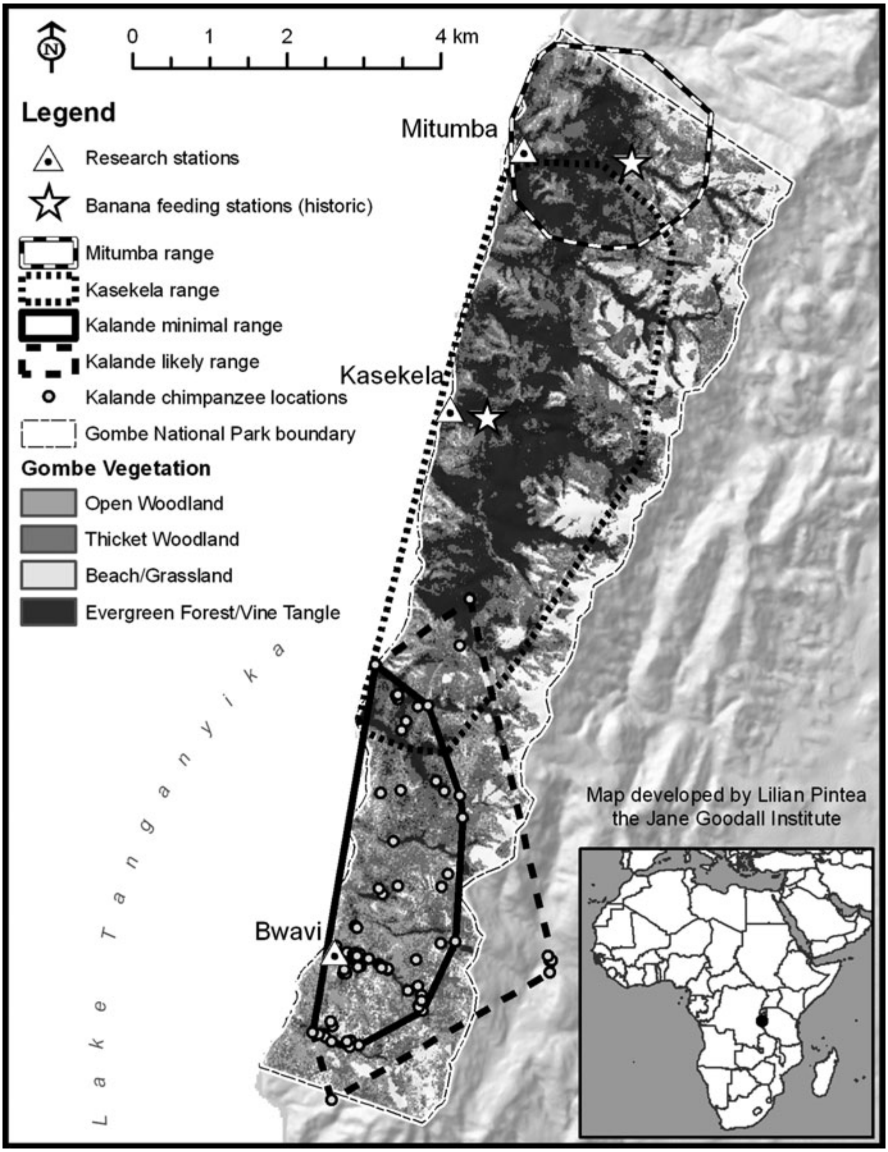

Fig. 16.1 Map of Gombe National Park, showing the locations of the research stations and former banana feeding stations, the 2007 ranges of the Mitumba and Kasekela communities, and the minimum and likely ranges of the Kalande community, based on sightings within the park and nest locations found near the park (2002–2009). The vegetation coverage within the park is based on classification from satellite images. The inset shows the location of Gombe within Tanzania. (Map based on Rudicell et al. (2010), Fig. 1, courtesy Lilian Pintea, the Jane Goodall Institute)

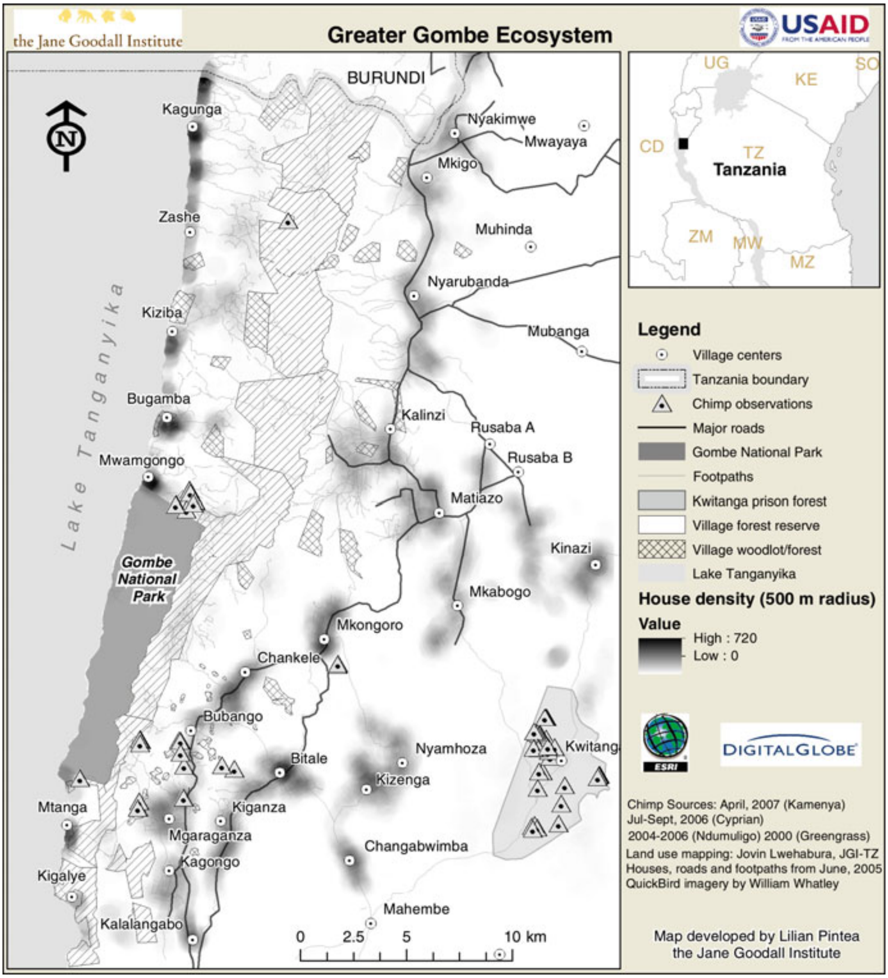

Fig. 16.2 Map of the greater Gombe ecosystem, showing Gombe National Park, the recently established village forest reserves, the location of chimpanzee sightings outside the park, and the density of houses, derived from 2005 QuickBird satellite imagery. (Map courtesy Lilian Pintea, the Jane Goodall Institute)

16.1.2 Study Population

Three chimpanzee communities have existed in Gombe throughout the duration of the study: Mitumba in the north, Kasekela[1] in the center, and Kalande in the south. As of January 2010, approximately 101–105 chimpanzees inhabited the park,

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[1] Spelled "Kasakela" in earlier publications; "Kasekela" is the preferred local spelling.

including 25 in Mitumba, 61 in Kasekela, and perhaps 15–19 in Kalande. The Kahama community split from the Kasekela community in the early 1970s but survived only through 1977. Life history details are known for 292 chimpanzees in the Mitumba and Kasekela communities, with less detailed information available for another 40 or so in the Kalande community.

Most research has focused on the Kasekela community, which Goodall began studying in 1960. Efforts to habituate the Mitumba community began in 1985. It was originally intended to serve as a focus for tourism, but was subsequently excluded from tourism because of its small size (TANAPA 2005). Several efforts to habituate the Kalande community from 1968 to 1990 proved unsuccessful, but a monitoring program begun in 1999 continues to the present (Rudicell et al. 2010).

16.1.3 Data Collection Methods

Early efforts to observe wild chimpanzees faced challenges common to many other primate studies: chimpanzees use large ranges and generally flee from people. To overcome these challenges, Goodall employed an observational approach that differed greatly from previous attempts to study chimpanzees (e.g., both Nissen (1931) and Kortlandt had tried to watch chimpanzees from blinds), but is now nearly ubiquitous in primate studies. Like Carpenter (1934) had done in his pioneering field study, Goodall approached the animals in plain view, allowing them to become habituated to human presence gradually. Goodall searched for and watched chimpanzees from hilltops and other vantage points, and gradually observed them in more detail as habituation improved. By the end of her fourth month, Goodall had observed chimpanzees eating meat (Goodall 1963) and making and using tools to “fish” for termites (Goodall 1964).

During the 1960s, the study developed from a single researcher recording data *ad libitum* throughout the forest to a large research team focused on systematic collection of behavioral data in the vicinity of a banana provisioning area (“Camp”) located near the center of the Kasekela community’s range. Goodall began provisioning chimpanzees in 1963 to speed habituation and improve observation and filming conditions. She hired her first research assistant in 1964, and in 1965, she formally established the Gombe Stream Research Centre, which rapidly grew to host a large research team. Researchers kept daily records of chimpanzees seen in camp and of their interactions (“A-record”). Collection of these data continued until banana feeding ended in 2000. Starting in 1967, and then more regularly from 1970, chimpanzees were weighed in camp using a hanging spring balance baited with bananas (Pusey et al. 2005). Robert Hinde developed a check-sheet for recording mother–infant behavior in 1969, forming the basis of data collection that continues to the present. Banana feeding also attracted baboons, and by 1967 Goodall had established a long-term baboon study, which continues today (Ransom 1981; Collins et al. 1984; Packer et al. 1998).

Researchers began to follow chimpanzees away from Camp around 1968, for studies including hunting (Teleki 1973) and sexual behavior (McGinnis 1979). Tragically, in 1968, Ruth Davis fell to her death from a cliff while following chimpanzees in Kahama valley (Goodall 1986). Subsequently, researchers were required to work in teams of at least two for safety, and Goodall began hiring Tanzanian field assistants, starting with Hilali Matama in 1968. Initially, the Tanzanians simply accompanied the foreign students, but their excellent skill at tracking chimpanzees and observing their behavior led to the start of formal training in standardized data collection in 1970. In 1974, Larry Goldman and Donna Anderson began more intensive training of field assistants, introducing the use of check-sheets and reliability tests (Goodall 1986).

Focal follows, necessary for unbiased estimates of behavior rates (Altmann 1974), were first conducted in 1968, as students followed individual chimpanzees through the forest. Richard Wrangham initiated all-day focal sampling that involved following chimpanzees between consecutive night-nesting sites (Wrangham 1977). Focal data were called B-Record to distinguish them from the A-Record data. Field assistants conducted some focal follows in 1973 and have conducted daily all-day focal follows of individuals in the Kasekela community regularly since 1974. Comparable data collection for the Mitumba community began in 1994. Observers record map location, party composition, and female reproductive status at 15-min intervals ("travel and group check-sheets"); continuously record the focal subject's feeding behavior; note all occurrences of mating, agonistic interactions, grooming, and tool use by the focal subject; and take ad libitum narrative notes on other events, including hunting, boundary patrols, and intergroup interactions.

In the early 1970s, Goodall developed an affiliation with Stanford University through David Hamburg. From 1971 to 1975, Goodall was a visiting professor at Stanford. A series of Stanford undergraduates visited Gombe from 1972 to 1975, first receiving training in chimpanzee behavior at the Stanford Outdoor Primate Facility ("Gombe West") before spending 6 months at Gombe. Students also visited Gombe from the Zoology program at the University of Dar es Salaam, where Goodall was a guest lecturer.

The growing and productive international research effort at Gombe, including the partnership with Stanford, abruptly halted in 1975 with the kidnapping of four students by rebels from Zaire (Goodall 1986). All four students were eventually safely returned to their families, but Tanzanian authorities considered the park unsafe for foreign researchers, including Goodall, for many years following the kidnapping. The Tanzanian field assistants took over day-to-day operations at Gombe, which Goodall oversaw from her home base in Dar es Salaam. Thanks to the dedication of the Tanzanian research team, data collection was able to continue at Gombe throughout this time. To raise the funds necessary to continue long-term research, Goodall founded the Jane Goodall Institute in 1977, which continues to fund Gombe research while also expanding into a broader global mission.

In the 1980s, foreign researchers were gradually allowed to return to Gombe for increasing periods. Chris Boehm conducted studies of vocal communication and behavior (1984–1990) and introduced the use of portable video cameras, which field assistants used to document behavior during B-record observations (Boehm 1989). Anthony Collins, who had studied baboons at Gombe in 1972–1975, returned in 1987 to oversee the baboon project, and since then has also been closely involved in management of the chimpanzee study.

By the 1980s, data accumulating from other sites made comparisons with Gombe possible. The first comparisons were between Gombe and Mahale and focused on diet (Nishida et al. 1983), habitat (Collins and McGrew 1988), and positional behavior (Hunt 1992). In 1990 and 1992, Christophe Boesch visited Gombe to compare hunting behavior at Gombe and Taï Forest, Côte d'Ivoire (Boesch 1994).

Foreign researchers returned to Gombe in greater numbers in the 1990s, including graduate students (e.g., Charlotte Uhlenbroek) and postdoctoral researchers (e.g., Craig Stanford). Several students started as volunteers habituating the Mitumba community, including Bill Wallauer, who subsequently began a 14-year-long video project to document chimpanzee behavior at Kasekela (Nishida and Wallauer 2003; Wilson et al. 2004; Pusey et al. 2008a). By the 2000s, Gombe once again hosted a regular contingent of graduate students from several universities. Many came from Anne Pusey's laboratory at the University of Minnesota and did work combining analysis of long-term data with new data collection. The 1990s and 2000s saw increased training of Tanzanian scientists, starting with Shadrack Kamenya, who studied red colobus monkeys (Kamenya 1997). In the 2000s, Tanzanian students conducted research for master's (Bakuza 2006; Ndimuligo 2007) and doctoral (Mjungu 2010) degrees.

While behavioral data collection continued using the same methods developed in the early 1970s, new technologies have greatly broadened and deepened our understanding of chimpanzees and their habitat. Advances in molecular technology permitted genetic analyses, including determination of kinship from noninvasively collected samples of hair (Morin et al. 1994) and feces (Constable et al. 2001; Wroblewski et al. 2009). Fecal samples also provided information for hormonal analyses (Emery Thompson et al. 2008), parasites (Gillespie et al. 2010), and virology (Keele et al. 2009). Hand-held video cameras have made possible more detailed analyses of behavior, including termite fishing (Lonsdorf et al. 2004) and meat sharing (Gilby 2006). Laser imaging technology has allowed creation of 3D models for analyzing skeletal materials (Kirchhoff 2010). The entry of demographic, ranging, feeding, and other behavioral data into a relational database has made decades worth of data available for analysis (e.g., Williams et al. 2002, 2004; Gilby et al. 2006; Murray et al. 2007; Wroblewski et al. 2009; Mjungu 2010). On a landscape scale, remote sensing images, from aerial photographs to satellite images, combined with Geographical Information Systems (GIS) software, have enabled the study of changes in habitat and land use in and around Gombe (Pintea et al. 2010). The phenology of key chimpanzee foods is regularly monitored in all three communities, and vegetation plots have been established and sampled throughout the park (Murray et al. 2006; Rudicell et al. 2010). Comparative studies using data from multiple field sites have been conducted on topics including demography (Hill et al. 2001; Emery Thompson et al. 2007), reproductive ecology (Emery Thompson 2005), and culture (Whiten et al. 1999; Nakamura et al. 2000; Nishida and Wallauer 2003; Schöning et al. 2008).

16.1.4 Infrastructure

Initially, Gombe research infrastructure consisted of a few simple tents, followed by prefabricated metal huts with thatched roofs. In 1971, George Dove helped upgrade the research infrastructure substantially, building breezeblock houses and offices along the lakeshore. The central office block still provides office and laboratory space, and an array of solar panels has provided electricity for lighting, computers, and other purposes, including a freezer for storing laboratory samples, since 2005. A small storage building has been converted into a necropsy laboratory. A herbarium cabinet stores plant samples for identification, and is now located in the JGI office in Kigoma for better protection from humidity. Breezeblock houses provide living quarters for research staff in Kasekela. Simple metal huts house research staff in Mitumba and in the Bwavi station in the Kalande community's range. To reduce risks of disease transmission, garbage pits and latrines are covered, and the entries to staff houses have been enclosed with wire mesh to provide "baboon-proof" outdoor living areas. Because of the rugged terrain, no roads reach the park, and Gombe is thus accessible only by foot or boat. The research center relies on wooden boats, with small ones stationed at Mitumba and Bwavi and larger ones at Kasekela.

16.1.5 Standardization and Management of Long-Term Data

The long-term study has produced many hundreds of thousands of pages of data. Analyzing these by hand is difficult and time consuming, and not really feasible for datasets that span many years, or for complicated analyses. Since 1990, Anne Pusey has worked with Goodall to develop an archive for housing all these datasheets, from which data are extracted and entered into a computer database. The Jane Goodall Institute's Center for Primate Studies operated at the University of Minnesota (1995–2009) and the archive has now moved to Duke University. Pusey has worked with computer scientists, including John Carlis, Shashi Shekhar, and their students, to develop a relational database, which keeps track of demographic data as well as behavioral data from the focal follows, including party composition, map location, and feeding, aggression, mating, and grooming. Data on ranging, party composition, and feeding are entered into the database from the maps and travel and group charts.

Extracting data from the B-record notes takes several steps, because the data are recorded in Swahili and written in a narrative instead of recorded on check-sheets.

(Several attempts have been made to design check-sheets to replace the narrative notes, but given the complexity of the data currently being collected, and the flexibility of the current system for recording both systematic data and descriptions of unusual events, designing check-sheets that are both sufficiently comprehensive and still practical to use in the field has been difficult.) The narrative notes are translated into English, and then entered into a database. Specific datasets such as mating, grooming, and aggression are extracted from the translated narrative notes and entered into tables, which are uploaded into an Access database; this allows efficient analysis of datasets that span many years (e.g., Williams et al. 2004; Gilby et al. 2006; Murray et al. 2006, 2007; Wroblewski et al. 2009; Rudicell et al. 2010). Work in progress includes the development of a searchable video database and computerizing of mother–infant data.

In the 1990s, the field maps used for recording the location of focal chimpanzees were redrawn from aerial photos rectified with the help of Global Positioning System (GPS) measurements. However, GPS signals are often difficult to obtain under heavy tree cover and in steep valley bottoms, so hand-drawn maps are still the main source of information on ranging. Comparison with GPS locations found that hand-drawn maps had a mean error of 133 m (Gilby et al. 2006). To document habitat change in and around the park, Pusey and Pintea have acquired remote sensing datasets, including aerial photographs and a series of satellite images of Gombe and the surrounding area, and have developed a digital elevation model for the park (Pintea et al. 2010).

16.2 Life Histories and Demography

16.2.1 Life Histories

Because chimpanzees can live nearly as long as humans, it has taken many years of study at Gombe and other sites (e.g., Mahale: Nishida et al. 2003; Bossou: Sugiyama 2004) to gain a clear picture of their life histories. During 50 years at Gombe, many individuals have been followed from birth to death. For example, researchers followed Goblin's life, from infancy (Goodall 1971, 1986, 1990), weaning (Pusey 1983), and adolescence (Pusey 1990) through his maturation into a politically savvy alpha male (Goodall 1986; Boehm 1992), followed by his fall from power in a brutal gang attack (Goodall 1992), his coalitionary behavior as a post-prime male (Gilby et al. 2009), and eventual old age and death (Williams et al. 2008; Terio et al. 2011). Necropsy revealed that Goblin had suffered from a multinodule infection of the nematode *Oesophagostomum* (Williams et al. 2008; Terio et al. 2011). Analysis of Goblin's skeleton found dental problems, including severely worn teeth and abscess drainage points (Kirchhoff 2010), which likely made it difficult for him to feed during the severe dry season of 2004, when he weakened and died.

Chimpanzees mature more rapidly and grow larger in captivity than in the wild, probably due to the abundance of food and protection from immunological and other stressors. Field data are thus necessary to obtain accurate measures of the timing of life history events in the context of the ecological constraints under which chimpanzee life history evolved. Moreover, life histories vary among sites; the following focuses on what has been learned from Gombe, especially from studies explicitly focused on development (e.g., Pusey 1983, 1990; Plooij 1984; Goodall 1986).

In the wild, chimpanzees grow slowly, being weaned at 50–86 months (Pusey 1983) and not reaching reproductive maturity until around 14–15 years for females and 15–16 years for males (Goodall 1986). At most chimpanzee study sites, the great majority of females transfer into new communities once they reach sexual maturity, whereas males universally stay in their natal communities (Pusey 1979; Stumpf et al. 2009; Nakamura and Nishida 2012). Females presumably disperse from their natal communities to avoid mating with close kin (Pusey 1979). About half of all females born into the Kaselela community, however, have stayed in their natal community (Pusey et al. 1997), perhaps due to limited dispersal opportunities. The proximate factors affecting dispersal and settlement decisions remain unclear, largely because data from neighboring habituated communities are limited. However, at least one Kasakela female that attempted to immigrate into Mitumba was repelled by aggressive attacks by resident females (Pusey et al. 2008a), suggesting that Mitumba is currently crowded, as far as female chimpanzees are concerned.

Once chimpanzees reach reproductive maturity, they focus their efforts on activities associated with reproductive success. Males and females both spend most of their time searching for and eating food, but important sex differences exist in reproductive strategies. Females must establish themselves in suitable areas, often in new communities, that have sufficient food to raise their young, are relatively safe from intergroup aggression, and have suitable mates (mature, unrelated males). Once established, females spend most of their time gestating, lactating, and otherwise caring for their offspring. For males, the main jobs in life are trying to attain high dominance rank, mating with estrous females, and joining with other males to defend and possibly expand the group territory.

By adulthood, male and female chimpanzees thus lead very different social lives. In general, males are more gregarious, often foraging in large parties, competing for dominance rank, grooming with allies, displaying at opponents, and mating with estrous females (Mitani 2009). Females are generally less gregarious than males (Pepper et al. 1999), perhaps because carrying infants makes mothers more sensitive to the costs of scramble competition associated with larger foraging parties (Wrangham 2000). Wrangham and Smuts (1980) found that Gombe mothers spent more than half of their time alone or with just their families. Females at some other sites, such as Taï and Ngogo, are more gregarious than Gombe females, likely due to greater abundance of food, but are still less gregarious than males (Lehmann and Boesch 2008; Wakefield 2008). When females have fully tumescent sexual swellings, they become more social, traveling with large parties of males or going off on consort with individual males (Goodall 1986).

