PRIMATOLOGY MONOGRAPHS

Takeshi Furuichi · Juichi Yamagiwa · Filippo Aureli *Editors*

Dispersing Primate Females

Life History and Social Strategies in Male-Philopatric Species

Springer

Primatology Monographs

Series editors
Tetsuro Matsuzawa
Inuyama, Japan

Juichi Yamagiwa
Kyoto, Japan

More information about this series at http://www.springer.com/series/8796

Takeshi Furuichi • Juichi Yamagiwa • Filippo Aureli
Editors

Dispersing Primate Females

Life History and Social Strategies in Male-Philopatric Species

Springer

Editors
Takeshi Furuichi
Department of Ecology and Social Behavior
Primate Research Institute
Kyoto University
Inuyama, Aichi, Japan

Juichi Yamagiwa
Kyoto University
Kyoto, Japan

Filippo Aureli
Instituto de Neuroetología
Universidad Veracruzana
Xalapa, Veracruz, Mexico

ISSN 2190-5967 ISSN 2190-5975 (electronic)
Primatology Monographs
ISBN 978-4-431-55479-0 ISBN 978-4-431-55480-6 (eBook)
DOI 10.1007/978-4-431-55480-6

Library of Congress Control Number: 2015938580

Springer Tokyo Heidelberg New York Dordrecht London

Cover illustration:
Front cover: From top, clockwise: A female bonobo suckling her infant female at Wamba, the Luo Scientific Reserve, D.R. Congo (photo by Takeshi Furuichi). A female chimpanzee with her two offspring in the Kalinzu Forest Central Reserve, Uganda (photo by Takeshi Furuichi). A female woolly monkey with her infant in Cueva de Los Guácharos National Park, Colombia (photo by Johanna Paez). A Geoffroy's spider monkey female from Santa Rosa sector, Área de Conservación Guanacaste, Costa Rica (photo by Filippo Aureli).
Spine: A female bonobo suckling her infant female at Wamba, the Luo Scientific Reserve, D.R. Congo (photo by Takeshi Furuichi).
Back cover: From top, clockwise: Adult female, infant, and silverback mountain gorillas resting together after rain in Bwindi Impenetrable National Park, Uganda (photo by Martha M. Robbins). A girl of |Gui singing a song and beating out a rhythm with a bundle of grass when gathering food with elder women in the Central Kalahari Game Reserve, Botswana (photo by Kaoru Imamura). Female northern muriquis known to each other from their natal group staying together in a new group in the Reserva Particular do Patrimônio Natural – Feliciano Miguel Abdala, Minas Gerais, Brazil (Photo by Carla de B. Possamai). Female bonobos trying to remove a snare on the hand of a newly immigrant female at Wamba, the Luo Scientific Reserve, D.R. Congo (photo by Takeshi Furuichi).

Printed on acid-free paper

Springer Japan KK is part of Springer Science+Business Media (www.springer.com)

Preface: Introduction to Dispersing Primate Females

During my master's course at Kyoto University, I carried out several studies about the social relationships among wild Japanese macaques living on Yakushima Island. It was fascinating to see their behaviors, which were considerably different from those reported in studies of artificially provisioned, free-ranging groups of Japanese macaques that had been conducted for more than 30 years. Many males visited my study group every year and stayed there only during the mating season or settled down after the mating season ended. The dominance rank of newly immigrant males rose gradually, but they eventually left the group after several years, even if they had reached a high dominance rank by that time, probably to seek better mating opportunities as females tended to avoid males with a long tenure in the group (Furuichi 1985; Suzuki et al. 1998). It was very interesting to observe such male dynamism, and I developed a great interest in the entire life history of males.

Although the life history of females had been well documented through long-term studies by that time, we had very limited knowledge about how males behaved after leaving their natal group, how many months or years they lived solitarily before immigrating into new groups, which kinds of groups males chose to immigrate into, and how many groups they belonged to throughout their lifetime. This apparent lack of knowledge stems from the impossibility of tracing the identified males after they left the study group. We could recognize them by facial features and other characteristics as long as the animals were in the study group, but it was very difficult to re-identify animals using such feeble characteristics when we encountered them in other study groups.

In order to overcome such difficulties, I captured more than 30 males of different ages in various study groups on Yakushima Island using an anesthetic blowpipe and released them after tattooing their faces. I expected to trace some of those males shifting between groups because many researchers had been observing different adjacent groups on Yakushima Island. However, this study was completely unsuccessful, because after those males left the groups where they had been tattooed, none of them immigrated into the groups under our observation. It seemed that those males did not immigrate into adjacent groups, but rather traveled much further to join new groups.

When I shifted my study subject to bonobos at Wamba in the former Republic of Zaïre (now the Democratic Republic of the Congo) in 1983, I found myself again interested in the life history of the difficult-to-study sex – this time it was the female. After a decade of study by previous researchers, we had learned that the bonobos of our study sites typically formed male-philopatric groups (Kano 1992; Hashimoto et al. 1996). All the females born to our study group emigrated during juvenile or adolescent ages, and many strange females temporarily visited or immigrated into our study groups, while males rarely disappeared from the study groups and there was no case of immigration of unknown males. I therefore reconstructed the life history of females by comparing social and sexual behaviors of females at different ages in the study group (Furuichi 1989). However, even though we have studied the life history of female bonobos for 30 more years since then, we still do not know how females behave after leaving their natal groups, how many groups they visit before finally settling down, and which kinds of groups they choose to immigrate into. Young female bonobos sometimes temporarily visit neighboring groups before leaving their natal groups. However, when they finally leave their natal groups, many of them seem to travel much further to find a group to settle down. Regrettably, the life history of individuals of the dispersing sex may remain unknown, although its knowledge is indispensable for understanding the dynamic structure of primate societies.

After studying the basic structure of the female-philopatric societies of Japanese macaques (*Macaca fuscata*) and male-philopatric societies of eastern chimpanzees (*Pan troglodytes schweinfurthii*), Itani (1972, 1977) constructed a hypothesis about the phylogenetic evolution of the social structure of primates based on fragmental information of various primate species. He proposed that matrilineal and non-matrilineal societies are mutually exclusive forms that evolved in different pathways, and that gorillas, chimpanzees, and humans belonged to the group of non-matrilineal societies. On the other hand, Clutton-Brock and Harvey (1977) suggested that the social structure of each primate species was determined or largely influenced by its ecological condition. They examined variables including body weight, group size, home range size, socionomic sex ratio, and sexual dimorphism among 100 primate species, and discussed the relationships between those variables and food habits and habitat conditions of each species.

We know now that the social structures of primate species, as well as those of other mammalian species, are largely influenced by both phylogeny and ecological conditions. Species belonging to the same taxon, such as Cercopithecinae and Callitrichinae, tend to show similar social structure or type of philopatry, but different types of social structure and dispersal patterns sometimes appear in the same taxon (Fleagle 1992; DiFiore and Rendall 1994; Aureli et al. 2008). Furthermore, although the female-philopatric society had been considered the most typical social structure of group-living primates owing to the predominance of studies on papionines, there is variation in dispersal patterns, and female-philopatric society is not the predominant type of primate social structure (Strier 1994). For example, male-philopatric/female-dispersal social structure is commonly found not only in African Hominidae (Morin et al. 1994; Hashimoto et al. 1996; Furuichi et al. 1998, 2012; Gerloff et al. 1999; Yamagiwa et al. 2003; Robbins et al. 2009a) but also in Atelinae (Shimooka et al. 2008; Di Fiore et al. 2009; Strier and Mendes 2012), and male dispersal, female dispersal, and both-sex dispersal are all found in Colobinae (Fashing 2011; Kirkpatric 2011; Sterk 2012). More recent information about female dispersal of each taxon will be provided in this book. Thus, comparative studies of species showing different dispersal patterns have gained great interest in primatology.

Although there are many differences between female-philopatric and male-philopatric species, one of the most important differences seems to lie in the extent of variation in social relationships and life history of individuals of the dispersing sex. Females of male-philopatric species show much larger variations than do males of female-philopatric species. This discrepancy was the main reason why we wanted to publish this book about dispersing primate females.

In female-philopatric species, males usually leave their natal groups. Males of those species show variation in the age of natal emigration, the choice of group to enter, the dominance status obtained in the new group, and the patterns of secondary dispersal (e.g., long-tailed macaque: van Noordwijk and van Schaik 1985; Japanese macaque: Suzuki et al. 1998; white face capuchin: Jack and Fedigan 2004a, b). Additional variations can be observed in the number of groups males visit throughout their life or the time spent solitarily or in all-male groups. However, males do not show substantial variation in the occurrence of natal dispersal before maturation.

In contrast, females in male-philopatric societies show much larger variation in life history. For example, although most females of northern muriquis dispersed from their natal group before the onset of sexual activity, some females reproduced in their natal group and the age at first reproduction was significantly earlier compared to females that dispersed (Strier and Mendes 2012). Similarly, although most female chimpanzees left their natal group before sexual maturation, some females reproduced in their natal group and emigrated with their offspring or remained there for life (Pusey et al. 1997; Boesch and Boesch-Achermann 2000; Nishida et al. 2003; Sugiyama 2004; Stumpf et al. 2009). Although females usually belong to one group at a time, they sometimes associate with two different groups at the same time (Williams et al. 2002). The importance of association with other females differs considerably between the closely related chimpanzees and bonobos (Goodall 1986; Nishida 1989; Wrangham et al. 1992; Kano 1992; Furuichi 2011). A large variation is also found in dispersal patterns of female gorillas. Females of *Gorilla beringei beringei* and *G. b. graueri* may transfer to other groups alone or with other females; join solitary males, one-male groups, or multi-male groups; or stay in their natal groups (Yamagiwa et al. 2003, 2009; Robbins et al. 2009a, b).

Although groups or group ranges are very important entities for males to protect in male-philopatric species, protection of such entities might be less important for dispersing females in male-philopatric species because they do not necessarily need to stay in the group to which they belong. The most important focus for a female is her own survival and that of her offspring. Therefore, females seek better strategies to succeed in these goals in the local population. Although it has been suggested that females need to leave their natal groups to avoid mating with close kin in male-philopatric species, such norms in life history can frequently be violated, as mentioned above. Females may leave or stay in their natal group for better feeding conditions or lower risk for predation (Wrangham 1979), and they may leave or stay in their natal group for more effective protection from infanticide according to the relative number of adult males in their natal group compared to other groups (Yamagiwa et al. 2003). Such flexibility in choice of life history strategies, due to weak constraints from kin relations, might be why females in human societies came to show enormous variations in the pattern of marriage, residence, and mating activities.

Thus, due to the large variation and flexibility and the difficulty of tracking females after natal dispersal, it has been a challenge to understand the patterns of life history and their underlying factors. The aim of this volume is therefore to present up-to-date knowledge about the life history and social relationships of females in male-philopatric primate species. Because male-philopatric species are found in various primate taxa, we focused on the two major taxa whose members live in multi-male, multi-female, male-philopatric groups: Atelinae in Part I (Chaps. 1, 2, 3) and Hominidae except *Pongo* in Part II (Chaps. 4, 5, 6, 7, 8). In Part III, factors influencing variations in the dispersal pattern across primates are examined (Chap. 9), and social patterns are compared across Colobinae species that show a large variation in dispersal patterns (Chap. 10). Finally, a hypothesis for the formation of human families from the perspectives of female life history is proposed by exploring recently gained knowledge in various fields of research (Chap. 11).

Inuyama, Aichi, Japan Takeshi Furuichi

References

Aureli F, Schaffner CM, Boesch C, Bearder SK, Call J, Chapman CA, Connor R, Di Fiore A, Dumber RIM, Henzi SP, Holekamp K, Korstjens AH, Layton R, Lee P, Lehmann J, Manson JH, Ramos-Fernandez G, Strier KB, van Schaik CP (2008) Fission-fusion dynamics: new research frameworks. Curr Anthropol 49:627–654

Boesch C, Boesch-Achermann H (2000) The chimpanzees of the Taï Forest. Oxford University Press, New York

Clutton-Brock TH, Harvey H (1977) Primate ecology and social organization. J Zool 183:1–39

Di Fiore AF, Rendall D (1994) Evolution of social organization: a reappraisal for primates by using phylogenetic methods. Proc Natl Acad Sci U S A 91:9941–9945

Di Fiore A, Link A, Schmitt C, Spehar S (2009) Dispersal patterns in sympatric woolly and spider monkeys: integrating molecular and observational data. Behaviour 146:437–470

Fashing PJ (2011) African colobine monkeys: their behavior, ecology, and conservation. In: Campbell CJ, Fuentes A, MacKinnon KC, Bearder SK, Stumpf RM (eds) Primates in perspective, 2nd edn. Oxford University Press, Oxford, pp 203–229

Fleagle JG (1992) Trends in primate evolution and ecology. Evolut Anthropol 1:78–79

Furuichi T (1985) Inter-male associations in a wild Japanese macaque troop on Yakushima Island, Japan. Primates 26:219–237

Furuichi T (1989) Social interactions and the life history of female *Pan paniscus* in Wamba, Zaire. Int J Primatol 10:173–197

Furuichi T (2011) Female Contributions to the peaceful nature of bonobo society. Evolut Anthropol 20:131–142

Furuichi T, Idani G, Ihobe H, Kuroda S, Kitamura K, Mori A, Enoimoto T, Okayasu N, Hashimoto C, Kano T (1998) Population dynamics of wild bonobos (Pan paniscus) at Wamba. Int J Primatol 19:1029–1043

Furuichi T, Idani G, Ihobe H, Hashimoto C, Tashiro Y, Sakamaki T, Mulavwa MN, Yangozene K, Kuroda S (2012) 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. In: Kappeler PM, Watts DP (eds) Long-term field studies of primates. Springer, Berlin/Heidelberg, pp 413–433

Gerloff U, Hartung B, Fruth B, Hohmann G, Tautz D (1999) Intracommunity relationships, dispersal pattern and paternity success in a wild living community of bonobos (*Pan paniscus*) determined from DNA analysis of faecal samples. Proc R Soc Lond 266:1189–1195

Goodall J (1986) The chimpanzees of Gombe: patterns of behavior. Harvard University Press, Cambridge

Hashimoto C, Furuichi T, Takenaka O (1996) Matrilineal kin relationship and social behavior of wild bonobos (*Pan paniscus*): sequencing the D-loop region of mitochondrial DNA. Primates 37:305–318

Itani J (1972) Reichourui no shakai kouzou (social structure of primates). Kyoritsu Press, Tokyo (in Japanese)

Itani J (1977) Evolution of primate social structure. J Hum Evol 6:235–243

Jack KM, Fedigan L (2004a) Male dispersal patterns in white-faced capuchins, *Cebus capucinus*: part 1: patterns and causes of natal emigration. Anim Behav 67:761–769

Jack KM, Fedigan L (2004b) Male dispersal patterns in white-faced capuchins, *Cebus capucinus*: part 2: patterns and causes of secondary dispersal. Anim Behav 67:771–782

Kano T (1992) The last ape: pygmy chimpanzee behavior and ecology. Stanford University Press, Stanford

Kirkpatrick RC (2011) The Asian colobines: diversity among leaf-eating monkeys. In: Campbell CJ, Fuentes A, MacKinnon KC, Bearder SK, Stumpf RM (eds) Primates in perspective, 2nd edn. Oxford University Press, Oxford, pp 189–202

Morin P, Moore J, Chakraborty R, Jin L, Goodall J, Woodruff D (1994) Kin selection, social structure, gene flow, and the evolution of chimpanzees. Science 265:1193–1201

Nishida T (1989) Social interactions between resident and immigrant female chimpanzees. In: Heltne P, Marquardt L (eds) Understanding chimpanzees. Harvard University Press, Cambridge, MA, pp 68–89

Nishida T, Corp N, Hamai M, Hasegawa T, Hiraiwa-Hasegawa M, Hosaka K, Hunt KD, Itoh N, Kawanaka K, Matsumoto-Oda A, Mitani JC, Nakamura M, Norikoshi K, Sakamaki T, Turner L, Uehara S, Zamma K (2003) Demography, female life history, and reproductive profiles among the chimpanzees of Mahale. Am J Primatol 59:99–121

Pusey AE, Williams JM, Goodall J (1997) The influence of dominance rank on the reproductive success of female chimpanzees. Science 277:828–831

Robbins AM, Stoinski T, Fawcett K, Robbins MM (2009a) Leave or conceive: natal dispersal and philopatry of female mountain gorillas in the Virunga volcano region. Anim Behav 77:831–838

Robbins AM, Stoinski TS, Fawcett KA, Robbins MM (2009b) Socioecological influences on the dispersal of female mountain gorillas – evidence of a second folivore paradox. Behav Ecol Sociobiol 63:477–489

Shimooka Y, Campbell CJ, Di Fiore A, Felton AM, Izawa K, Link A, Nishimura A, Ramos-Fernández G, Wallace RB (2008) Demography and group composition of *Ateles*. In: Campbell CJ (ed) Spider monkeys: behavior, ecology and evolution of the genus *Ateles*. Cambridge University Press, Cambridge, pp 329–348

Sterk EHM (2012) The behavioral ecology of colobines monkeys. In: Mitani JC, Call J, Kappeler PM, Palombit RA, Silk JB (eds) The evolution of primate societies. The University of Chicago Press, Chicago/London, pp 65–90

Strier KB (1994) Myth of the typical primate. Am J Phys Anthropol 37(S19):233–271

Strier KB, Mendes SL (2012) The northern muriqui (*Brachyteles hypoxanthus*): lessons on behavioral plasticity and population dynamics from a critically endangered species. In: Kappeler PM, Watts DP (eds) Long-term field studies of primates. Springer, Berlin/Heidelberg, pp 125–140

Stumpf RM, Thompson ME, Muller MN, Wrangham RW (2009) The context of female dispersal in Kanyawara chimpanzees. Behaviour 146:629–656

Sugiyama Y (2004) Demographic parameters and life history of chimpanzees at Bossou, Guinea. Am J Phys Anthropol 124:154–165

Suzuki S, Hill DA, Sprague DS (1998) Intertroop transfer and dominance rank structure of nonnatal male Japanese macaques in Yakushima, Japan. Int J Primatol 19:703–722

van Noordwijk M, van Schaik CP (1985) Male migration and rank acquisition in wild long-tailed macaques (*Macaca fascicularis*). Anim Behav 33:849–861

Williams JM, Pusey AE, Carlis JV, Farm BP, Goodall J (2002) Female competition and male territorial behaviour influence female chimpanzees' ranging patterns. Anim Behav 63:347–360

Wrangham RW (1979) On the evolution of ape social systems. Soc Sci Inform 18:335–368

Wrangham RW, Clark AP, Isabirye-Basuta G (1992) Female social relationships and social organisation of the Kibale forest chimpanzees. In: Nishida T, McGrew WC, Marler P, Pickford M, de Waal FBM (eds) Topics in primatology. University of Tokyo Press, Tokyo, pp 81–98

Yamagiwa J, Kahekwa J, Basabose AK (2003) Intra-specific variation in social organization of gorillas: implications for their social evolution. Primates 44:359–369

Yamagiwa J, Kahekwa J, Basabose AK (2009) Infanticide and social flexibility in the genus *Gorilla*. Primates 50:293–303

Contents

Part I Dispersing Ateline Females

1 Dispersal Patterns of Female Northern Muriquis: Implications for Social Dynamics, Life History, and Conservation ... 3
Karen B. Strier, Carla B. Possamai, and Sérgio L. Mendes

2 Association Networks and Life History of Female Spider Monkeys .. 23
Yukiko Shimooka

3 Social Interactions and Proximal Spacing in Woolly Monkeys: Lonely Females Looking for Male Friends 45
Pablo R. Stevenson, Diego A. Zárate, Mónica A. Ramírez, and Francisco Henao-Díaz

Part II Dispersing Hominine Females

4 Dispersal Patterns of Females in the Genus Gorilla 75
Andrew M. Robbins and Martha M. Robbins

5 Sex Differences in Ranging and Association Patterns in Chimpanzees in Comparison with Bonobos 105
Chie Hashimoto and Takeshi Furuichi

6 Intergroup Transfer of Females and Social Relationships Between Immigrants and Residents in Bonobo (*Pan paniscus*) Societies 127
Tetsuya Sakamaki, Isabel Behncke, Marion Laporte, Mbangi Mulavwa, Heungjin Ryu, Hiroyuki Takemoto, Nahoko Tokuyama, Shinya Yamamoto, and Takeshi Furuichi

7 Human Female Dispersal and Social Organization: A Case of Central African Hunter-Gatherers 165
Naoki Matsuura

8 Life History and Sexual Relationships of Female Kalahari Hunter-Gatherers 185
Kaoru Imamura

Part III Evolution of Female Dispersal

9 Complexities of Understanding Female Dispersal in Primates 215
Phyllis C. Lee and Karen B. Strier

10 Factors Influencing Grooming Social Networks: Insights from Comparisons of Colobines with Different Dispersal Patterns 231
Ikki Matsuda, Keiichi Fukaya, Cristian Pasquaretta, and Cédric Sueur

11 Evolution of Hominid Life History Strategy and Origin of Human Family 255
Juichi Yamagiwa

Conclusion: Emerging Patterns and Challenges for Dispersing Female Primates 287
Filippo Aureli

Index 295

Part I
Dispersing Ateline Females

Chapter 1
Dispersal Patterns of Female Northern Muriquis: Implications for Social Dynamics, Life History, and Conservation

Karen B. Strier, Carla B. Possamai, and Sérgio L. Mendes

Introduction

Female dispersal is widespread across the Primate Order (Moore 1984). Yet an early field research emphasis on the Old World cercopithecines during the 1950s–1970s has resulted in the persistent misperception that most primates live in matrilocal societies with extended matrilineal kin groups and male-biased dispersal. This "myth" has prevailed despite increasing evidence that bisexual dispersal and female-biased dispersal are more common than male-biased dispersal at the genus level in all major clades except the cercopithecines (Strier 1994). Moreover, the phylogenetic signals for male-biased dispersal among cercopithecines (Di Fiore and Rendall 1994) and for female-biased dispersal in panini and atelins are quite strong (Lee and Kappeler 2003). This distinction between the dispersal patterns of matrilineal cercopithecines and other primates raises numerous questions about the social and ecological conditions that favor matrilocal female kin groups versus those in which females either avoid competition with close kin by dispersing or are relatively indifferent toward one another and therefore more responsive to the reproductive strategies of males (e.g., Wrangham 1980; Sterck et al 1997; Isbell and Young 2002).

