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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P.M. Kappeler and D.P. Watts (eds.), *Long-Term Field Studies of Primates*,
DOI 10.1007/978-3-642-22514-7_5,

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)

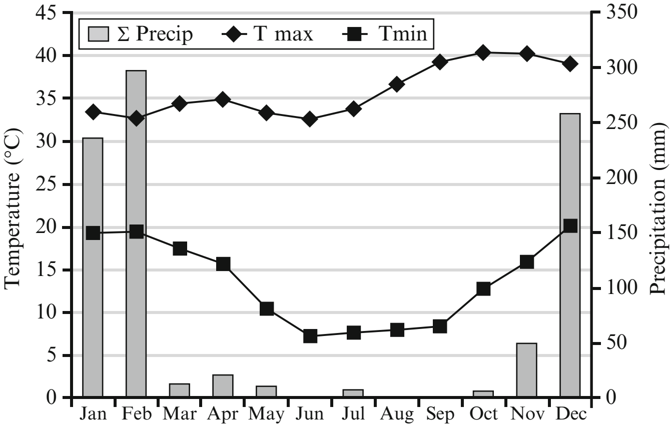

Fig. 5.2 Climate at Kirindy. Mean monthly maximum (*diamonds*) and minimum (*squares*) temperature as well as monthly precipitation (*bars*)