Besides differing in overall gregariousness, the sexes differ in foraging patterns and range use. Females spend more time foraging for insects such as termites (Pandolfi et al. 2003), whereas males spend more time hunting and eating mammalian prey such as red colobus monkeys (Stanford et al. 1994). Males generally use the community's entire range, patrolling the borders and sometimes making deep incursions into neighboring ranges, whereas females generally use a smaller proportion of the community's total range (Williams et al. 2002). At Gombe, females spend much of their time in smaller "core areas" (Wrangham 1979; Wrangham and Smuts 1980). The extent to which males and females differ in their ranging patterns varies among sites (e.g., Lehmann and Boesch 2008), but evaluating these differences is complicated by the use of different definitions and methods of analysis across sites. At Gombe, female home ranges have been analyzed based on points from all-day follows in which females were "alone" (that is, unaccompanied by adults other than their female relatives) (Williams et al. 2002; Murray et al. 2006), a method not used at other sites. However, analysis of all ranging points indicates that Kanyawara females use different "neighborhoods" within the total range (Wilson 2001; Emery Thompson et al. 2007).

Early observations of these sex differences in space use suggested that the sexes might differ in community membership as well. Wrangham (1979) described three alternative models of chimpanzee social structure, in which females (1) ranged equally over the entire community with males, (2) ranged in smaller core areas but associated only with males of a particular community, or (3) ranged in smaller core areas distributed across the landscape independently of male ranging behavior. Studies at Gombe support the second model (Goodall 1983; Williams et al. 2002), while studies at Taï support the first model (Lehmann and Boesch 2008). In general, though, it appears that each female belongs to a specific community and that community memberships are stable. Exceptions to this rule occur when the number of males in a community declines precipitously, and parous females begin visiting or even transferring to neighboring communities (Nishida et al. 1985; Rudicell et al. 2010).

Both male and female chimpanzees compete for access to key resources. Early studies suggested that chimpanzees had completely egalitarian social relations (e.g., Reynolds and Reynolds 1965). Studies of habituated chimpanzees soon revealed that males compete vigorously for status (Bygott 1979). For females, though, decided agonistic interactions are infrequent and often subtle, leading to early speculations that dominance is not an important aspect of their social relationships (de Waal 1984; Wrangham 1980). Moreover, variation exists among sites; for example, Wakefield (2008) found no evidence for linear female dominance hierarchies at Ngogo. At Gombe, however, both males and females can be assigned dominance ranks based on the outcome of dyadic contests (Murray et al. 2006). At Gombe, higher dominance rank is associated with greater reproductive success for both males and females (Pusey et al. 1997; Constable et al. 2001; Wroblewski et al. 2009; Jones et al. 2010).

Rank appears to affect female reproductive success largely through access to better feeding areas, which in turn allows females to shorten their inter-birth intervals. In general, female chimpanzees reproduce slowly (Emery Thompson et al. 2007). Kasekela females had a median inter-birth interval of 4.9 years, including intervals where the previous infant died (Jones et al. 2010). High-ranking females at Gombe produce surviving infants at higher rates than low-ranking females and have daughters that mature at younger ages (Pusey et al. 1997). Vegetation plots conducted throughout the Kasekela community's range revealed that high-ranking females had smaller core areas with higher densities of preferred food trees (Murray et al. 2006). Fertility also varies with age (Emery Thompson et al. 2007; Jones et al. 2010), but considerable variation cannot be explained by either rank or age, suggesting that phenotypic quality is an important component of fertility (Jones et al. 2010). Phenotypic quality likely encompasses a broad range of traits, including maternal and other social skills plus immune system function.

Determining male reproductive success is challenging in chimpanzees, because females generally mate with multiple males. Goodall initially characterized the chimpanzee mating system as promiscuous (Goodall 1965). While it eventually became clear that high-ranking males tended to monopolize mating with available females, especially during the peri-ovulatory period (or "POP"; Tutin 1979), only with the advent of noninvasive genetic sampling did patterns of paternity become clear (Constable et al. 2001; Wroblewski et al. 2009). As it turned out, high-ranking males do have more offspring at Gombe (Constable et al. 2001; Wroblewski et al. 2009) and elsewhere (e.g., Taï: Boesch et al. 2006; Budongo: Newton-Fisher et al. 2010). However, by competing for access to peri-ovulatory females and by using alternative mating tactics (e.g., consortship) as well as mating with younger, less preferred females, lower-ranking males can achieve higher reproductive success than predicted by the priority-of-access model (Wroblewski et al. 2009).

Like other primates (Charnov and Berrigan 1993), chimpanzees live long lives compared to other mammals their size. Nonetheless, chimpanzees have higher age-specific mortality than human foragers, and appear to senesce more rapidly (Hill et al. 2001). A study compiling data from Gombe and several other sites found that mean life expectancy at birth was below 15 years for both males and females (Hill et al. 2001). The main causes of death were disease and conspecific aggression (Williams et al. 2008). Predation by leopards (Boesch 1991; Furuichi 2000) and lions (Inagaki and Tsukahara 1993) can be important sources of mortality at other sites, and probably were in the past at Gombe, before lions were extirpated and leopards reduced in numbers (Pierce 2009). Chimpanzees are considered "old" by their mid-30s (Goodall 1986), and by their late 30s, they often suffer from ailments of old age such as worn teeth and degenerative joint disease (Morbeck et al. 2002; Kirchhoff 2010). However, because exceptional individuals can live well beyond 50 years, even the 50-year-long Gombe study has not lasted long enough to document the longest chimpanzee lives fully. The oldest chimpanzee in Kasekela, Flo, was initially thought to be 41 ± 5 years old when she died (Goodall 1983). Flo's estimated age was later revised upward to 53 years, based on comparison with other chimpanzees (Williams et al. 2008). The oldest individual currently alive at Gombe, Sparrow, is approximately 52 years, and, with her full coat of hair and generally robust appearance, looks younger than Flo did at the end of her life.

Because Flo was already old in 1960 when the study started, and because Sparrow immigrated into the study community as an adolescent, neither individual's age is known precisely. Despite the longevity of these exceptional individuals, very few chimpanzees at Gombe have lived past 40 years. Among the individuals followed since infancy, the oldest female, Fifi, lived to be 46 years and appeared to be in good health when last seen. The oldest female followed since birth, Gremlin, is now 40 years. Several males are estimated to have lived to 40 years old or just beyond: Evered, Huxley, and McGregor. The oldest male followed since birth, Goblin, died 13 days before he would have turned 40 years.

Like most other mammals, but in contrast to humans, reproductive senescence in chimpanzee follows approximately the same schedule as somatic aging. The interval between births increases with age (Jones et al. 2010), and eventually some very old females may stop cycling altogether (Nishida et al. 2003; Nakamura and Nishida 2012), but females do not typically experience a post-reproductive life phase, or menopause (Emery Thompson et al. 2007).

16.2.2 Population Size

While Gombe is a small park, the park's total chimpanzee population remains uncertain. Estimates of the total population prior to about 2000 rely largely on guesswork. Goodall's estimate for the 1960s was 100–150 chimpanzees (van Lawick-Goodall 1968). Estimates made by extrapolating back from the known and estimated sizes of the Mitumba and Kalande communities yielded a similar range of 120–150 chimpanzees in the 1960s (Pusey et al. 2008b). Estimates of the population since about 2000 are more precise, thanks to the genotyping of fecal samples from the unhabituated Kalande community (Rudicell et al. 2010). Based on detailed demographic data for Mitumba and Kasekela and estimates for Kalande, the minimum population estimate ranged from 91 to 101 chimpanzees (median = 95) from 2000 to 2010, and the maximum estimate ranged from 100 to 109 chimpanzees (median = 103), with no clear upward or downward trend over time.

Despite the recent stability of the total population, the sizes of the individual communities have varied considerably. Although research on the Kasekela community began in 1960, it was not until 1966 that all individuals were known, at which time 60 individuals lived in Kasekela. By 1973, Kasekela had divided into two communities: Kasekela, with 40 chimpanzees, and Kahama, with at least 14 (and probably more, given the likelihood that Kahama also included unidentified, unhabituated females). Males from Kasekela killed at least five individuals from Kahama (Goodall 1986). By the end of 1977, the Kahama community no longer existed, as all the males had been killed or disappeared and the surviving females and offspring had rejoined Kasekela or dispersed elsewhere (Goodall 1986). Following a respiratory epidemic in 1987 that killed nine individuals, Kasekela reached its smallest recorded population size, 38, in 1989. Kasekela's population gradually recovered in the 1990s, and, thanks to immigration, grew rapidly in the 2000s, numbering 61 chimpanzees by the start of 2010.

The size of the Mitumba community has been documented only since 1985. Goodall (1986) estimated that Mitumba contained 50 individuals in the 1970s and early 1980s. During this time, the Mitumba successfully defended its boundaries against the Kasekela community, and even expanded its range at the expense of Kasekela in the early 1980s, suggesting that it was similar in size to Kasekela (which contained 51–58 individuals in 1978–1983). However, records from the first years of direct observation indicate that probably at least 20 individuals, but no more than 31, were alive in 1985 (Mjungu 2010). We do not know whether Mitumba's population declined in the early 1980s, whether some individuals were not recorded at that time, or if the pre-habituation estimates of the community's size were too high. However, by the mid-1990s, the chimpanzees were sufficiently well habituated, and observations sufficiently frequent, that all individuals were likely identified. A respiratory epidemic in 1996 caused Mitumba's population to drop from 25 to 20 (Mjungu 2010). The community's population declined to a minimum of 19 at the start of 1999, followed by a gradual recovery to 25 individuals at the start of 2010 (Mjungu 2010; Rudicell et al. 2010). Despite the overall increase, the number of adult males decreased from five in 1994 to only two from 2005 on (Mjungu 2010). The number of adult males in Mitumba may yet recover, though. The community has six males aged 8–13 years, suggesting that the Mitumba males might yet again pose a significant challenge to the Kasekela males in adulthood.

In 1969, Gale identified more than 20 individuals in the Kalande community and estimated that it totaled at least 40 (Rudicell et al. 2010) and might have been substantially larger. By the late 1990s, though, Kalande chimpanzees rarely met Kasekela chimpanzees, suggesting that Kalande had declined substantially. Estimates based on sightings, molecular genetics, and likely migration patterns indicate that Kalande contained 19–43 individuals in 1998, but declined to only 15–19 by the start of 2010, with a particularly severe loss in 2002 (Rudicell et al. 2010). During this time, Kalande had an unusually high prevalence of the virus SIVcpz, which is known to increase mortality in chimpanzees (Keele et al. 2009), suggesting that at least some of the decline resulted from the impact of SIVcpz infection (Rudicell et al. 2010).

As recently as the 1970s, forest and woodland habitat outside the park likely connected Gombe to other chimpanzee populations (Pintea et al. 2010). Intergroup encounters observed in 1975 to the extreme east of Kasekela's range suggest that an "Eastern" or "Rift" community might have persisted to the east of the park (Goodall et al. 1979), though those encounters might have simply involved individuals from Kalande moving north along the eastern margin of their rivals' range (Goodall 1986). By the late 1990s, however, rapid deforestation had turned Gombe into a largely isolated island of chimpanzee habitat (Pintea et al. 2010). Nonetheless, an unknown number of chimpanzees survive in forest fragments outside the park, including a small population (perhaps 15 weaned individuals) in Kwitanga Forest

Fig. 16.3 Goblin through the ages (**a**) juvenile in ~1969, (**b**) as a young adolescent in ~1972, (**c**) as alpha male in 1985, presiding over a red colobus carcass, (**d**) as an old male with severely worn teeth in 2003, (**e**) shortly before his death in August 2004, and (**f**) his skull in the Gombe skeleton collection. Photos ©David Bygott (**a**, **b**), ©Chris Boehm (**c**), ©Michael Wilson (**d**, **e**), and ©Claire Kirchhoff (**f**)

(Ndimuligo 2007), which may be close enough for chimpanzees to travel between there and Gombe. Chimpanzee nests have also been found near Zashe village, in the hills along the rift escarpment to the north of Gombe, near the border with Burundi (Fig. 16.3).

16.3 Research Highlights

16.3.1 Intergroup Dynamics

One topic for which Gombe is especially well known and that is relevant to many aspects of the long-term study is intergroup dynamics. Only long-term data provide information needed to understand the consequences of interactions between communities. As Goodall noted (1986:3), “Had my colleagues and I stopped after a mere 10 years, we should have had a very different picture of the Gombe chimpanzees than we do today. We would have observed many similarities in their behavior and ours, but we would have been left with the impression that chimpanzees were far more peaceable than humans”.

Because chimpanzees live in fission–fusion societies, many years were required just to determine the boundaries of social groups at Gombe. Goodall initially supposed that the entire chimpanzee population interacted freely and peacefully (Goodall 1965). Reynolds formed a similar impression of “loose unstable groupings and apparent lack of group social organization” at Budongo (Reynolds and Reynolds 1965:422). In contrast, Itani and Suzuki (1967) inferred that chimpanzees lived in stable “large-sized groups.” In 1965, Nishida began research in the Mahale Mountains, 150 km south of Gombe, with the specific goal of understanding the social organization of wild chimpanzees (Nishida 1979; Nakamura and Nishida 2012). By 1968, Nishida had inferred that chimpanzees lived in socially bounded fission–fusion societies. Observations at Gombe, and eventually other sites, confirmed that chimpanzees indeed live in socially bounded, mutually hostile groups called “communities” (Goodall et al. 1979).

Once observers began to follow Kasekela chimpanzees away from the feeding station in the late 1960s, they witnessed encounters with neighboring communities (Goodall et al. 1979). Around the same time, the Kasekela community began to fission. By 1970, two subgroups could be discerned. Six adult males, an adolescent male, and three adult females began avoiding the northern part of the range and spending more time in the south, while 8 adult males and 11 adult females occupied the north and avoided the south. The chimpanzees that ranged to the south were called the Kahama community, while those that stayed in the north retained the name Kasekela. Besides the three habituated females that became part of the Kahama community, an unknown number of unhabituated females also probably associated with the Kahama males (Goodall 1983). By 1973, the two communities were clearly distinct, and threatened each other when they met – with only occasional friendly contacts among some of the older males giving any hint that the two communities had once been one (Goodall 1983, 1986).

The first observed intergroup violence involved the killing of the infant of an unfamiliar female in 1971 (Bygott 1972). In 1973, observers following three males from the Kahama community found a freshly dead adult female, possibly a Kalande female killed by Kahama males (Wrangham 1975). Observers then witnessed a series of attacks from 1974 to 1977, during which Kasekela males fatally wounded four adult males and an adult female from Kahama; the freshly killed body of a fifth male was also found (Goodall 1986). By the end of 1977, all of Kahama's males had died or disappeared, and the remaining females either returned to Kasekela or joined other communities. Intergroup infanticides continued, with two in 1975 and one in 1979 (Goodall 1986). These attacks took place to the south of Kasekela's range, indicating that the infants' mothers were either unhabituated members of the Kahama community, or members of the Kalande community.

Goodall describes the extermination of the Kahama community as "The Four Year War" (Goodall and Berman 1999). While the rate of killings appears to have been particularly high during the 1970s, it also seems that chimpanzee communities are never fully at peace. In the late 1970s, having vanquished the Kahama community, the Kasekela chimpanzees experienced hostile encounters with their powerful neighbors to the north and south. By 1983, outside males were making deep incursions into the heart of Kasekela's range (Goodall 1986). Several otherwise healthy adult males disappeared, suggesting they might have been killed (*ibid.*), but no intergroup killings were directly observed in the 1980s. This may be at least partly due to the reduced number of observation hours per year compared to that in the preceding and following decades, resulting in fewer follows to border areas where intergroup interactions are most likely. The intergroup encounters that were observed were hostile, and severe attacks on females from neighboring communities were seen (Williams et al. 2004).

By the early 1990s, the Kasekela community had begun recovering in population size and range size. In March 1993, the Kasekela chimpanzees killed Rejea, an infant from the Mitumba community (Wilson et al. 2004). By the late 1990s, the expansion of the Kasekela range accelerated, largely at the expense of the Kalande community, which apparently started a steep population decline (Rudicell et al. 2010). On deep incursions into Kalande's range in 1998, Kasekela males attacked two infants, killing one, and severely attacked and likely killed an adolescent male (Wilson et al. 2004). During the 2000s, the Kasekela community maintained a large range, and intergroup violence continued intermittently. Kasekela males likely killed a Mitumba male, Rusambo, in 2002 (Wilson et al. 2004), and killed a Mitumba infant, Andromeda, in 2005 (Wrangham et al. 2006). In turn, Mitumba males killed Patti, an adult female from Kasekela (Wrangham et al. 2006; Williams et al. 2008).

Intergroup aggression has been a major source of mortality at Gombe (Williams et al. 2008). Intergroup killings have also been reported for all of the other long-term study sites, including Mahale, Kanyawara, Ngogo, and Budongo (summarized in Wrangham et al. 2006; Mitani et al. 2010), and Taï (Boesch et al. 2008). Killings have also occurred at some sites where studies have less time depth, such as Kalinzu (Hashimoto and Furuichi 2005) and Petit Loango (Boesch et al. 2007). Overall, the evidence strongly suggests that intergroup killing is a species-typical behavior.

16.3.1.1 Causes of Intergroup Aggression

Studies at Gombe and elsewhere have helped to clarify the causes of intergroup aggression. Males apparently benefit from defending and expanding territories by excluding rival males; by increasing the amount of food available for self, mates, and offspring; and by making territories more attractive to potential immigrants (Wilson and Wrangham 2003; Mitani et al. 2010). Females benefit from male territorial defense and expansion due to improved safety and improved food resources (Williams et al. 2004).

Male chimpanzees are hostile to foreign males, and genetic evidence supports the view that males are generally successful at preventing outside males from mating with their females. At Gombe, all infants tested in the Kasekela community had fathers from within their own community (Constable et al. 2001; Wroblewski et al. 2009). Paternity tests of Mitumba chimpanzees have likewise found no evidence of extra-community paternity (Wroblewski unpublished data). One female from the Kalande community apparently has an infant fathered by a Kasekela male (Rudicell et al. 2010). This conception might have occurred during a prolonged visit by that female to the Kasekela community (*ibid.*). No extra-group paternities have been reported for Budongo (Reynolds 2005), though extra-group paternity accounted for 7–11% of offspring born into communities at Taï (Vigilant et al. 2001; Boesch et al. 2006).

Several lines of evidence support the view that chimpanzees benefit by increasing the size of their territories. Analysis of 33 years of body mass data found that individuals in Kasekela were heavier when territory size was larger and population density was lower (Pusey et al. 2005). Analysis of 18 years of data for Kasekela found that females reproduced more quickly, individuals traveled in larger parties, and males encountered receptive females more often when the territory size was larger (Williams et al. 2004). Females dispersing from the declining Kalande community settled more often in the larger Kasekela territory than in the smaller Mitumba territory (Rudicell et al. 2010).

The quality of a territory may depend on other factors besides size, including food abundance and the density of competitors. When the number of adult males in Kalande was reduced to one, parous females began to visit the Kasekela community, and at least one emigrated permanently (Rudicell et al. 2010). This resembles the mass transfer of mothers from Mahale's K-group following the reduction of the community to a single adult male (Nishida et al. 1985) and suggests that females base their residence decisions on having enough males in the community to provide some or all of the following benefits: defense of food resources, protection from intergroup aggression, and providing sufficient mating partners. Investigations are currently under way to determine how food abundance and distribution affect the timing and location of intergroup encounters (Wilson et al. 2010).

Overall, the causes of intergroup aggression in chimpanzees are similar to those of many other group territorial species (Crofoot and Wrangham 2010). In most such species, though, intergroup conflict is rarely fatal. In contrast, among chimpanzees, humans, some social carnivores, and several social insects, intergroup conflict can account for a substantial portion of adult mortality. Manson and Wrangham (1991; cf. Wrangham 1999) argued that among mammals, fatal fighting is most likely in species with fission–fusion social systems, coalitionary bonds, and intergroup hostility, which together create opportunities for killing rivals at relatively low cost to the attackers (Manson and Wrangham 1991). Killing rivals, rather than merely chasing them off, benefits the killers by reducing the coalitionary strength of their opponents (Wrangham 1999). This "imbalance of power hypothesis," based on observations at Gombe, where the attackers generally greatly outnumbered the victims (Goodall 1986), has been supported by evidence from other sites, including the Kanyawara and Ngogo communities in Kibale National Park (Watts 2012). Playback experiments found that Kanyawara males were more likely to approach a simulated intruder the greater their numerical superiority (Wilson et al. 2001). Kanyawara males visited borders more often when in parties with more males (Wilson et al. 2007), and Ngogo males conducted boundary patrols more often when with many males (Mitani and Watts 2005).

16.3.2 Disease Ecology

Disease is the major cause of death for chimpanzees at Gombe (Williams et al. 2008), as at other sites (e.g., Mahale: Nishida et al. 2003 and Taï: Boesch and Boesch-Achermann 2000). Many deaths have occurred during epidemics, which included suspected polio, respiratory infections, and mange (Goodall 1986; Lonsdorf et al. 2006; Williams et al. 2008). Because chimpanzees and humans are so closely related, they share many of the same diseases. Molecular evidence indicates that at least some of the infections suffered by chimpanzees at research and tourism sites originate from humans (Köndgen et al. 2008). Humans may also contract diseases originating in chimpanzees (Wolfe et al. 1998). Understanding disease ecology is thus important for several reasons, such as guiding conservation management decisions, ensuring the health of people visiting and working in primate conservation areas, and understanding the origins and natural history of diseases that affect humans.

Various health data have been collected over the course of the study (Lonsdorf et al. 2006). Since March 2004, Lonsdorf and colleagues have been collecting systematic health data on the Kasekela and Mitumba chimpanzees (Lonsdorf et al. 2006; Travis et al. 2008). For each regular B-record follow, observers visually assess the health of the focal subject and collect a fecal sample for parasitological analysis. Gillespie and colleagues (2010) found that parasite prevalence was higher at Mitumba than Kasekela, perhaps due to the proximity of the Mitumba chimpanzees to the densely populated village of Mwamgongo. The health monitoring project has also provided tools and training to improve the recovery of samples and information during necropsies, which has proven invaluable in investigating the impact of another infection at Gombe: SIVcpz.