Although female dispersal should limit opportunities for the development of extended, multigenerational matrilines, it does not necessarily sever all female kin bonds if females transfer into groups where older matrilineal kin have gone or if

---

K.B. Strier (✉)
Department of Anthropology, University of Wisconsin–Madison, 1180 Observatory Drive, Madison, WI 53706, USA
e-mail: kbstrier@wisc.edu

C.B. Possamai • S.L. Mendes
Programa de Pós Graduação em Biologia Animal, Departamento de Ciencias Biológicas, Universidade Federal do Espírito Santo, Vitória, Brazil

T. Furuichi et al. (eds.), *Dispersing Primate Females*,
Primatology Monographs, DOI 10.1007/978-4-431-55480-6_1

they transfer with familiar age cohorts, which may also be close paternally related kin (Strier 2008). In chimpanzees, female dispersal rarely leads to associations among close female kin (Langergraber et al. 2009), but in at least one study of gorillas, females were found to disperse preferentially into groups with female kin (Bradley et al. 2007). Among northern muriquis, females disperse prior to the onset of sexual activity and puberty (Strier and Ziegler 2000; Strier 2008) and then appear to remain in their new groups for the duration of their lives. The absence of female secondary dispersal in this and most other female dispersing species may result in lifelong associations among close female kin outside of their natal groups. Such associations may be especially prevalent in small, isolated populations where dispersal opportunities are limited, and correspondingly, the probability of encountering related females in other groups is quite high (Strier 2004). Understanding female dispersal patterns can provide important insights into the underlying social and genetic structure of these populations and thus contribute to conservation efforts on their behalf.

Dispersal represents a major life history milestone, particularly if it occurs prior to the onset of puberty. Delayed sexual maturation may be considered to be a cost of dispersal, especially if it corresponds with a delay in a female's age at first reproduction that results in an overall shorter reproductive lifespan (reviewed in Strier 2008). However, the timing of dispersal may also be affected by seasonality in social or ecological conditions that can simultaneously affect both opportunities to disperse and constraints on dispersal. For example, seasonal food scarcity might stimulate expanded ranging patterns that bring females into greater contact with other groups and facilitate intergroup transfer. Alternatively, seasonal concentrations of preferred foods that lead to an increase in the frequency of intergroup encounters might facilitate female group transfers compared to times of food scarcity, when ranging and energy are more limited and intergroup encounters are rare. Such effects of seasonality on female dispersal patterns may be especially pronounced in populations living at high densities with correspondingly high potential levels of both intra- and intergroup feeding competition. Indeed, the avoidance of intragroup feeding competition when fruit resources are scarce may account for the fluid patterns of association and fluctuating party sizes of females in groups with a high degree of fission–fusion dynamics (reviewed in Aureli et al. 2008).

Most considerations of dispersal by female primates focus on evaluating the social, reproductive, or ecological correlates, with little attention to the implications of female dispersal for assessments of population persistence and for the development of informed conservation management programs. Here, we present a unique set of data on female dispersal patterns in an isolated population of northern muriquis over a 10-year period during which time all individuals in the entire population have been monitored. We use long-term data on female ages, natal groups, and mother identities to examine whether dispersing females exhibit social preferences toward maternally related or familiar females in their new groups and whether females that disperse into different groups differ in their ages at first reproduction. We also discuss the implications of female northern muriqui dispersal patterns for the conservation and management of this critically endangered species.

Northern Muriquis

The northern muriqui was once classified together with the southern muriqui, but it is now recognized as a separate species, *Brachyteles hypoxanthus*, distinct from the southern muriqui, *B. arachnoides*, on the basis of genetic and morphological differences. Today, the two species occur allopatrically, with the northern muriqui restricted to about a dozen of the remaining fragments of Brazilian Atlantic forest in the states of Minas Gerais, Espírito Santo, and southern Bahia (Mendes et al. 2008). Although comparative field studies have been conducted or are now under way, most of our current knowledge about northern muriqui behavioral ecology comes from long-term field research on our study population at the Reserva Particular do Patrimônio Natural – Feliciano Miguel Abdala (RPPN-FMA), a privately owned, federally protected forest in Caratinga, Minas Gerais (19°44′S, 41°49′W). The 957 ha forest reserve is surrounded by pasture and agricultural lands that separate it from other smaller forest fragments still standing on some of the neighboring properties (Fig. 1.1). However, there are no other muriquis in these fragments except for females from our study population that have recently begun to colonize them (Tabacow et al. 2009a). More details about the study site and the muriquis' isolation from other populations can be found elsewhere (Strier 2014; Strier and Mendes 2012).

In contrast to most other primates, including those with similarly female-biased dispersal patterns and at least one population of southern muriquis in São Paulo state (e.g., Talebi et al. 2009), northern muriqui society is distinguished by the nonhierarchical, egalitarian relationships among and between males and females. Philopatric males are highly tolerant toward one another and toward females, which may be related to their sexual monomorphism in both body and canine size (Rosenberger and Strier 1989; Lemos de Sá and Glander 1993). Mating occurs in full view of other group members without overt aggression (Strier 1997; Possamai et al. 2007), and the muriquis' large relative testes size and copious production of ejaculate suggest selection for sperm competition (e.g., Dixson 2012). Recent genetic paternity analyses of a cohort of infants in our study population revealed extremely low levels of male reproductive skew, consistent with their relaxed behavioral promiscuity (Strier et al. 2011).

Adult and subadult males associate preferentially with one another and maintain strong, affiliative social networks (Strier et al. 2002; Tokuda et al. 2012), whereas females tend to socialize less often and with fewer partners and to actively avoid their closest female associates when feeding (Strier 1990, 2011; Arnedo et al. 2010). Indeed, the avoidance of feeding competition may also explain the shift from cohesive to fluid, fission–fusion grouping patterns that accompanied the large increase in group size and in population density in our study population over time (Dias and Strier 2003). Although other behavioral and demographic responses to our study population's continued growth have been documented (e.g., Tabacow et al. 2009b; Strier and Ives 2012; Strier and Mendes 2012; Tokuda et al. 2012, 2014), there is no evidence that rates of aggression or other forms of overt competition have increased.

Fig. 1.1 View of the surroundings of the forest fragment of the RPPN-Feliciano Miguel Abdala, in Caratinga, Minas Gerais (Photo by Carla de B. Possamai)

Considering their overall tolerance toward one another and avoidance of direct competition, it is not at all clear what stimulates female northern muriquis to leave their natal groups. In the Matão group years ago, females close to dispersal age were found to socialize less and become more peripheral than their male age cohorts, but there was no evidence that they were targets of aggression or actively evicted by other members of their natal group (Strier 1993; Printes and Strier 1999). Recent immigrant females were similarly peripheral, but tended to associate more with adult males and less with adult females in their new group (Printes and Strier 1999). The playful relationships that at least some immigrants establish with smaller juveniles might also contribute to their integration and ultimate acceptance (Strier 1999). However, data on the social dynamics of a larger number of individuals are necessary to evaluate whether these are normative social patterns for new female immigrants and whether access to familiar females from their natal groups might alter their social dynamics.

Documenting Dispersal Events

Following a brief pilot study in 1982, systematic observations were initiated on the Matão group in June 1983. Observations of this group have been continuous except for the period between August 1984 and June 1986, when only episodic demographic data were collected. The other group, Jaó, also present since 1982 is known to have split on two separate occasions, creating the daughter groups M2 in 1987–1988 (Strier et al. 1993) and Nadir in 2002–2003 (Strier et al. 2006). From 2002 to 2003, systematic studies were initiated on the Jaó group and extended to include the Nadir group as it became established (Tokuda et al. 2014) and the M2 group. Northern muriquis have distinct facial markings and fur and facial features that make it possible for trained observers to recognize them individually. Thus, we now have life history data on all females born in the Matão group since 1983 and on all females born in the entire population since 2002–2003.

Because of this research history, our dispersal data prior to 2002 are restricted to females that were born in the Matão group or that immigrated into the Matão group (Strier 2005). The nearly continuous monitoring of the Matão group has provided reliable data on natal female birth dates and thus on female age at dispersal, as well as on the interval from immigration to first birth for females that joined this group from the outset. Elsewhere (Strier and Mendes 2012), we have shown that natal female age at dispersal from the Matão group has not changed over time, despite an increase in this group's size from 23 individuals in July 1983 to 117 individuals as of July 2012 due to births and immigrations offsetting deaths and emigrations (e.g., Strier et al. 2006; Strier 2014).

Since the onset of systematic monitoring of the population in 2002, we have been able to track the dispersal trajectories of all females in all four groups that have reached dispersal age (Fig. 1.2). Ages of females born in the Jaó, Nadir, and M2 groups prior to the onset of monitoring were estimated based on comparisons of visible characteristics with females of known age in the Matão group. Age estimates for these females are those employed in the Primate Life History Database (Strier et al. 2010). Here, we describe the dispersal patterns of females during the period from March 2002 through July 2012.

The four groups in the population all grew in size over the study period. In June 2012, group sizes ranged from 52 individuals (M2), to 78 (Jaó), to 79 (Nadir), to 119 (Matão). Dispersal in this population is a dynamic process because although there is no secondary dispersal after the onset of puberty and sexual activity, females may initially visit different groups or return to their natal groups before ultimately – and apparently, permanently – transferring. We have never observed a female to return to her natal group after becoming sexually active and reproducing, and on only one occasion, described below, did a female leave a group after mating in that group.

We define the onset of the dispersal process by having at least one confirmed sighting of the female in association with one or more members of a non-natal group in the absence of proximity to her natal group. The dispersal process is considered to be complete once the female stops returning to her natal group or visiting other

Fig. 1.2 Females known from natal group (Matão) hanging out together in their new group, Jaó (Photo by Carla de B. Possamai)

groups; often this coincides with the onset of sexual activity, which also coincides with the onset of ovarian cycling (Strier and Ziegler 2000). Initially, new females that appeared in the Matão group could only have come from the Jaó group, but by the early 1990s, a female who had been born in the M2 group would have been old enough to disperse. Because we were not following either Jaó or M2 groups prior to 2002, we could not distinguish between these potential natal groups for the females that immigrated into the Matão group, and therefore, we do not include them in the analyses presented here.

Conversely, natal Matão females that were sighted with other muriquis in the forest were classified as having dispersed (e.g., Strier 2005, 2014; Strier and Mendes 2012), even though their subsequent fates in their new groups were not systematically monitored until 2002, when some of the females could be confidently reidentified (Strier et al. 2006). Once the population-wide monitoring was initiated, however, females have been tracked more closely from the last sighting date in their natal groups until their first appearance date in another group, as well as during their visits to other groups or returns to their natal groups; all females continue to be monitored in their new groups after they have permanently transferred.

The fates of females that were never relocated after they were last sighted in their natal groups were recorded as undetermined; these females could not be classified as having emigrated because we could not exclude the possibility that they died before dispersing. If a female was resighted in another group after leaving her natal group, she was retroactively assigned an emigration date corresponding to the last day she was observed in her natal group and a temporary immigration date corresponding to the first day she was observed with the new group. The temporary immigration date was subsequently adjusted depending on whether the female remained in the new group, visited other groups, or returned to her natal group. Females that dispersed out of the Reserve into neighboring forest fragments have emigration dates based on their last sighting in their natal groups; although they dispersed into the fragments, they are not considered to have immigrated because there were no established groups in these fragments into which they could immigrate. These females might be best classified as colonizers of these forest fragments.

Precision of the dates assigned to dispersal events was affected by a combination of factors including observer sampling effort, visibility conditions in the areas in which females were last and first observed, and the behavior and temperament of the individual females. Specifically, emigration dates could have been assigned too early (and therefore female age at emigration underestimated) if a female continued to travel with her natal group after the last date she was recorded by observers to be with it. Conversely, immigration dates could be assigned as later than actually occurred (and female age at immigration overestimated) if a female had joined a new group before she was first observed associating with it. The dates on which females were resighted in the forest fragments to the south of the Reserve are likely to be later than their arrival in the fragments because of the sporadic and opportunistic nature of the censuses in these areas.

The dispersal process was classified retrospectively based on whether females were sighted in a single group (or in the fragments) where they remained for at least a year after last sighting in their natal group (Direct) or in more than one non-natal group before either remaining in one of the visited groups (Visit) or returning to the natal group (Test). It was necessary to revise these classifications whenever females moved between groups prior to their permanent transfers. Because the study site is isolated, there are no other muriquis in surrounding areas that could immigrate into the study population. Hence, all immigrations since the onset of the population-wide monitoring in 2002 involved females in the four study groups that comprise the study population; all of them are individually recognizable to trained observers and monitored systematically as part of the long-term research at this site (Strier and Mendes 2012).

Timing of Dispersal: Female Age

Females during this study period emigrated at a mean (± sd) age of 5.73 ± 0.50 year (median = 5.72 years; minimum–maximum = 4.82–6.74 years; N = 44). There was no difference in the minimum dispersal ages of females that were known from birth (5.78 ± 0.50 year, $N = 26$) versus those whose ages were estimated at the time monitoring began (5.71, ±0.12, $N = 18$; Mann–Whitney U = 244.5, $N_1 = 26$, $N_2 = 18$, $p > 0.05$). Median age at natal group emigration ranged from 5.22 years for females born in Nadir group ($N = 3$), to 5.69 years for those born in M2 group

($N = 11$), to 5.76 years for those born in Jaó group ($N = 14$), to 5.88 years for those born in Matão group ($N = 16$). Although Matão females spent from 0.125 years to nearly 0.67 years months longer in their natal group than females born in the other groups on average, variation in dispersal age was not significantly greater between groups than it was within groups during this 10-year study period (Kruskal–Wallis $K = 3.36$, $\mathrm{df} = 3$, $p > 0.05$). Moreover, the more intensive monitoring of the Matão group may have made these emigration dates more accurate than those for females in the other groups, where less frequent sampling may have resulted in earlier assignments of female emigration dates based on the last sightings in them in their natal groups (Fig. 1.3).

Differences in sampling intensity, in the distances between groups, and in whether females transferred directly or visited or tested different groups around may have also affected immigration dates. Indeed, any of these factors might explain why the difference between emigration dates and dispersal dates was greater for some of the females that moved into the fragments than for those that remained in the reserve and immigrated into other established groups (Fig. 1.3). While it is possible that at least some of the females were slow to move into the fragments, we have no way to evaluate this because they were not encountered by observers during these intervals.

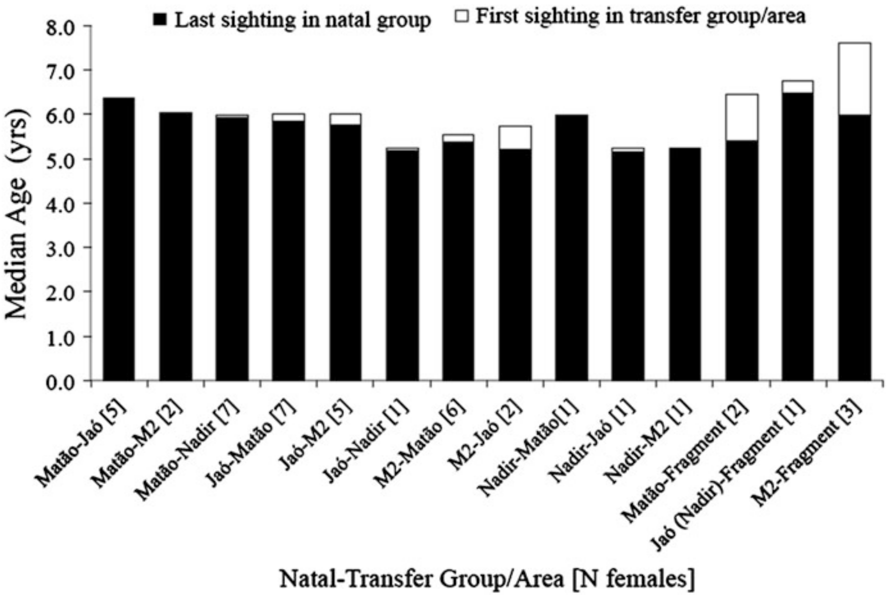


Fig. 1.3 Dispersal ages of female northern muriquis, April 2002–July 2012. The last recorded sighting of a female traveling with her natal group is considered to be her emigration date. Her first recorded sighting with the group (or area) in which she remains is considered to be her transfer date. Variation in the lags between emigration and transfer dates, especially for females that moved into the fragments, can be attributed, at least in part, to variation in the intensity with which groups were followed and the long intervals between censuses in the fragments (Tabacow et al. 2009a; Strier and Ives 2012)

Timing of Dispersal: Seasonality

The timing of dispersal events was highly seasonal, with all 44 of the dispersing females (100 %) for which we have reliable data being last sighted in their natal groups between October and May (Fig. 1.4). The RPPN-FMA is characterized by a distinct rainy season from November to March and a dry season from April to October (Strier et al. 2001). Although births have been recorded in every month of the year, some 66.4 % of known birthdates ($N = 295$, as of December 2012) have occurred during the dry season months (updated from Strier et al. 2001). Correspondingly, conceptions that lead to live births (after a 7.2-month gestation; Strier and Ziegler 1997) are concentrated during the rainy season months (Strier 1997; Strier et al. 2003). The restriction of female dispersal events during these years to the mating and conception seasons is paradoxical, however, because females in this population experience an average delay of more than 3 years between dispersal and their first reproduction (Strier and Mendes 2012; for this study, see below).

This delay suggests that factors other than immediate reproductive opportunities may underlie the seasonal timing of dispersal. For example, the rainy season months also correspond to the times of year when preferred new leaves, fruits, and flowers are most abundant (Strier 1991; Strier and Boubli 2006) and when intergroup encounters are more common (Strier, unpublished data). The seasonality in food abundance and in social opportunities might therefore reduce the energetic and social costs of dispersal during the rainy season, despite the delays between dispersal and the onset of puberty (Strier and Ziegler 2000; Strier and Mendes 2012, respectively). The fact that 19 of the 23 emigrations of Matão females recorded between 1987 and 1999 also occurred during the rainy season months

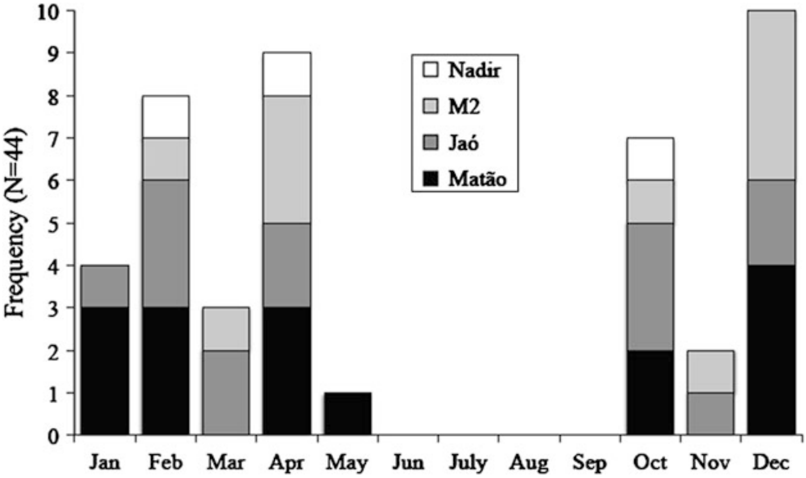


Fig. 1.4 Monthly distribution of natal emigration events by female northern muriquis, April 2002–2012 (Legend shows the different natal groups)

(see Strier and Ziegler 2000) despite the smaller group size and lower population density suggests that seasonal dispersal may be more strongly linked to ecological and energetic factors than to demographic ones. Nonetheless, intergroup encounters at any time could still provide opportunistic conditions for low-cost dispersal.

Social Preferences

Females varied in whether they transferred directly from their natal group into a new group versus whether they visited one or more non-natal groups before either remaining in one of them or returning to visit their natal group again. However, secondary dispersal after a female reproduced has never been reported in this species, and only one female in our study population was observed to mate in a group and then subsequently leave it (see below). Of the 12 females for whom visits were reliably recorded, two visited one group before joining another, five visited a group and then returned to their natal group before either joining or visiting other groups, and five visited at least two other groups (or the fragment) before settling in one of them (Table 1.1). However, there are no obvious patterns that might predict or explain the variation in individual dispersal patterns. For example, one natal Matão female (NT) visited the Nadir group and then the M2 group and then returned to reside in the Nadir group, where she had older maternal sisters, within 9 days of leaving her natal group. Another female (COL) dispersed from the Matão group only 46 days after NT, but was only sighted again 133 days later, traveling with the Jaó group. COL had a maternal sister (CR) that had immigrated into the Nadir group less than 2 years earlier, but she opted to immigrate into the Jaó group, where she joined an even older maternal sister who she would never have known from her natal group. Both NT and COL would have encountered other females with whom they were familiar from their natal group in both the Jaó and Nadir groups; thus, it is unclear why they opted to join the different groups that they did.

At the group level, females born in the Jaó and M2 groups were more likely to join the Matão group than to join the other non-natal groups (Fig. 1.5). Matão females, by contrast, were more likely to join the Jaó and Nadir groups than M2 group. However, two of the four most recent Matão emigrants have been associating with the M2 group; if these females transfer permanently into the M2 group, then their presence may attract other familiar and possibly related females from their natal Matão group in the future.