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

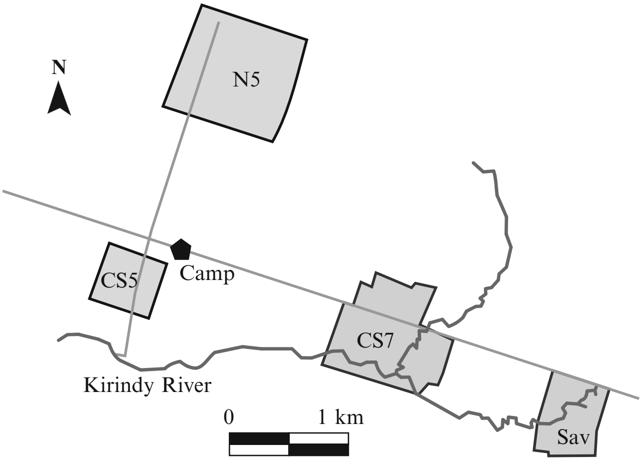

Fig 5.3 Map of local study areas at Kirindy Forest

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

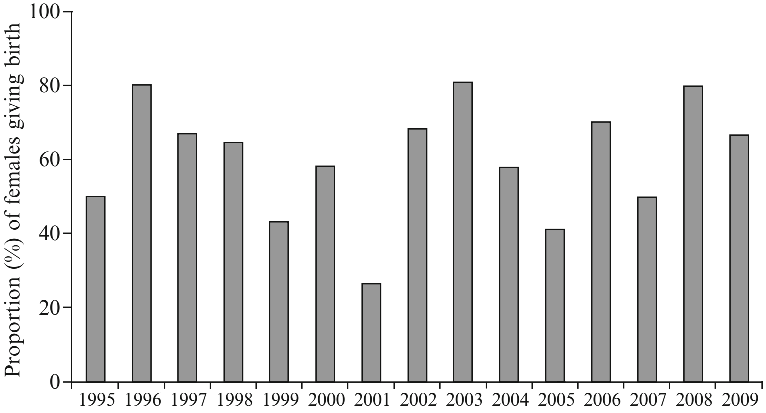

Fig. 5.4 Proportion of sifaka females giving birth between 1995 and 2009

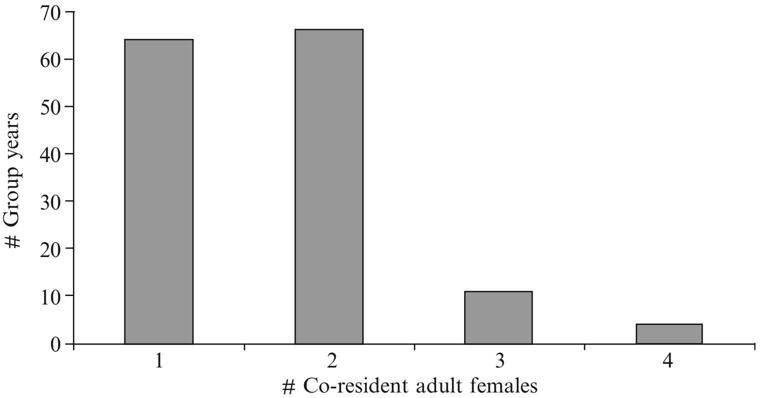

Fig. 5.5 Number of co-resident sifaka females per group over 149 group years

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

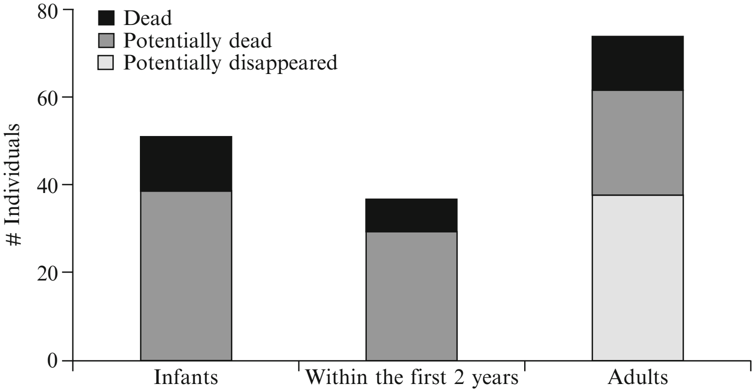

Fig. 5.6 Number of infants, juveniles within the first 2 years, and adults that either died are potentially dead or potentially disappeared. Individuals that disappeared at an age under the average age of natal dispersal (males median 60 months (IQR 12); females median 54 months (IQR 18)) were considered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

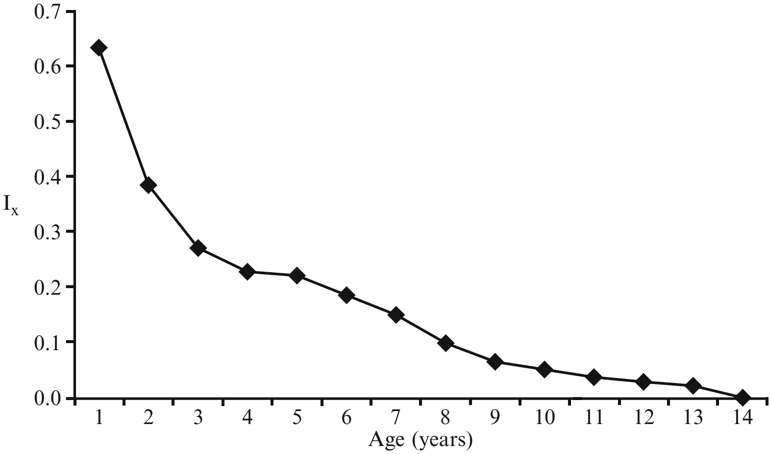

Fig. 5.7 Age-dependent survival of sifakas at Kirindy Forest

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.

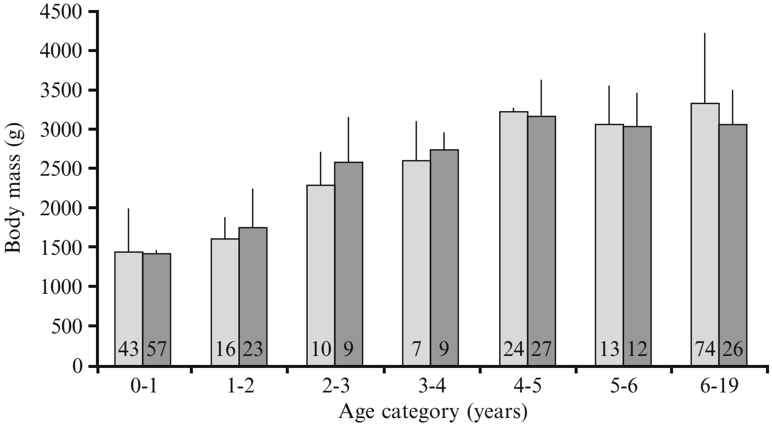

Fig. 5.8 Mean (±SD) body mass of female (*light*) and male (*dark*) sifakas per age category. Numbers inside bars denote sample size. Please note that most individuals were weighed repeatedly at different ages

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.

Acknowledgments Our foremost thanks go to our field assistant Tiana Andrianjanahary for his reliable and enthusiastic collection of census data. Enafa, Mily, Elysée, Léonard Razafimanantsoa, Rodin Rasoloarison, Mamitiana Razafindrasamba, Jean-Pierre Ratolojanahary, Nielsen Rabarijaona, Remy Ampataka, the late Jean-Claude Beroboka, Dietmar Zinner, Rebecca Lewis, and numerous student baby-sitters helped with the capture of sifakas. Dr. Joelison Ratsirarson supported our sifaka study in numerous ways. The CFPF/CNFEREF, Département Biologie Animale Université d'Antananarivo, and the Ministère Forêts et Environnement de Madagascar continue to authorize and support our research. The Bundesamt für Naturschutz provided the permits for tissue imports, and Heike Klensang was instrumental in obtaining them. Ulrike Walbaum managed the sifaka data base for many years, and Katharina Peters helped in extracting relevant information. Without the ground-breaking activities of Jörg Ganzhorn and the continuous financial support of the Deutsches Primatenzentrum and the Deutsche Forschungsgemeinschaft, this ongoing long-term project would have been impossible. We thank all these individuals and institutions for their support, and David Watts for helpful comments on this chapter.

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