Current evidence indicates that HIV-1, the cause of the global AIDS pandemic, originated in the transmission of SIVcpz from chimpanzees to humans (Hahn et al. 2000). The strains of SIVcpz most closely related to HIV-1 occur in west-central Africa (Keele et al. 2006). Related strains of SIVcpz occur in the eastern Congo basin, but the virus is distributed unevenly and has not been detected in Uganda or Mahale (ibid.). Gombe is thus the only site with habituated chimpanzees at which some of the chimpanzees are naturally infected with SIVcpz (Santiago et al. 2002; Keele et al. 2006). SIVcpz infection was initially thought to be harmless (Silvestri 2008). However, detailed demographic data have revealed that it increases the mortality risk of infected chimpanzees by 10–16 times, and analysis of tissues collected from necropsies revealed that infected chimpanzees suffered AIDS-like damage to immune system tissues (Keele et al. 2009). Implications of this discovery for the future of Gombe's chimpanzees are sobering. The Kalande community, which has a much higher prevalence of the virus than Mitumba or Kasekela, has suffered a dramatic decline that may at be due at least partly to SIVcpz infection (Rudicell et al. 2010). Population models indicate that infected populations are likely to decline. Nonetheless, in small populations like Gombe, the virus may go extinct before the host population does. Moreover, factors such as immigration may help prevent population decline.

16.4 Discussion and Conclusions

In five decades of long-term research at Gombe, researchers have learned a great deal about the behavior and life histories of wild chimpanzees. While some striking behaviors such as tool use and hunting were observed early, only in the second decade of study did the outlines of chimpanzee social structure began to emerge, including group territorial defense, lethal aggression, and female transfer. The importance of female dominance rank was not clear until the study's fourth decade. Direct measures of male reproductive success were not obtained until the study's fifth decade, and we are still learning how female settlement patterns and ecology affect reproductive success. While many complete life histories have now been documented, the study has still not exceeded the lifespan of the longest lived chimpanzees. Gombe is small, but we are only now getting accurate estimates of the total chimpanzee population, and only two of the park's three communities are fully habituated. A wealth of data has been accumulated on intergroup dynamics, yet we are just starting to understand what influences frequencies of intergroup conflict. An integrated, multidisciplinary effort has begun to address disease, the major source of mortality, yet much work is needed to reduce the risk of disease transfer from humans to chimpanzees. Moreover, Gombe has unexpectedly emerged as a key site in the study of a virus that was unknown in 1960, but which has since claimed the lives of millions of people around the world. The presence of SIVcpz in Gombe presents both a fascinating opportunity for research and a challenging threat to the population.

Meanwhile, other field studies across Africa have broadened our understanding of chimpanzees and have confirmed that many patterns of behavior observed at Gombe are species typical. These studies have also found important differences among chimpanzee societies, revealing a diversity of social customs and raising questions about the extent to which behavioral differences depend on genetic differences, ecology, or social learning.

Many questions remain, even within a specific topic, such as aggression. For example: Will the Kasekela males kill the remaining Mitumba and Kalande males? If they eliminate their rivals, will they control a single super community, or will the community fission? Instead, if the adolescent males of Mitumba survive into adulthood, will they take back territory from Kasekela?

In the coming decades, molecular analyses of noninvasively collected samples will no doubt continue to yield new ways of detecting and analyzing viruses, parasites, genes, hormones, and more. The analysis of entire genomes will become practical. Molecular studies will continue to complement behavioral work in important ways, helping to confirm the identities of individuals as they move among communities and identifying likely maternal and paternal relationships, even among unhabituated chimpanzees (Rudicell et al. 2010). Yet however much technology advances, the core of the research must remain the individual chimpanzees, with their distinctive personalities and sometimes unexpected behavior. The more we learn about these individuals and their relationships, the more potential there is to ask interesting questions, including many that we have not yet thought of.

One of the most pressing questions is whether chimpanzees will survive in the wild. As human populations grow and forests become fragmented by logging and conversion to agriculture, many chimpanzee populations face a future similar to Gombe: living in ecological islands, surrounded by people, and heavily impacted by human activities and climate change (see also Jolly 2012). Gombe provides a field laboratory for promoting the survival of chimpanzees across Africa. Current efforts seek to address two major threats: disease risk, and habitat loss and subsequent population isolation. The health monitoring project is collecting baseline data essential for assessing chimpanzee health. Efforts have been made to improve sanitation around human settlements and minimize contact between chimpanzees and humans, including researchers, park staff, and tourists. Improvements in sanitation and enforcement of existing rules are still needed. The Jane Goodall Institute has been working with local villages to establish an interconnected network of village forest reserves around Gombe (Fig. 16.2). These could provide benefits both to villagers, in terms of protected watersheds, reduced erosion, and better conservation of forest products, and to chimpanzees, by providing a buffer and by enabling them to move more easily between Gombe and other remnant populations in the area (Pintea et al. 2010). If chimpanzees begin moving through these forest reserves, efforts will be needed to maintain local good will and prevent poaching.

Despite many threats, the Gombe chimpanzee population has remained stable over the past 10 years, giving some hope that it will survive well into the future.

Moreover, the government of Tanzania continues to demonstrate that it regards Gombe as one of the nation's natural treasures. In 2010, President Kikwete announced that the Tanzanian government would nominate Gombe for consideration as a World Heritage Site. Moreover, plans are underway to extend the park boundaries 1.5 km into the lake to protect freshwater species, resulting in a total park area of over 56 km^2 (Kayanda 2010). Gombe will need continued national and international support to ensure that its chimpanzees continue to survive, and that we will continue to learn from them.

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Chapter 17
Long-Term Research on Grauer's Gorillas in Kahuzi-Biega National Park, DRC: Life History, Foraging Strategies, and Ecological Differentiation from Sympatric Chimpanzees

Juichi Yamagiwa, Augustin Kanyunyi Basabose, John Kahekwa, Dominique Bikaba, Chieko Ando, Miki Matsubara, Nobusuke Iwasaki, and David S. Sprague

Abstract We have conducted long-term research on sympatric gorillas and chimpanzees in Kahuzi-Biega National Park since 1987. The demographic history of habituated gorillas has provided insights into their reproductive strategies. Infanticide by male gorillas, which has occurred frequently in the Virunga mountain gorilla population, had not been reported in Kahuzi for more than 20 years. However, soon after the large-scale killing of gorillas during a war in the late 1990s, it occurred three times within a few months. The infanticidal male might have discriminated between infants who were not his offspring and an infant whom he presumably sired based on past interactions with their mothers. At Kahuzi, births occurred most frequently during the period of ripe fruit abundance, and female Grauer's gorillas show longer inter-birth interval than female mountain gorillas in the Virungas. A comparison of reproductive strategies among different gorilla populations suggests that seasonal fluctuation in food abundance may lead to slow reproduction, whereas the potential pressure of infanticide may promote rapid reproduction. The reduced ranges and increased encounters between unfamiliar groups induced by large human disturbance, such as wars or conversion of their habitat to farmland, might have produced conditions leading to infanticide.

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Long-term data on diet composition indicate extensive overlap in fruit foods between sympatric gorillas and chimpanzees. However, their ranging and fallback strategies differed. The gorillas tended to use a large area evenly, whereas the chimpanzees visited small areas repeatedly. When preferred fruits were scarce, gorillas increased consumption of vegetative foods including leaves, pith, and barks, and chimpanzees ate more leaves, pith, and animal foods. These differences are tied to differences in food processing and digestive abilities, positional behavior, and cognitive abilities that mitigate feeding competition between the two species. The growing human population and political instability caused by the recent war have increased pressures on wildlife in and around the park. Conflicts between the park authorities and unemployed local people could be an important additional factor that predisposes individuals to hunt gorillas. The role of local conservation NGOs has become increasingly important for mitigating such conflicts and reducing destructive activities. We should use our knowledge of gorillas and chimpanzees gained by long-term studies for creating appropriate conservation measures.

17.1 Research History of Gorillas and Chimpanzees in Kahuzi-Biega National Park

Most primates have relatively long life spans and slow reproduction (Ross 1998; Kappeler et al. 2003). The great apes, in particular, have the slowest reproduction and the longest period of immaturity (Goodall 1986; Watts 1990; Nishida et al. 2003; Wich et al. 2004; Harcourt and Stewart 2007). Gorillas and chimpanzees are gregarious, and association with other individuals in social groups and individual transfer between groups greatly influence their survival and reproductive success (Fossey 1983; Goodall 1986; Harcourt and Stewart 2007). Therefore, long-term studies of demography, social changes, and reproduction are necessary to obtain the life history data crucial for understanding social and behavioral evolution in these species. In addition, long-term studies allow us to analyze (a) how apes and other nonhuman primates make behavioral adjustments to environmental changes, (b) how dispersal influences social structure, (c) how demographic changes influence intergroup relationships, and (d) how niche divergence allows primate species to live sympatrically.

Long-term research projects on primates living in natural habitats should also involve conservation efforts in response to increasing human disturbance such as deforestation, mining, and poaching. Ecotourism has been promoted as part of conservation strategies in many protected areas. Kahuzi-Biega National Park (KBNP), in the eastern Democratic Republic of Congo (DRC), has been a suitable site for both long-term research and ecotourism. Several groups of Grauer’s gorillas (*Gorilla beringei graueri*) were habituated for research and tourism, and their demography has been recorded for more than 20 years. Eastern chimpanzees (*Pan troglodytes schweinfurthii*) are sympatric with Grauer’s gorillas, and a group of chimpanzees was also habituated for research. In this chapter, we describe some of the major results of our long-term research on these gorillas and chimpanzees and of conservation efforts in Kahuzi.

Grauer's gorillas are only found in eastern DRC. They occur in two national parks (Maiko and Kahuzi-Biega) and two national reserves (Itombwe and Tanya), with the largest population in Kahuzi-Biega (Hall et al. 1998). Eastern chimpanzees also occur in these habitats. Kahuzi is divided into a lowland sector (5,400 km^2 at an altitude of 600–1,800 m) covered with lowland moist evergreen forest and a highland sector (600 km^2 at an altitude of 1,800–3,308 m) covered with montane forest. The two sectors are connected by a corridor that is 4 km wide and 20 km long (Fig. 17.1). The highland sector was gazetted as a national park in 1970, mainly for the protection of Grauer's gorillas (Mankoto 1988). The park was extended into the lowland sector in 1975, and the whole park was inscribed in the World Heritage List in 1980.

A team from Kyoto University and Centre de Recherche en Sciences Naturelles (CRSN) carried out preliminary research on the Kahuzi gorillas and chimpanzees from 1987 to 1991 and estimated population densities for both species. This team found extensive overlap in diet and ranging, documented frugivory and insectivory by the gorillas, and found that frugivory had a positive effect on gorilla daily path length (Yamagiwa et al. 1989, 1991, 1994; Yamagiwa and Mwanza 1994). Population surveys were also conducted in the lowland sector and adjacent forest by WCS in 1994 (Hall 1994; Hall et al. 1998). The density of apes in the lowland sector was estimated to be 0.27–0.33 gorillas/km^2 and 0.27–0.32 chimpanzees/km^2 by nest counts along reconnaissance walks (Yamagiwa et al. 1989), and 0.26–0.58 gorillas/km^2 and 0.81–1.78 chimpanzees/km^2 by nest counts along transects (Hall et al. 1998).

In the highland sector, four groups of gorillas were habituated for a gorilla tourism program (Fig. 17.2). The Mushamuka Group and the Maeshe Group were habituated in the early 1970s, and demographic changes in these groups have been recorded since the late 1970s (Yamagiwa 1983; Mankoto et al. 1994). The Mubalala Group was habituated in 1987 (Mankoto 1988), and the Nindja Group formed in 1989, when several females and immatures from the Mushamuka and Maeshe Groups joined a young silverback who had been born in the Mushamuka Group. Research on the Mushamuka and Maeshe Groups was conducted in the 1970s and focused on ranging patterns, feeding ecology and nutrition, social relationships, and relationships between groups (Casimir and Butenandt 1973; Casimir 1975; Goodall 1977; Yamagiwa 1983). The first gorilla census in the highland sector was conducted using nest counts in 1978, and the population was estimated at 223 gorillas (Table 17.1; Murnyak 1981).

In 1985, the Institut Zairois pour la Conservation de la Nature (IZCN, now ICCN) launched a conservation project in cooperation with the German Technical Cooperation Agency (GTZ) to train guides and regulate the gorilla tourism program (von Richter 1991). Gorilla tourism was well organized during this time, and it generated significant revenue. From 1989 to 1993, annual revenue was about US$ 210,000 (Butynski and Kalina 1998). A second census, conducted in 1990

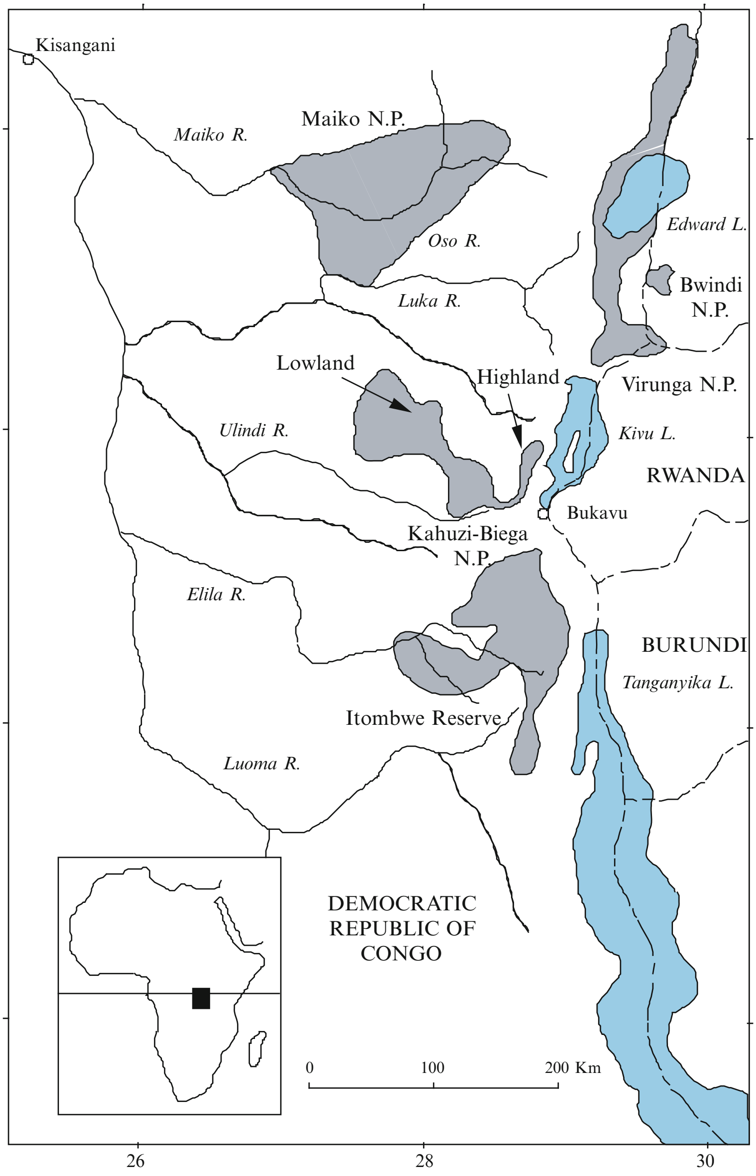

Fig. 17.1 Map showing the location of Kahuzi-Biega National Park. Gray areas represent a national park or forest reserve. *Blue* areas represent a lake

by Kyoto University, GTZ, CRSN, and IZCN, found about 258 gorillas (Yamagiwa et al. 1993). The first census of chimpanzees in the highland sector was conducted simultaneously, and three chimpanzee groups (communities) were confirmed by nest counts. Their nests were found in the small areas covered with primary forest,

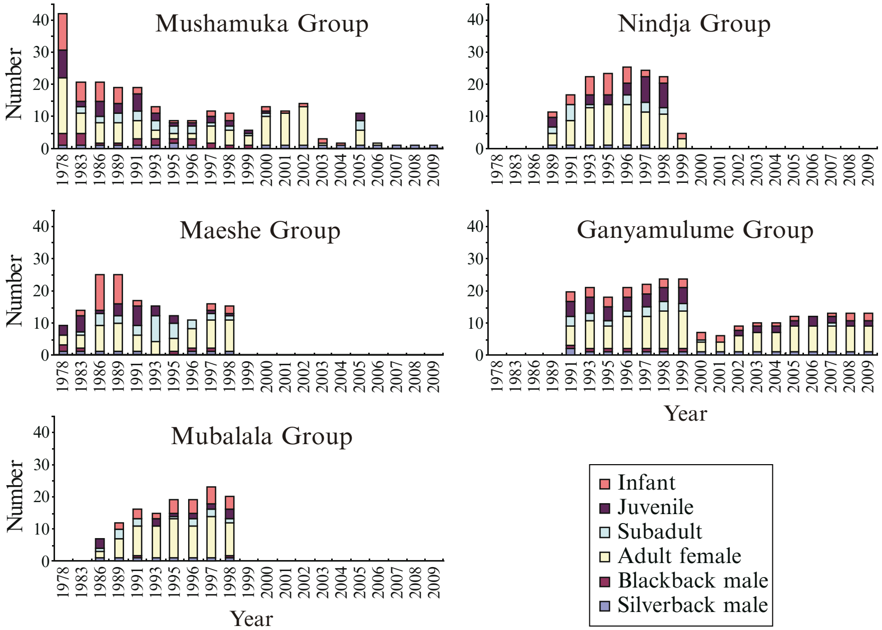

Fig. 17.2 Annual change in group size and composition of habituated gorilla groups at Kahuzi

and their density was estimated to be 0.13 chimpanzees/km^2 (Yamagiwa et al. 1992). During this survey, we found extensive overlap between one group of chimpanzees and four groups of gorillas, and decided to habituate these groups for long-term studies (Yamagiwa et al. 1996). By 1994, we had habituated the Ganyamulume Group (21 gorillas) and the Kaboko Group (22 chimpanzees) for research on diet and ranging (Yamagiwa and Basabose 2006a, b).

However, political instability in the Kivu region interrupted our research many times in the 1990s. The problems started with the outbreak of riots in Kinshasa in 1991 and were exacerbated in 1994 when the Rwandan genocide provoked the influx of about 450,000 refugees into the area around the park (Hall 1994). During the subsequent war from 1996 to 1999, these refugees were driven from the area, and many people died. Insecurity has continued on and off to the present day, associated with the presence of *Interahamwe* who caused the genocide in Rwanda and of other armed groups. Most of the elephants and half the gorilla population in the highland sector were lost during the war when park rangers were disarmed and prohibited by the rebel government from patrolling the park (Yamagiwa 1999). Armed militia groups frequently camped in the lowland sector and poaching there was probably more intense than in the highland sector (Hart et al. 2007). Three population surveys did not show a marked decline in the population of chimpanzees, but clearly indicated a sudden decrease in the number of gorilla groups during the war and a gradual increase in group size and in the proportion of infants (Table 17.1).

Table 17.1 Population census in the highland sector of KBNP

	1978[1]	1990[2]	1996[3]	2000[4]	2004[5]
Population size	223	258	247	130	163
# Groups	14	25	25	13	15
Mean group size	15.6	10.8	9.8	9.6	17.3
% Infant	17.0	8.4	12,7	9.3	15.9
# Solitary males	5	9	2	4	2

Source: 1, Murnyak, 1981; 2, Yamagiwa et al., 1993; 3, Inogwabini et al., 2000; 4, 5, Amsini et al., 2007.

Since 1994, we have followed fresh trails of the Ganyamulume Group and the Kaboko Group (up to one-day old) between consecutive nest sites and used GPS data to record their ranging. We confirmed estimates of group size and composition by direct observation and by counting night nests and measuring the feces they contained. We estimated diet composition from direct observations, evaluation of feeding remains along fresh trails, and fecal analysis. Fresh feces were collected mainly at nest sites, washed in 1-mm mesh sieves, dried in sunlight, and stored in plastic bags. The contents of each sample were examined macroscopically and listed as seeds, fruit skins, fiber, leaves, fragments of insects, and other matter. Fruit seeds and skin were identified at the species level macroscopically. We also kept track of changes in the composition of the groups habituated for tourism and used data on these groups to investigate gorilla life history strategies.

The home ranges of the Ganyamulume Group and the Kaboko Group were composed mainly of bamboo (*Sinarundinaria alpina*) forest, primary montane forest, secondary montane forest, and *Cyperus* (*Cyperus latifolius*) swamps. We set up a belt transect 5,000 m long and 20 m wide at an altitude of 2,050–2,350 m within the Ganyamulume Group's home range in 1994, and recorded 2,033 individual trees and woody vines above 10 cm in diameter at breast height (DBH) belonging to 49 species. The diversity of tree species in the highland sector is distinctly lower than that in the lowland sector, where we identified 6,922 trees and vines belonging to at least 150 species found in a belt transect 8,000 m long and 10 m wide. To estimate fruit abundance, we have monitored 28 species of trees and shrubs twice each month since 1994; chimpanzees and gorillas eat fruit from 24 of these and the other four are not ape food species. For each species, fruits (ripe and unripe) of at least ten reproductively mature trees were monitored. The monthly datum of the presence of fruit was the average of the two records. To estimate fruit abundance (biomass and number) of tree species, we used DBH (Chapman et al. 1992). We calculated a monthly fruit index (F_{m}) as

$$F_{\mathrm{m}} = \sum_{k=1}^{s} P_{\mathrm{km}} B_k,$$

where P_{km} denotes the proportion of the number of trees in fruit for species k in month m, and B_{k} denotes the total basal area per ha for species k in the line transect. The ripe fruit index was calculated from six fruit species preferred by gorillas and 12

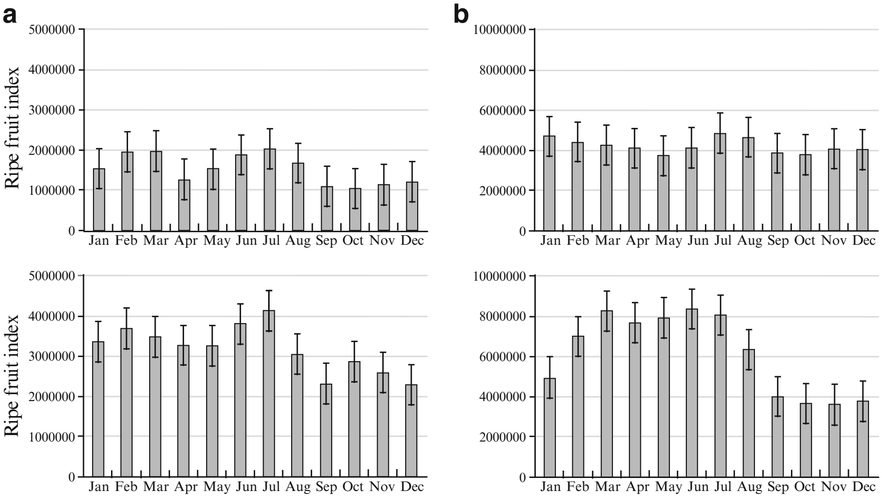

Fig. 17.3 Monthly fluctuation in the ripe fruit index for gorillas (**a**) and chimpanzees (**b**) in the primary (*upper*) and the secondary (*lower*) forests

preferred by chimpanzees, where preferred fruit species were defined as those ranked in the top three fruit species by fecal analysis in a month (Yamagiwa et al. 2008).