Because we do not know the natal groups or maternal relatedness of females other than those born in Matão group prior to the onset of population-wide monitoring in 2002, we cannot evaluate whether kinship and familiarity affect female decisions to join particular groups. Nonetheless, we examined the relative strength of associations among female dyads in the three groups into which Matão females have immigrated. Although a previous behavioral study found that recent immigrant females in the Matão group associated more often with adult females in their new group than did the natal females that were old enough but had not

Table 1.1 Visits and tests during the dispersal process

Female ID	Natal group	1st group visit	Return home (1)	2nd group visit	Return home (2)	2nd visit to 1st group	2nd visit to 2nd group	Group at last sighting
Val	Matão	Nadir						Jaó (not visited)
EA-J	Jaó	Matão						M2 (not visited)
OL-N	Jaó/Nadir	Matão		M2				Matão (visited 1st)
NT	Matão	Nadir		M2				Nadir (visited 1st)
BRD-J	Jaó	Matão		M2				Matão (visited 1st)
TP-M2	M2	Nadir		Matão		Nadir	Matão	Fragment (not visited)
RT-J	Jaó	Matão		Nadir		Matão	Nadir	Matão (visited 1st)
Neo	Matão	M2	Matão					M2 (visited 1st)
NK-N	Jaó/Nadir	Fragment	Nadir	Matão				Fragment (visited 1st)
CLR-J	Jaó	Nadir	Jaó	Matão				Matão (visited 2nd)
RN-M2	M2	Nadir	M2	Matão	M2			Matão (visited 2nd)
OD-N	Nadir	Jaó	Nadir	Matão	Nadir			Matão (visited 2nd)

Columns from left to right follow the temporal sequence from the female’s first departure from her natal group. Only females that visited at least one other group prior to emigration during this study period are shown

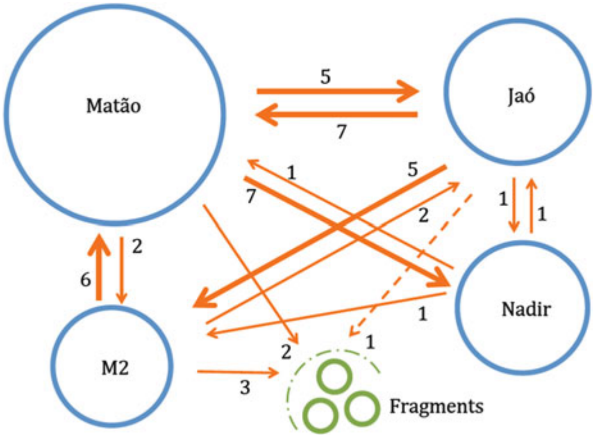


Fig. 1.5 Female northern muriqui natal group transfers, April 2002–2012. The four muriqui groups in the reserve are indicated by *blue circles*, drawn roughly proportionate to their respective sizes (see Methods for group sizes). The discontinuous forest fragments to the south of the reserve are shown in *green*. *Arrows* and *numbers* show female dispersal from their natal groups into their adult groups. The *dashed arrow* indicates the natal group (Jaó) of a female whose mother was among the founders of the Nadir group after the Jaó group fissioned (Strier et al. 2006; Tokuda et al. 2014). This female was an infant at the time of the fission and grew up in the Nadir group with her mother

yet dispersed (Printes and Strier 1999), the small sample size and lack of history for the immigrant females precluded more fine-grained assessments of their social relationships. In an effort to fill this gap, one of us (CBP) collected systematic data on the association patterns of 31 females that had emigrated from either the Matão group ($N = 22$), Jaó group ($N = 5$), M2 group ($N = 2$), or Nadir group ($N = 1$) or had remained in the Nadir group ($N = 1$) since the onset of the population-wide monitoring in 2002 (Strier et al. 2006). A total of 1,036 observations, or individual records, of target females were obtained from 1,608 scan samples conducted at 30-min intervals from January to December 2011 on the Jaó, M2, and Nadir groups.

We used scan sample data on target females' nearest neighbors within a 5 m radius as an indicator of their closest spatial associates, following other analyses of social dynamics among muriquis in this population (e.g., Strier 1990, 2011; Printes and Strier 1999; Possamai et al. 2007). Target females were observed with at least one adult or subadult nearest neighbor within a 5 m radius in about two-thirds of the samples (Jaó group and M2 group: median proportion of observations in proximity = 0.61, $N = 14$ and $N = 5$ target females, respectively; Nadir group: median = 0.68, $N = 12$) and with one or more other target females in about 30 % of the observations in the groups to which they immigrated (Fig. 1.6), despite differences in the number of target females, and the number of available associates, in each group (Jaó group: median proportion of observations in proximity = 0.33, $N = 14$ target females; Nadir group: median = 0.28, $N = 12$; M2 group: median = 0.27, $N = 5$).

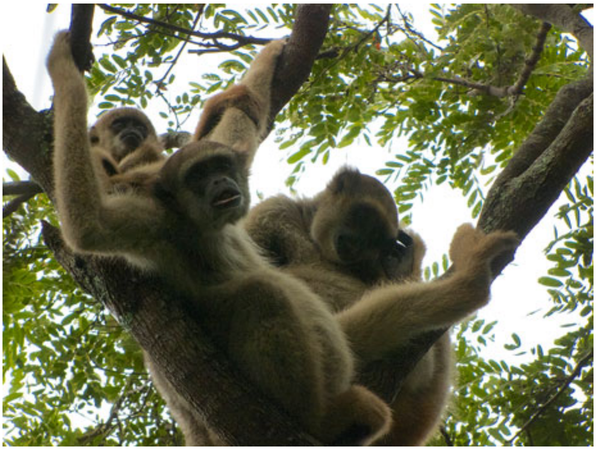


Fig. 1.6 Females known from natal group (Matão) hanging out with older resident female of Nadir group (Photo by Carla de B. Possamai)

Dyadic association indices, DAIs (Martin and Bateson 1986; calculated as $N_{AB}/N_A + N_B + N_{AB}$, where N_{AB} is the number of observations of females A and B in proximity, N_A is the number of observations of female A alone, and N_B is the number of observations of female B alone), ranged from 0 to 0.60 across all dyads. Preliminary analyses suggest there were no significant differences in the DAIs of females with shared histories in the same natal groups where they would have been familiar with one another ($N = 63$ dyads) versus those that were unfamiliar ($N = 104$ dyads; $z = 1.68$, $p > 0.05$) or among maternal sisters ($N = 10$ dyads) versus non-maternal sisters ($N = 157$ dyads; $z = -0.50$, $p > 0.05$). However, other factors, including female age and length of residency in their adopted groups, as well as differences in group size and composition could be involved. For example, among Taï chimpanzees, females social relationships appear to develop over time (Lehmann and Boesch 2009), similar to what has been observed among long-term female residents versus recent immigrants in the Matão group recent (Strier 1996).

Dispersal and Age at First Reproduction

If dispersing females opted to disperse into particular groups based on their assessments of habitat quality, we might have expected to see evidence of these differences in female age at first reproduction (AFR). Mean (± sd) AFR for the 18 (of 43; excludes NK-N) females for which both the mother's and the offspring's birthdates were known to within ± 15 days was 9.27 ± 1.16 years (median = 9.00 years, minimum–maximum = 7.25–11.98 years). All but one of these females was born in the Matão group; two were females that remained to reproduce in their natal Matão group. Excluding these two females, ten of the females had dispersed during the study period and six had dispersed prior to this study period. Although AFR appeared to be earlier for females that immigrated into and reproduced in the M2 and Matão groups, there were no significant differences in AFR for females that dispersed into different reproductive groups in this sample (Kruskal–Wallis $K = 4.78$, $df = 3$, $p > 0.05$) or for females that dispersed during or prior to the present study period ($MWU = 1.0$, $N_1 = 10$, $N_2 = 6$, $p > 0.05$). Thus, although our sample size is small, there is no evidence at present that a female's choice of reproductive group affects the onset of her reproductive career.

Demographic Consequences of Dispersal

Only one group (Nadir) experienced a net gain of +5 females through immigration; the other groups had net losses ranging from −2 females (Matão), to −3 females (M2), to −6 females (Jaó). These losses result from the dispersal of six (14 %) of the 44 females into an adjacent patch of forest fragments outside of the reserve. Two of these females were observed in association with one or more non-natal groups prior to dispersing into the fragments; the other four females were initially recorded as having disappeared from their natal groups; they were next seen during opportunistic censuses of the fragments, from 0.69 to 1.85 years after their last sighting in the reserve (see Fig. 1.3 and Table 1.1; updated from Tabacow et al. 2009a).

One of these females (THA-M2) followed her older maternal sister (TP-M2), who had previously emigrated with another female from her natal cohort (EE-M2) with whom she was ultimately seen in the fragments. The other three females (NK-N, MC, and FELC) apparently opted to colonize the fragments instead of joining any of the established mixed-sex groups living within the reserve.

These six females emigrated from their natal groups between December 2007 and March 2011, during which time ten other females that had survived to dispersal age from the same natal groups succeeded in immigrating into other groups in the Reserve. Indeed, three of these ten females (30 %) had already given birth to their first offspring by April 2012, in contrast to only one of the six (16.67 %) females that had dispersed into the forest fragments during the same period.

This female, NK-N, was seen in her natal group (Nadir) on 8 February 2009 and then next seen in the Matão group from 27 February 2009 to 1 March 2009. She was resighted in her natal group on 17 April 2009, but then missing until 23 July 2009, when she was seen in the forest fragments. She was still in the forest fragment on 2 October 2009; but she returned to the Reserve and was observed traveling with her natal group in November 2009, and by early January 2010, she was traveling with the Matão group. In early February 2010, she copulated with at least one Matão male; she was last seen in the Matão group on 16 February 2010. Female NK-N had been born in the Jaó group between 1 October 2002 and 29 November 2002 and was thus a dependent infant whose mother moved into the newly formed Nadir group soon after she was born (Tokuda et al. 2014). During a census on 1 April 2012, NK-N was resighted in the fragments carrying an infant estimated to be approximately 1½ years old (Tabacow, Pers. Comm.). Considering the 7.2-month gestation length for females in this population (Strier and Ziegler 1997), it is probable that NK-N had conceived during her visit to the Matão group in early 2010. This would make her younger (approximately 8 years) at her first reproduction than the median age at female first reproduction recorded for other females in this population during the same study period. It also illustrates the potential of dispersing females to colonize unpopulated forests, as discussed below.

Conservation Implications and Caveats

Our population-wide monitoring of northern muriqui female dispersal patterns over more than a decade reveals surprisingly little intergroup variation in female age at dispersal or at first reproduction. Indeed, both the slight (but not statistically significant) tendency of females to disperse later from the Matão group and begin reproducing earlier in the Matão group can be most parsimoniously attributed to our more intensive, near daily monitoring of this group and therefore to the greater accuracy of records for this group. Females in the other groups are monitored for roughly 1-week at up to 3-week intervals, and failure to locate a female in any particular month would increase the possible error around both her last sighting versus real dispersal date and her first sighting with a new infant and thus her AFR.

These potential sources of bias, together with the more than twofold difference between the size of the smallest (M2) and largest (Matão) groups, make the consistency in female dispersal age a potentially valuable guideline for future management programs involving the translocation of females. It also highlights the need for developing reliable physical criteria by which the ages of female muriquis can be accurately assessed (Strier et al. unpublished data).

Habitat fragmentation has resulted in the isolation of small groups of muriquis across what is considered to be a metapopulation of muriquis in Santa Maria de Jetibá, Espírito Santo. The pasture and farmland that separate the forest fragments represent dispersal barriers for females, who sometimes leave their natal group but remain as solitary adults within the same forest fragment as their natal groups (Mendes et al. 2005). Previously, one of us (SLM) led an effort to evaluate the effectiveness of translocation as a management tactic for these females. A young female estimated to be about 6 years old (and thus close in age to the average dispersal ages known from the Caratinga muriquis) was targeted for translocation while she was still in her natal group. In October 2005, the female was successfully captured and transported to another isolated forest fragment about 10 km away, where she was released near another muriqui group that was being monitored. Initially, the translocated female was harassed by the adult females in the new group when she approached them, similar to what has previously been described for new female immigrants in the Caratinga population (Strier 1999). However, 20 days after the translocation, this aggression ceased and the female began to interact peacefully with her new group. In 2008, 3 years after her translocation, the female had her first parturition, but the infant disappeared about 1 year later and is presumed to have died. However, in 2011, the female gave birth to a second infant that was still alive as of July 2013.

The strong seasonal avoidance of any dispersal events during the peak dry, winter season months (June–August) also emerged as a consistent pattern across groups. Whether it reflects the shorter period of daylight with reduced activity during these months (Strier 1987), shorter day ranges or shifts in subgroup size (Dias and Strier 2003), or the lower rates of intergroup interactions that typically occur during these months (Strier, unpublished data), is not clear. Nonetheless, distinguishing between these possible explanations for seasonality in female dispersal patterns has potentially important implications for translocations in which solitary females were captured and then released into established areas where they subsequently succeeded in reproducing (Mendes et al. 2005, unpublished data; Barros et al. 2011). If females avoid dispersal during the peak dry months because of limited opportunities such as lack of intergroup encounters, then there might not be any risks to planning future translocations during peak dry season months. However, if seasonal dispersal reflects avoidance of social, ecological, or energetically stressful times, then translocations might be more securely implemented at times other than the peak dry months, as has so far proven to be the case with the successful translocations conducted elsewhere.

There were no obvious criteria with which to predict or interpret the variation in female dispersal patterns or in their choice of which group to ultimately join. Preliminary behavioral analyses show no evidence that female–female associations in their reproductive groups are biased in favor of either familiar individuals from their natal groups or females known to be maternal kin. However, further analyses may provide more insights into how their social relationships develop over time. Whether these social preferences affect female survival or reproductive success is unclear, especially considering the lack of variation in female muriqui AFR across groups and over the decades during which this population has been monitored (Strier 2014).

The transfer of 14 % of dispersing females over the past decade into the otherwise empty fragments outside the reserve is consistent with other indications of habitat saturation inside the reserve (e.g., Tabacow et al. 2009b; Strier and Ives 2012). The colonization of these fragments may be advantageous in terms of supporting ongoing efforts to increase the available habitat for muriquis by establishing protected corridors (Tabacow et al. 2009a). However, at present and until these fragments can be secured, they represent a “sink” (sensu Pulliam 1988) for females dispersing from this population because of the absence of mature males and, thus, breeding opportunities, available to the females that have moved there. Establishing corridors into these fragments and protecting them is now an even more urgent conservation management priority.

Combining our long-term knowledge of population demography and individual life histories with ongoing analyses of dispersal patterns can extend our ability to develop informed conservation management plans, not only for our study population but also for muriquis living under different conditions elsewhere (Strier, and Ives 2012; Strier 2014). Extrapolating from the consistent patterns we found in female dispersal age over time (Strier and Mendes 2012) and across groups (this study) and in the seasonal distribution of dispersal events in our population to other muriqui populations can help insure that there will be females of this species to disperse in the future.

Conclusion

Similar to other atelins, female northern muriquis (*Brachyteles hypoxanthus*) typically disperse from their natal groups. This discovery has played an important role in conservation management programs involving translocations for this critically endangered species. However, information about variation in age at dispersal or about how social, reproductive, and ecological conditions might affect female muriqui dispersal decisions and age at first reproduction has been limited, in part due to the length of time required to accumulate individual-based data on long-lived females that mature and reproduce slowly. Although data on female dispersal and life history from our main study group at the Reserva Particular do Patrimônio Natural – Feliciano Miguel Abdala (RPPN-FMA) in Caratinga, Minas Gerais, Brazil over a 30-year period have been presented elsewhere (Strier 2005, 2014; Strier and Mendes 2009, 2012), the data presented here on female dispersal patterns across the entire population of four muriqui groups at our study site over a 10-year period from April 2002 through July 2012 are unique. During this period, a total of 44 females dispersed from their natal groups at mean (± sd) age of 5.73 ± 0.50 year (median = 5.72 years). Dispersal was strongly seasonal, with no emigrations occurring during the peak dry season months, from June to August. At least 12 females visited one or more groups before ultimately dispersing; some females also returned to their natal groups during the dispersal process. However, as reported previously for this population (Strier 2008, 2014), no secondary dispersal after reproduction has occurred. We found no evidence that females associate preferentially in their reproductive groups with familiar or maternally related females. Moreover, six females (14 % of the dispersing females in this study period) left the reserve and were last sighted in adjacent forest fragments that did not support other muriqui groups. Median age at first reproduction was 9.00 years and did not vary significantly across groups. These unique data on the dispersal patterns of all females in the four groups that comprise one of the largest populations of northern muriquis emphasize the range of social, reproductive, and ecological factors that may affect female dispersal patterns and that should be considered in conservation management programs for this and other critically endangered species.

Acknowledgments KBS thanks Drs. T. Furuichi and J. Yamagiwa for their invitation to participate in the symposium on female dispersal they organized at the International Primatological Society Meetings in Cancun, Mexico, in August 2012, where most of the data described in this paper were presented. We also thank CNPq and the Abdalla family for the permission to conduct research at the RPPN-FMA and Preserve Muriqui and CI-Brasil for logistical support in the field. The field study has been supported by a variety of sources, including the National Science

Foundation (BNS 8305322, BCS 8619442, BCS 8958298, BCS 9414129, BCS 0621788, and BCS 0921013), the National Geographic Society, the Liz Claiborne and Art Ortenberg Foundation, the Fulbright Foundation, the Sigma Xi Grants-in-Aid, Grant #213 from the Joseph Henry Fund of the NAS, the World Wildlife Fund, the L.S.B. Leakey Foundation, the Chicago Zoological Society, the Lincoln Park Zoo Neotropic Fund, the Center for Research on Endangered Species (CRES), the Rufford Foundation, the Margot Marsh Biodiversity Foundation, Conservation International, the University of Wisconsin–Madison, CNPq – Brazilian National Research Council, Fundação de Amparo à Pesquisa do Espírito Santo – FAPES, and the Primate Action Fund – CI. This research has complied with all US and Brazilian regulations. We thank the many people who have contributed to the long-term demographic data records from 1983 to 2012 (in alphabetical order): L. Arnedo, M.L. Assunção, N. Bejar, J.P. Boubli, P.S. Campos, T. Cardoso, A. Carvalho, D. Carvalho, C. Cäsar, A.Z. Coli, C.G. Costa, P. Coutinho, L. Dib, Leonardo G. Dias, Luiz. G. Dias, D.S. Ferraz, A. Ferreira, F. Fernandez, J. Fidelis, A.R.G. Freire Filho, J. Gomes, D. Guedes, V.O. Guimarães, R. Hack, M.F. Iurck, M. Kaizer, M. Lima, M. Maciel, I.I. Martins, W.P. Martins, F.D.C. Mendes, I.M. Mourthé, F. Neri, M. Nery, S. Neto, C.P. Nogueria, A. Odalia Rímoli, A. Oliva, L. Oliveira, F.P. Paim, R.C. Printes, J. Rímoli, S.S. Rocha, R.C. Romanini, R.R. dos Santos, M. Schultz, B.G.M. da Silva, J.C. da Silva, A.B. Siqueira de Morais, V. Souza, D.V. Slomp, F.P. Tabacow, W. Teixeira, M. Tokudo, K. Tolentino, and E.M. Veado. We thank Amanda Alves de Melo for technical assistance with the manuscript. We also thank the editors of this volume for their comments on an earlier version of this manuscript.

References

Arnedo LF, Mendes FDC, Strier KB (2010) Sex differences in vocal patterns in the northern muriqui (*Brachyteles hypoxanthus*). Am J Primatol 72:122–128

Aureli F, Schaffner CM, Boesch C, Bearder SK, Call J, Chapman CA, Connor R, Di Fiore A, Dunbar RIM. Henzi SP, Holekamp K, Korstjens AH, Layton R, Lee P, Lehmann J, Manson J.H, Ramos-Fernandez G, Strier KB, van Schaik CP (2008) Fission-fusion dynamics: new research frameworks. Curr Anthropol 49:627–654

Barros JBG, da Rocha Vilela DA, de Melo FR (2011) Parâmetros fisiológicos, hematológicos e morfométricos de exemplar de muriqui-do-norte (*Brachyteles hypoxanthus*) submetido à captura e contenção química para fins de translocação em Minas Gerais. In: Melo FR, Mourthé I (eds) A Primatologia no Brasil, vol 11, Sociedade Brasileira de Primatologia. MG, Belo Horizonte, pp 175–186

Bradley BJ, Doran-Sheehy DM, Vigilant L (2007) Potential for female kin associations in wild western gorillas despite female dispersal. Proc R Soc B 274:2179–2185

Di Fiore A, Rendall D (1994) Evolution of social organization: A reappraisal for primates by using phylogenetic methods. Proc Natl Acad Sci U S A 91:9941–9945

Dias LG, Strier KB (2003) Effects of group size on ranging patterns in *Brachyteles arachnoides hypoxanthus*. Int J Primatol 24:209–221

Dixson AF (2012) Primate sexuality: comparative studies of the prosimians, monkeys, apes, and humans. Oxford University Press, Oxford

Isbell L, Young TP (2002) Ecological models of female social relationships in primates: similarities, disparities, and some directions for future clarity. Behaviour 139:177–202

Langergraber K, Mitani J, Vigilant L (2009) Kinship and social bonds in female chimpanzees (*Pan troglodytes*). Am J Primatol 71:840–851

Lee PC, Kappeler PM (2003) Socioecological correlates of phenotypic plasticity of primate life histories. In: Kappeler PM, Pereira ME (eds) Primate life histories and socioecology. Cambridge University Press, Cambridge, pp 41–65

Lehmann J, Boesch C (2009) Sociality of the dispersing sex: the nature of social bonds in Western African female chimpanzees, *Pan troglodytes*. Anim Behav 77:377–387

Lemos de Sá RM, Glander KE (1993) Capture techniques and morphometrics for the woolly spider monkey, or muriqui (*Brachyteles arachnoides* E. Geoffroy 1806). Am J Primatol 29:145–153

Martin P, Bateson P (1986) Measuring behavior. Cambridge University Press, New York

Mendes SL, Santos RR, Carmo, LR (2005) Conserving the northern muriqui in Santa Maria de Jetiba, Espirito Santo. Neotrop Primates 13(Suppl):31–35

Mendes SL, de Oliveira MM, Mittermeier RA, Rylands AB (2008) *Brachyteles hypoxanthus*. In: IUCN 2013. IUCN red list of threatened species. Version 2013.1. www.iucnredlist.org. Downloaded 2 Sept 2013

Moore J (1984) Female transfer in primates. Int J Primatol 5:537–589

Possamai CB, Young RJ, Mendes SL, Strier KB (2007) Socio-sexual behavior of female northern muriquis (*Brachyteles hypoxanthus*). Am J Primatol 69:766–776

Printes RC, Strier KB (1999) Behavioral correlates of dispersal in female muriquis (*Brachyteles arachnoides*). Int J Primatol 20:941–960

Pulliam HR (1988) Sources, sinks, and population regulation. Am Nat 132(5):652–661

Rosenberger AL, Strier KB (1989) Adaptive radiation in the ateline primates. J Hum Evol 18:717–750

Sterck EHM, Watts DP, van Schaik CP (1997) The evolution of female social relationships in nonhuman primates. Behav Ecol Sociobiol 41:291–309

Strier KB (1987) Activity budgets of woolly spider monkeys, or muriquis (*Brachyteles arachnoides*). Am J Primatol 13:385–395

Strier KB (1990) New World primate, new frontiers: insights from the woolly spider monkey, or muriqui (*Brachyteles arachnoides*). Int J Primatol 11:7–9

Strier KB (1991) Diet in one group of woolly spider monkeys, or muriquis (*Brachyteles arachnoides*). Am J Primatol 23:113–126

Strier KB (1993) Growing up in a patrifocal society: sex differences in the spatial relations of immature muriquis (*Brachyteles arachnoides*). In: Pereira ME, Fairbanks LA (eds) Juveniles primates: life history, development and behavior. Oxford University Press, New York, pp 138–147

Strier KB (1994) Myth of the typical primate. Yearb Phys Anthropol 37:233–271

Strier KB (1996) Reproductive ecology of female muriquis. In: Norconk M, Rosenberger A, Garber P (eds) Adaptive radiations of New World primates. Plenum Press, New York, pp 511–532

Strier KB (1997) Mate preferences of wild muriqui monkeys (*Brachyteles arachnoides*): reproductive and social correlates. Folia Primatol 68:120–133

Strier KB (1999) Faces in the forest: the endangered muriqui monkeys of Brazil. Harvard University Press, Cambridge, MA

Strier KB (2004) Sociality among kin and nonkin in nonhuman primate groups. In: Sussman RW, Chapman AR (eds) The nature and evolution of sociality. Aldine de Gruyter, New York, pp 191–214

Strier KB (2005) Reproductive biology and conservation of muriquis. Neotrop Primates 13(Suppl):41–47

Strier KB (2008) The effects of kin on primate life histories. Annu Rev Anthropol 37:21–36

Strier KB (2011) Social plasticity and demographic variation in primates. In: Sussman RW, Cloninger CR (eds) The origins and nature of cooperation and altruism in non-human and human primates. Springer, New York, pp 179–192

Strier KB (2014) Northern muriqui monkeys: behavior, demography, and conservation. In: Yamagiwa J, Karczmarski L (eds) Primates and cetaceans: field studies and conservation of complex mammalian societies. Springer, New York, pp 233–247

Strier KB, Boubli JP (2006) A history of long-term research and conservation of northern muriquis (*Brachyteles hypoxanthus*) at the Estação Biológica de Caratinga/RPPN-FMA. Primate Conserv 20:53–63

Strier KB, Ives AR (2012) Unexpected demography in the recovery of an endangered primate population. PLoS One 7(9):e44407

Strier KB, Mendes SL (2009) Long-term field studies of South American Primates. In: Garber PA, Estrada A, Bicca-Marques JC, Heymann EW, Strier KB (eds) South American primates: comparative perspectives in the study of behavior, ecology, and conservation. Springer, New York, pp 129–155

Strier KB, Mendes SL (2012) The northern muriqui (*Brachyteles hypoxanthus*): lessons on behavioral plasticity and population dynamics from a critically endangered primate. In: Kappeler P, Watts D (eds) Long-term studies of primates. Springer, Heidelberg, pp 125–140

Strier KB, Ziegler TE (1997) Behavioral and endocrine characteristics of the reproductive cycle in wild muriqui monkeys, *Brachyteles arachnoides*. Am J Primatol 42:299–310

Strier KB, Ziegler TE (2000) Lack of pubertal influences on female dispersal in muriqui monkeys, Brachyteles arachnoides. Anim Behav 59(4):849–860

Strier KB, Mendes FDC, Rímoli J, Odalia Rímoli A (1993) Demography and social structure in one group of muriquis (*Brachyteles arachnoides*). Int J Primatol 14:513–526

Strier KB, Mendes SL, Santos RR (2001) Timing in births in sympatric brown howler monkeys (*Alouatta fusca clamitans*) and northern muriquis (*Brachyteles arachnoides hypoxanthus*). Am J Primatol 55:87–100

Strier KB, Dib LT, Figueira JEC (2002) Social dynamics of male muriquis (*Brachyteles arachnoides hypoxanthus*). Behaviour 139:315–342

Strier KB, Lynch JW, Ziegler TE (2003) Hormonal changes during the mating and conception seasons of wild northern muriquis (*Brachyteles arachnoides hypoxanthus*). Am J Primatol 61:85–99

Strier KB, Boubli JP, Possamai CB, Mendes SL (2006) Population demography of northern muriquis (*Brachyteles hypoxanthus*) at the Estação Biológica de Caratinga/Reserva Particular do Patrimônio Natural-Feliciano Miguel Abdala, Minas Gerais, Brazil. Am J Phys Anthropol 130(2):227–237

Strier KB, Altmann J, Brockman DK, Bronikowski A, Cords M, Fedigan LM, Lapp H, Liu X, Morris WF, Pusey AE, Stoinski TS, Alberts SC (2010) The primate life history database: a unique shared ecological data resource. Methods Ecol Evol 1:199–210

Strier KB, Chaves PB, Mendes SL, Fagundes V, Di Fiore A (2011) Low paternity skew and the influence of maternal kin in an egalitarian, patrilocal primate. Proc Natl Acad Sci U S A 108:18915–18919

Tabacow FP, Possamai CB, de Melo FR, Mendes SL, Strier KB (2009a) New sightings of northern muriqui (*Brachyteles hypoxanthus*) females in forest fragments surrounding the Estação Biológica de Caratinga- RPPN Feliciano Miguel Abdala, Minas Gerais, Brasil. Neotrop Primates 16:67–69

Tabacow FP, Mendes SL, Strier KB (2009b) Spread of a terrestrial tradition in an arboreal primate. Am Anthropol 111:238–249

Talebi MG, Beltrao-Mendes R, Lee PC (2009) Intra-community coalitionary lethal attack of an adult male southern muriqui (*Brachyteles arachnoides*). Am J Primatol 71:860–867

Tokuda M, Boubli JP, Izar P, Strier KB (2012) Social cliques in male northern muriquis (*Brachyteles hypoxanthus*). Curr Zool 58:342–352

Tokuda M, Boubli JP, Mourthé I, Izar P, Possamai CB, Strier KB (2014) Males follow females during fissioning of a group of northern muriquis. Am J Primatol 76:529–538. doi:10.1002/ajp.22244

Wrangham RW (1980) An ecological model of female-bonded primate groups. Behaviour 75:262–299

Chapter 2
Association Networks and Life History of Female Spider Monkeys

Yukiko Shimooka

Introduction

Four species of spider monkey (*Ateles geoffroyi*, *A. paniscus*, *A. belzebuth*, and *A. hybridus*) are distributed in Central and South America (Collins 2008). All spider monkey species share various characteristics with chimpanzees and bonobos, such as a dispersal regime characterized by male philopatry and female dispersal (Symington 1988; Strier 1994; Di Fiore and Campbell 2007; Shimooka et al. 2008). A recent genetic analysis of a large group of *A. belzebuth* – in which adult males were more related to each other than were adult females – confirms that, under natural demographic conditions, males are related and philopatric while females disperse into other groups (Di Fiore et al. 2009). There is one exceptional report of a group of *A. geoffroyi* wherein there were two separate cases of male immigrations. These resulted in take-over and concomitant disappearance of resident males (Aureli et al. 2013), demonstrating that male immigration may occur under certain demographic circumstances.

Another characteristic shared with chimpanzees and bonobos is that spider monkeys live in social communities with a relatively high degree of fission–fusion dynamics, in which group members are rarely all together and frequently split and merge into fluid subgroups (Klein 1972; Cant 1977; Symington 1990; Chapman 1990; Di Fiore and Campbell 2007; Asensio et al. 2008). Such a social characteristic influences the opportunities for group members to interact with one another, which in turn has an impact upon social relationships (Aureli et al. 2008). These fission–fusion dynamics are also suggested to regulate intragroup scramble

---

Y. Shimooka (✉)
Faculty of Life and Environmental Sciences, Teikyo University of Science, 2828 Yatsusawa, Uenohara, Yamanashi, Japan
e-mail: shimooka@ntu.ac.jp

T. Furuichi et al. (eds.), *Dispersing Primate Females*,
Primatology Monographs, DOI 10.1007/978-4-431-55480-6_2

and contest competition for feeding on fruit, via the relationship between party size and habitat-wide food availability (Chapman et al. 1995; Asensio et al. 2008, 2009).

Spider monkeys are described as living in sex-segregated communities, in which females are reported to be "less social" and males are reported to be "social" and "gregarious" (Fedigan and Baxter 1984). Female spider monkeys have been observed frequently traveling alone or in small subgroups with only their offspring (*A. paniscus*: van Roosmalen and Klein 1988; *A. geoffroyi*: Chapman 1990; Fedigan and Baxter 1984), although in *A. belzebuth*, females were found in larger subgroups than males when fruit was abundant (Shimooka 2003). Hartwell et al. (2014) has examined temporal pattern of sexual segregation of *A. geoffroyi yucatanensis* at Runaway Creek Nature Reserve in Belize using a test that distinguishes sexual segregation from aggregation and random association between the sexes and found that spider monkeys' subgroups were significantly sexually segregated in 15 of the 23 months and were more likely to segregate when food availability was high.

Recently, social network theory (see review by Newman 2003) has been increasingly applied to the analysis of social structure of animals (Lusseau and Newman 2004; Croft et al. 2004; Henzi and Lusseau 2009; Krause et al. 2009). In spider monkeys, Ramos-Fernández et al. (2009) analyzed annual social networks from 6 years of study and revealed that female–female association indices are higher but less selective than male–male association indices. Females formed tightly linked clusters that were stable over time with the exceptions of immigrant females, who showed little association. Centrality, a measure of how strongly linked an individual is to other strongly linked individuals, was higher for females than for males. Ramos-Fernández et al. (2009) also showed that strength of association for females, defined as the sum of all association indices for each individual in the network, was also higher than that of males and over the years is more equally distributed among them.

Until now, studies on association pattern have been conducted on an annual basis (Klein 1972; Fedigan and Baxter 1984; Chapman 1990; Ramos-Fernández et al. 2009). However, the patterns of fission–fusion dynamics change seasonally (Shimooka 2003), and the reproductive status of a female can change within a year from cycling to pregnant or from pregnant to lactating, which may affect the pattern of their association. In chimpanzees, for example, reproductive status has been demonstrated to affect patterns of association: the number of estrous females influences party size (Hashimoto 2001), and estrous females are more gregarious than anestrous females (Pepper et al. 1999). Analysis restricted to an annual basis might bury such a variation in association patterns. Here, I focus on short-term association patterns in periods of 2–3 months and examine its variation through Association Network Analysis (Newman 2003; Lusseau and Newman 2004).

Observations and Analyses

The subjects are wild long-haired spider monkeys (*Ateles belzebuth belzebuth*) at La Macarena, Colombia. The Centro de Investigaciones Ecológicas La Macarena (CIEM) study site is in Tinigua National Park (Izawa and Mizuno 1977) on the right

Fig. 2.1 View of Duda River from a ridge in Centro de Investigaciones Ecológicas La Macarena, Tinigua National Park, Meta, Colombia

bank of the lower Duda River (2°40 N, 74°10 W, 350 m asl.). Many channels and wide, low gradient ridges characterize the terrain (Fig. 2.1). Annual rainfall ranges from 2,200 to 2,900 mm (Kimura et al. 1994), and there are distinct rainy and dry seasons. The dry season normally lasts for 3 months (late December–early March), when monthly rainfall is less than 100 mm.

At CIEM, Dr. Kosei Izawa and several Japanese and Colombian researchers including myself have conducted a 6-year study from 1997 on three groups of spider monkeys around the research station (Shimooka 2005). The monkeys were well habituated and individually identified (Fig. 2.2). This study features the research conducted in three periods within 20 months: Period 1, February–March 2000; Period 2, September–November 2000; and Period 3, August–October 2001. This study focused on MB-2 group, consisting of 28–30 animals including 16–18 adults and subadults (Table 2.1). During the research period, two adult females disappeared from MB-2 group, and there were no new immigrants.

During this study, I analyzed only adults and subadults that were independent from others. I used data from party follows when I observed them for more than 30 min continuously (Fig. 2.3). Observation was conducted for 185–237 h in each period (Table 2.1). In all periods, I recorded every fission and fusion event when I detected it. Based on those records, I determined the party membership of every

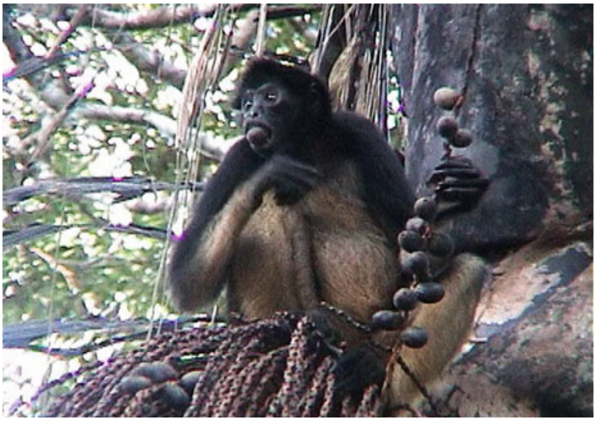


Fig. 2.2 Adult female Rico (F7) eating fruits while sitting on a fruit bunch of palm *Oenocarpus bataua*

Table 2.1 Group composition of MB-2 group

Age class	Sex	Number of individuals		
		Period 1	Period 2	Period 3
Adult	Male	5	5	5
	Female	11	11	10
Subadult	Male	2	2	2
	Female	0	0	0
Juvenile	Male	0	0	1
	Female	3	3	3
Infant	Male	2	4	2
	Female	5	5	7
Total number of individuals		28	30	30

15 min and used those data for analysis (see Shimooka 2003 for the details of observation method and definition of party). Party size varied among periods, mean party size was largest in Period 1 and smallest in Period 3 (Fig. 2.4).

Female reproductive status changes over time. Thus, the reproductive status of each female was estimated in each period based on birth records and observation of copulation and categorized into five status: pregnant, lactating, cycling, possible cycling, and young immigrants (Table 2.2).

Pregnant: As the gestation length in spider monkeys is 7–7.5 months (Eisenberg 1973; Milton 1981; Nunes and Chapman 1997), a female was categorized as pregnant for 7.5 months before giving birth. Three females were estimated as already pregnant at the beginning of Period 1 and gave birth to an infant between Periods 1 and 2 or at the beginning of Period 2.

Lactating: Although there seems to be variation in the age of weaning in *A. geoffroyi* (Vick 2008), most offspring of *A. belzebuth chamek* at Cocha Cashu are weaned by the age of two years (Symington 1987). Thus, here a female who has an infant or juvenile less than 2 years old was categorized as lactating.

Fig. 2.3 A party of spider monkeys resting on tree branch. An adult male Ogi (M5, *left*) and two adult females and a juvenile (*right*)

Cycling: Females confirmed to be not pregnant who copulated during the study period, or who had a juvenile older than 2 years of age, were categorized as cycling.

Young Immigrant: Age at emigration in spider monkeys was observed to be between 4.9 and 6.3 years in eight females of *A. geoffroyi* (Vick 2008), and in other studies, it is estimated as 4–5 years (Fedigan and Baxter 1984; Symington 1987; Shimooka et al. 2008). When a young nulliparous female was first observed in January of 2000, her body size was slightly larger than the 4–5 years resident female juvenile. It was not clear exactly when she immigrated from other group, but from her body size, she was estimated to have immigrated into this group recently. In Period 1, her reproductive status was unclear; thus, she was treated aside as a young immigrant.

Possible Cycling: Five females gave birth to an infant in early 1999 (with dates estimated from infant size and locomotion patterns in January of 2000). Those individuals born in 1999 could reach 2 years of age in Period 3, but reproductive status of these females in Period 3 was unclear because of lack of subsequent observation. These females were categorized as possible cycling. The immigrant female, who first gave birth in Period 3, was also categorized as possible cycling in Period 2, which is 9–11 months before giving birth.

Association indices (AI; Nishida 1968) between adults and subadults were calculated in each period based on scanning of party composition every 15 min. AI between individuals A and B was given by $R/(P+Q+R)$, where P is the number of parties containing only A, Q is the number of parties containing only B, and R is the number of parties containing both A and B.

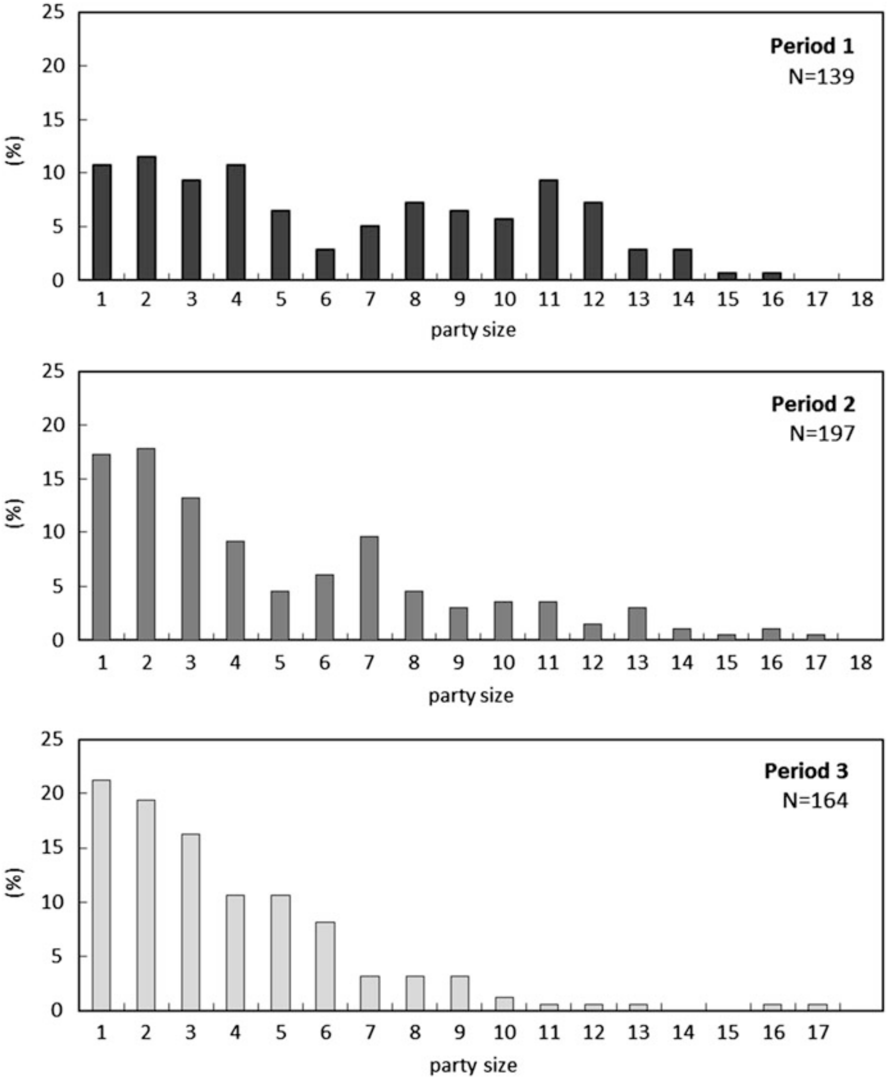


Fig. 2.4 Party size distribution in each period (edited from Shimooka 2003). Overall distribution of party size was significantly different between all periods (Kolmogorov–Smirnov two-sample test; Periods 1–2: $D_{139,197} = 0.21$, $P < 0.01$; Periods 1–3: $D_{139,164} = 0.35$, $P < 0.01$; Periods 2–3: $D_{197,164} = 0.19$, $P < 0.01$)

Social network was analyzed based on a matrix of association indices using NetDraw (Borgatti 2002) and UCINET 6.2. In social networks, nodes and ties represent individuals and association indices, respectively. The spring embedding algorithm with node reputation was used to layout the position of nodes using the "Gower scaling" starting positions (Borgatti 2002; Ramos-Fernández et al. 2009).