Meteorological data are available from the Meteorological Station at CRSN (1,600 m above sea level), which is located 4 km from the study area. The mean annual rainfall from 1994 to 2009 was 1,607 mm (range: 1,316–2,180 mm), with a distinct dry season in June, July, and August, in which the mean monthly rainfall was below 100 mm. The mean monthly temperature was 20.1°C (mean maximum: 26.5°C; mean minimum: 13.8°C).

In the lowland tropical forests that gorillas and chimpanzees inhabit sympatrically, the dry season is regarded as a period of fruit scarcity (Lope, Gabon: Tutin and Fernandez 1993; Ndoki, Congo: Kuroda et al. 1996; Moukalaba, Gabon: Takenoshita et al. 2008). In contrast, more ripe fruits are available during the dry season in Kahuzi (Fig. 17.3).

17.2 Life History of Kahuzi Gorillas

Starting in 1983, we named each individual and used the names for systematic recording of demographic changes, J. Kahekwa worked as a guide for gorilla tourism and named all individuals of the habituated groups, and J. Yamagiwa confirmed demographic changes with J. Kahekwa every year. Although the exact dates of birth, death, immigration, and emigration of some individuals were recorded, most demographic data were only collected weekly or monthly, due to the limits on the time that tourists were allowed to contact the gorillas per day.

Unfortunately, large-scale poaching when the war resumed in 1998 and 1999 decimated half of the gorilla population in the highland sector (Table 17.1). Habituated groups were the focus of poaching, and Maeshe, Mubalala, and Nindja Groups disintegrated after the majority of members were killed (Fig. 17.2). In Mushamuka Group, a blackback male (11 years old in 1998) led the 11 survivors. In Ganyamulume Group, a silverback male and three females were killed by poachers in 1998, and a solitary silverback joined the group after 6 months as a new leader. However, a blackback male started regularly forming a subgroup with several females, and finally formed another group in 2000. The park rangers were disarmed by the rebel force and could not enter the park for 9 months. The park staff resumed regular patrols without arms and started to habituate other groups in 1999. They succeeded in habituating Mishebere Group and Mufanzala Group in 2001, and Birindwa Group, Chimanuka Group, Langa Group, and Mankokoto Group afterward (Fig. 17.4). A silverback male of Mishebere Group was killed by poachers and the group disintegrated in 2003, and the young male of Mushamuka Group recently lost all females and immature to become solitary, but other groups have survived until 2009. Data collection on the habituated groups has continued so far, but life history data are incomplete due to frequent movements of individuals between habituated and unhabituated groups.

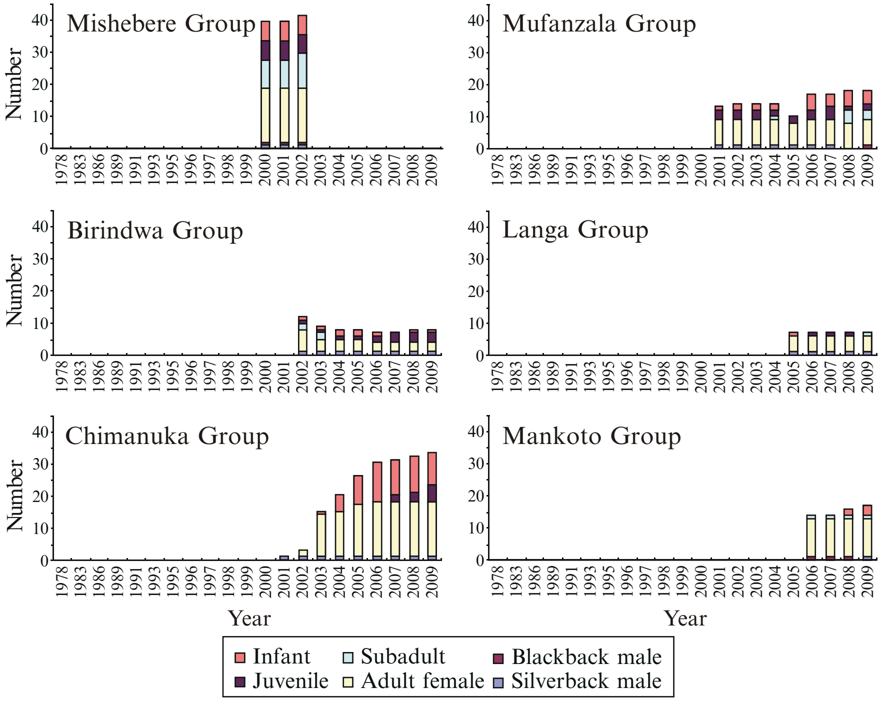

Fig. 17.4 Annual change in group size and composition of newly habituated gorilla groups at Kahuzi

We reconstructed the demographic history of habituated groups from fragmented records on each individual, mainly from data before the large-scale killing in 1998, and compared them with those of mountain gorillas in the Virungas (Table 17.2). Most previous information on gorilla social organization and life histories has come from the long-term data on mountain gorillas (*G. beringei*) gathered by the Karisoke Research Center. Mountain gorillas are year-round breeders, and no evidence of birth seasonality exists (Watts 1991). They form cohesive groups, and the home range of neighboring groups overlaps extensively (Schaller 1963; Harcourt 1978). Low variation in habitat quality and high home range overlap reduce the ecological cost of dispersal, while reproductive strategies strongly influence patterns of female transfer (Watts 1990, 1996; Robbins 1995; Harcourt and Stewart 2007).

Infanticide by males is a major source of infant mortality in the Virunga population (Fossey 1984; Watts 1989, 1991; Robbins et al. 2009). The contexts in which it occurs and its effects on female transfers and reproductive rates are consistent with the sexual selection hypothesis (Hrdy 1979; Sommer 1994; van Schaik 2000). Female mountain gorillas might respond to the threat of infanticide by seeking effective male protection. For example, they tend to transfer into multi-male groups instead of to single-male groups or solitary males, presumably because defense by multiple males is more effective and because the presence of multiple males reduces that chance that male death leaves a female with a dependent infant without any protection (Watts 1989, 1996, 2000). Multi-male groups attract more

Table 17.2 Reproduction and life history features of gorillas in Kahuzi and Virungas

Life history parameter	N	Kahuzi	N	Virunga
Seasonality in birth	47	$p<0.05$	65	N.S.
Sex ratio at birth (number of males/number of females	64	0.94	59	0.79
Infant mortality 1 Primiparous	21	33.3%	14	42.9%
Parous	25	20.0%	45	17.8%
Infant mortality 2 First year	46	19.6%	65	26.2%
Second year	46	6.5%	65	7.7%
Minimum age at first observed copulation		5.2 years		5.8 years
Number of producing their first infant in natal group	18	5	16	7
Number of producing their first infant in non-natal group	18	9	16	9
Number of females emigrating from their natal group after the first birt	5	4	7	4
Age at first parturition	6	10.6 years (9.1-12.1)	8	10.1 years (8.7-12.8)
Interval between surviving births	9	4.6 years (3.4-6.6)	26	3.9 years (3.0-7.3)
Age at male emigration from natal group	6	12.7 years (9.6-14.4)	9	13.5 years (12-15)
Maximum number of silverback males within a group		2		7
Proportion of multi-male group in the population		8%		40%

Source: Watts (1990, 1991); Robbins (1995), Yamagiwa & Kahekwa (2001) Yamagiwa et al (2003); Robbins et al (2007) females than single-male groups; this in turn might prevent maturing males from leaving their natal groups because they have good chances of mating within those groups (Robbins 1995, 2001; Robbins and Robbins 2005; Harcourt and Stewart 2007). This could explain the high proportion of multi-male groups (about 40%) in the Virunga population (Weber and Vedder 1983; Robbins 1995).

In contrast, births at Kahuzi are significantly clumped in May and June – the early dry season (Fig. 17.5; $X^2 = 23.6$, $df = 11$, $p < 0.05$), at which time the abundance of ripe fruit increases (Fig. 17.3a). Infant mortality was lower at Kahuzi than in the Virungas, especially that of infants born to primiparous females and mortality in the first year after birth (Table 17.2). Infanticide might have caused this difference. In Kahuzi where infanticide had not been observed until recently, females tended to transfer with immatures, and 9 cases of females with infants were observed between 1989 and 1997 (Yamagiwa and Kahekwa 2001). After the death of silverback males, females did not disperse but maintained cohesive groups without any mature males for prolonged periods (Maeshe Group for 29 months, Mushamuka Group for 15 months, and Nindja Group for 9 months). In the Virungas, single-male groups of mountain gorillas always disintegrated after the death of silverback males, and females joined neighboring groups or solitary males within a few months. The absence of infanticide might have facilitated natal dispersal by maturing males either alone or with other individuals before maturity. The high probability of co-transfer by multiple females may make it relatively easy for solitary males to form new groups and for males to form new groups via fissioning of existing ones; this might explain the small proportion of multi-male group (8%) in the Kahuzi population (Yamagiwa et al. 1993, 2003).

We thought that male Grauer's gorillas were not infanticidal (Yamagiwa and Kahekwa 2001), but social and demographic changes following the war showed this to be wrong (Yamagiwa and Kahekwa 2004). The first case of infanticide at Kahuzi was observed in 2003. When a female transferred with other females from the Mugaruka

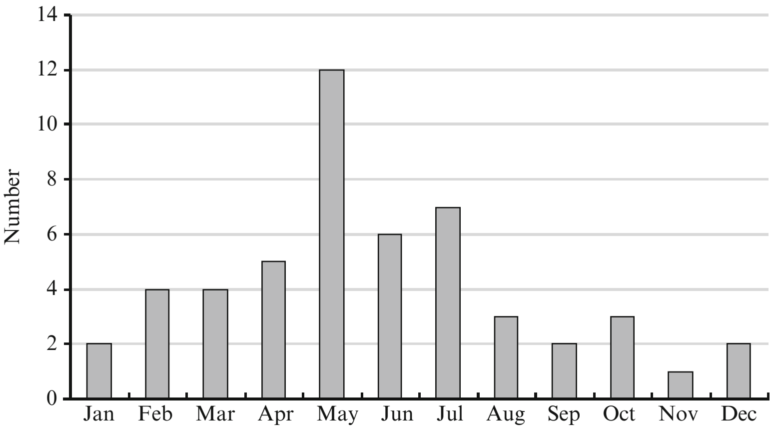

Fig. 17.5 Monthly fluctuation in the number of births observed in the habituated groups

(the former Mushamuka) Group to the Chimanuka Group, her newborn infant was killed by Chimanuka, the silverback male of that group. The victims in the second and the third cases were newborn infants whose mothers transferred into Chimanuka Group 1 and 2 months before giving birth, respectively. But another newborn infant whose mother transferred into the same group more than 1 year before was not killed by Chimanuka. These observations suggest that the infanticidal male discriminated between infants who were not his offspring and an infant whom he had presumably sired, probably based on past interactions with their mothers (Yamagiwa et al. 2009).

The occurrence of infanticide might have changed patterns of female association. A female transferred from the Mugaruka Group to the Chimanuka Group 1 month after the last infanticide, and she left a dependent infant (31-month old). She might have learned from the first case of infanticide that she witnessed and effectively responded to the threat by abandoning her infant at transfer. Since the first infanticide occurred, female transfer with dependent infants or formation of all-female groups have never been seen again.

Although infanticide did not promote the formation of multi-male groups at Kahuzi, it might have accelerated female reproduction. In the Chimanuka Group, many females gave birth soon after the last case of infanticide, and the number of infants rapidly increased (Fig. 17.4). Between 2005 and 2010, four twins were born in the Chimanuka Group, and two pairs have survived until present. Age at first birth is slightly older at Kahuzi than in the Virungas, and inter-birth intervals are slightly longer (Table 17.2). Both ecological and social factors are responsible. Seasonal fluctuation in food abundance may lead to slow reproduction. Greater frugivory, stronger habitat seasonality, lower densities of herbaceous foods, and lower abundance of weaning foods may promote slower development and reproduction in western lowland gorillas (Doran and McNeilage 2001; Nowell and Fletcher 2008), which mature more slowly and have a later age at first parturition and longer inter-birth intervals than mountain gorillas (Robbins et al. 2004; Breuer et al. 2009). In contrast, the potential pressure of infanticide may promote rapid reproduction in the Virungas (Fig. 17.6). Although no difference is found in the mean group size across gorilla populations in different habitats, the maximum group size is larger in eastern gorillas than western gorillas, and the proportion of multi-male groups in the population is larger in mountain gorillas than in Grauer's gorillas and western gorillas (Yamagiwa et al. 2003). The more frugivorous diets of western gorillas may set lower limits on maximum group size because they lead to stronger within-group feeding competition, which in turn makes it easier for single males to monopolize females and prevents the formation of multi-male groups (Harcourt and Stewart 2007; Breuer et al. 2009).

The probability of infanticide may be increased by rapid changes in density of gorilla social units and associated changes in relationships between groups like those that followed large-scale poaching at Kahuzi. The leading silverbacks in all five habituated groups were killed by poachers, and group disintegrations and frequent female transfers occurred after their deaths, although females continued to associate with each other and without silverbacks for several months in some groups. Young silverbacks who had been solitary males survived during the war and joined these female groups as the new leading males. Among eight groups newly monitored by the

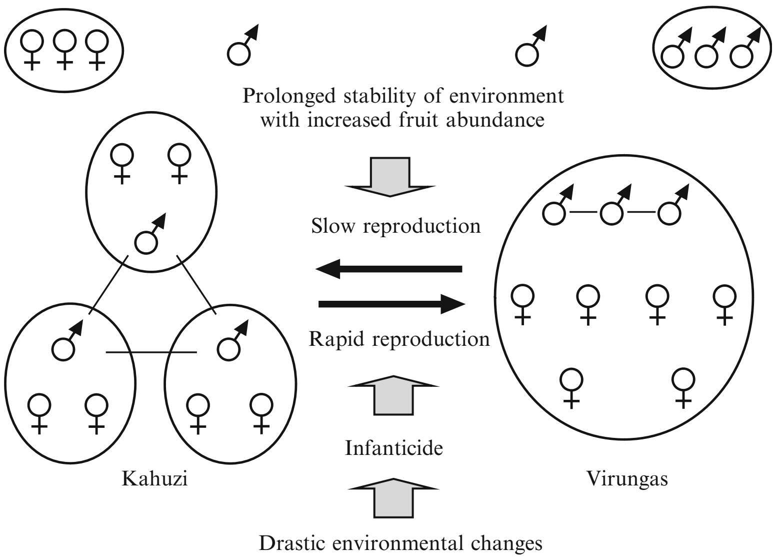

Fig. 17.6 Two types of social structure shifting to each direction by environmental changes

park and by us after large-scale poaching, seven groups were led by young silverbacks estimated to be less than 20 years old (Yamagiwa et al. 2009). Chimanuka, the infanticidal male, was 17 years old when he killed three newborn infants. Mugaruka, who lost all his females to Chimanuka, was one year younger than Chimanuka. Both males were born in different habituated groups (Maeshe and Mushamuka Groups) and were presumably unrelated. These maturing silverbacks are strongly motivated to attract females in order to establish their own groups (Harcourt 1978; Yamagiwa 1986), and they show a greater potential to commit infanticide than do group males in the Virungas (Watts 1989). The sudden changes in the population of mountain gorillas following the large conversion (40%) of their habitat to farmland might also have promoted infanticide in the Virunga region. The gorilla population was reduced by half after the conversion, as was observed in Kahuzi. The reduced ranges and increased encounters between unfamiliar groups induced by such disturbances might have produced conditions leading to infanticide.

17.3 Research on Sympatric Populations of Gorillas and Chimpanzees

The pioneering studies of sympatric populations of gorillas and chimpanzees in the 1950s and 1960s suggested that several aspects of niche differentiation, including differences in diet, habitat choice, and use of forest strata, allow coexistence of gorillas and chimpanzees (Schaller 1963; Jones and Sabater Pi 1971). Field studies on allopatric populations of gorillas and chimpanzees have also reported distinct differences in their socioecology. Gorillas are more folivorous, and the continuous availability and relatively uniform quality of their terrestrial food resources reduce the potential for feeding competition and enable them to form cohesive groups in which females have egalitarian social relationships. Gorillas are not territorial and groups show weak site fidelity (Stewart and Harcourt 1987; Watts 1991, 1996, 1998a,b; Harcourt 1992). In contrast, pronounced frugivorous diets and frequent use of depletable high-quality fruit patches prevent chimpanzees from forming cohesive groups and promote a fission–fusion sociality as a way to reduce feeding competition (Nishida 1968; Goodall 1986; Chapman et al. 1995; Wrangham et al. 1996). Chimpanzees form communities (unit groups) that have stable memberships. They defend territories against members of neighboring communities, and male chimpanzees occasionally patrol the peripheral parts of their ranges, where lethal intercommunity aggression can occur (Goodall et al. 1979; Nishida et al. 1985; Watts and Mitani 2001; Wilson and Wrangham 2003; Boesch et al. 2007; Watts 2012; Wilson 2012).

However, most of the data on gorillas have come from long-term studies on a single population of mountain gorillas in the Virunga volcanoes living at the upper altitudinal extreme of the species' geographic distribution. Research on western lowland and Grauer's gorillas, and that on mountain gorillas inhabiting the low altitudinal forest of Bwindi show that they are considerably more frugivorous than Virunga gorillas and often feed and nest in trees (Tutin and Fernandez 1984; Williamson et al. 1990; Yamagiwa et al. 1994; Kuroda et al. 1996; Remis et al. 2001; Robbins and McNeilage 2003; Stanford and Nkurunungi 2003; Rogers et al. 2004). Nevertheless, they also tend to form cohesive groups like mountain gorillas (Harcourt et al. 1981; Tutin 1996; Doran and McNeilage 1998). Average group size and home range size of gorillas vary little among habitats, although the proportion of multi-male groups is higher in mountain gorillas than in eastern and western lowland gorillas (Watts 1996; Doran and McNeilage 2001; Yamagiwa et al. 2003; Yamagiwa and Basabose 2006b).

In contrast, the members of a chimpanzee community form temporary parties that frequently change size and composition in association with variation in fruit availability and with social factors such as the presence of estrous females and conflict among males, and their annual range size varies among habitats (Chapman et al. 1995; Matsumoto-Oda et al. 1998; Yamagiwa 1999; Anderson et al. 2002; Mitani et al. 2002; Basabose 2004). Thus, gorillas and chimpanzees have great social and ecological flexibility, but they respond differently to variation in food abundance and distribution. Both gorillas and chimpanzees have unspecialized digestive systems, and they are less able to digest unripe fruits and mature leaves than Old World monkeys (Chivers and Hladik 1980; Fleagle 1984; Remis 2000). Consequently, their diet is highly diverse and includes a broad range of non-fruit foods (van Schaik et al. 2004; Yamagiwa 2004). Their behavioral and social flexibilities have possibly evolved to cope with these dietary constraints.

Niche separation between sympatric primate species becomes more pronounced during periods of food shortage (Ungar 1996; Tan 1999; Powzyk and Mowry 2003). Fallback foods, which are used more when preferred foods are scarce, might have had particularly important evolutionary influences on the morphology and behavior of the African apes (Lambert 2007; Marshall and Wrangham 2007). Research on sympatric populations is the best way to elucidate the impact of fallback foods and other environmental factors on morphological and behavioral differentiation between gorillas and chimpanzees.

In Kahuzi, long-term data on diet composition indicate extensive overlap in fruit foods between gorillas and chimpanzees (Yamagiwa and Basabose 2006a). However, patterns of frugivory were different. For gorillas, the monthly abundance of ripe fruit from preferred species was positively correlated with the diversity of fruit in the monthly diet (the monthly mean number of fruit species per fecal sample: $R^2 = 0.436$, $p < 0.0001$) and with the monthly mean proportion of fruit remains per fecal sample ($R^2 = 0.244$, $p < 0.001$). For the chimpanzees, the abundance of preferred fruit was positively correlated with the monthly proportion of fruit in fecal samples ($R^2 = 0.197$, $p < 0.01$), but the diversity of fruits consumed was not significantly related to the abundance of ripe fruit ($R^2 = 0.005$, $p = 0.623$). Among fruit species preferred by both apes, both consumed ripe fruit of *Myrianthus holstiii* in proportion to its abundance ($R^2 = 0.482$, $p < 0.001$ for gorillas; $R^2 = 0.281$, $p < 0.001$). However, consumption of figs by both apes was not significantly correlated with the abundance of ripe fruits, and chimpanzees always consumed more figs than gorillas.

These differences in feeding patterns are reflected in differences in ranging patterns. We plotted daily movements of the study groups on a grid of 250 × 250 m quadrats superimposed on a 1:25,000 vegetation map of the study area (Yamagiwa and Basabose 2006b). Based on the number of grid squares visited by the study groups, the total home range of the gorilla group (42.3 km^2 for 92 months) was three times larger than that of the chimpanzee group (15.7 km^2 for 82 months). Both annual range (average 15.5 km^2) and core area (average 3.4 km^2) of the gorilla group were about twice as large as those of chimpanzees (7.1 km^2 and 1.5 km^2, respectively). The gorillas tended to use a large area evenly, whereas the chimpanzees visited small areas repeatedly. The proportion of the total home range reused within 1 month was larger for chimpanzees (55%) than for gorillas (25%). The gorillas tended to shift their range monthly and yearly, while the chimpanzees showed high site fidelity. The number of new grid squares visited by the gorilla group tended to increase every year, while that of chimpanzees did not increase substantially after the first 2 years (Yamagiwa and Basabose 2006b). The chimpanzees covered more than half their total home range within the first year (Basabose 2005).