Table 2.2 Reproductive status and birth records of adult females and age category of males

			Reproductive status			
			Period 1	Period 2	Period 3	
ID	Sex	Name	Feb.–Mar. 2000	Sep.–Nov. 2000	Aug.–Oct. 2001	Record of birth/giving birth
F1	Female	Cinnamon	Lactating	Cycling	Lactating	1994–1995[a], Apr.–Jul. 1998, Jun.–Jul. 2001
F2	Female	Nawa	Lactating	–	–	Apr.–Jul. 1998
F3	Female	Futaba	Lactating	Lactating	Possible cycling	1995–1996[a], 1999
F4	Female	Hana	Pregnant	Lactating	Lactating	Early in 1996,[a] Jun.–Aug. 2000,[b] Aug. 2001
F5	Female	Popy	Lactating	Lactating	Possible cycling	1999
F6	Female	Quatro	Pregnant	Lactating	Lactating	Sep. 2000
F7	Female	Rico	Lactating	Lactating	Possible cycling	1999
F8	Female	Vina	Lactating	Lactating	Possible cycling	1999
F9	Female	Wild	Pregnant	Lactating	Lactating	1996 –1997[a], Sep. 2000
F10	Female	Sepa	Lactating	Lactating	–	1994–1995[a], Oct. 1998[b], 1999
F11	Female	Joya	Young immigrant	Possible cycling	Lactating	Aug. 2001
F12	Female	Mask	–	Lactating	cycling	Oct. 2001
M1	Male	Black	Adult	Adult	Adult	Unknown
M2	Male	Delta	Adult	Adult	Adult	Unknown
M3	Male	G	Adult	Adult	Adult	Unknown
M4	Male	Kakeru	Adult	Adult	Adult	Unknown
M5	Male	Ogi	Adult	Adult	Adult	Unknown
M6	Male	Comino	Subadult	Subadult	Subadult	Born in 1994–1995, son of F1
M7	Male	Zero	Subadult	Subadult	Subadult	Born in 1995, son of F3

Nawa and Sepa disappeared from the group in the course of study. Mask was rarely observed in Period 1; thus it was deleted from the analysis. Ages of two subadult males M6 and M7 were estimated from their body size in 1997. They were observed in the same subgroups with the mother only occasionally in Periods 2–3. F11, who immigrated to MB-2 in 1998, was treated as adult although she was still nulliparous in the end of the study in 2002.

[a] The female had an infant or juvenile when first identified, and the age of infant or juvenile was estimated.

[b] The infant died soon.

Eigenvector centrality and strength of association are metrics related to the structure of the network (Newman 2004). These two metrics were calculated in each period using UCINET 6.2, based on all association indices regardless of whether the value of association index was below or above the mean association index.

Strength of association is the sum of all association indices of an individual with all other group members; thus, it indicates the individual's degree of gregariousness. An individual with high strength may be associated with many other group members or have very high association indices with a few group members. Strength was calculated for each individual considering all associations or only those with a particular sex class. The mean strength was calculated by dividing the strength of each individual by the number of possible individuals to associate with in each period, as this number strongly affects the value of strength.

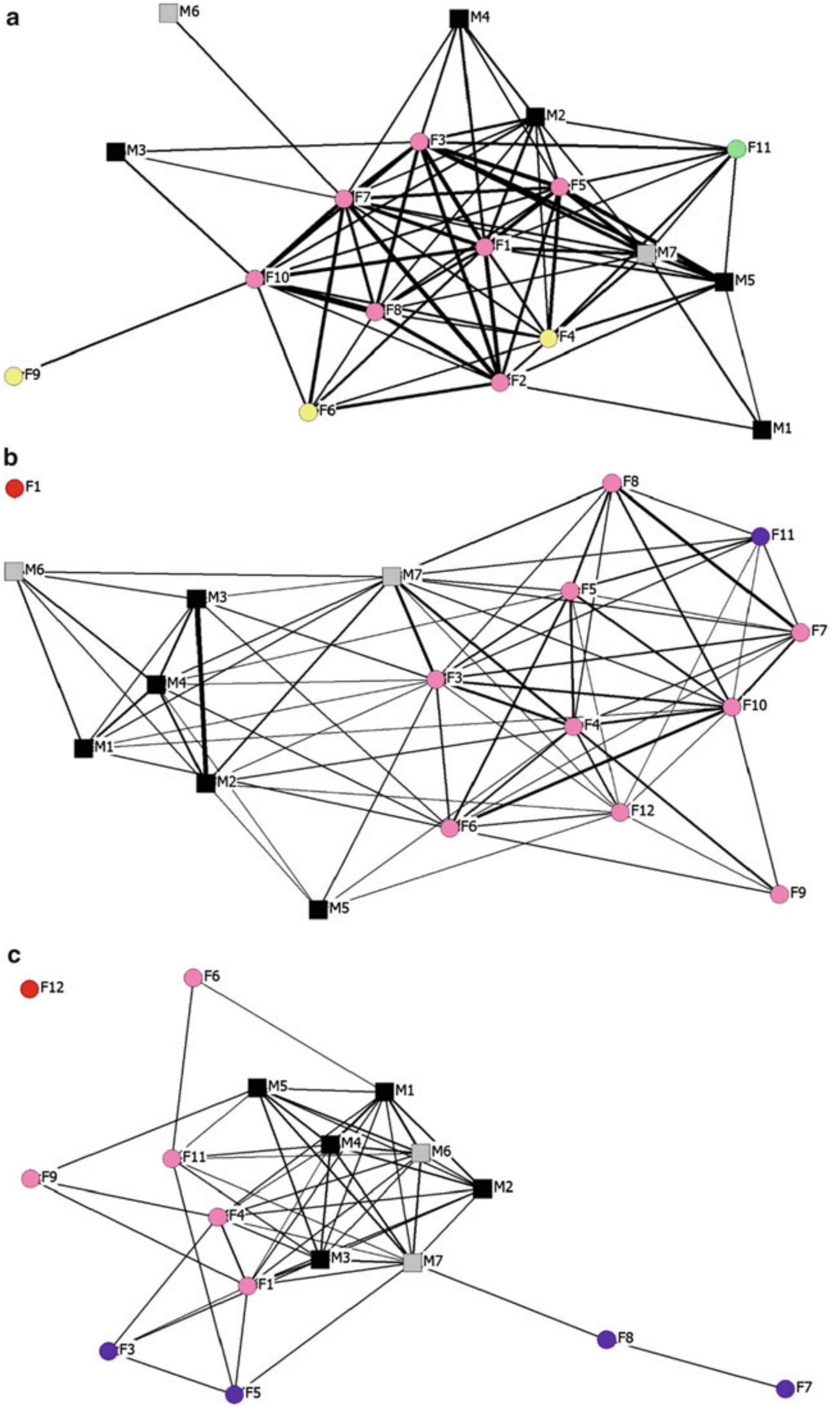
Eigenvector centrality is another index to measure how well connected an individual is within the network, which is mathematically the appropriate element of the first eigenvector of the matrix of association indices (Newman 2004). An individual can have high eigenvector centrality either because it has a high degree of strength of association or because it is connected to other individuals with a high degree of strength.

Difference in Social Networks Among Three Periods

Association networks for the three study periods are shown in Fig. 2.5. Although it is clear that there are same-sex preferences, there are also links between males and females in each period. The pattern changes dramatically among the three periods over 20 months. In Period 1, females are in the center of the network and connected to each other by thick bonds, whereas males are peripheral and connected to only a few individuals with narrow bonds. In Periods 2 and 3, males and females are placed apart; males are more gregarious in the network and connected by thicker bonds than females.

▶

Fig. 2.5 Diagrams of the association networks among the adults in each period. To clarify the presentation, only association indices higher than the mean in each period were presented as ties. The width of a tie between two nodes represents the value of association index between two individuals; thicker ties indicate the association indices were higher between the two individuals, and an individual, whose association indices with all other individuals were lower than the mean, is shown as a single node without any ties. Shape and color of nodes indicate sex or reproductive status of each individual. Black square, adult male; gray square, subadult male; pink circle, lactating female; yellow circle, pregnant female; red circle, cycling female; purple circle, possible-cycling female; green circle, young immigrant. (a) Period 1, (b) Period 2, (c) Period 3. Thicker ties indicate the association indices were high between the two individuals. An individual, whose association indices with all other individuals were lower than the mean, is described aside as a single node without any ties (F1 in (b) and F12 in (c))


a
M6
M4
M2
M3
F3
F11
F5
F7
F1
M7
F10
M5
F8
F4
F9
F2
F6
M1
b
F1
F8
F11
M6
M7
M3
F5
F7
M4
F3
F10
F4
M1
M2
F12
F6
F9
M5
c
F12
F6
M5
M1
M4
M6
F11
F9
M2
F4
M3
M7
F1
F8
F3
F5
F7

Width of bonds reflects the degree of strength, and strength is strongly affected by party size. Strength of each individual changed among the three periods, in all combination of sex classes: males or females with all associations or with only individuals of the same sex (Fig. 2.6). In Fig. 2.6, except for male–male strength (Fig. 2.6c), values of strength were highest in Period 1 when party size was largest and lowest in Period 3 when party size was smallest, which can be explained by largest party size in Period 1 when food availability was estimated highest and smallest party size in Period 3 when food availability was estimated lowest (Shimooka 2003). Male–male strength values, however, are contrary to these results: values were highest in Period 3 and lowest in Period 1 (Fig. 2.6c). This result indicates that males do not gather with each other simply for food gain but also for social reasons such as patrols of territory boundaries and searching for estrous females. Values of strength are relatively equally distributed among males (Fig. 2.6d), whereas those of females are quite variable among individuals (Fig. 2.6f). Strength of some females changed dramatically across periods. As reproductive status and length of residence in the group of each individual changes in each period, these factors are examined carefully below.

Values of eigenvector centrality also varied among periods, sex, and reproductive status of females. In Period 1, females showed higher centrality than males ($p < 0.05$, $U_{6,10} = 14.0$ Mann–Whitney U-test); in Period 2, there were no differences between them ($p = 0.29$, $U_{6,11} = 29.0$); and in Period 3, males showed higher centrality than females ($p < 0.001$, $U_{6,9} = 0.0$).

All males showed similar patterns through periods. Values were significantly higher in Period 3 (average = 0.31 ± 0.02) than in Period 1 (average = 0.20 ± 0.03, $p < 0.05$, $Z = 2.37$, Wilcoxon signed-rank test) and Period 2 (average = 0.21 ± 0.03, $p < 0.05$, $Z = 2.37$). By contrast, values of female centrality were higher in Period 1 (average = 0.24 ± 0.06, $p < 0.05$, $Z = 2.37$) and Period 2 (average = 0.22 ± 0.06, but not significant) than in Period 3 (average = 0.19 ± 0.04).

These results are generally consistent with those reported by Ramos-Fernández et al. (2009), which showed the transition of association networks of *A. geoffroyi* on a yearly basis for 8 years. Both studies show that female spider monkeys form tightly linked clusters, with the exception of immigrant females who show little association with any adult in the group. Individual variability in both strength of association and eigenvector centrality, however, is larger among females than among males in this study, whereas it is larger among males than among females in the work of Ramos-Fernández et al. (2009). This difference is probably driven by the length of period analyzed in each study: analysis on an annual basis will wash out the variation of association patterns in females that change over shorter periods of time.

Position of Females with Respect to Their Reproductive Status

Reproductive status of females varied among individuals in each period, which largely affected their centrality. Although the number of individuals in each reproductive category was too small to conduct statistical analyses, when data in all

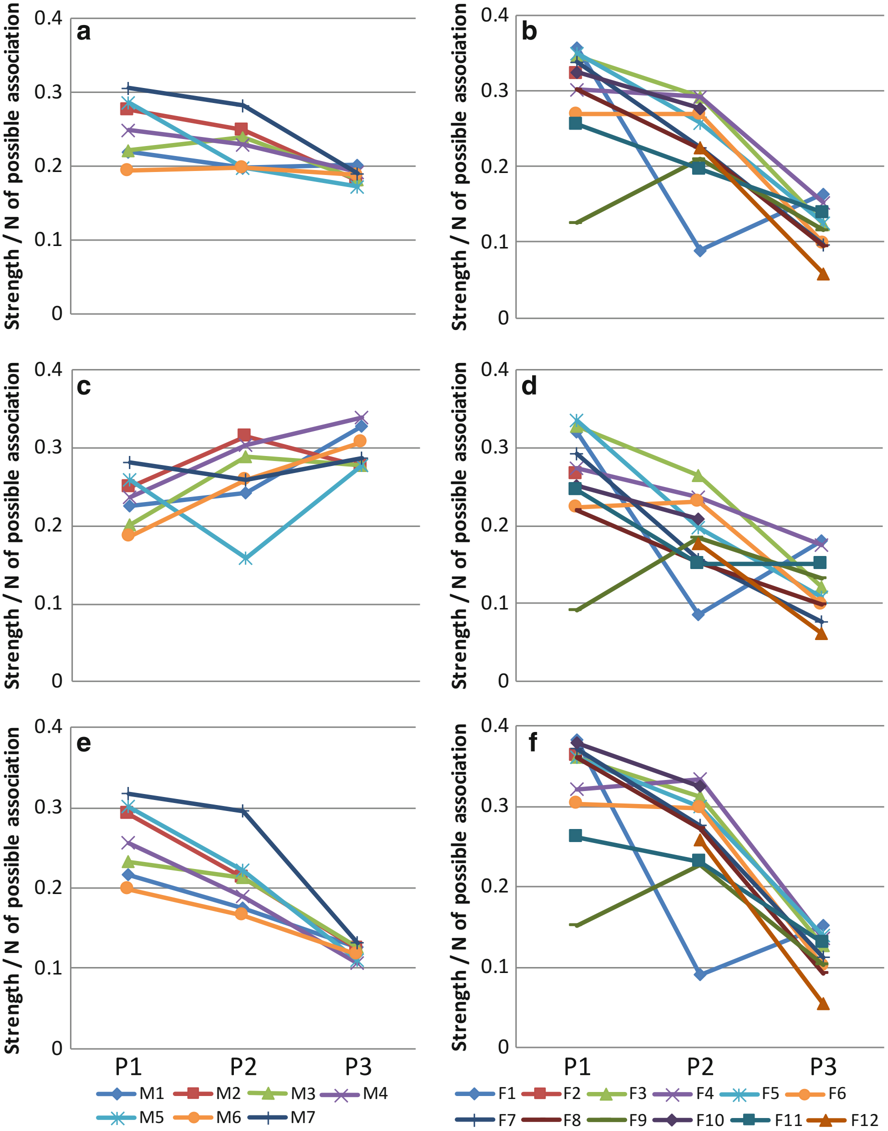


Fig. 2.6 Mean strength of association of each individual in each period. As the total number of individuals in one period differs among periods, the sum of all association indices for each individual in the network is divided by the number of individuals possible to associate with. (**a**) Male with all individuals, (**b**) female with all individuals, (**c**) male with male, (**d**) female with male, (**e**) male with female, (**f**) female with female

three periods were pooled, centrality was highest in lactating females (mean ± s.d. = 0.24 ± 0.04), followed by pregnant females (0.19 ± 0.07) and possible-cycling females (0.17 ± 0.03), and lowest in cycling females (0.08, $n = 2$).

Lactating females were always gregarious and often central in their networks (Fig. 2.5). Eigenvector centrality of lactating females was higher than that of other females when examined regardless of period ($p < 0.01$, $U_{21,\,11} = 24.0$ Mann–Whitney U-test). When all the females except for the reproductively inactive young immigrant were lactating or pregnant, lactating females were often together in one large party, which is shown qualitatively by their high strength in Period 1 (Fig. 2.5a).

Pregnant females were found only in Period 1. One of the three pregnant females, F9, was often found on the periphery and showed the lowest strength and eigenvector centrality. The other two pregnant females – F6 and F4 – were connected with others, but both values of strength and eigenvector centrality were lower than in lactating females. For pregnant females, traveling long distances by semi-brachiation with other females may be disadvantageous because of the high risk of falling or being involved in aggression, which may explain this relative lack of social association. Pregnant females have not been distinguished from others in preceding studies of spider monkey social networks, probably because pregnancy is not easily noted from visual observation: spider monkeys often look pregnant upon swallowing multiple fruits with large seeds, typically surprising researcher when females appear with a newborn infant.

Assuming that the nutritive demands of pregnant and lactating females are similar, the difference in their social networks suggests that the presence of dependent offspring is important in deciding association patterns. Avoidance of infanticide and predation may be possible factors. Although there are few observations of infanticide in spider monkeys, those reported indicate that victims are typically young males while aggressors are adult or subadult males (Gibson and Vick 2008; Shimooka, unpublished data). Previous reports also showed that spider monkey adults are preyed upon by jaguars and pumas (Matsuda and Izawa 2008), while juveniles and infants may also be preyed upon by crested eagles (Julliot 1994). Due to these potentially higher mortality risks, females with dependents may preferentially associate with other mothers to increase antipredator vigilance and predation dilution effects while also reducing the risk of infanticide by intragroup males. Whether or not such gregariousness in mothers decreases the risk of infanticide needs to be examined more closely through the behavior of mothers by investigating whether they associate more often with both other mothers and males or avoid association with males altogether. Another potential reason for the high gregariousness of lactating females may be the need for playmates and socialization opportunities for juveniles. Social and locomotor play may stimulate the development of motor abilities and may also give mothers the opportunity to concentrate on feeding or resting.

Cycling females were present only in Periods 2 and 3. Both F1 in Period 2 and F12 in Period 3 were not connected with any individual and stay completely outside of established social networks (Fig. 2.5b, c). Both strength of association and eigenvector centrality of these two females were lowest in both periods, and there are structural holes around them (Fig. 2.6d, f). It is important to note, however, that these results may mean that these females can have associations with a broad range of individuals.

F1 was a central female in Periods 1 and 3, but in Period 2 was not observed at all, although other group members were observed often together at a big fruiting tree of *Ficus* sp. After one and a half month's absence, she suddenly appeared back in the group while the other monkeys were resting. She approached emitting whinnies, which most of the other group members answered with whinnies. I recorded the number of vocalizations, but so many whinnies were exchanged that they were neither differentiable nor countable. After this encounter, F1 was observed quite often with other individuals and gave birth in June or July of 2001; thus, she was estimated to have conceived in Period 2 or shortly after. As multiparous females usually cycle for a few months prior to conception (3–6 months in *A. geoffroyi*, Campbell et al. 2001), it would be adequate to estimate that F1 was cycling while she was absent. Given that an estrous female usually copulates secretly or forms a consortship with a male (Campbell and Gibson 2008), typically in an area of low use for the social group (Shimooka, unpublished data), it is understandable that cycling females appear to temporarily leave established social networks while nonetheless continuing to be members of the group.

Possible-cycling females were observed only in Periods 2 and 3. They are included in the network but are very peripheral. None of them were connected with adult males, although two of them were connected with a subadult male, M7. Similar to cycling females, these possible-cycling females have relatively low eigenvector centrality (Fig. 2.7b), yet they also have medium levels of strength of association with both males and females (Fig. 2.6d, f). Although no further information on their reproductive status is available, it is assumed that they were in the early stage of cycling.

How Does a Subadult Female Become a Group Member After Immigration?

Van Roosmalen and Klein (1988) reported in *A. paniscus* that, although aggression is rare, "leading females" (believed to be oldest) occasionally direct severe aggression towards "non-leading females." Asensio et al. (2008) also reported that in *A. geoffroyi*, new immigrant females receive aggression from longer-term resident females. It is likely that in female–female relationships, how long a female has resided in a given group is an important factor determining the quality of female–female social relationships (Aureli et al. 2006). Symington (1987) determined whether a female was high ranking or low ranking based on agonistic displacements at food patches in *A. belzebuth*, but most of the previous studies described that dominance hierarchy among females is difficult to determine (Chapman 1990)

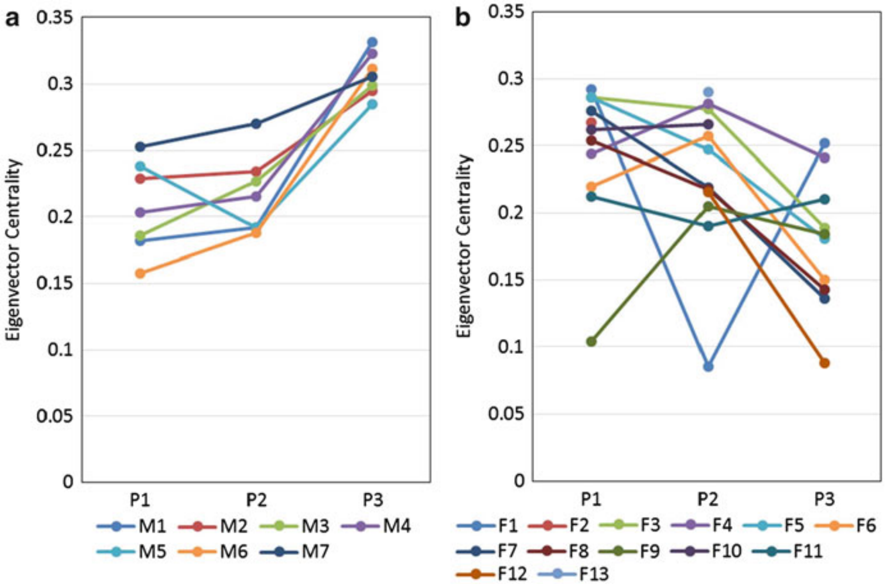


Fig. 2.7 Eigenvector centrality of each individual. (**a**) Adult (M1–M5) and subadult males (M6 and M7), (**b**) adult females

or this topic was not addressed (*A. belzebuth*: Klein 1972; Izawa et al. 1979; *A. geoffroyi*: Fedigan and Baxter 1984). It is likely that dominance hierarchy is unclear in many species of *Ateles* (Aureli et al. 2008).