The ranging patterns of the gorillas were similar to those of mountain gorillas in the Virunga region, and reflect a strategy to seek high-quality herbaceous vegetation and to avoid previously used areas that contained trampled vegetation (Vedder 1984; Watts 1987, 1998b). In contrast, the ranging patterns of the chimpanzee study group are similar to those of chimpanzees inhabiting lowland forests in Taï (Lehmann and Boesch 2003) and Gombe (Williams et al. 2004), and reflect a strategy to harvest fruit efficiently by adjusting search paths and patch revisitation to the current distribution of fruit (Waser 1984; Garber 1989).

Table 17.3 Range overlap between the gorilla and chimpanzee groups

	Total range	Core 75%	Core 50%
Overlap area	**11.0 km^2**	**2.1 km^2**	**0.25 km^2**
Primary forest	**21.5%**	**42.3%**	**62.5%**
Secondary forest	**65.8%**	**51.3%**	**35.6%**
*Cyperus*swamp	**1.9%**	**1.9%**	**2.2%**
Bamboo forest	**10.7%**	**4.5%**	**0%**
% in gorilla range	**25.9%**	**14.9%**	**4.0%**
% in chimpanzee range	**69.7%**	**41.3%**	**9.8%**

Most (70%) of the chimpanzee study group's home range overlapped with that of the gorilla study group (Table 17.3). However, the small core area overlap (10% from the chimpanzee perspective) suggests that the chimpanzee avoided the core area of the gorillas, which included primary forests, secondary forests, and swamps. In contrast, that of the chimpanzees consisted mainly of primary forest fragments. Several encounters between gorillas and chimpanzees were observed in the primary forest (Yamagiwa et al. 1996). All lasted for only a few minutes and ended with mutual avoidance. Chimpanzees possibly avoided visiting fruiting patches that the gorillas also used, especially when they were in small parties (Basabose 2002). Although high overlap in fruit diets predicts frequent encounters between gorillas and chimpanzees at fruiting crops, their different foraging strategies may reduce the opportunities for encounters. They may also avoid direct contact where their preferred fruits are available. Co-feeding between gorillas and chimpanzees has been observed in the lowland tropical forests at Ndoki and Goualago (Kuroda et al. 1996; Morgan and Sanz 2006), and aggressive interactions were observed in the montane forest at Bwindi (Stanford and Nkurunungi 2003).

September to January is a period of fruit scarcity in Kahuzi. The abundance of ripe fruits for chimpanzees decreased distinctly in the secondary forest that dominated their home range (Fig. 17.4). Chimpanzees possibly need to use the small patches of primary forest to seek fruit during this period. Gorillas usually shifted to the bamboo forest and fed on bamboo shoots (Casimir and Butenandt 1973; Goodall 1977). However, from 1994 to 1997, many bamboo stands withered and died after flowering, and the gorillas only occasionally visited the bamboo forest, probably to search bamboo shoots, and returned to the previous ranging area in the primary or the secondary forest after a few days (Fig. 17.7). When bamboo shoots appeared in 1998, the gorillas used the bamboo forest more.

When fruit was scarce, gorillas and chimpanzees relied on different fallback foods in Kahuzi. We examined their fallback foods using the definition of staple/filler fallback foods by Marshall and Wrangham (2007). Fecal analysis showed that gorillas regularly consumed vegetative foods (leaves, pith, and bark) in every month, and in certain months, all gorilla fecal samples (100%) were composed entirely of vegetative plant parts (Yamagiwa and Basabose 2009). The mean proportion of vegetative foods per fecal sample of gorillas was negatively

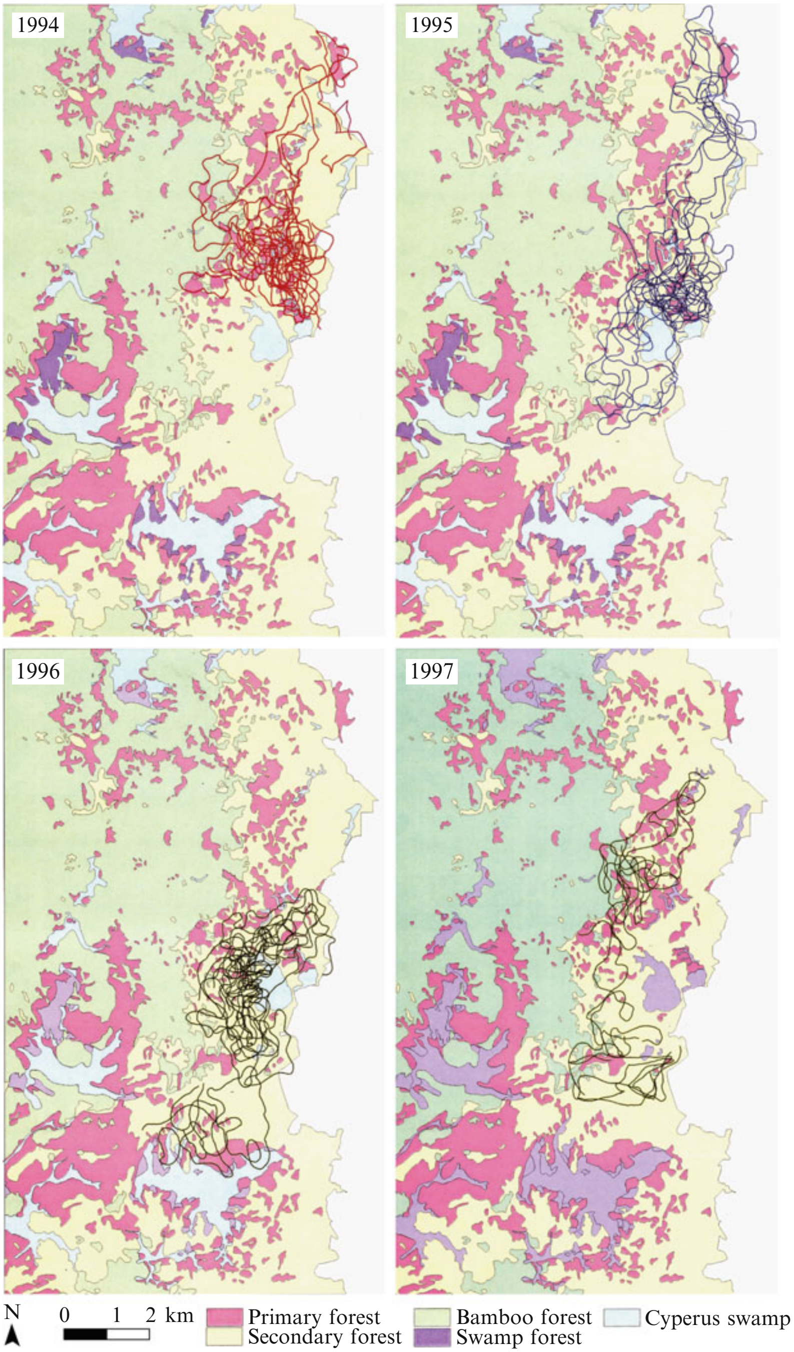

Fig. 17.7 (Continued)

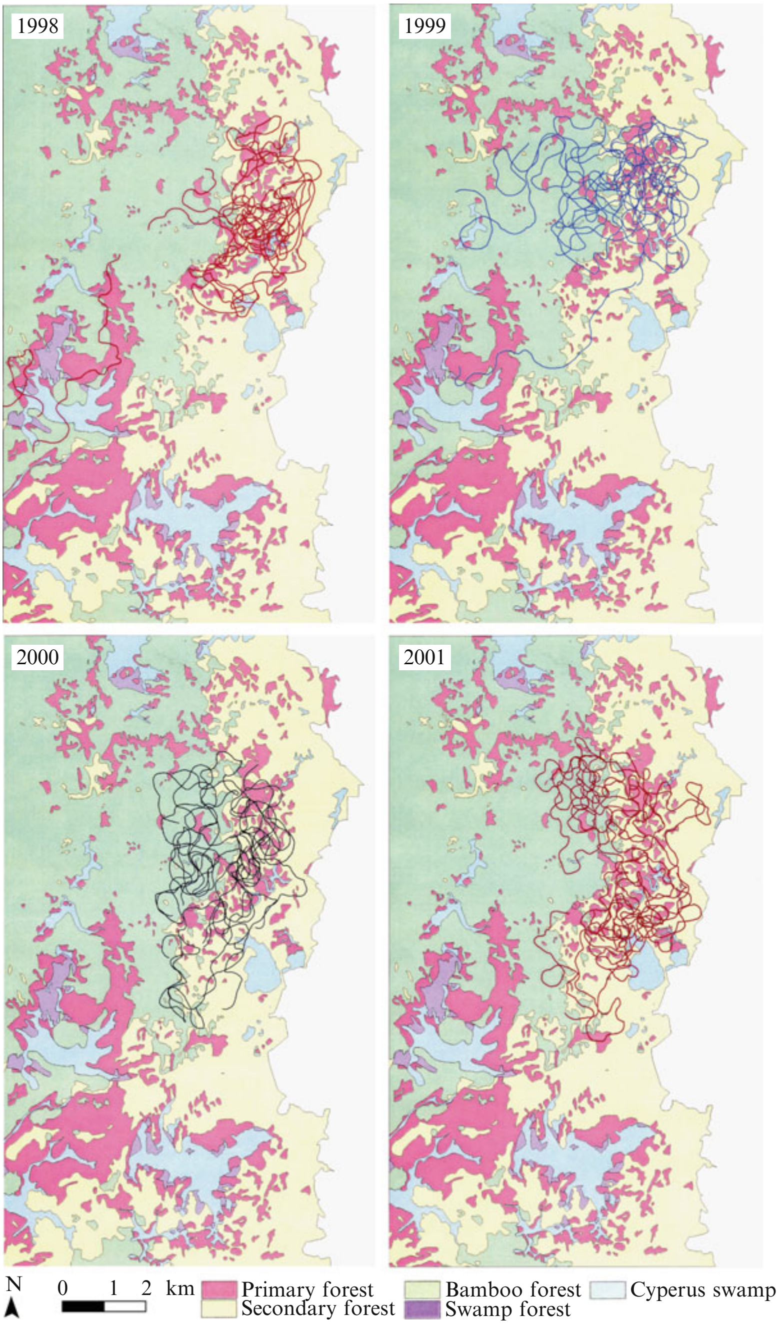

Fig. 17.7 Daily travel routes of gorillas during the period of bamboo flowering (1994–1997) and after bamboo shoots become available (1998–2001)

correlated with the ripe fruit index ($R^2 = 0.242$, $p < 0.001$). We calculated the daily food scores (DFS) as the number of days in which the gorillas of the study group ate each food item (Yamagiwa et al. 2005). These observations suggest that some vegetative foods, such as leaves of *Basella alba* and *Jasminium abyssinicus*, are staple fallback foods for gorillas.

On the contrary, vegetative foods did not constitute 100% of the chimpanzee's diet in any month. Due to their negative correlation with the ripe fruit index ($R^2 = 0.152$, $p < 0.01$), they are regarded as filler fallback foods. Animal foods are another important set of fallback foods for chimpanzees, who eat at least five species of insects (*Apis mellifera*, *Meliplebeia tanganyikae* aff. *Nigrita*, *Crematogaster* spp., and *Dorylus* sp.) and prey on two *Cercopithecus* monkeys (*C. mitis* and *C. l'hoesti*) and the giant squirrel (*Protoxerus stangeri*). They also use sticks to dig out subterranean bee nests (Yamagiwa et al. 1988). The monthly mean proportion of chimpanzee fecal samples including animal foods was negatively correlated with the monthly mean proportion of fruit remains per fecal sample ($R^2 = 0.131, p < 0.01$).

Gorillas in lowland tropical forests consume fruit during the entire year and tend to consume many kinds of leaves low in fiber and tannin contents, as reported for chimpanzees (Tutin and Fernandez 1993; Conklin and Wrangham 1994; Reynolds et al. 1998; Remis et al. 2001; Doran et al. 2002). These findings suggest that leaves and piths are filler fallback foods for gorillas in these habitats, while they are staple fallbacks, and bark serves as a filler fallback, in montane habitats. Leaves and piths are also filler fallback foods for chimpanzeesans, especially, for bonobos that inhabit lowland tropical forest where gorillas are not present, while both chimpanzees and bonobos rarely use barks as fallback foods (Tutin and Fernandez 1993; Malenky and Wrangham 1994; Kuroda et al. 1996; Basabose 2002).

Our study suggests that chimpanzees in some populations or habitats, including Kahuzi, feed more on animal foods, instead of bark, during the period of fruit scarcity. Chimpanzees use various tools for capturing social insects and for extracting edible parts from hard shells (McGrew 1992). Tool use by chimpanzees tends to increase when their preferred foods are scarce (Yamakoshi 1998). Such differences in fallback foods and fallback strategies might have led to different adaptations between gorillas and chimpanzees (Lambert 2007; Marshall and Wrangham 2007; Yamagiwa and Basabose 2009). Gorillas have morphological traits that facilitate consumption of higher fiber foods, while chimpanzees have locomotive abilities (climbing, clambering, and arm-swinging from branch to branch, and moving faster and longer distance than gorillas) to harvest dispersed fruit and leaf crops efficiently, and cognitive abilities to use tools. Bonobos do not coexist with gorillas, tend to consume terrestrial herbs frequently, and rarely feed on animal matters or use tools. These fallback strategies might have contributed to socioecological differences between them (Fig. 17.8). Sympatry might have promoted different fallback strategies in gorillas and chimpanzees to mitigate feeding competition; these differences in turn allowed range expansion into different habitats (gorillas to higher montane forest, and chimpanzees to more open and drier habitat).

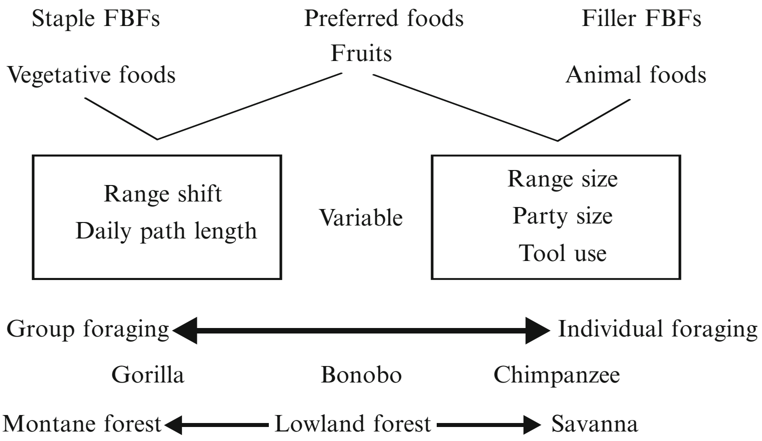

Fig. 17.8 Fallback strategies of the African apes. See text for explanation

17.4 Human Population Pressure and Conservation Measures

The South Kivu region, where the KBNP is located, has a high human density (over 300 people/km^2) and an annual population growth rate of 4%. People have extensively cultivated the highland region, which has highly fertile volcanic soils, and no natural forest remains outside the national park. Since the 1980s, people have suffered a severe economic crisis and faced political instabilities. As of the early 1990s, various projects funded by the World Bank and other international NGOs had improved infrastructure, and gorilla tourism was generating significant revenues, which helped boost support for gorilla conservation. However, the number of tourists has drastically declined and most foreign aid and cooperation has been suspended since 1994. Most of the elephants and half of the gorilla population were lost in the highland sector of the park during the war, and the situation is worse in the lowland sector where armed militia groups are still poaching wildlife (Yamagiwa 2003; Hart et al. 2007).

Deforestation, mining, charcoal production, cattle and goat encroachment, and slash-and-burn agriculture are the main destructive activities in the highland sector of the park. In 2000 and 2001, approximately 15,000 people rushed into the park to mine coltan when its price suddenly increased by more than ten times (Kasereka et al. 2006). In 2004, the military forces left the park and the park rangers resumed regular patrols, but more than 8,000 people were still mining coltan, cassiterite, and gold (Iyomi and Schuler 2004) and camped inside the park. Their subsistence activities (farming and hunting) also caused permanent damages to vegetation and wild animals. The human pressure was strongest in the corridor linking the highland and lowland sectors of KBNP. By 2008, 60% of the corridor had been degraded due to farming and mining, and the park authority has declared an urgent need to protect this area (Nishuli 2008). Recent damage to vegetation by humans is serious. Plants are collected for construction, food, fuel, and medicine. Sivha (1999) interviewed 213 people living around the highland sector of KBNP and reported that 93% of 249 wild plants they used came directly from the park. Suspension of public services such as clinics and transportation has accelerated exploitative activities of local people after the war.

The growing population has increased pressures on wildlife in and around the park. Various conservation activities in cooperation with international and national NGOs have been undertaken to support the park (Bikaba 2007). The IZCN-GTZ project funded by the World Bank, the World Wide Fund for Nature, and other international NGOs supported the wages and infrastructure of KBNP, improved public health, and helped lessen the workload of local women by providing water piped from natural sources (Steinhauer-Burkart et al. 1995). Park authorities decided to devote 40% of park revenues to park management and community development. The Gorilla Organization initiated a campaign to minimize the impact of mining, Partners In Conservation (PIC-Columbus Zoo) funded an animal breeding program that enabled 147 households around the park to obtain a goat, and the Rhodes Scholar's Southern Africa Forum (RSSAF/Oxford University) has funded a farming project that distributed agricultural tools and seeds to households around the park.

Starvation caused by the recent economic and political crisis is the main factor that led the people to destructive activities in the park. Conflict between the park authorities and unemployed local people could be an important additional factor that predisposes individuals to hunt gorillas. For many local residents, the park had been a long-standing source of resentment and conflict. When the national government created the park in the 1970s, it required many local villagers to abandon their lands and refrain from using the natural resources of the new reserve. They were also prohibited from shooting the elephants that frequently raided their crops. Furthermore, local villages were ordered to absorb the people who were evicted from the new reserve. To mitigate these growing conflicts, promote local conservation knowledge, and improve the quality of life in the area's communities, we established the Pole Pole Foundation (POPOF), a local NGO, in 1992. A few park rangers and some inhabitants of villages adjacent to the park constitute the bulk of the POPOF members, and researchers joined as advisers. POPOF sought to promote local community development through a variety of projects that would simultaneously benefit conservation in the park and neighboring lands. These included the establishment of a handicraft center, a tree nursery, and a school for environment education that employed local people, including former poachers. POPOF is currently working with 21 schools and running 11 adult literacy centers. In 2007, POPOF built a secondary school for environmental education, which has six class rooms and currently hosts 213 pupils. About 100,000 tree seedlings have been produced in the tree nursery center and distributed to villagers around the park. PIC, the Gorilla Organization, and POPOF-Japan have supported these projects.

Recently, we conducted a socioeconomic survey in two administrative sectors surrounding the highland sector of the park to understand the human community reliance on park's natural resources and to try implementing alternative subsistence measures that would reduce human impacts on the park. We selected five households in each sector and monitored foods and materials for subsistence they harvested, got, gave, sold, or purchased every day for 13 months in 2007 and 2008. The results showed that the local people obtained barely enough grains and vegetables necessary for subsistence and got hardly animal protein and not enough fuel (Fig. 17.9). Wood is their main source of fuel, supplemented with charcoal and kerosene obtained mainly by purchase or barter. Cooking heavily depends on palm oil, transported from lowland forests areas and usually purchased with cash. Income declines caused by the economic collapse triggered by the wars have increased such needs and have stimulated the local people to collect natural resources in the park for subsistence. The following alternative measures are proposed.

1. Promote animal breeding projects and fish farming to increase the availability of meat and milk.
2. Resume and strengthen the trees planting projects around the park to supply communities with wood and other natural resources to be managed rationally.
3. Promote farming projects to improve food security around the park, including sustainable land management.
4. Promote projects that use appropriate sustainable technologies to meet fuel needs and rational management strategies for using farmland, such as production of vegetable oil from locally grown crops such as peanuts and sunflowers.
5. Promote socioeconomic and income-generating activities. Development of a fair trade system accompanied by ecotourism is one of our recommended activities.

The role of local NGOs in conservation of natural resources has become increasingly important in the areas with political instability, such as Kahuzi. With weak enforcement of rules and regulations and national institutions in disarray, local people in this region have made decisions according to short-term personal or local interests (Kasereka et al. 2006; Bikaba 2007). Park authorities are powerless to stop local people from using protected areas for agricultural production and mining. The local

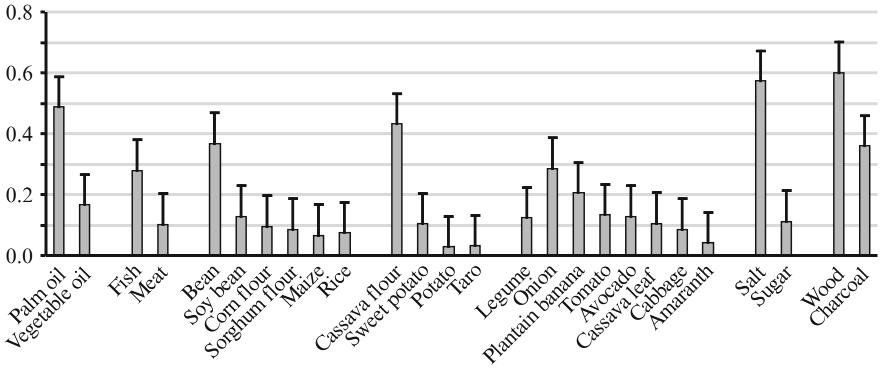

Fig. 17.9 Mean frequency of usage for each material of subsistence per meal by ten families inhabiting near the Kahuzi-Biega National Park

NGOs, such as POPOF, should cooperate with international NGOs to reinforce conservation knowledge among local people and provide alternatives to destructive activities. Scientists should also cooperate with them to use scientific knowledge for creating appropriate conservation measures. We should use our understanding of the ecological and social flexibility of gorillas and chimpanzees gained by long-term studies to help with management of the park, and we urgently need to inspire positive participation by local people in research and conservation activities.