In this study, F11 was first observed alone in January of 2000 (the beginning of Period 1) in the peripheral area of MB-2 home range. When she was first observed, she was still young, estimated to be a 6–7 years old subadult. She was often found alone on the periphery of the group, but could be found easily because she often repeatedly made long-loud calls. During Period 1, she began to spend time with other females, but was often the target of aggression. The aggression towards F11 often took place at feeding trees, especially at palms such as *Astrocaryum chambira* and *Oenocarpus bataua*. Due to the size of these palm trees, only one or two individuals can feed at once, although the amount of food in a patch is large. Most aggression at feeding trees in this study occurred at such palm trees, and F11 was often chased down the trunk by other females. F11 was the only individual who clearly was of low rank. In the network, she is not in the females' cluster in Period 1, although in Period 2 she began to associate often with F5, sitting on a tree branch side by side. The relatively thick line connecting F11 and F5 in Fig. 2.5b and the shorter distance between F11 and other females in Fig. 2.5b than in 2.5a show this change in her social position. After F11 gave birth in Period 3, aggression towards her decreased and she looked as if she was finally accepted and included as a member of MB-2 group, although centrality was still low. In Period 3, values of strength with males or females and eigenvector centrality were relatively higher among females, which means F11 finally became central after a year and half. This case study shows the gradual process of how a subadult female is integrated into a social group after immigration.

Ramos-Fernández et al. (2009) showed that in wild *A. geoffroyi*, three new adult female immigrants maintained associations mostly among themselves with lower values of strength of association compared to long-term resident females, and then their value of strength showed a substantial increase from the first year to the second year. The presence of young infant itself may temporarily enhance female–female relationships (Aureli et al. 2008): several studies in *A. geoffroyi* report that females with young infants receive or exchange more embraces than females without infants (captive: Schaffner and Aureli 2005; wild: Fedigan and Baxter 1984; Eisenberg and Kuhn 1966; Slater et al. 2007). These results indicate that both long-term residence in a group and having an infant are the primary factors determining the centrality of new immigrant females.

A Female Repeats Cycling, Pregnancy, Lactating, and Then?

F1 was the only one female who had three offspring simultaneously in the group. When I began study on MB-2 group at the end of 1996, she already had a juvenile son (M6). Subsequently, she gave birth to a female ("Citron") in 1998, followed by another female ("Cilantro") in 2001. Since then, all three offspring have remained in MB-2 group. This is relatively rare because in order to have three offspring in a group at once, the eldest one must be a male; if not, a daughter will emigrate at around 6 years old before the birth of her second younger sibling. In order to have more than two offspring in a group, a female needs to have multiple sons. Furthermore, male juveniles appear to have higher mortality than female juveniles (Shimooka et al. 2008) and can be the target of lethal aggression by adult or subadult males (Gibson and Vick 2008). Thus, not many females are able to have several surviving sons. Although there were two other females that gave birth to three offspring during the course of the project, one or two of the infants died or disappeared.

The reproductive status of F1 changed from lactating (for Citron) in Period 1 to cycling in Period 2 and then to lactating again (for Cilantro) in Period 3. She was in the very center of the network in Period 1, but moved to outside of the network while cycling in Period 2 and then moved again in the center in Period 3 (Fig. 2.5). Quantitatively, eigenvector centrality of F1 is the highest among females in Periods 1 and 3 and lowest in Period 2 (Fig. 2.7b). Her case shows that female association changes dramatically in relation with reproductive status, although F1's high centrality might also be related with her long residence in this group. She was estimated to be relatively old in 1997, considering physical characteristics such as wrinkles on her facial skin. As there is no more information about the history of individuals, it is impossible to know how long she had been resident. Longitudinal study is needed to clarify if and how long-term residence in a group affects the social relationships of females.

Relationships Between Mother and Son

To date, there have been no reports on the relationship between adult males and their mothers in spider monkeys. In this study, we do have information on the social relationships between two mothers and their subadult male sons. M6 is estimated to have been born in 1994–1995 from F1, and M7 is estimated to have been born in 1995–1996 from F3. M7 was smaller than M6 and is estimated to be a year younger. Both M6 and M7 have been observed traveling independently of their mothers since September 1998. Lacking observations from the period of obligate dependence when very young, it was difficult to determine the mother–son relationship.

In the network data, F1 and M6 were not located near each other in any period. However, when the association index of M6 was more carefully examined, the index with F1 in Period 3 was highest among those with females, albeit much lower than those with other males. As a male of 5–6 years old, M6's relationships with other males seem to be more important than that with his mother; similarly, for F1 – who was lactating during this period – relationships with other lactating females seem to be more important than that with her independent son.

By contrast, in Periods 1 and 2, M7 was often observed near his mother F3 who was lactating a male infant but not in Period 3 when F3 was possibly cycling. The association index also shows that M7 associated with F3 most often among females in Period 2 and the second most often in Period 1. F3 also associated with M7 most often among males both in Periods 1 and 2. It is possible that the relationship between mother and son becomes estranged when the mother's reproductive status changes to cycling. It is also interesting that the node position of M7 is located between a male cluster and a female cluster in Period 2 and between a male cluster and possibly cycling females in Period 3. This close association with males and his mother shows that he plays an important role in the network that bridges separate clusters of males and females.

How mother–son relationships change when subadult males take on the social role of an adult is not yet known, as there is no follow-up research in our study group. Symington (1990) showed that, in *A. belzebuth chamek,* male–female relationships both in association pattern and affiliative behaviors were intermediate between those of female–female and male–male dyads and that male–female grooming is less common than male–male grooming and more common than female–female grooming. Similar patterns were also found in *A. geoffroyi* (Aureli et al. 2008; Slater et al. 2009). However, because no information about kinship was available in these studies, it is still unknown how mother–son relationships differ from those of other male–female dyads. In chimpanzees in Mahale, Tanzania, orphaned chimpanzees' sons die younger than expected even if they lose their mothers after weaning (Nakamura et al. 2013), which suggests that longitudinal but indirect maternal investment continues after weaning and is vital to the survival of sons. In bonobos at Salonga NP, DR Congo, mothers and sons have high association rates, and mothers provide aid to sons in conflict with other males (Surbeck 2011). In bonobos at Wamba, DR Congo, mothers support their sons in agonistic interactions among males, whereas sons never support their mothers in agonistic interactions among females (Furuichi 1997; Furuichi 2011). Compared to chimpanzees or bonobos, the frequency of agonistic and affiliative interactions in spider monkeys is much less; thus, it is not easy to clarify whether or not aids in conflict or any kind of investments by mothers after weaning bring substantial influences on the development or reproductive success of their sons. Only studies based on longitudinal data can reveal the existence of such direct mother–son interactions. Under such situations, network analysis on association patterns might be helpful to examine indirect relationships among individuals, such as if a female who has adult sons may play a more central role or if mother–son relationships may function to connect males and females in a group.

Males' Association Also Varied Among Periods

Spider monkey males travel more frequently at the boundary area of their home ranges (*A. belzebuth chamek*: Symington 1988; *A. belzebuth belzebuth*: Shimooka 2005; *A geoffroyi*: Chapman et al. 1995), where they engage in boundary patrols and intergroup aggression (*A. belzebuth chamek*: Symington 1988; *A. belzebuth belzebuth*: Klein 1974), which is possibly related to female defense by males. Aureli et al. (2006) reported that males raided well into the home range of neighboring groups while walking on the ground and chasing encountered residents. Male spider monkeys are known to form strong bonds associating with each other, the purpose of which may be reinforced by these raids (Fedigan and Baxter 1984; van Roosmalen and Klein 1988; Symington 1990; Chapman 1990).

In this study, males' association pattern varied among periods. No cluster of males existed in the network during Period 1, whereas a clear cluster existed in Periods 2 and 3. Both values of strength of association and centrality of males were more equally distributed among them than those of females. It is interesting that when party size is smaller (in Periods 2 and 3), males form tighter clusters. Not only party size but also the number of cycling females may affect males' associations. These two are not independent, as females' reproductive status affects their own association and ranging patterns. Males need to check females' reproductive status distributed widely over the home range by searching and visiting each female and sniffing the genital area or touching the clitoris (Campbell and Gibson 2008); thus, regardless of whether males cooperate or not, the presence of cycling females will attract males and affect their associations.

Campbell (2006) and Valero et al. (2006) have reported that in *A. geoffroyi*, there were male–male intragroup coalitionary lethal aggressions towards younger males. It seems that relationships between adult males and young males are not as strong as those of adult males. In this study, the node position of two subadults, M6 and M7, shows clear differences. In Period 1, M6 is linked with only one adult female, but M7 is connected with various individuals of both sexes. In Period 2, M6 is in the male cluster and connected only with males, but M7 is still between the male and female clusters. In Period 3, M7 belongs to the male cluster but is still connected with more females than M6. The two subadult males are only one year apart from each other, but their association patterns differ greatly.

From the position of the nodes in Fig. 2.5, no two males showed tight associations lasting for three periods. From physical characteristics, M3 and M5 were estimated to be relatively old, and their nodes were relatively near to the female cluster in Periods 2 and 3. Age, residency time in a group, relationship with females, and potential dominance rank are all possible factors affecting these associations. Information about their kin relationships, such as brotherhood and mother–son, or about their tenure in the group will provide more insight into how males decide their association partners.

Conclusion

Until now, spider monkey females have been described as less social than males, because social interactions such as grooming, aggregation, and coalitionary behaviors occur at very low rates (Symington 1987; Slater et al. 2007). With permutation tests that examine whether association rates are higher or lower than chance expectation, Ramos-Fernández et al. (2009) revealed that female associations on a yearly basis could not be distinguished from random aggregations and concluded that female association patterns are mostly the result of encounters by chance. However, by estimating reproductive status of each female and analyzing their social networks in shorter time periods, this study reveals that each individual female showed variable patterns of associations according to her reproductive status. If females truly aggregate by chance, changes in their reproductive status should not affect their associations. Social circumstances around a female change dramatically through life, and females will behave adaptively in each situation. Changes in females' association will also affect males' association. Therefore, analyses with reference to female reproductive status are essential for understanding fission–fusion dynamics in spider monkeys. In this study, I analyzed only association patterns involved in party formation, which is just one aspect of spider monkey social characteristics. Although social interactions are infrequent in spider monkeys, parameters such as proximity or approach may be useful to reveal more complex social relationships among them.

Females are not just black dots moving on a computer screen. They may be dots, but each dot changes size and color as it grows and changes according to its reproductive status. In spite of long-term studies on spider monkeys, we still do not know much about the two biggest events of females: reproduction and intergroup transfer. We rarely know where cycling females stay, what they do, with whom they associate while away from other group members, and why they copulate secretly. This dearth in information is primarily because copulation is performed in secrecy (Campbell and Gibson 2008). In Tiputini, Ecuador, for example, an estrous female copulated with one or two males for several weeks in an area that other individuals typically did not use (Shimooka, unpublished data). To reveal the behavioral patterns of cycling females, we may need to employ technologies for remote observation, such as radio collars with GPS.

The most difficult aspect of observing individuals of the dispersing sex is to follow them when they transfer between groups. It is totally unknown how a spider monkey female transfers between groups, how they decide the group into which to immigrate, what they do while they are not belonging to any groups, and how long they spend alone. Studies with limited dispersal potential – such as in fragmented forests or on an island with multiple resident groups – and the use of GPS radio collars may more feasibly provide more information about female life history. In order to further understand female life history, knowledge about long-term personal history of each individual is essential. Ultimately, long-term study on several neighboring groups will be the only way to clarify the changes in female social relationships throughout the life course.

Acknowledgments I appreciate Dr. Kosei Izawa, Dr. Carlos Mejia, Dr. Akisato Nishimura, Dr. Koshin Kimura, Ms. Agumi Inaba, Dr. Andres Link, and Dr. Pablo Stevenson. And I also thank Mr. Alvaro Sanabria, Mr. Nelson Silva, Mr. Ramiro Montealegre, and all the people at La Macarena, and I hope the people in La Macarena are surviving and having a safe life there. I also thank Dr. Cédric Sueur for his help in network analysis, Dr. Christopher A. Schmitt for his advice in English, and the editors of this book for the many comments and advice on the draft. I appreciate Dr. Nobuharu Suzuki and Takaharu Suzuki for their support and understanding. This study was supported by COE program promoted by the Ministry of Education, Science, Sports, and Culture, Japan, and Grant-in-Aid from the Ministry of Education, Science, Sports, and Culture, International Scientific Research No. 09041144.

References

Asensio N, Korstjens AH, Schaffner CM, Aureli F (2008) Intragroup aggression, fission–fusion dynamics and feeding competition in spider monkeys. Behaviour 145:983–1001

Asensio N, Korstjens AH, Aureli F (2009) Fissioning minimizes ranging costs in spider monkeys: a multiple-level approach. Behav Ecol Sociobiol 63:649–659

Aureli F, Schaffner CM, Verpooten J, Slater KY, Ramos-Fernández G (2006) Raiding parties of male spider monkeys: insights into human warfare? Am J Anthropol 131:486–497

Aureli F, Schaffner CM, Boesch C et al (2008) Fission-fusion dynamics: new research frameworks. Curr Anthropol 49:627–654

Aureli F, Di Fiore A, Murillo-Chacon E et al (2013) Male philopatry in spider monkeys revisited. Am J Phys Anthropol 152:86–95

Borgatti S (2002) NetDraw software for network visualization. Anal. Technol, Lexington

Campbell CJ (2006) Lethal intragroup aggression by adult male spider monkeys (*Ateles geoffroyi*). Am J Primatol 68(12):1197–1201

Campbell C, Gibson K (2008) Spider monkey reproduction and sexual behavior. In: Spider monkeys Behav. Ecol. Evol. genus *Ateles*, Campbell CJ (ed) Cambridge University Press, Cambridge. pp 266–287

Campbell CJ, Shideler SE, Todd HE, Lasley BL (2001) Fecal analysis of ovarian cycles in female black-handed spider monkeys (*Ateles geoffroyi*). Am J Primatol 54:79–89. doi:10.1002/ajp.1014

Cant J (1977) Ecology, locomotion, and social organization of spider monkeys (*Ateles Geoffroyi*). University of California, Davis

Chapman C (1990) Association patterns of spider monkeys: the influence of ecology and sex on social organization. Behav Ecol Sociobiol 26:409–414. doi:10.1007/BF00170898

Chapman CA, Chapman LJ, Wrangham RW (1995) Ecological constraints on group size: an analysis of spider monkey and chimpanzee subgroups. Behav Ecol Sociobiol 36:59–70

Collins A (2008) The taxonomic status of spider monkeys in the twenty-first century. In: Spider monkeys Behav. Ecol. Evol. genus *Ateles*, Campbell CJ (ed) Cambridge University Press, Cambridge. pp 50–78

Croft D, Krause J, James R (2004) Social networks in the guppy (*Poecilia reticulata*). Proc R Soc Lond Ser B Biol Sci 271:S516–S519

Di Fiore A, Campbell CJ (2007) The atelines: variation in ecology, behavior, and social organization. In: Campbell CJ, Fuentes A, MacKinnon K, Bearder S, Stumpf R (eds) Primates in perspective. Oxford University Press, New York, pp 155–185

Di Fiore A, Link A, Schmitt C, Spehar S (2009) Dispersal patterns in sympatric woolly and spider monkeys: integrating molecular and observational data. Behaviour 146:437–470

Eisenberg JF, Kuehn RE (1966) The behavior of *Ateles geofforoyi* and related species. Smithson Misc Coll 151(8):1–63

Eisenberg J (1973) Reproduction in two species of spider monkeys, Ateles fusciceps and Ateles geoffroyi. J Mammal 54:955–957

Fedigan L, Baxter M (1984) Sex differences and social organization in free-ranging spider monkeys (*Ateles geoffroyi*). Primates 25:279–294

Furuichi T (1997) Agonistic interactions and matrifocal dominance rank of wild bonobos (*Pan paniscus*) at Wamba. Int Primatol 18(6):855–875

Furuichi T (2011) Female contributions to the peaceful nature of bonobo society. Evol Anthropol 20:131–142

Gibson K, Vick L (2008) Intra-community infanticide and forced copulation in spider monkeys: a multi-site comparison between Cocha Cashu, Peru and Punta Laguna, Mexico. Am J Primatol 70:485–489

Hartwell KS, Notman H, Bonenfant C, Pavelka MS (2014) Assessing the occurrence of sexual segregation in spider monkeys (*Ateles geoffroyi yucatanensis*), its mechanisms and function. Int J Primatol 35:425–444

Hashimoto C, Furuichi T, Tashiro Y (2001) What factors affect the size of chimpanzee parties in the Kalinzu Forest, Uganda? Examination of fruit abundance and number of estrous females. Int J Primatol 22:947–959

Henzi S, Lusseau D (2009) Cyclicity in the structure of female baboon social networks. Behav Ecol Sociobiol 63:1015–1021

Izawa K, Mizuno A (1977) Palm-fruit cracking behavior of wild black-capped capuchin (*Cebus apella*). Primates 18:773–792

Izawa K, Kimura K, Nieto AS (1979) Grouping of the wild spider monkey. Primates 20:503–512

Julliot C (1994) Predation of a young spider monkey (*Ateles paniscus*) by a crested eagle (*Morphnus guianensis*). Folia Primatol 63:75–77

Kimura K, Nishimura A, Izawa K, Mejia C (1994) Annual changes of rainfall and temperature in the tropical seasonal forest at La Macarena Field Station, Colombia. Field Stud New World Monkeys La Macarena, Colomb 9:1–3

Klein L (1972) The ecology and social behavior of the spider monkey, *Ateles belzebuth*. University of California, Berkeley

Klein LL (1974) Agonistic behaviour in neotropical primates. In: HOLLOWAY L (ed) Primate aggression, territoriality, and xenophobia. Academic Press, New York, pp 77–122

Krause J, Lusseau D, James R (2009) Animal social networks: an introduction. Behav Ecol Sociobiol 63:967–973

Lusseau D, Newman M (2004) Identifying the role that animals play in their social networks. Proc R Soc Lond Ser B Biol Sci 271:S477–S481

Matsuda I, Izawa K (2008) Predation of wild spider monkeys at La Macarena, Colombia. Primates 49:65–68

Milton K (1981) Estimates of reproductive parameters for free-ranging *Ateles geoffroyi*. Primates 22:574–579

Nakamura M, Hayaki H, Hosaka K et al (2013) Orphaned male chimpanzees die young even after weaning. Am J Phys Anthropol 153:139–143

Newman M (2003) The structure and function of complex networks. SIAM Rev 45:167–256

Newman M (2004) Analysis of weighted networks. Phys Rev E 70:056131

Nishida T (1968) The social group of wild chimpanzees in the Mahale Mountains. Primates 9:167–224

Nunes A, Chapman C (1997) A re-evaluation of factors influencing the sex ratio of spider monkey populations with new data from Maraca Island, Brazil. Folia Primatol 68:31–33

Pepper JW, Mitani JC, Watts DP (1999) General gregariousness and specific social preferences among wild chimpanzees. Int J Primatol 20(5):613–632

Ramos-Fernández G, Boyer D, Aureli F, Vick LG (2009) Association networks in spider monkeys (*Ateles geoffroyi*). Behav Ecol Sociobiol 63:999–1013

Schaffner CM, Aureli F (2005) Embraces and grooming in captive spider monkeys. Int J Primatol 26(5):1093–1106

Shimooka Y (2003) Seasonal variation in association patterns of wild spider monkeys (*Ateles belzebuth belzebuth*) at La Macarena, Colombia. Primates 44(2):83–90. doi: 10.1007/s10329-002-0028-2

Shimooka Y (2005) Sexual differences in ranging of *Ateles belzebuth belzebuth* at La Macarena, Colombia. Int J Primatol 26:385–406

Shimooka Y, Campbell CJ, Di Fiore A, Felton AM, Izawa K, Link A, Nishimura A, Ramos-Fernández G, Wallace RB (2008) Demography and group composition of *Ateles*. In: Spider monkeys: behavior, ecology and evolution of the genus *Ateles*, Campbell CJ (ed) Cambridge University Press, Cambridge. pp 329–348

Slater KY, Schaffner CM, Aureli F (2007) Embraces for infant handling in spider monkeys: evidence for a biological market? Anim Behav 74(3):455–461

Slater KY, Schaffner CM, Aureli F (2009) Sex differences in the social behavior of wild spider monkeys (*Ateles geoffroyi yucatanensis*). Am J Primatol 71(1):21–29

Strier K (1994) Brotherhoods among atelines: kinship, affiliation, and competition. Behaviour 130(3):151–167

Surbeck M (2011) Mothers matter! Maternal support, dominance status and mating success in male bonobos (*Pan paniscus*). Proc R Soc B Biol Sci 278:590–598

Symington M (1987) Sex ratio and maternal rank in wild spider monkeys: when daughters disperse. Behav Ecol Sociobiol 20:421–425

Symington M (1988) Demography, ranging patterns, and activity budgets of black spider monkeys (*Ateles paniscus chamek*) in the Manu National Park, Peru. Am J Primatol 15:45–67

Symington M (1990) Fission-fusion social organization in *Ateles* and *Pan*. Int J Primatol 11:47–61

Van Roosmalen M, Klein L (1988) The spider monkeys, genus *Ateles*. Ecol Behav Neotrop Primates 2:455–537

Valero A, Schaffner CM, Vick LG, Aureli F, Ramos-Fernandez G (2006) Intragroup lethal aggression in wild spider monkeys. Am J Primatol 68(7):732–737

Vick L (2008) Immaturity in spider monkeys: a risky business. In: Spider monkeys Behav. Ecol. Evol. genus *Ateles*, Campbell CJ (ed) Cambridge University Press, Cambridge. pp 288–328

Chapter 3
Social Interactions and Proximal Spacing in Woolly Monkeys: Lonely Females Looking for Male Friends

Pablo R. Stevenson, Diego A. Zárate, Mónica A. Ramírez, and Francisco Henao-Díaz

Introduction

Social systems depend on social organization, social structure, and mating systems (Kappeler and van Schaik 2002). Social systems in primates are believed to be determined mainly by resource availability, predation risk, parental care, and infanticide (Wrangham 1980; Terborgh and Janson 1986; van Schaik 1989; Sterck et al. 1997; Isbell and Young 2002; Koenig 2002). It has been suggested through socioecological models that the simultaneous influence of these factors may generate social behaviors that promote the reproductive fitness of individuals (Kappeler and van Schaik 2002). Most primate socioecological models establish that predation risk promotes group formation by the females. However, groups are prevented from growing indefinitely by the effects of competition over resources. In contrast, the distribution of males depends mainly on female availability, but associations of females can be also influenced by risk of infanticide (Sterck et al. 1997), and females may seek protective males to increase the chances of infant survival. In this way, female–female association together with habitat saturation determines the competitive regimen and, with it, the social relationships within the group (van Schaik 1989; Sterck et al. 1997).