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Chapter 18
Long-Term Studies on Wild Bonobos at Wamba, Luo Scientific Reserve, D. R. Congo: Towards the Understanding of Female Life History in a Male-Philopatric Species

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Abstract Long-term studies on wild bonobos began at Wamba, in the current Luo Scientific Reserve, in 1973. Except for several interruptions due to political instability and civil war, we have been conducting studies of identified individual bonobos over 35 years, providing valuable data on their population dynamics and life history. Although the number of groups and number of individuals in the northern section of the reserve decreased by half during the interruptions of the study, the number of members of the main study group has steadily increased since 2002 when we resumed the study. Our long-term data demonstrated the male-philopatric structure of the group. There is no confirmed case of emigration of males from the study group, and no case of immigration of males into the group. On the other hand, all females born into the study group disappeared by the age of 10 years, and females with estimated ages of 6–13 years immigrated into the study group. These ages of intergroup transfer are much earlier than those reported for chimpanzees. Exceptional cases of immigration of two adult males and two adult

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females with offspring occurred right after the war. It is likely that remnants of extinct groups joined the study group. Such integration of members of foreign groups highlights the peaceful nature of bonobo society. The study group is characterized by an extremely high tendency for female aggregation. Various factors, including high density of food patches, female initiative in ranging, prolonged estrus of females, and high social status of females, seem to be responsible for the high attendance ratio of females in mixed-sex parties. Our long-term observations therefore provided evidence for interesting behavioral contrasts with chimpanzees.

18.1 Introduction

The so-called last ape, or bonobo (*Pan paniscus*), which lives only in areas bordered by the Congo River, was first described as a subspecies of chimpanzee in 1929 (Schwarz 1929). It attracted the interest of many anthropologists and primatologists because of its morphological similarity to human ancestors and unique sexual behaviors (Susman 1984; Kano 1992). Long-term studies on wild bonobos began in the 1970s at two study sites, Wamba and Lomako in the Republic of Zaïre. However, mainly due to the country's political instability, it was very difficult to continue these studies. The economic situation worsened through the 1980s, and the first violent riot arose in the capital city of Kinshasa in 1991, when many researchers had to evacuate their study sites. Though studies gradually resumed at various sites, a civil war occurred in 1996 and a new regime was established, bringing with it a new name for the country: Democratic Republic of Congo. Security conditions improved somewhat and researchers returned or attempted to return to their field sites around 1998, but again a war involving several African countries occurred in August of the same year. Researchers could do nothing until around 2002, when a ceasefire was agreed upon.

Because of these difficulties, there are even now only a few long-term study sites at which researchers are carrying out behavioral studies of wild bonobos. Studies in Lomako were interrupted by the wars that occurred in 1996 and 1998. The Lomako-Yokokala Faunal Reserve was created in 2006, and studies of bonobos are currently being undertaken (Dupain et al. 2000; White et al. 2008), but not mainly on the same study groups or identified individuals. Very active research programs studying wild bonobos have been undertaken at Lui Kotale since 2002 (Hohmann and Fruth 2003), but even this study remains shorter than those at many chimpanzee study sites. Therefore, we have much to learn from studies at Wamba, which have continued for more than 35 years except during periods of political instability and war, especially concerning the life history of wild bonobos.

In this chapter, we will first provide an overview of the history of our research and conservation activities at Wamba. We will describe changes in the bonobo population structure during times of economic and political instability, focusing on the general effects of such instability. Second, we will summarize the outcome of our studies concerning the life history of bonobos at Wamba, using the data available for the main study group. Bonobos form semiclosed social groups, called unit groups (Nishida 1979) or communities (Goodall 1983), which we refer to as "groups" in this chapter. Groups of bonobos are male-philopatric, and females transfer between them before the onset of sexual maturation (Furuichi 1989; Kano 1992). Therefore, long-term data are indispensable for understanding the life history of females. We will also briefly review our findings pertaining to female sexuality and social behavior. Though bonobos are close relatives of chimpanzees, there are many interesting differences between the sexual and social behaviors of these two species, particularly among females. Therefore, the investigation of female life histories and behavior should greatly improve our understanding of what bonobos can tell us about the evolution of hominoids.

18.2 History of Research and Conservation Activities

18.2.1 Onset of Studies at Wamba and the Creation of the Luo Scientific Reserve

After the Congo crisis of 1960–1966, Toshisada Nishida carried out a preliminary survey of wild bonobos in an area adjacent to Lake Tumba in 1971, and confirmed that bonobos still survived in the Congo Basin (Nishida 1972). Using the information provided by this survey, Takayoshi Kano conducted a survey over a wider area to find an appropriate site to begin observation of wild bonobos in 1973 (Kano 1992). This trip was extremely difficult, partly because he had to roam an enormous area in the Congo basin on a bicycle, and partly because the indigenous people were not accustomed to non-African visitors at that time. People of some villages were afraid of him and did not treat him with much respect, forcing him to continue his journey without staying at their villages. When he reached a village called Wamba, however, the people welcomed him. He also heard vocalizations of bonobos from the village. Thus, he decided to choose this village for his field research.

In 1974, Kano sent Suehisa Kuroda to Wamba to begin the study of bonobos there. Kuroda first tried to habituate the bonobos ranging around the Bokela stream by artificial provisioning, but was unsuccessful. He then changed his target to another group that sometimes visited agricultural fields to feed on sugar cane. He named this group "E group," after "elanga," which refers to an agricultural field in the local language. He successfully habituated most bonobos in E group and, with Kano, identified its members by 1976. Bonobos of E group came to regularly visit the sugar cane fields in 1977, and the first artificial provisioning site was opened in the forest in 1978 (Kano 1992; Kano et al. 1996).

Since then, many researchers of the team headed by Kano have visited Wamba and carried out research on bonobo ecology and behavior. Bonobos used the forest around the village and had little fear of local people, who were tolerant of them because of their traditional belief that they and the bonobos both descended from the same family of bonobos that had lived in the forest in the past. According to this belief, an older brother in a family of bonobos held to their traditional lifestyle and his descendants thus remained in the forest as bonobos. However, his younger brother was tired of eating raw foods. Once upon a time, he was roaming in the forest, crying, a spirit of the forest taught him to make fire, after which he left the forest and began eating cooked food. His descendants became humans. Therefore, the village people consider the bonobos akin to distant brothers and do not kill or eat them.

In fact, there were no suspected cases of poaching before 1983, but during the absence of researchers in 1984, one of the young adult males of E1 group was killed by a poacher from outside of Wamba who tried to sell its body as meat. A second poaching incident that occurred during the absence of researchers in 1987 was more serious. A military troop ordered village people to capture two infants, and their mothers and some other adults of the study groups were killed during this attempt. According to an unconfirmed report, the two infants were carried to the capital Kinshasa and were given by the government as a gift to the King of Belgium. These incidents, together with a growing awareness of the importance of bonobos at Wamba for conservation and research purposes, encouraged us to create a reserve in the Wamba area (Kano et al. 1996).

Following discussions with our research team, our counterpart organization (Research Center of Natural Science, or CRSN, of the Republic of Zaïre) decided to create a reserve for scientific research, and we agreed to provide technical and financial aid to help with its creation. Delimitation of the proposed reserve area started in 1987, and in 1988, CRSN and the local communities signed agreements that created a reserve named the Reserve Scientifique de Luo (called “Luo Reserve” hereafter; Fig. 18.1). The reserve was officially recognized by the Ministry of the Environment in March 1990.

After some argument about what status the reserve should have, we chose to create a special reserve for scientific research instead of a national park, the creation of which would have required local people to leave. Though there were only small hunting camps in the southern section of the reserve, there were six homesteads and more than 1,000 people living in the northern section where we had been carrying out research. We therefore made efforts to help local people maintain their traditional ways of coexistence with the bonobos. Hunting primates and the use of guns or wire snares were prohibited, but hunting other animals with traditional techniques was allowed. Also, clearing of new fields in primary or old secondary forest to grow cash crops was prohibited, but reusing or even creating new fields for cassava or other subsistence crops was allowed within limited areas, mostly within 1 km of the road. To compensate people for these limits on forest use, the CRSN promised to support local development, including provision of support for local schools and medical services. Our research team has since tried to help CRSN, now CREF (Research Center of Ecology and Forestry), to provide such support.

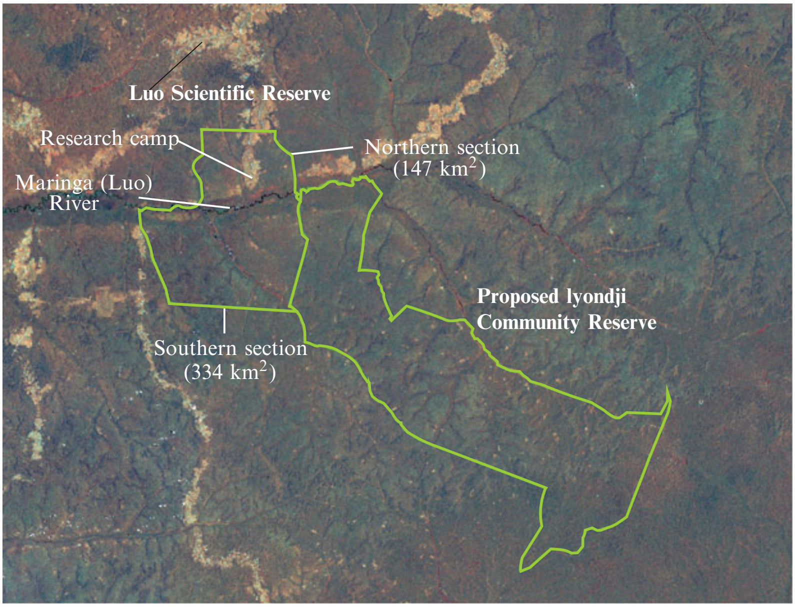

Fig. 18.1 The Luo Scientific Reserve and the proposed Iyondji Community Reserve. Image: NASA Landsat Program, c. 1998–2002 image composite. The *pale colorations* show roads, homesteads, agricultural fields, and young secondary forest

These efforts were initially fairly successful. However, promoting both conservation and the well-being of local people long term is extremely difficult, particularly when the conditions of human societies change rapidly. At Wamba, requests by local people for support became very serious when their lives were badly affected by political instability and war in the 1990s. Furthermore, requests for assistance by local people increased when the globalization of information made them more aware of the importance of bonobos to the conservation community and of the gaps between their standard of living and those of people in the developed world. Previously successful strategies to balance nature conservation with the local peoples' quality of life needed modification in subsequent years. The trials of achieving coexistence between the ever-changing needs of humans with unchanging nature seem to be endless.

18.2.2 Changes in Bonobo Population Structure in the Reserve

The Luo Reserve is divided into two sections by the Maringa (or Luo) River (Fig. 18.1), which bonobos cannot cross. A large portion of the northern section, where most of our research activities have been carried out, consists of young secondary forest and both abandoned and currently used homesteads and fields.

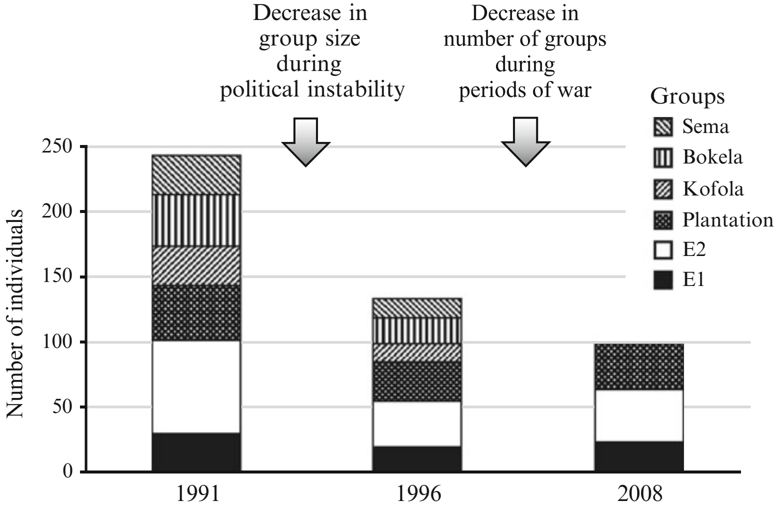

Fig. 18.2 Changes in the bonobo population structure in the northern section of the Luo Reserve. Figure modified from Hashimoto et al. (2008) using data from 1991 to 2008

In the beginning of 1991, six groups of bonobos with about 250 individuals used the northern section (Fig. 18.2). However, the population decreased by half during our absence, which began in 1991 because of political instability. When we resumed our studies in 1994, the number of bonobos estimated by direct observations was about 130, and their density estimated by nest counts was 0.54 independent animals per km^2 in 1996 (Hashimoto and Furuichi 2001). We were again forced to leave the site in 1996 due to the civil war. When we returned to the site in 2002, we could not find three of the six groups, and only about 100 bonobos remained in the northern section.

In contrast to the northern section, most of the southern section is primary or old secondary forest, and there are fewer villages, although many small hunting camps exist. Unfortunately however, the situation in this section seems to be even worse than in the north. The density of bonobos in the western area of the southern section was estimated to be 0.28 in 1996 (Hashimoto and Furuichi 2001). However, there were almost no bonobos in the western area in 2007 (Mulavwa unpublished data). Apparently, the population of bonobos in the area near the road was significantly reduced during the war. Though a good number of bonobos seems to remain in the eastern area of the southern section, an intensive survey in this section is urgently needed.

The main cause of the loss of bonobos during the war seemed to be hunting, especially by or on the orders of soldiers. Because many of the soldiers deployed in the Luo Reserve were from other areas of the country and many did not have a taboo against killing and eating bonobos, they sometimes hunted or asked villagers to hunt these animals for them. The village people might also have hunted the bonobos spontaneously to sell the meat as a means of surviving the war. Vegetation in the

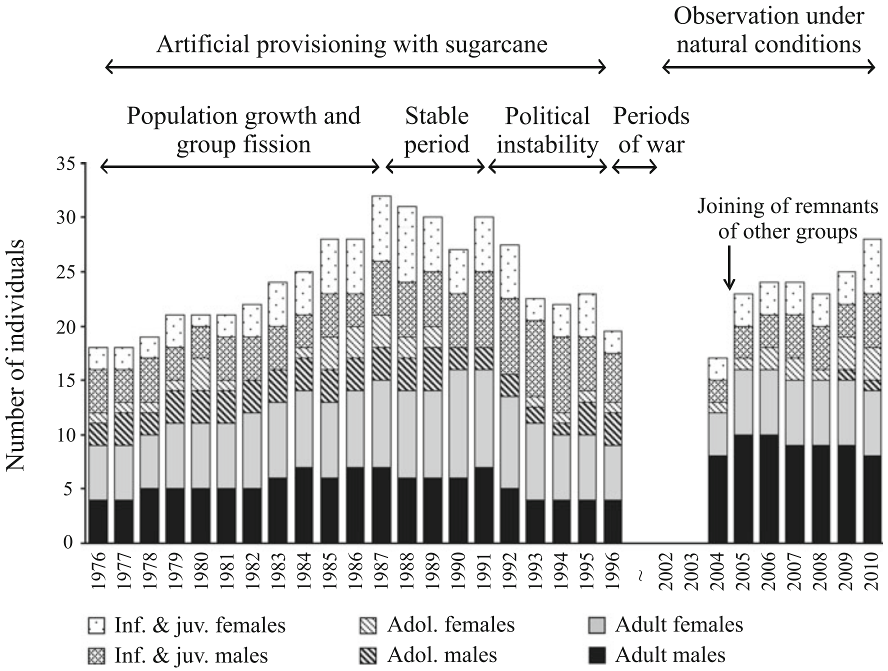

Fig. 18.3 Changes in the number of bonobos in the main study group. Figure modified from Hashimoto et al. (2008) using data from 1976 to 2010

primary forest was also damaged during the war. Many people fled from the villages along the road and lived instead in hunting camps within the forest, making cassava fields in the areas surrounding their encampments. Thus, political instability and war considerably damaged the fauna and flora in the reserve, although no fighting actually occurred in this area.

The number of bonobos in the main study group was also strongly influenced by the political conditions. The main study group, E, split into two groups, E1 and E2, by 1983 (Furuichi 1987). Figure 18.3 shows changes in the number of bonobos in the subgroup of E that eventually became E1 before 1983, and the number of bonobos in E1 since 1984. The group increased steadily in size until the split, and continued to increase thereafter. However, these increases stopped in 1987, and the group rapidly decreased in size during the period of political instability beginning in 1991. Though we lack data on group size during the war that started in 1996, E1 had 17 confirmed members in the beginning of 2004. Thus, the number of bonobos in E1 group did not decrease significantly during the 1996–2004 period.

Although we had been employing artificial provisioning for our observations before 1996, we decided to resume our research without this practice to avoid disease transmission and to observe bonobos under more natural conditions. Starting in 2004, the size of E1 group rapidly increased, seemingly because remnant individuals of other disappearing groups joined them (see below). Since then, the number of bonobos of E1 has steadily increased, attaining a current number close to that of 1991.

It was surprising that, in spite of the disappearance of three neighboring groups, the size of E1 group did not significantly decrease during our war-induced absence. It may seem that this occurred because the group was ranging in the middle of the northern section where our research camp is located. However, the risk of hunting was likely higher in this central area because a troop of soldiers was staying at our research camp. In fact, one of our research assistants was repeatedly ordered by soldiers to guide them to the sites where E1 group was sleeping. Although he intentionally guided them to the wrong sites several times, he was finally forced to guide them to a sleeping site after being told “guide us, or you will be killed.” When they arrived at the sleeping site, soldiers asked him which one to shoot. He could not help but point to an adolescent male that was the first to appear from a bed. Soldiers fired at the bonobo from close range, but they still needed to fire several times before finally killing it. Although the soldiers did take it back and eat it, they stopped killing bonobos in that area because they were afraid that some “magical power” had prevented their bullets from hitting the animal. The research assistant hid one of the bonobo’s bones in his house; he showed it to us late at night when he reported these events after our return to the site in 2002. Probably the biggest reason that this group survived the war was that our assistants and other local people tried to protect it, in the hope that the researchers would return after the war.

One of the more positive outcomes of our conservation activities is that the people of an adjacent village, Iyondje, proposed to create a community reserve for the conservation of bonobos in 2007 (Fig. 18.1). They wanted to stimulate research activities and tourism in the area and to protect their forest against intrusion by farmers from other villages. This reserve would be connected to the Luo reserve and would triple its size. Our research team is now working to help local people achieve this goal, in collaboration with the US Fish and Wildlife Service and the African Wildlife Foundation.

18.3 Life History of Bonobos at Wamba and Characteristics of Female Behavior

18.3.1 Intergroup Transfer of Individuals

Like chimpanzees, bonobos were thought to form male-philopatric groups, among which only females transferred (Nishida 1979; Wrangham 1986; Furuichi 1989; Kano 1992). This assumption was supported by the fact that the genetic distances between male bonobos of the same group were shorter than those between females (Hashimoto et al. 1996; Gerloff et al. 1999). However, there are many reports of exceptions to male philopatry and female transfer in chimpanzees. For example, some females at Gombe remain in their natal group for entire lives (Goodall 1986).

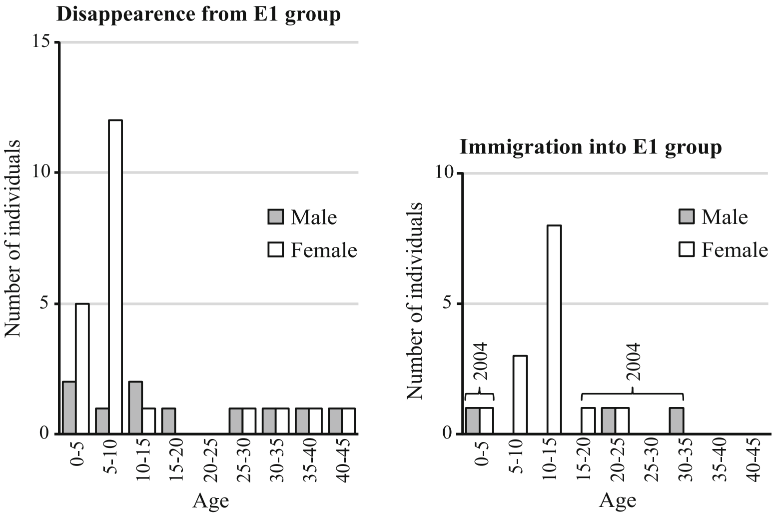

Fig. 18.4 Disappearance and immigration of individuals from and to E1 group. Figure modified from Hashimoto et al. (2008) using data from 1976 to 2009

At Bossou, Guinea, both males and females disappeared from their natal group, and some extra-group males were observed to visit the study group and stay temporarily (Sugiyama 1999, 2004). Therefore, the patterns of transfer of individuals need to be examined through long-term studies of specific groups.

Figure 18.4 shows the number of individuals of different age classes that disappeared from, or immigrated into, the study group at Wamba. Many females disappeared between the ages of 6 and 10 and presumably emigrated (Hashimoto et al. 2008). Only a few individuals in other age classes disappeared; their disappearances might have been deaths. If we exclude mergers between the remnants of adjacent groups in 2004, only females at estimated ages of 6–13 years old immigrated into E1 group. Females who immigrated into the study group under the age of 10 years disappeared shortly thereafter. However, most females who appeared in E1 at the age of 10 or older eventually had offspring, and settled into the group permanently.

Based on this information, we can infer that females leave their natal groups at the age of 6–10, and settle into new groups at the age of 10–13, when they start to reproduce. Because there is only one case of a supposed emigration by a female at 6 years old, this might in fact be a disappearance due to death rather than emigration. However, all the other females born into the study group disappeared between 7 and 10 years of age (Hashimoto et al. 2008), which is much younger than the age of first transfer among female chimpanzees; for example, females leave their natal groups between the ages of 8 and 16 at Mahale, Tanzania (Nishida et al. 2003). One of the unanswered questions concerns what females are doing during the years after leaving their natal groups and before settling down in new groups. To date, there are many cases in which we observed unknown females of 10 years or younger visiting our study group and disappearing after a short period. Therefore, it seems possible that young adolescent females who have left their natal groups move from group to group before finally immigrating permanently into a group in late adolescence.

Disappearance of males occurred almost evenly across the different age classes, and this probably reflects their deaths. By contrast, except for mergers of the remnants of adjacent groups in 2004, there were no observed cases of immigration by males. This strongly suggests that bonobos form male-philopatric groups (Kano 1982; Hashimoto et al. 1996). There were, however, some cases in which adolescent or adult males disappeared from the study group before coming back after absences of several months. Males ranging alone were sometimes seen by village people, albeit infrequently. In one case, an adult male that had been absent for several months had a number of new scars when he returned to the group. We still have little indication of what these males are doing during their absence, in particular whether they stay on their own within the ranges of their own groups or visit other areas or other groups temporarily.

One exception regarding the transfer of males occurred in 2004 (Hashimoto et al. 2008). Researchers sometimes observed two strange females with infants, and two strange adult males traveling with the study group. In the beginning, this happened only when the study group was in the eastern area of its home range, near the home range of the extinct K group. The north-eastern area was undoubtedly in the home range of K group, and E1 was never observed to use this area before the wars. It is likely that E1 group expanded their home range into this newly vacant area, and the remnants of the extinct K group subsequently joined them. By 2006, each of those six individuals was completely integrated into E1 group, even ranging with other E1 members into western parts of the group's home range, far from the range of their likely original group, K. The two adult males were usually found in the central part of mixed-sex parties, and we could not distinguish their behavioral tendencies from those of the original E1 males.

Another example of transfer of male bonobos was reported from Lomako (Hohmann 2001). When Hohmann resumed observation in 1997 after the first war, he found two strange males in the range of the study group, Eyengo. They were severely attacked by resident males and females, and one of them was no longer observed after 6 months. However, the other male established affiliative relations with resident members and remained with the group for at least 11 months, after which observations were interrupted by the second war. Though possibly a coincidence, it is noteworthy that these cases at Wamba and Lomako both occurred immediately following a period of war.

Such facultative intergroup transfers have also been observed under similar circumstances in Japanese macaques (*Macaca fuscata*), which form female-philopatric groups among which only males typically transfer (Suzuki et al. 1998). In one case, a group gradually decreased in size, and when only two females remained, they finally immigrated into a neighboring group (Takahata et al. 1994). Such a transfer of individuals of the normally nondispersing sex may occur in unusual situations involving group extinctions. In addition, these incidents in bonobos also reflect their relatively peaceful nature. Unlike the intensely hostile intergroup relationships among chimpanzees, when two groups of bonobos at Wamba meet, they frequently merge temporarily and travel together while engaging in affiliative social and sexual interactions (Idani 1990; Kano 1992). Although some aggressive interactions occur in the beginning of encounters, they are mostly displays without physical attacks. Although Hohmann reported that encounters between neighboring groups at Lomako were often agonistic, he also noted that aggressive behaviors were mainly restricted to displays (Hohmann et al. 1999). Such tolerance of members of different groups might allow for the immigration of adult males under conditions such as those outlined here.

18.3.2 Cohesive Grouping of bonobos

Both chimpanzees and bonobos have fission–fusion social systems, which are characterized by group members splitting into smaller subgroups, called parties, which change flexibly in membership over time (Kuroda 1979; Kano 1982; Nishida 1979; Wrangham 1979; Chapman et al. 1994; van Elsacker et al. 1995). Early studies on the grouping of bonobos reported that their party sizes were larger than those of chimpanzees (Kuroda 1979; Kano 1986), and various hypotheses to explain this difference were presented (White and Wrangham 1988; Kano 1992; Furuichi 2009). However, more recent analyses showed that party size varies considerably among sites in both species, leading to uncertainty about the differences between species (Furuichi 2009). If we compare the data obtained using similar definitions of a “party,” the number of individuals ranges from 4.0 to 10.3 for chimpanzees and from 4.9 to 14 for bonobos in studies including independent individuals only, while it ranges from 4.0 to 10.0 for chimpanzees and from 8.5 to 22.7 for bonobos in studies including all individuals. Thus, there is no statistically significant difference in party size between the two species. However, relative party size (Boesch 1996) or attendance ratio (Furuichi et al. 2008), defined as party size relative to the size of the whole group, differs significantly. This value ranges from 9 to 30% for chimpanzees but from 27 to 51% for bonobos. This might partly be explained by the larger size of chimpanzee groups, but it also seems to reflect real differences in behavior.

Fission–fusion events typically occur at high frequencies in chimpanzees (e.g., Mahale: Nishida 1968). Different chimpanzee parties may simultaneously use distant areas within the group home range, and it is therefore very rare that a researcher can observe all members of the group within a single day. In Kalinzu Forest, Uganda, where we have been studying the ecology of chimpanzees since 1992, we could not see some females for as long as 4–5 years, probably because they ranged alone or in small parties while pregnant and lactating. In contrast to chimpanzees, different bonobo parties at Wamba usually range in similar areas while keeping track of each other’s position through vocal exchanges. As a result, especially during the high-fruiting season when these bonobos form large parties

(Mulavwa et al. 2008), all members of E1 group are often observed on a single day's observation. For example, all of the group members were observed on 35 of the 125 days on which E1 group was observed from sleeping site to sleeping site in 2008. Thus, the grouping pattern of bonobos at Wamba is considerably different from that of chimpanzees, although the term "fission and fusion" is often used for the grouping patterns of both species.

When we follow bonobos in the forest, we are impressed by some behavioral tendencies that we rarely or never observe in chimpanzees. Though the daily travel distances of bonobos tend to be shorter than those of chimpanzees (Furuichi et al. 2008), bonobos sometimes travel long distances to shift between different areas in the home range. During such long-distance travel, they sometimes split into several parties that often exchange vocalizations, and some bonobos in the leading party sit on the ground and look back, awaiting the arrival of those left behind. Another interesting contrast with chimpanzees is that the first individuals to arrive at big fruiting trees usually do not climb up immediately, but instead wait for the arrival of other members of the party. When these other members arrive, they make a chorus of soft vocalizations, and then all climb the tree together. Our observations at Kalinzu suggest that chimpanzees sometimes give loud calls to attract other members to feeding trees, but they do not wait for other members to arrive before climbing up.

The behavior of bonobos in the evening also warrants consideration. When the time to sleep approaches, parties that are travelling separately but in the same vicinity start calling to each other. We call these vocalizations "sunset calls." Parties sometimes approach each other while exchanging sunset calls, and begin to make nests after they join. This happens more frequently during the high-fruiting season. Bonobos usually forage in large parties during the daytime and aggregate to form even larger parties in the evening, before again splitting into several parties the next morning to forage (Kuroda 1979; Fruth and Hohmann 1994; Mulavwa et al. 2010). We do not hear such typical calls in the evening among chimpanzees at Kalinzu, and there is a report from Budongo, Uganda, that the party sizes of chimpanzees decrease towards the evening (Reynolds 2005). All these behaviors seem to show that bonobos are strongly motivated to maintain as much cohesion as ecological circumstances allow.

18.3.3 Aggregation of Females

Unlike the tendency for female chimpanzees to range alone or in small parties, female bonobos tend to attend parties more frequently than do males, which contributes greatly to their group's overall cohesion (Kuroda 1979; Kano 1982, 1992; Furuichi 1987; White 1988; Furuichi et al. 2008). Even at Taï, Côte d'Ivoire, where chimpanzees form larger parties than at other sites, females have a lower tendency than males to attend such parties (Boesch 1996; Boesch and Boesch-Achermann 2000). As an example, this difference can be illustrated by comparing

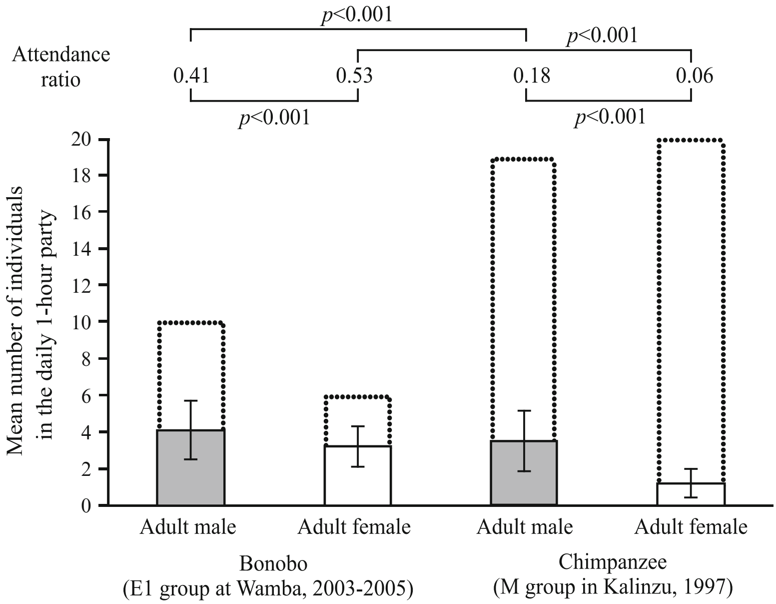

Fig. 18.5 Comparison of the group size and the mean 1-h party size between bonobos at Wamba and chimpanzees in the Kalinzu Forest. The length of the *bars with solid lines* represents the average numbers of individuals found in the 1-h party, and the length of the *bars with dotted lines* represents the number of all individuals belonging to the unit-group. The 1-h party is a method developed for comparison of party sizes between different species and sites (Hashimoto et al. 2001). Figure modified from Mulavwa et al. (2008)

party sizes relative to group sizes for bonobos of E1 group with chimpanzees at Kalinzu (Fig. 18.5). Although there are various definitions for party size, we employed the same 1-h party size method (Hashimoto et al. 2001) at both sites for a direct comparison. The numbers of individuals in the 1-h parties were not substantially different between the two species. However, while almost half of the group members were found in the 1-h parties of bonobos on average, a smaller proportion of the group members were found in parties of chimpanzees. In particular, we found a marked difference between species in female attendance in parties. While less than one-tenth of the females were found in parties of chimpanzees on average, almost two-thirds of the females were found in parties of bonobos. Female bonobos do not only attend parties frequently, but usually aggregate in the central part of the parties (Fig. 18.6).

The tendency for female chimpanzees to range alone or in small parties has been explained by various hypotheses. Due to their subordinate status relative to males, female chimpanzees may be subject to larger costs from contest competition at feeding sites than males are. Furthermore, foraging in a larger party may increase the frequency of shifts between food patches, which increases the cost from scramble competition for the slower moving females because they require longer travelling times between food patches and then arrive late to feeding sites

Fig. 18.6 Aggregation of females and their offspring in the central part of a mixed-sex party of bonobos

(Chapman et al. 1995; Wrangham et al. 1996; Wrangham 2000; Furuichi 2009). If true, the difference in the attendance ratio between males and females should be greater in larger parties because females should avoid attending such large parties. In fact, such a tendency has been confirmed in chimpanzees at Kanywara in Kibale National Park, Uganda (Wrangham 2000). However, this prediction was not verified in bonobos (Furuichi et al. 2008). As seen in Fig. 18.7, the attendance ratio of female bonobos was always higher than that of males, irrespective of party size. This suggests that influences of participation in parties differ quantitatively and/or qualitatively for female bonobos and female chimpanzees.

There are four major factors that may be responsible for the difference between the two species (Fig. 18.8; Furuichi 2011). The first factor is the difference in the density of food patches, which may typically be higher in bonobo habitats. Though we have not yet analyzed the data quantitatively, we encounter fruiting trees or food remains at much shorter intervals when following bonobos at Wamba than when following chimpanzees in the Kalinzu Forest. These food sources are not necessarily large fruiting trees, but include terrestrial herbs and the fruit and leaves of small trees that are more abundant in bonobo habitats (White and Wrangham 1988; Malenky and Wrangham 1994). The existence of such food sources between

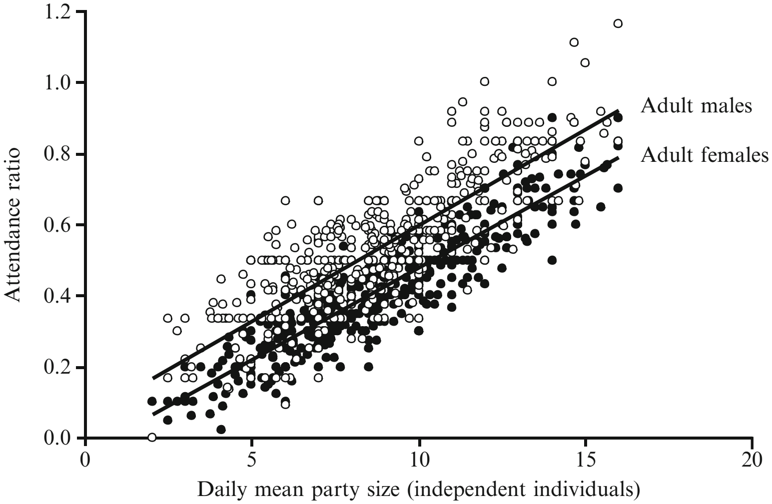

Fig. 18.7 Attendance ratio of males and females. Each *dot* in this figure shows the daily mean attendance ratio, which is the mean probability that each male or female was observed in a 1-h party. The *x* axis is the daily mean 1-h party size. Figure cited from Furuichi et al. (2008)

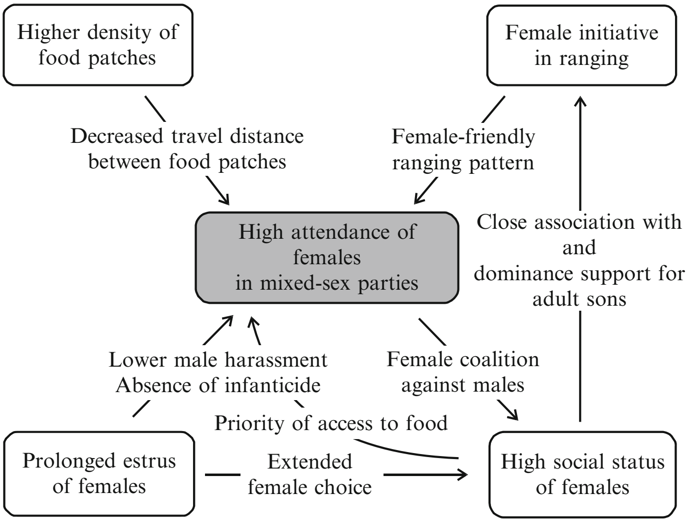

Fig. 18.8 Factors related to the aggregation of females. Figure cited from Furuichi (2011)

large food patches may decrease both the rate and distance of travel between the large food patches, thus reducing the costs for the slower moving females (Wrangham 2000).

The second factor to consider is the extent of female initiative in ranging (Furuichi et al. 2008). At Wamba, party movements typically occur when members descend from tall fruit trees and take short breaks in lower layers of the forest. They observe one another's movements as if to confirm which way others want to travel. Sitting on low trees seems to provide better visibility than sitting on the ground. Some individuals, most frequently males, climb down and perform branch-dragging displays, seemingly to propose a direction of movement. However, the entire party does not move until high-ranking females climb down and initiate movement in a direction of their own choice. Parties of E1 group usually range in one area for up to several weeks and then shift to another area. They typically move only short distances per day while in particular areas. Even when males travel farther, seemingly to shift to another area, they usually abandon these attempts if the females do not follow them, at which point they return to the original area to rejoin the females by evening (Furuichi et al. 2008). If females can control the direction and distance of travel, they can avoid incurring large costs associated with ranging in large mixed-sex parties.

The third factor is the prolonged estrous periods of females (Savage-Rumbaugh and Wilkerson 1978; Thompson-Handler et al. 1984; Furuichi 1987; Kano 1992; Furuichi and Hashimoto 2002). Female chimpanzees usually do not resume cyclic estrus until 4–5 years after parturition when their infants survive, and they stop showing signs of estrus by two months after conception. Thus, if we extrapolate from reproductive parameters recorded at Gombe and Mahale, female chimpanzees are in estrus on only about 5% of days in their adult life (Furuichi and Hashimoto 2002). By contrast, female bonobos resume swelling cycles only 1 year after parturition. Because these females are still experiencing postpartum amenorrhea, this is a pseudo-estrus without possibility of conception. They also show pseudo-estrus during pregnancy until about 1 month before parturition. Thus, female bonobos show estrus for as much as about 27% of their adult lives (Furuichi and Hashimoto 2002). Though this difference is smaller than Wrangham's (1993) estimate of 36 estrus (or pseudo-estrus) days between births for chimpanzees vs. 497 days for bonobos, bonobos still show estrus on more than five times as many days as do chimpanzees.

Such a difference must greatly alter the relationships between males and females. Male chimpanzees compete for a very limited number of estrous females, and alpha males usually have priority of access to them. Although females sometimes perform opportunistic mating or form consortships with lower ranking males, females cannot usually refuse sexual solicitation by alpha males. In some large groups with many males, such as at Ngogo and Kalinzu, opportunistic mating occurs more frequently than in smaller groups but females are sometimes cooperatively herded by a few high-ranking males, and do not usually refuse solicitation by those males. Females are subject to aggressive behaviors during the solicitation of copulations, and female choice for mating partners is very limited (Tutin 1979; de Waal 1982; Hasegawa and Hiraiwa-Hasegawa 1983; Watts 1998; Stumpf and Boesch 2005; Boesch et al. 2006; Hashimoto and Furuichi 2006a, b; Muller et al. 2007).

Among bonobos, in contrast, there are typically many estrous females in a group, and even high-ranking males cannot monopolize all of them. Therefore, males do not frequently fight with each other over access to estrous females, but instead devote greater effort to soliciting females for copulation. Copulation success is therefore largely dependent upon whether females accept such sexual solicitations. Under such circumstances, males rarely attack females, and females can easily ignore even solicitations of the alpha male. Thus, female choice of mating partners is enhanced in bonobos. In addition to reducing sexual coercion, the prolonged estrus of female bonobos may also contribute to paternity confusion, which may help to prevent infanticide (Kano 1992; Wrangham 1993; de Waal 1995; Furuichi 1997; Furuichi and Hashimoto 2002, 2004).

The fourth and final factor discussed here is the relatively high social status of female bonobos. Although there has been dispute regarding whether female bonobos are dominant to males or whether both males and females share equal status, the balance of power between the sexes certainly differs between the two species (Kano 1992; Parish 1996; Furuichi 1997; Vervaecke et al. 2000; Stevens et al. 2007). The high social status of females may contribute to the aggregation of female bonobos in three ways. First is that the contest competition with males over food is not a constraint for females to attend the mixed-sex parties because females have priority of access to food (Kano 1992; Parish 1994; Furuichi 1997; Vervaecke et al. 2000). Second is that females can avoid harassment and infanticide by males because of their high status (Parish 1996; Furuichi 1997; Kano 2001). Third is that they can take the initiative in ranging through the close association with their adult sons. Males usually range with their mothers and frequently exchange grooming with them, and females support their sons in the agonistic interactions between males and help them to attain higher dominance rank (Furuichi 1989, 1997, in press; Kano 1992; Furuichi and Ihobe 1994; Surbeck et al. 2011). Reciprocally, the high degree of aggregation among females may contribute to their high social status through the formation of coalitions (Parish 1996; Furuichi 1997). Furthermore, the social status of females may be enhanced by the extended female choice in mating resulting from the prolonged estrus.

Thus, many factors seem to synergistically contribute to the aggregation of female bonobos. Although we do not yet know how this entire system evolved, Fig. 18.8 may suggest that the evolution of physiological traits concerning prolonged estrus may be one of the key candidates capable of initiating this system. For a better understanding of the evolutionary significance of sexual, behavioral, and sociological divergence between our closest living relatives, we undoubtedly need more information concerning the life history of females. We hope that our long-term studies at Wamba will continue to provide such information.

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Part VI
Summary

Chapter 19
Long-Term, Individual-Based Field Studies

Tim Clutton-Brock

19.1 Introduction

This book syntheses the result of 18 long-term individual-based studies of primates, of which the shortest has spanned over 10 years and the longest now exceeds 50 years. Its production is timely, for primate studies have now reached a stage where individual-based data extending over several decades are available for a wide range of species spanning all the continents where primates occur and are being used to explore an increasing range of fundamental questions in ecology, evolutionary biology and behaviour (Robbins 2010).

Although some of the longest running individual-based field studies of mammals have involved primates, primate studies are neither the longest running field studies of vertebrates nor the most extensive. The first long-term field studies of vertebrates that could recognise and monitor the life histories of large samples of individuals were of blue tits and great tits in Holland (Kluijver 1951) and Britain (Lack 1954, 1966) and a similar approach was subsequently extended to the studies of other passerine birds (Fig. 19.1). Most early studies of birds followed the lead of Kluijver and Lack and used records of individual life histories to extend research on population dynamics and demography. Individuals were normally recognised from leg rings and were rarely habituated to close observation. The same approach was subsequently extended to the studies of other passerine birds (Grant 1986; Grant et al. 2001; Smith et al. 2006), seabirds (Dunnet et al. 1979), waders (Harris 1970; Ens et al. 1995), waterfowl (Cooke and Rockwell 1988; Scott 1988) and raptors (Newton 1985, 1986).

The first systematic field studies of mammals began in the 1930s, but long-term studies that tracked the behaviour of individuals over part or all of their lifespan were not initiated until three decades later, starting in the late 1950s and early 1960s

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Fig. 19.1 Six of the longest running individual-based studies of birds, showing the date when systematic data began to be collected (great tits, Wytham Wood, UK; fulmar petrels, Orkney, Scotland; Bewick's swans, Slimbridge, UK; scrubjays, Florida, USA; acorn woodpeckers, California, US; song sparrows, Mandarte Island, Canada). All six studies continue today

Fig. 19.2 Six of the longest running studies of mammals: chimpanzees, Gombe, Tanzania; *yellow-bellied marmots*, Colorado, USA; African lions, Serengeti, Tanzania; savannah baboons, Amboseli, Kenya; bighorn sheep, Alberta, Canada; *red deer*, Rum, Scotland

(Fig. 19.2). Several of the first studies were of primates (Itani 1958; Kawamura 1958; Schaller 1963; DeVore 1965; van Lawick-Goodall 1968; Kummer 1968) but a similar approach was soon extended to the studies of ungulates and other large herbivores (Geist 1971; Douglas-Hamilton 1973; Clutton-Brock et al. 1982; Festa-Bianchet 1989), carnivores (Kruuk 1972; Schaller 1972) and rodents (Armitage 1975; Hoogland 1995) and later, cetaceans (Connor and Smolker 1985; Mann et al. 2000), bats (Racey 1982; Kerth 2008a, b) and marsupials (Jarman and Southwell 1986).

Compared to mammals, many birds have the great advantage that adults can be caught and marked with relative ease, nests and chicks are commonly accessible and many species are diurnal and relatively visible. In addition, many hole-nesting species, like the tits, can be induced to breed in artificial nest sites that can be designed to maximise the ease of observation at the nest. Relatively few wild mammals offer the same range of advantages. Many species are partly nocturnal and are relatively difficult to observe unless individuals have been habituated to the presence of humans. Permanent, visible marks are often difficult to produce or are undesirable for other reasons. In some groups of mammals, it is possible to catch and mark unhabituated individuals repeatedly (including some bats (Kerth 2008a, b), rodents (Schradin 2005), nocturnal lemurs (Kappeler 1997) and pinnipeds (Campagna et al. 1988; Le Boeuf and Reiter 1988)), but many others (including many diurnal primates) have to be habituated to close observation before it is possible to monitor behaviour and life histories of individuals on a regular basis. Habituation is almost always time consuming to establish and costly to maintain and limits the number of individuals and groups that can be sampled, constraining both the range of questions that can be asked and the generality of conclusions. As a result, it is unsurprising that detailed field studies of birds preceded those of mammals and that, even today, mammalian field studies are less advanced than those of birds.