P.R. Stevenson (✉) • M.A. Ramírez • F. Henao-Díaz
Departamento de Ciencias Biológicas, Centro de Investigaciones Ecológicas la Macarena, Universidad de los Andes, Cr. 1 No. 18A-10, Bogotá, Colombia
e-mail: pstevens@uniandes.edu.co

D.A. Zárate
Departamento de Ciencias Biológicas, Centro de Investigaciones Ecológicas la Macarena, Universidad de los Andes, Cr. 1 No. 18A-10, Bogotá, Colombia

Centro de Investigaciones en Ecosistemas (CIEco), Universidad Nacional Autónoma de México, Mexico City, Mexico

T. Furuichi et al. (eds.), *Dispersing Primate Females*,
Primatology Monographs, DOI 10.1007/978-4-431-55480-6_3

Female association is regarded as a key element when defining socioecological models and social systems. Wrangham (1980) proposed a model of female association in which the distribution of resources is the main determinant. According to this model, relatively high-quality resources with a discrete distribution can be defended. Therefore, under this situation, it is expected that related females (who are more dependent on resources for reproductive success than males) will associate for the long term, deriving in female philopatry. On the other hand, high-quality resources with a uniform distribution, or low-quality resources, cannot be defended. In these cases, female associations are not expected, as there is no motivation for them to do so. This could be related to a low aggression rate among groups, which does not promote coalition formation among females. Likewise, if resources cannot be monopolized, dominance hierarchies are not expected to be formed (Isbell and Young 2002). Then, when there are no defendable resources and no dominance hierarchies are formed, female dispersal is expected. Although some aspects of the sociological models have been supported with empirical data, recent studies have also shown that some of the assumptions are not correct and other points are difficult or impossible to test (Clutton-Brock and Janson 2012). Therefore, the study of the potential effects of ecological factors on the social structure of primate groups is still a matter of debate, where cooperation, including the role of males and phylogenetic signals, also seems to play an important role (Koenig et al. 2013; Thierry 2013).

Female Dispersal

In mammals, males are viewed as the dispersing sex, while females are usually philopatric (Greenwood 1980; Dobson 1982). This pattern was also believed to be the most common in primates (Pusey 1987a), but these ideas have been reevaluated by several researchers (Di Fiore and Rendall 1994; Strier 1994a). Dispersal occurs at approximately the beginning of the reproductive age, and it has been suggested that this behavior may be a strategy mainly to avoid endogamy; however, it also helps to increase the probabilities of reproductive success, to reduce competition for resources or mates, and to reduce the unequal impact of reproductive costs (Pusey 1987b; Perrin and Mazalov 2000). High immigration and emigration rates have been registered under conditions of high predation risk, aggression, and even starvation, which would suggest that the benefits of dispersal are higher than the costs (Pusey 1987a; Bradley et al. 2004; Jack and Fedigan 2004a, b; Broquet et al. 2006; Clobert et al. 2009).

In primates, male dispersal and female dispersal occur commonly. For instance, atelines show a bias towards female dispersal (Di Fiore et al. 2010). Atelines are the largest Neotropical monkeys, currently including spider monkeys (genus *Ateles*), woolly monkeys (*Lagothrix*, including yellow tailed woolly monkeys, formerly *Oreonax*), and woolly spider monkeys or muriquis (*Brachyteles*). In *Ateles* spp., dispersal is mainly performed by females (Symington 1987; Shimooka et al. 2008; Di Fiore et al. 2009, but see Aureli et al. 2013). Moreover, the high degree of fission–fusion dynamics characteristic of spider monkeys can lead to a certain degree of segregation by sex. This means that adult females and their infants spend most of the time foraging together and usually away from adult males, who travel for longer distances than females (Fedigan and Baxter 1984; Ahumada 1989). Similarly, *Brachyteles* spp. also shows female dispersal, male philopatry, and flexible grouping patterns, but foraging subgroups are larger than those of spider monkeys (Strier 1987, 1991). Moreover, in chimpanzees (*Pan troglodytes*), whereas most females disperse from their natal group, males are philopatric and show strong affiliation and cooperation (Boesch and Boesch-Achermann 2000; Nishida et al. 2003; Sugiyama 2004). This is important for the defense of the community's feeding range, which in turns affects the reproductive rates of resident females (Williams et al. 2004). Chimpanzees also share other ecological traits with atelines such as a predominantly frugivorous diet, a high degree of fission–fusion dynamics, formation of multi-male–multi-female groups, promiscuous mating, and associating in temporary parties that vary in size, duration, and composition (Goodall 1986; Nishida 1979; Mitani et al. 2002).

Different observational studies have suggested that the natural dispersal pattern of woolly monkeys is consistent with male philopatry, while females tend to disperse from their natal groups (Stevenson et al. 1994; Nishimura 1994, 2003; Defler 2010; Di Fiore et al. 2010). However, there are reports of juvenile males changing groups when their mothers migrate, and solitary males, possibly dispersing from their group, have also been observed (Di Fiore and Fleischer 2005; Di Fiore et al. 2009; Defler 2010). Secondary dispersal (subsequent migration of females after the first dispersal event) has also been observed. For example, an unmistakable adult female ("Cabeciplana") was observed to migrate to one of the study groups (CR-12) at Tinigua National Park (Colombia) in 1996, and then it was seen in a different group in 2000. Therefore, this female migrated at least twice during her lifetime (P. R. Stevenson, unpublished observations).

Social and Ecological Characteristics of Woolly Monkeys

Woolly monkeys live in multi-male–multi-female groups, which show considerable variation in size and composition (ranging from 9 to 49 individuals, Table 3.1, Fig. 3.1), where full adult males are larger than adult females (Fig. 3.2 a, b). Comparisons among groups of different sizes (or for the same group at different years), in terms of feeding rates and daily traveled distance, have been made for the population at Tinigua Park, Colombia (Stevenson and Castellanos 2000; Stevenson 2006). In general, feeding rates on fruits are similar in all groups, but larger groups consistently move more than medium-sized groups to get resources, suggesting a strong role of intragroup competition. Small groups also travel more than medium-sized groups, unless they inhabit good quality home ranges in terms of fruit production (Stevenson 2006). This trend has been observed in other populations, but significant differences between groups differing in size were not found (Zárate-Caicedo 2009).

Table 3.1 Size and composition of woolly monkey groups reported in several studies

Site/group (year)	AM	AF	SM	SF	Juv	Inf	Total	Source
Peneya	11	15	3	2	5–6	6	42–43	Izawa (1976)
Peneya	4–7	3–12	1–3	3–3	2–12	0–8	13–45	Nishimura (1990)
Isla Cahuana	5	5	0	1	4	2	17	Soini (1990)
Cahuana/#5	3	2	1	0	1	2	9	Soini (1990)
Cahuana/#7	4	6	1	1	3	3	18	Soini (1990)
Tinigua/CR-1 (1988)	4	5	0	2	2	1	14	Stevenson et al. (unpublished)
Tinigua/CR-1	4	6	1	0	5	3	19	Nishimura, (personal communication)
Tinigua/CR-2 (1988)	8	10	0	4	5	2	29	Izawa and Nishimura (1988)
Tinigua/CR-D	4	4	1	1	3	1	14	Stevenson et al. (unpublished)
Tinigua/CR-Z	5	7	2	0	5	2	21	Stevenson et al. (unpublished)
Yasuni	4–2	8–11	5–5	0	4–5	1–1	22–24	Di Fiore (1997)
Urucu	7	12–14	2	0	15–18	5–8	44–49	Peres (1996)
Caparu	5	8			6	4	20–24	Defler (2010)
Trueno/Grand(I 2008)	14	16	0	0	0	2	32	Zárate-Caicedo (2009)
Trueno/Grand(II 2008)	14	16	0	0	2	11	43	Zárate-Caicedo (2009)
Guacharos/Col (2013)	4	7	2	1	5	3	22	Paez and Garcia (unpublished)
Tinigua/CR-12 (1990)	4	5–6	1	1	3–6	2–4	18–21	Stevenson (1998)
Tinigua/CR-12 (1996)	4	7	2	0	6	2	21	Stevenson et al. (unpublished)

The groups corresponding to the case study are shown in the gray zone

Some researchers have reported small groups and solitary individuals (Di Fiore 2002; Defler 2010); however, in most of these cases, it is likely that they correspond to subgroups. For instance, Soini (1990) described three groups in Cahuana Island (Perú) of 6, 8, and 3 individuals. These "groups" spent some days and nights away from each other, but in other occasions, they spent the night together and were in close proximity during the day, suggesting that they could be considered as subgroups of the same social unit. Defler (2010) also reported a population near the Apaporis River (Caparu Biological Station in Colombia), whose groups exhibit temporal divisions in two or more dispersed foraging subunits and showing regrouping throughout the day. This phenomenon was supposed to be affected by the low availability of food sources in this site, which has low fertility soils. Similarly, in Cueva de Los Guacharos National Park, we installed collars and GPS devices on four individuals (Fig. 3.2c). Preliminary information and direct observations have shown that one adult female has been in close proximity to the largest male in the group, while a second female was in close proximity only during some days and more than 1 km apart most of the time (Stevenson and Link unpublished data).

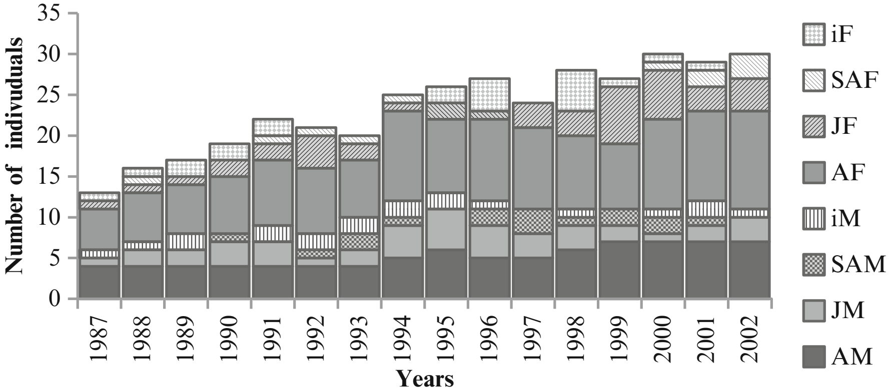


Fig. 3.1 Changes in size and composition in the study group CR1, studied continuously by Dr. A. Nishimura in Tinigua NP, Colombia. Each pattern corresponds to the number of individuals in different age–sex classes (*AM* adult male, *AF* adult female, *SAM* subadult male, *SAF* subadult female, *JM* juvenile male, *JF* juvenile female, *iM* infant male, *iF* infant female)

In fact, some studies have characterized the social grouping of woolly monkeys as showing fission–fusion dynamics, while others as cohesive units (Di Fiore and Rodman 2001; Defler 2010). It seems likely that the degree of fission–fusion dynamics is site dependent. We hypothesize that cohesion increases in populations with high density and more groups as competitors (i.e., more potential for intergroup and interspecific encounters), because relatively cohesive groups have been reported for two populations of woolly monkeys that are sympatric with spider monkeys (Tinigua National Park: Nishimura 1994; Stevenson et al. 1998; Yasuni National Park: Di Fiore and Rodman 2001).

Woolly monkey groups are more cohesive than those of spider monkeys when living in sympatry (Stevenson et al. 1998), and this has been suggested to be possible due to their relatively higher dietary flexibility. Even though both spider and woolly monkeys are considered highly frugivorous primates, woolly monkeys consume a larger variety of items including insects, other arthropods, and occasionally small vertebrates (Fig. 3.2d, e, f), which tend to be more evenly distributed in the forest than fruit patches. Then, it has been suggested that contest competition, which seems to be stronger for fruits that are easily monopolizable (Stevenson et al. 1998), may have a less negative influence on subordinates that can forage for arthropods when fruit patches are occupied (Stevenson et al. 1994). In woolly monkey groups, a female in estrous usually mates with the majority of males (Nishimura et al. 1992; Nishimura 1994), which may allow multiple males to contribute to the genetic representation of the new generations. In fact, Escobar-Páramo (1999) provided molecular evidence indicating for the first time that juveniles from a single group have more than one father. However, mating by large older males is more frequent than by younger ones (Nishimura 1994). In the most studied population in terms of social aspects (Tinigua National Park), mating events are distributed along the

Fig. 3.2 Examples of the study animals. (**a**) An adult male at Tinigua NP (Meta). (**b**) An adult female of the Tinigua population. (**c**) An adult male ("Neimar") carrying a collar with a GPS device in Cueva de Los Guacharos NP (Huila). (**d**) An adult female carrying an infant in El Trueno station (Guaviare). (**e**): An adult male opening a palm inflorescence (*Wettinia kalbreyeri*) at Guacharos. (**f**): An adult male feeding on a frog in Amacayacu NP (Amazonas)

year in a relatively uniform manner (Nishimura et al. 1992). However, it has been reported that the majority of births usually happen in the second semester of the year (Nishimura 2003), when fruit production is scarce and woolly monkeys rely on young leaves, unripe fruits, and flowers (Stevenson et al. 1994; Stevenson 2006). Although woolly monkeys tend to increase the consumption of other items in fruit scarcity periods, the relevance of different kinds of fallback resources varies between populations (Caparu: González and Stevenson 2010; El Trueno: Zárate and Stevenson 2014; Guacharos National Park: Cifuentes et al. 2013).

Social interactions in woolly monkey groups normally represent less than 5 % of their activity budget (Stevenson et al. 1994; Defler 1995; Di Fiore 1997; Stevenson 2006) and usually show marked differences across time. A positive relationship between the time invested in social interactions and fruit abundance has been found in various years for the Tinigua population (Stevenson 2006). This suggests that, in times of fruit scarcity, energetic limitations reduce the possibility of performing this type of energy-demanding activities (Stevenson et al. 1994; Di Fiore and Rodman 2001), especially those that do not directly affect reproductive success, such as play. However, this pattern is less clear in other studied populations (Gonzalez and Stevenson 2010; Zárate and Stevenson 2014; Vargas et al. 2014). Even though these differences could be due to the different ecological conditions, it is also clear that adequate ways to quantify the variables of interest require extensive sampling. For instance, a detailed quantification of fruit abundance in the forest needs a huge sampling effort (Stevenson and Vargas 2008), and in some cases, the estimates are not reliable because of small sample size.

Studies on the Tinigua and Yasuni populations have reported group transfer mainly by subadult and adult females and only a few cases of male dispersal (e.g., male juveniles that migrate with their mothers) (Nishimura 1994; Stevenson et al. 1994; Di Fiore and Fleischer 2005). The best demographic data comes from a group studied for 15 continuous years by Dr. A. Nishimura. During the study, 16 females were born in the group, and five of them remained in the group and were less than five years old at the end of the study (i.e., had not reached subadult age). Six disappeared at ages 1–4 years, including two that died of the "white faced" disease. The remaining five females disappeared and presumably dispersed just after reaching subadult age (5–7 years). None of the born females reached the adult stage in the group. On the other hand, 14 males were born in the group during the study; four of them remained in the group and were less than 5 years old at the end of the study; three disappeared at ages 3–5 years (including two that died of the "white faced" disease). In contrast to females, only one male disappeared after reaching subadult age (5–7 years), and six of them continued in the group at the adult stage (>7 years) (Nishimura, pers. comm.). Similar patterns were observed in other study groups in the area (Stevenson pers. obs.); however, these groups were not as rigorously monitored as Nishimura's group. Therefore, it seems safe to conclude that female dispersal is quite common at the subadult stage, while male dispersal is unlikely for males, at least in the Tinigua population.

In other woolly monkey populations, male philopatry has been questioned based on relatedness analyses (i.e., Ecuadorian populations, Di Fiore et al. 2009) and cases where rehabilitated males have been successfully incorporated into natural groups (Maldonado and Botero 2009). However, in other populations studied so far, individual recognition is difficult, making it impossible to have a reliable quantitative assessment of female and male dispersal. This occurs, for instance, in Yasuni National Park in Ecuador (Di Fiore, pers. com.) and Caparú Research Station in Colombia (González and Stevenson 2010). When individual recognition is possible, the assessment is usually based on sex, size, broken fingers, facial traits, and genital marks (Fig. 3.3).

Woolly monkeys exhibit strong male dominance over females (Nishimura 1990, 1994; Stevenson et al. 1994; Stevenson 1998), and high aggression rates from adults (especially males) towards subadult females can motivate them to leave their natal group. Grooming activities are relatively frequent between females and their young offspring, whereas adult males receive substantial grooming from juveniles and adult females (Nishimura 1990; Stevenson 1998). Grooming is more frequent between individuals with the shortest interindividual distances, suggesting that affiliative interactions occur more often among individuals that spent substantial time in close proximity (Stevenson 1998). Therefore, close proximity is a good indicator of affiliative behavior. In fact, the sex and age classes with the highest social affinity were females and their young (which spend a lot of time in close spatial proximity), followed by adult males and females; while affinity among males and among females tends to be low (Stevenson 1998). Moreover, close proximity between mothers and offspring decreases through time (Table 3.2); therefore, overall patterns of proximity vary along time as a function of the number and age of juveniles in the group (i.e., close average proximity when the number of young juveniles in the group is high). Social interactions within the group can also change depending on the reproductive status of females. For example, females with a dependent infant usually receive less aggression than females without a dependent infant (Stevenson 2006). Since most information on the social aspects of woolly monkey populations comes from studies performed at Tinigua, it is unknown whether these patterns can be generalized to other populations. However, proximity patterns seem to hold in Yasuni, where adult females are not commonly found in proximity to other adult females (although they tolerate each other in most contexts), similar to what happens to adult males (Di Fiore and Fleischer 2005).

In addition, woolly monkeys are among the most sensitive primate species to habitat disturbance (Defler 2010). This species is found in Colombia, Venezuela, Brazil, Perú, and Ecuador (Di Fiore et al. 2010), and the most threatened subspecies is the Colombian woolly monkey (*L. lagothricha lugens*), distributed along central and eastern ridges and adjacent lowlands (Bennett 2003; Defler 2010). Increasing human population densities and deforestation rates in this part of the country have caused severe forest fragmentation (Stevenson and Link 2008); however, the effects of anthropogenic disturbance on the behavior and ecology of woolly monkeys are just in their initial phase (Zárate and Stevenson 2014).

Fig. 3.3 Key features for individual recognition in woolly monkeys, including facial traits and marks on genitals. All the examples belonged to the Guacharos population. (**a**) Adult male "Toniño" with conspicuous forehead line. (**b**) Adult male "Romario" with vanished forehead line. (**c**) Adult male "Neimar" penis tip. (**d**) Adult male "Zico" penis tip. (**e**) Adult female clitoris "Leika". (**f**) Broken finger of an adult male "Pibe"

Table 3.2 Changes in proximal spacing between young woolly monkeys and their mothers as the offspring becomes older

	Distance to mother	
Age (mo)	Contact	% > 5 m
0–4	100 %	0 %
4–10	<80 %	0 %
10–14	<50 %	>15 %
14–24	<15 %	>30 %
30–36	<5 %	>60 %

From Stevenson et al. (1998)

Here, we review what is known about the social interactions of woolly monkeys, and we evaluate whether there are similar proximity patterns across populations at Tinigua and Guacharos National Parks (continuous forests) and El Trueno station (forest fragment), focusing especially on female relations. To achieve this, social relationships among adult individuals of both sexes and their temporal and spatial differences were explored. Given the female-biased dispersal pattern in woolly monkeys, female–female associations should be weaker than male–male associations. However, populations inhabiting fragmented habitats are expected to show altered social relationships compared to populations in pristine habitats, since habitat saturation could exacerbate agonistic interactions among individuals due to resource competition (Irwin 2007). Additionally, discontinuity in the forest matrix may limit dispersal routes (Di Fiore et al. 2009; Oklander et al. 2010).

Study Groups and Their Habitat

Our study sites included Tinigua and Cueva de Los Guacharos National Parks and El Trueno experimental station. Tinigua NP is located on the western flank of the Sierra de la Macarena, Meta (2°40′N, 74°10′W). La Macarena Ecological Research Center (CIEM) is located within the park, on the western margin of the Duda River at an altitude of 350 masl (Stevenson 2006). This study site has continuous canopy cover and extensive forests without strong anthropogenic disturbance, at least since 1950s. Cueva de Los Guacharos NP (here after Guacharos) is located in the Acevedo municipality, Huila (1°36′22.99″N, 76° 6′3.44″W). This territory has been under the protection of the National Parks Unit since 1960, which controls deforestation and hunting within the park (UAESPNN 2005). The park has a continuous forest area of approximately 9,000 ha in an altitudinal gradient from 1,660 to 2,850 masl. The El Trueno experimental station, of the Amazonian Institute of Scientific Research (SINCHI), is located in El Retorno municipality, Guaviare (2°22′28″N, 72°41′27″W), at 219 masl. This station contains a forest fragment with an area of approximately 136 ha (Zárate and Stevenson 2014). Woolly monkey population densities vary between study sites: El Trueno station has the highest estimated density (50 indiv./km^2), similar to the one found in Tinigua NP (41–50 indiv./km^2, Stevenson 2007) and higher than the estimated density at Guacharos NP (20 indiv./km^2, Vargas et al. 2014). Interestingly, fruit production values estimated by transect methods have shown higher productivity for both El Trueno and Tinigua sites, than for Guacharos (Stevenson 2014).