In contrast to early studies of birds, which focussed primarily on population ecology, many of the early individual-based studies of mammals concentrated on describing and investigating the structure and organisation of societies. However, as field studies developed, these contrasts have disappeared. Long-term, individual-based studies of birds and mammals are now commonly used both to explore ecological processes and to investigate the costs and benefits of different phenotypic traits or behavioural strategies. In addition, an increasing number of studies of birds are exploring the structure of social groups and the development of social relationships between individuals (Koenig and Dickinson 2004). Like studies of mammals, some now rely on habituating individuals to close observation and on recognition using natural markings, while others have habituated individuals to close observation to a point where it is possible to weigh them repeatedly. Conversely, several field studies of mammals now monitor multiple groups and several 100 individuals, marking individuals with tags, dye-marks or transponders and individual-based studies are now commonly used to investigate the dynamics and demography of populations as well as the organisation and structure of social groups.

Few people who initiate long-term field studies set out with the objective of working at a particular site on a particular species for a protracted period and most long-term studies start with limited objectives and short time horizons and only develop into lengthy research programmes because of the opportunities they provide. One consequence is that long-term studies commonly develop on a hand-to-mouth basis and little time is spent considering alternative courses or strategic decisions. However, as anyone who has run a long-term field study knows only too well that they are demanding, time-consuming, expensive and commonly absorb a large proportion of the working lives of the people that run them, so it is important to be clear about the reasons for conducting and maintaining them.

In this chapter, I focus on some of the strategic issues affecting long-term studies. In the second section, I examine the benefits of long-term studies, extending several of the arguments outlined by Kappeler et al. in the first chapter. It is also important to recognise the strengths and limitations of particular systems and to adapt research objectives to match them, for if politics is the art of the possible, research is the art of the soluble (Medawar 1967) and there are few prizes for battling unsuccessfully against overwhelming odds. In the third section, I provide a brief (and subjective) evaluation of the particular strengths and some of the limitations of research on primates and argue that future studies of primates will need to recognise both the constraints that working on primates commonly involve and the opportunities they provide. Finally, there are a number of dilemmas that many long-term studies are either facing already or are likely to face in the future. Some of these were discussed at the VII. Freilandtage, ranging from the need to prevent disease transmission to the protection of field staff against bandits, but many of the most fundamental ones were never discussed and some of them have yet to be confronted. In the final section, I briefly review some of these issues.

19.2 The Benefits of Long-Term Studies

Longitudinal studies of animal populations fall into two main groups (Clutton-Brock and Sheldon 2010a). First there are studies at the population level that measure the size, structure and distribution of particular populations but do not depend on individually marked or recognisable animals. Second, there are studies based on data collected from recognisable (or marked) individuals, like all of those represented in this book. Since laboratory-based scientists (including a substantial proportion of referees) often fail to appreciate the important differences between them, it is important to be clear about their differences.

Long-term studies at the population level can measure the size and stability of populations, the relative numbers of animals of different age and sex, the size, composition and movements of groups, the timing of breeding seasons and the proportion of juveniles that survive (Lack 1966; Riney 1982). Where individuals can be aged reliably before or after death, they can investigate age-related changes in fecundity, rearing success and survival (Sinclair 1977). Protracted long-term research is necessary partly because many of the most important ecological and evolutionary processes affecting populations – including the demographic processes controlling animal numbers and the evolutionary processes generating adaptation – commonly occur over multiple years or decades rather than across hours, weeks or months, and partly because the ecological factors affecting animal numbers fluctuate over time and extreme circumstances or events can have long lasting consequences. Studies at the population level provided the base for the first investigations of the regulation of animal numbers (Lack 1966) and have continued to play an important role in research on the demography and dynamics of animal populations and into the environmental factors that affect recruitment, dispersal and survival (Hanski et al. 1991; Sinclair and Arcese 1995; Newton 1998; Lawler et al. 2006). More recently, they have played an important role in documenting the effects of global climate change and investigating their consequences (Crick and Sparks 1999; Cotton 2003; Edwards and Richardson 2004; Langvatn et al. 2004; Lawler et al. 2006; Thackeray et al. 2010).

Although population level studies have an important part to play in ecological research and will continue to be the normal level of investigation for studies of many taxonomic groups, they have important limitations, especially for research into the ecology and behaviour of long-lived iteroparous organisms with overlapping generations (Clutton-Brock and Sheldon 2010a). In particular, they are unable to investigate the extent or consequences of individual differences in reproductive success, which are pronounced in most natural populations and can have important consequences for population dynamics (Clutton-Brock 1988; Newton 1989). In addition, they often have difficulty in distinguishing between the effects of changes in fecundity, survival and dispersal (or immigration) and in identifying the reasons for changes in each of these parameters. Their estimates of age-related changes in reproductive success and survival are often compromised by the shorter life spans of inferior phenotypes, with the result that superior individuals are over-represented in older age groups and the effects of age are underestimated. Although they can assess the distribution of genotypes, they can seldom reconstruct the detailed kinship structure of social groups reliably. Finally, they are not in a position to explore the wide range of social mechanisms operating within groups that affect the distribution of breeding success, emigration and survival among group members.

Long-term studies that are able to monitor the development and life histories of individually recognisable animals are able to investigate many ecological and evolutionary process that are inaccessible to population level studies, as Kappeler et al. described in Chap. 1. In particular, they make it possible to measure individual differences in growth, behaviour and reproductive success throughout the lifespan, generating estimates of the magnitude of individual differences and providing insight into the causes of demographic change (Clutton-Brock 2001; Clutton-Brock and Sheldon 2010a, b). They also permit investigation of relationships between events or decisions at one stage of the lifespan and subsequent growth, reproduction and survival, providing insight into the costs and benefits of different strategies and the evolution of trade-offs between reproduction and survival. They allow comparison of these effects between categories of individuals, based either on phenotype or genotype, so that it is possible to measure the strength of interactions between environmental and genetic factors (Kruuk and Hill 2008). Where they extend over multiple generations, genetic pedigrees can be constructed (Pemberton 2008) and used to measure both the heritability of traits (Kruuk et al. 2000, 2002), the extent to which environmental factors have trans-generational effects (Albon et al. 1987; Clutton-Brock 2004) and the evolution of phenotypic plasticity (Brommer et al. 2005; Nussey et al. 2005, 2007; Clutton-Brock and Sheldon

2010a). Finally, they provide a basis for accurate descriptions of the social environment that individuals live in (including variation in social organisation, mating systems and social structure) and for investigating the causes and consequences of variation in social behaviour (Silk 2007; Clutton-Brock and Sheldon 2010a).

Because of the range of questions that they can investigate, many long-term, individual-based studies come to involve multiple scientists working on different but complementary aspects of biology, providing opportunities to investigate relationships between social parameters and encouraging interdisciplinary research. One practical consequence of the development of multi-faceted research teams working on the same animals is that individual projects can maintain unusually high rates of publication which commonly increase with the duration of the research. To confirm our impression of this effect, Kelly Moyes and I carried out a survey of the output of long-term individual-based field projects based in the UK. Our sample included records for 51 long-term (>10 years) individual-based studies of which the longest had been running for more than 50 years (Fig. 19.3a) and included most of the well-known long-term studies in Britain. Almost all of these studies were productive – but a quarter of them had unusually high rates of publication, producing multiple papers each year and large numbers over the total period they had been running (Fig. 19.3b). Analysis of publication trajectories of the studies in our sample shows that, in general, the longest running studies are the most productive. In the majority of cases, the first publications only appear after studies have been

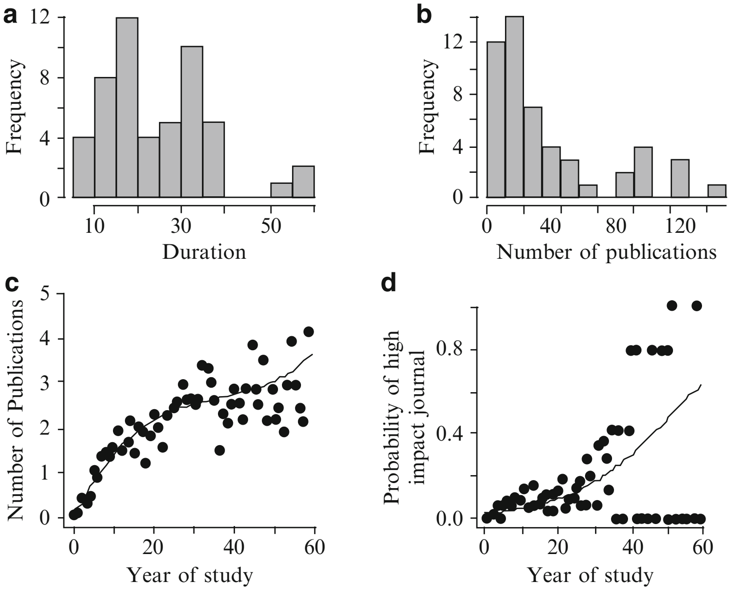

Fig. 19.3 Output of 51 long-term, individual-based studies based in the UK (**a**) frequency of studies of different duration; (**b**) total publications per study; (**c**) publications per year of study; (**d**) probability of producing a paper in *Science*, *Nature*, *PNAS* or *Current Biology*

running for several years but, subsequently, annual rates of publication increase rapidly – and continue to do so for at least two decades (Fig. 19.3c). In addition, the probability that studies will publish at least one paper per year in a high-impact journal (defined for the purposes of this study as a paper in *Science*, *Nature*, *PNAS* or *Current Biology*) increases with time (Fig. 19.3d), suggesting that the originality of the work increases rather than decline with the duration of studies. We believe that analyses of this kind could play an important role in convincing funding agencies of the role played by long-term field studies in the development of research in ecology, evolutionary biology and animal behaviour and of the importance of maintaining them and that there would be benefits in extending the analysis shown in Fig. 19.3 to include a wider range of studies.

One conclusion to be drawn from surveying the results of long-term field studies is the need for careful choice of species. While long-term data will (almost) always generate broader opportunities and more credible results than short-term ones, species differ in the extent to which they are likely to justify the effort and cost of long-term research. There are substantial benefits to focussing on species where relatively large numbers of individuals and groups can be recognised and monitored; where it is feasible to catch, mark and weigh individuals at regular intervals; where samples of skin, blood, faeces and urine can be collected to establish paternity and monitor hormonal variation; where visibility is good and it is possible to monitor the breeding cycles of individuals throughout the year; where emigrating individuals can be followed to ascertain their fate; where the quality and availability of food supplies can be monitored; where it is feasible and permissible to carry out experiments in natural populations; and where life spans are sufficiently short that it is feasible to track several cohorts throughout their lives (Clutton-Brock and Sheldon 2010a). Few, if any, mammals meet all of these criteria but some meet more than others – and there are some species (including many primates) that meet very few of them. This is not to suggest that only the most tractable species should always be the target of long-term research, for there are other criteria that affect research priorities, but it is important to recognise these limitations and to adjust the objectives of research programmes in relation to what is feasible.

19.3 Primates and Other Animals

The studies in this book provide an opportunity to compare long-term studies of primates with those of other animals and to identify both their strengths and their limitations. In his opening chapter, Kappeler et al. review the history of primate studies and the subsequent chapters provide extensive support for their claims. Perhaps the single greatest achievement of long-term primate studies has been their documentation and investigation of diversity in social behaviour – in particular, of social organisation in different species, of social structure within groups, of social relationships between individuals and of their effects on feeding behaviour development, survival and breeding success (Smuts et al. 1986; Campbell et al. 2007).

In this area, long-term studies of primates that have been able to habituate individuals to close observation have led the field, providing data of greater depth and resolution and field experiments of greater sophistication than are available for any other group of mammals. Comparisons of research on social behaviour in primates with studies of rodents (Wolff and Sherman 2007), bats (Kerth 2010), ungulates (Jarman 1974; Jarman and Kruuk 1996), carnivores (Gittleman 1989; Creel and Creel 2002), cetaceans (Mann et al. 2000) and macropods (Jarman 2000) emphasise how relatively far advanced studies of social behaviour in primates still are. It is no accident that many of the most novel discoveries have come from research on cercopithecine monkeys (and baboons and macaques in particular) where research projects have been running for several decades and individuals can be habituated to close observation (Silk 2007; Alberts and Altmann 2011). Other areas where primate field studies have generated pioneering studies and produced ground breaking results include research on behavioural development; on the structure and content of signals; on food choice and differences in feeding behaviour within and between species; and on ranging behaviour and selective habitat use.

In contrast, the difficulties of studying many primates in their natural habitats have constrained research on other topics. The need for habituation often limits the number of groups that can be sampled and has restricted research on the dynamics of populations and on the effects of population density and of density-independent parameters with the result that demographic research is less developed in primates than in rodents or ungulates (Sinclair and Arcese 1995; Hanski et al. 2001), where more extensive data sets have made it possible to sample larger numbers of individuals and groups, to test predictive models of population size (Coulson et al. 2001) and to explore the effects of changes in global climate (Thackeray et al. 2010; Moyes et al. 2011). The relatively long life spans of most primates have delayed accurate assessments of age-related changes in reproduction and survival, with the result that research on the causes of variation in life-history parameters (including pre-natal effects of environmental variation and of variation in genotype) are more developed in other animals (Kruuk and Hill 2008). Until the recent development of non-invasive sampling methods, the difficulties of catching and anaesthetising individuals have also impeded research on reproductive physiology and development as well as on the genetic structure of populations. In particular, pedigree-based studies spanning multiple generations than can assess the heritability of traits, measure the intensity of selection and compare selection coefficients between the sexes or between animals of different ages, which are available for some other vertebrates (Pemberton 2008), have not yet been developed in primates. Finally, with the important exception of research on vocal communication (where research on primates has led research on other mammals), opportunities for experiments and, in particular, for experiments that investigate trade-offs between life-history parameters are usually limited with the result that studies that are able to investigate the causal basis of observed relationships is low.

As the duration of primate field studies increases and sample sizes rise, the range of questions that can usefully be investigated will increase and, in future, we can expect to see primate studies exploring many of the ecological, physiological and evolutionary questions that are currently being investigated in other animals where larger and more complete data are available. In particular, the unusual opportunities for close observation and the detailed knowledge of kinship and social relations that primate studies allow will provide important opportunities to investigate the way in which aspects of the physical and social environments interact to affect breeding success and survival, as well as the extent to which behavioural and developmental strategies are modified to respond to these effects.

19.4 Problems and Dilemmas

Long-term studies of primates face a wide range of problems and dilemmas, some practical, others more conceptual (Clutton-Brock and Sheldon 2010b). Most long-term studies necessarily involve the collection of data by many individuals requiring detailed protocols and regular checks on accuracy and consistency. In addition, the very large data sets they generate require careful organisation and regular updating. Modern methods of data storage and customised databases have an important role to play (see Alberts and Altmann 2012; Wilson 2012) but new dilemmas continue to emerge. For example, the recent tendency for many journals and some granting agencies to require authors to provide public access to all data used in published papers (Whitlock 2011) is likely to present difficulties to many long-term projects. In addition, all long-term projects will eventually face the problem of transferring expertise, data and control between successive principal investigators.

One particular dilemma facing anyone running a long-term field study is the extent of reliance on observational data versus field experiments. It is scarcely necessary to emphasise the need for field experiments to determine the causal basis of relationships and studies of the evolution of behaviour in other animals rely increasingly on experimental studies (Krebs and Davies 1993). However, while some experiments can be performed without jeopardising records of individual life histories, others have inevitable effects on the life histories of experimental animals that may affect other members of their social groups. One way of alleviating this difficulty is to conduct research on two or more separate populations and to restrict experiments to one of them – but this is only possible where habituation is rapid or unnecessary and, more commonly, it is necessary to decide between the benefits of field experiments and their costs to naturalistic records of individual life histories.

Long-term primate studies also face a range of conceptual dilemmas, many of them related to the aims and priorities of primatology itself. Is the principal aim of primate field research is to use the unusual opportunities that primates provide to investigate ecological and evolutionary questions of general importance both to primates and to other animals? Or is it, rather, to extend the breadth of knowledge of the ecology and evolution of primates despite the limitations involved? Or a bit of both? This issue is important because it affects answers to a range of more specific questions about research priorities that primatologists are likely to face both in determining their own research priorities and as referees. For example, what relative priority should be given to extending taxonomic coverage by descriptive studies of previously unstudied species versus to detailed research on more specific questions in species whose behaviour and ecology has already been extensively described? How important are repeated studies of the same species across a range of habitats? And what priority should be given to extending longitudinal studies of particular populations?

There may be no general answers to these questions but there are some obvious guidelines. The highest priority should be given to research that is likely to answer novel questions relevant to understanding the biology of both primates and other animals. The case for initiating the studies of previously unstudied species depends both on their feasibility and on the probability that they will confirm, refute or extend explanations of interspecific differences, so that the highest priority is typically for studies of taxonomically or ecologically divergent species. Repeated studies of the same species in contrasting habitats are important to establish the extent and causes of intraspecific variation but need to cover a sufficient number of populations to demonstrate credible relationships between ecological and behavioural parameters. Finally, a very high priority should be given to longitudinal studies (and especially to long-term studies of the most accessible species) because of the wide range of questions that only long-term, individual-based studies can answer.

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Erratum to:

Chapter 4
Long-Term Lemur Research at Centre Valbio, Ranomafana National Park, Madagascar

Patricia C. Wright, Elizabeth M. Erhart, Stacey Tecot, Andrea L. Baden, Summer J. Arrigo-Nelson, James Herrera, Toni Lyn Morelli, Marina B. Blanco, Anja Deppe, Sylvia Atsalis, Steig Johnson, Felix Ratelolahy, Chia Tan, and Sarah Zohdy

P.M. Kappeler and D.P. Watts (eds.), *Long-Term Field Studies of Primates*,
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In this chapter, the following sentences are incorrect:

Section 4.3.4 Reproductive Hormones, 2nd paragraph:

While DHT levels were higher in males than in females, there was no significant sex difference in testosterone levels. Similar testosterone results were found in *M. rufus*.

Section 4.4.4 Habitat Disturbance, 4th paragraph:

In a comparative study of stress hormones in adult *E. rubriventer* in selectively logged versus minimally logged sites, patterns of cortisol excretion were similar in both sites, but those in the undisturbed site showed little response to variation in food availability and rainfall. In contrast, at the disturbed site, fecal cortisol levels were significantly higher when fruit was scarce (parturition and early lactation) compared with when fruit was abundant (prebreeding season).

The corrected versions are:

Section 4.3.4 Reproductive Hormones, 2nd paragraph:

While DHT levels were higher in males than in females, the relationship between sex and testosterone level varied across seasons, with each sex excreting higher levels at different times (Tecot et al. in prep.). Similar testosterone results were found in *M. rufus* (Zohdy et al. 2010).

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Section 4.4.4 Habitat Disturbance, 4th paragraph:

In a comparative study of stress hormones in adult *E. rubriventer* in selectively logged versus minimally logged sites, patterns of cortisol excretion were similar in both sites, but those in the disturbed site showed little response to variation in food availability and rainfall. In contrast, at the undisturbed site, fecal cortisol levels were significantly higher when fruit was scarce (parturition and early lactation) compared with when fruit was abundant (prebreeding season).

The online version of the original chapter can be found under
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Erratum to:

Chapter 13

The 30-Year Blues: What We Know and Don’t Know About Life History, Group Size, and Group Fission of Blue Monkeys in the Kakamega Forest, Kenya

Marina Cords

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In this chapter, figure 13.5 is incorrect.

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The corrected version is:

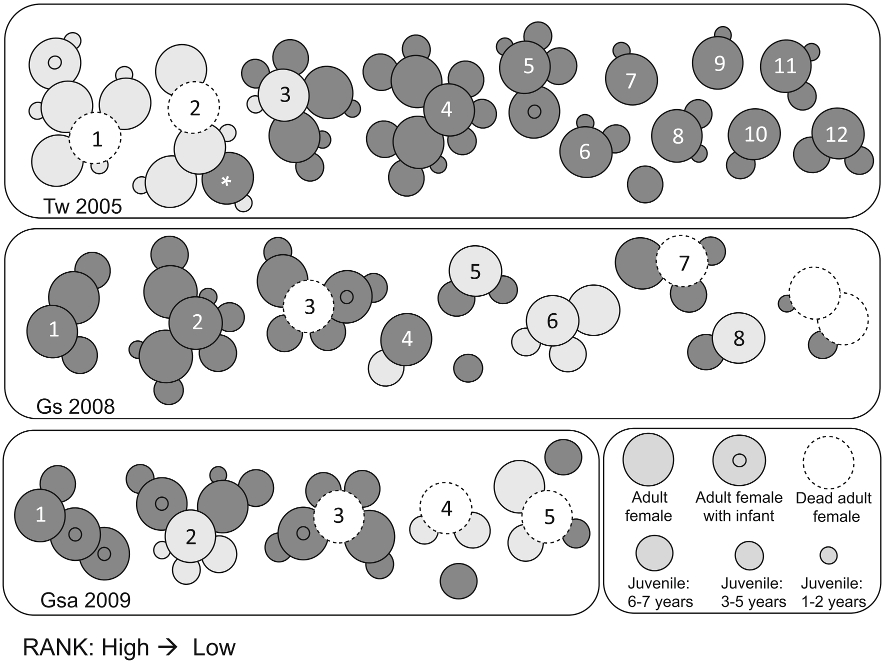

Fig. 13.5 Maternal kinship, rank, and group fission. For each of three fissions, individuals are represented as *circles*, with *shading* (*light vs. dark grey*) indicating group membership after fission, and size proportional to age (see legend). To indicate maternal relatedness, a large circle (mother) overlaps the circles representing her offspring. Matriline rank decreases from left to right, indicated by integer values (1 = highest). Matriline rank was derived from dyadic agonistic interactions among adult females, 9–12 months before fission; matrilines represented only by juveniles therefore have no rank and are randomly placed. Individual marked by *asterisk* is discussed in text

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