We analyzed data from focal individuals in groups that were followed continuously from dawn to dusk. Focal sessions were variable in length, mainly depending on topography and the possibility to observe the monkeys directly (e.g., in sub-Andean forest and very humid forest, there are more epiphytes and a dense understory vegetation that limits the observation of monkeys, and under these conditions, it is hard to follow focal animals for long periods of time). In general, focal sessions lasted a few hours, and under these follows instantaneous samples at 10 min intervals were used to gather information on activity, diet, and neighbors in proximity (within 5 m from the focal animal) (Altmann 1974; Stevenson and Quiñones 2004). Several group members were chosen as focal animals in each month, and we did not control the time or sequence in which they were observed (except for the El Trueno population, where the same individuals were chosen and observed for 12 h every month).

We collected a total of 720 sampling hours between August 1996 and July 1997 in Tinigua (here after 1997), which were then compared with 384 h of data gathered from August 1990 to March 1991 (here after 1991) and published in Stevenson (1998). In Guacharos, we completed 720 sampling hours between January and July 2010. In El Trueno station, we completed a total of 1,440 sampling hours between January and December 2008. At each instantaneous sampling, we registered the number, sex, and age-class of individuals at less than 5 m from the focal. We classified all individuals in four main categories: adult male, adult female, female with dependent infant (carrying offspring during long movements), and immature individuals. Individuals were classified as infants (0–1 year old), juveniles (>1–4 years old), subadults (>5–6 years old), and adults (>6 years). Subadult males and females were also differentiated in our analysis of temporal variation, and juveniles were excluded from the analysis of association between adults of both sexes. We used G tests to evaluate the statistical associations in the frequency of proximity among adult age classes and between years. These tests compare the frequency in which different age–sex classes are found in proximity and examine if the association differs in relation with expected frequencies (in this sense, it can be understood as a likelihood version of a chi-square test of independence) (Sokal and Rohlf 1995; Whitlock and Schluter 2009). The null hypothesis of this analysis is based on independent frequency; for instance, in our case, it means that neighbors of focal animals are males and females in the same proportion, independently of the sex of the focal animal.

We based our analyses on comparisons among focal individuals in each category and the category of nearby individuals. This procedure was performed for each locality; however, the majority of comparisons between localities showed no significant differences (Fig. 3.4). For this reason, data from the three study sites were also analyzed by pooling the information of all three populations to

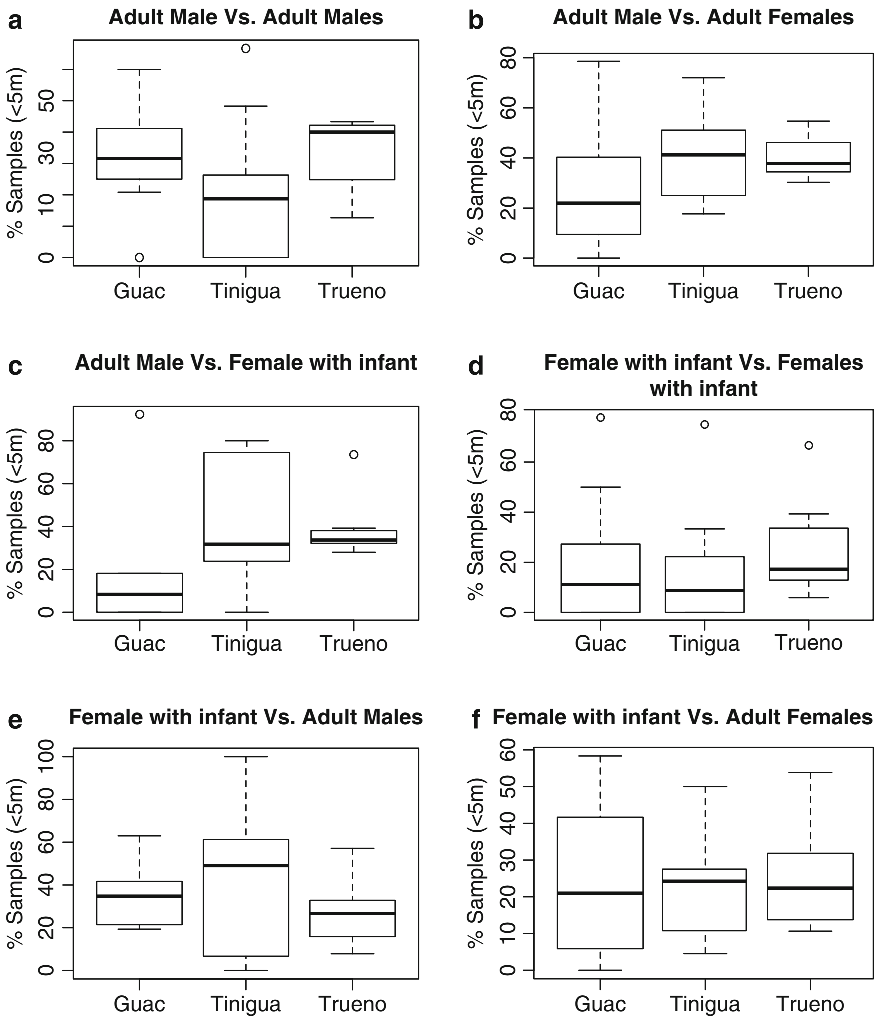


Fig. 3.4 Comparison of proximity between a focal adult woolly monkey and other adult monkeys in three different localities. The *Y* axis represents the percentage of samples in which a focal animal was in less than 5 m from other individuals of different age–sex categories. (**a**) Adult male as focal animal vs. other adult males, (**b**) adult male as focal animal vs. adult females, (**c**) adult male as focal animal vs. adult females with infant, (**d**) adult female with infant as focal animal vs. adult females with infant, (**e**) adult female with infant as focal animal vs. adult males, (**f**) adult female with infant as focal animal vs. adult females, (**g**) adult females as focal animal vs. adult females, (**h**) adult females as focal animal vs. adult females with infant, and (**i**) adult females as focal animal vs. adult males. We did not find significant differences between populations, except for the last comparison (i) ($p = 0.001$)

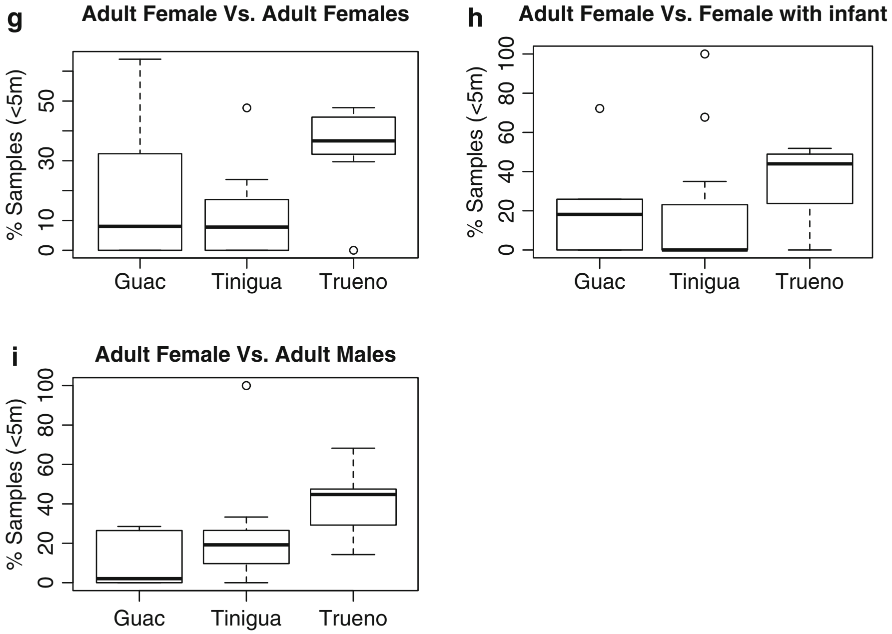


Fig. 3.4 (continued)

determine whether there were significant differences among categories. Finally, to evaluate the effects of fragmentation on the social behavior of woolly monkeys, we compared the frequency of social interactions for each population from the instantaneous samplings using G tests. All the analyses were performed using R software using a Pete Hurd code (http://www.pmc.ucsc.edu/~mclapham/Rtips/G%20test.txt, R Development Core Team 2012).

Case Studies

Between-Year Comparison in Tinigua

Despite finding statistical differences in the frequency of proximal spacing between years for the Tinigua population ($X^2 = 117$, df $= 18$, $p < 0.01$), we also found some consistent patterns (Fig. 3.5). For instance, adult females are commonly found in close proximity of juveniles (probably their offspring) most of the time or they are alone (mostly nulliparous full grown females). As expected, adult females were rarely in close proximity to other adult females due to their dispersal behavior and low affiliative relations. However, we found differences between years in these frequencies (Fig. 3.5a), probably due to the variation in the number of females with

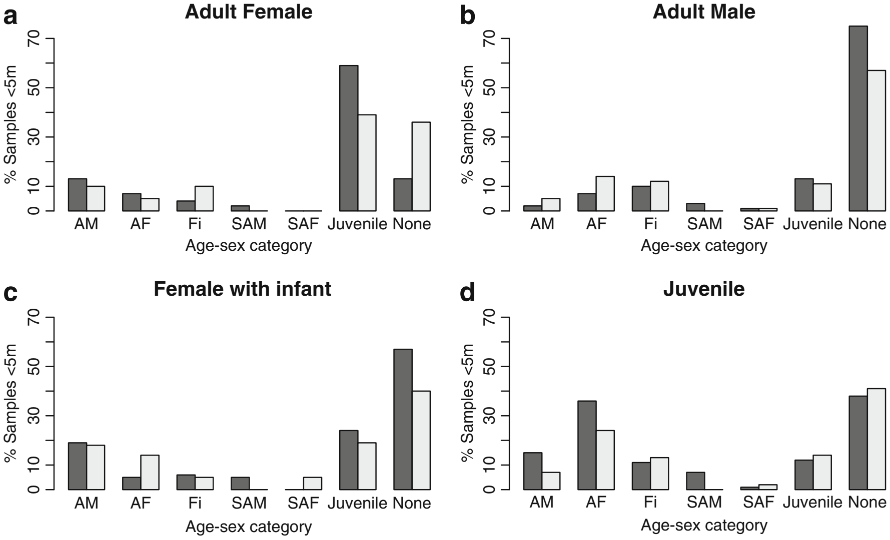


Fig. 3.5 Percentage of samples in which focal woolly monkeys were in proximity to individuals of different age–sex classes in Tinigua NP, comparing 2 years (*black* = 1991, *gray* = 1996). Each panel corresponds to a different focal animal age–sex class (**a**–**d**) that could be in proximity (<5 m) to individuals of other classes (*AM* adult male, *AF* adult female, *Fi* female with infant, *SAM* subadult male, *SAF* subadult female) or alone without close individuals (none)

associated juveniles (Table 3.1). For instance, in our main study group at Tinigua (CR12), there were four infants that became juveniles during the study period in 1991; in contrast, only two were in that age in 1996. Since young juveniles (1–2 years old) spend most of their time in close proximity to their mothers (Stevenson 1998), the higher frequency of proximity between females and juveniles in 1991 than in 1996 is possibly a reflection of the number of young juveniles in the group. Similarly, in other groups, we have found strong changes in the composition of groups: our large group at El Trueno fragment changed from no juveniles and two infants to two juveniles and eleven newborns within a single year (Table 3.1).

In both years, adult males were the most distant focal animals to other group members (Fig. 3.5b). In contrast to expectations from the socioecological theory, focal males were found in close proximity to other adult males less frequently than with adult females. This pattern, however, was observed in another group at the study site (Nishimura 1994) and was also found for the Ecuadorian populations of woolly monkeys (Di Fiore and Fleischer 2005). In the case of adult males, we found some differences between years, possibly due to the higher number of adult male–female associations observed during the second year. The higher number of females in the second year could explain this result (Table 3.1) and mainly the number of females without dependent infants.

Juveniles were frequently in proximity of their mothers (Fig. 3.5d), who for up to two or three years do not have new offspring. Juveniles of 4–5 years usually remain close to their mothers, and for this reason, we also observed a high frequency of association between juveniles and adult females with dependent offspring (Stevenson 1998). In addition, juveniles were observed gathering mainly to engage in play sessions and occasionally interacting with adult males. Accordingly, juveniles were the age class showing most neighbors around. We found large differences in the frequency of interactions between focal juveniles and adult females, which probably reflect differences in the age of the juveniles at the time of observations (since there is a gradual increase in spacing as juveniles grow, especially for juvenile males that start to go closer to adult males, Stevenson 1998, Table 3.2).

Focal females with dependent infant were often seen near adult males, and this frequency was quite consistent between years (Fig. 3.5c). As expected due to their low affiliative interactions, these females were also rarely found near other females, and in accordance with the results from juveniles, they were often found near to 3–5-year juveniles. For adult females with dependent infant, the largest between-year difference was related to the variation of other females in proximity.

Proximity Between Adult Monkeys

G tests analyzing the association between age–sex classes in terms of proximity showed no significant associations for two of the populations (Tinigua: $G = 0.26$, $df = 1$, $p = 0.31$ and El Trueno: $G = 1.14$, $df = 1$, $p = 0.14$). Figure 3.6 is a mosaic plot that resembles a bar plot with the bars stacked one on top of the other. The bar area in this type of graph shows the relative frequency or proportion within each category; also the numbers of observations are represented proportional in the width of each bar. We use this way to display the data because it is easier to compare the proportion between two categories than a grouped bar graph (Whitlock and Schluter 2009). In both sites, when adult females were focal individuals, they were more frequently found in proximity to males than to females. However, focal males were also found more frequently near males than females (Fig. 3.6a, b), thus resulting in a lack of association. In these two populations, females were found more frequently in close proximity to other adults than to adult males, which are frequently without close companion (Fig. 3.6a, b). For the population at Guacharos, the proximity association between adult age–sex classes was significant ($G = 4.21$, $df = 1$, $p = 0.04$). In this case, proximity between adult females was very infrequent.

When pooling the data from all three populations, we found that neither adult females without dependent infants (Kruskal–Wallis = 0.621, $df = 2$, $p = 0.73$) nor adult males (Kruskal–Wallis = 3.14, $df = 2$, $p = 0.21$) differ in the percentage of samples in close proximity to adult males or adult females (Fig. 3.7a, b). In contrast, differences were found when females with a dependent infant were the focal animals (Kruskal–Wallis = 8.54, $df = 2$, $p = 0.013$). Females with dependent infants were more frequently found near adult males than adult females (Fig. 3.7c).

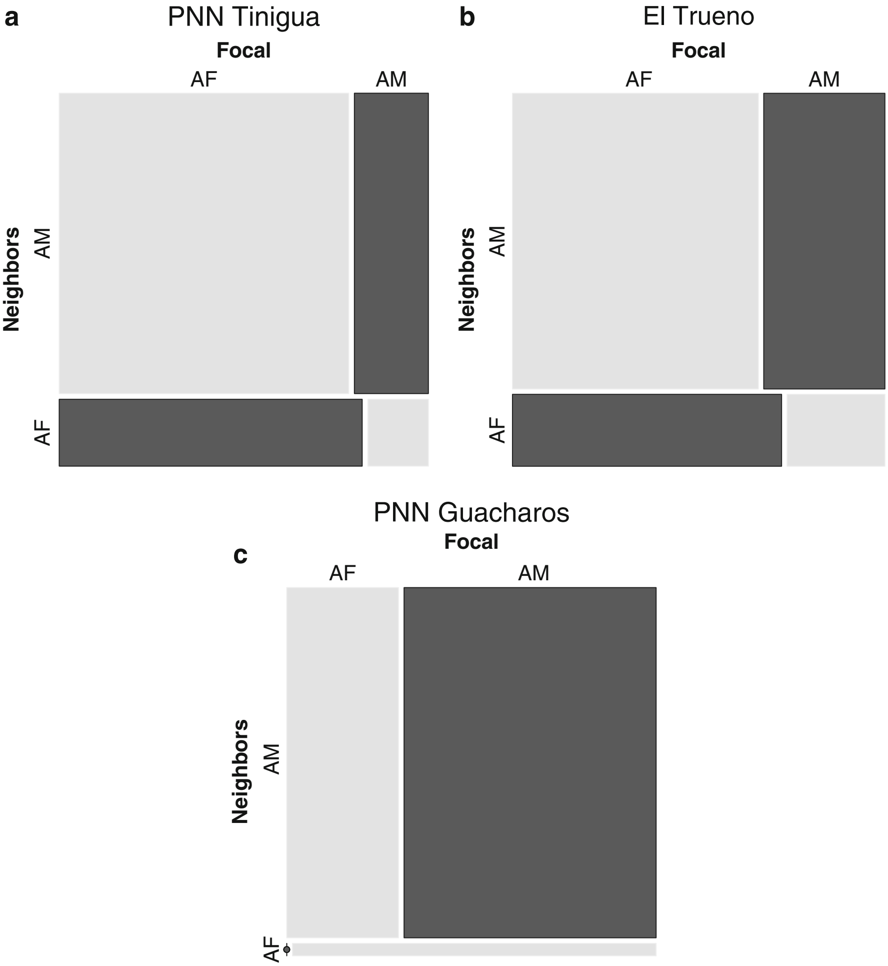


Fig. 3.6 Frequency of samples in which focal adult females and males were found near (<5 m) to other adult males and females (*AF* adult female – including both with and without dependent infant; *AM* adult male). The area for each combination is proportional to the frequency in which the combination was observed in proximity. (**a**) Tinigua NP, (**b**) El Trueno, and (**c**) Guacharos NP

Proximity and Context

We analyzed the average number of neighbors (<5 m) by age–sex focal category discriminating the focal activity. In this analysis, we found a significant difference in the focals' proximity due to their activity ($W = 682.03$, $\mathrm{df} = 7$, $p < 0.001$). This difference is mostly attributable to high frequency of individuals in proximity when the focal animal was engaged in social interactions and in resting (Fig. 3.8.a). Interestingly, we also found a significant difference in the focals' proximity due

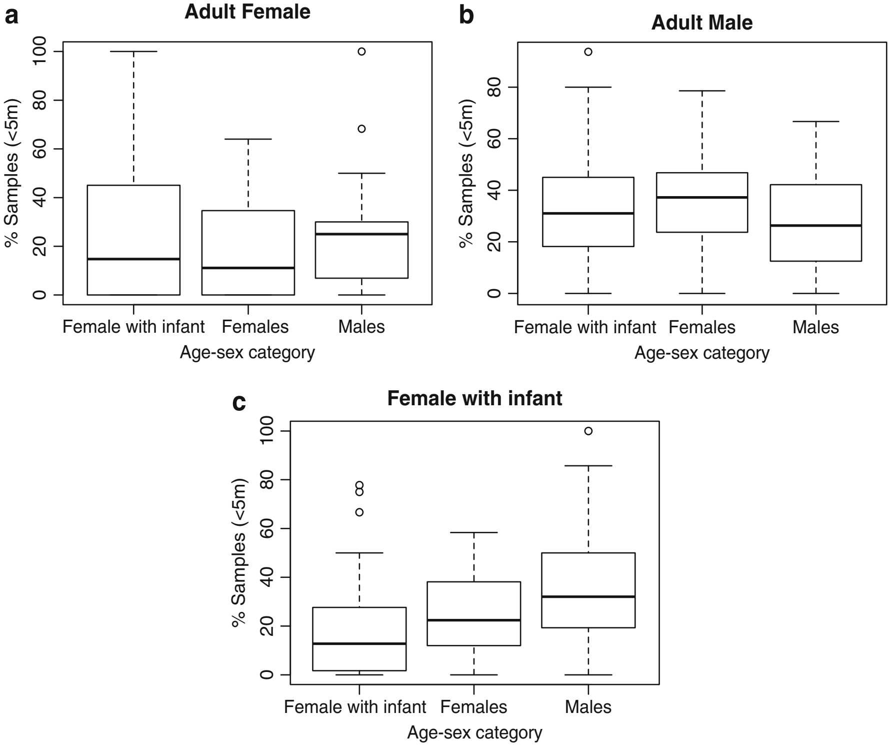


Fig. 3.7 Percentage of samples in which focal adult woolly monkeys, (**a**) adult females, (**b**) adult males, and (**c**) adult females with dependent infants, were found in close proximity (<5 m) to other adult individuals

to the type of food item they were found eating ($W = 157.76$, df $= 7$, $p < 0.001$). In particular, there were a higher number of individuals surrounding the focal when eating fruits than when foraging for arthropods (Fig. 3.8.b).

Social Interactions

Although woolly monkeys at Tinigua were engaged in social interactions more often than individuals at the other two sites (2 % vs. 1 %), monthly variation was high, and we found no significant differences among populations ($X^2 = 2.69$, df $= 2$, $p = 0.26$). Nevertheless, there were some differences in the main type of interactions observed at each site ($X^2 = 20.1$, df $= 4$, $p < 0.001$). For instance, the highest percentages of mating (54.7 %) and chest rubbing (9.4 %) were observed in Tinigua, the population in the El Trueno fragment showed the highest aggression rates (32 %), and the population at Guacharos presented the highest percentages of

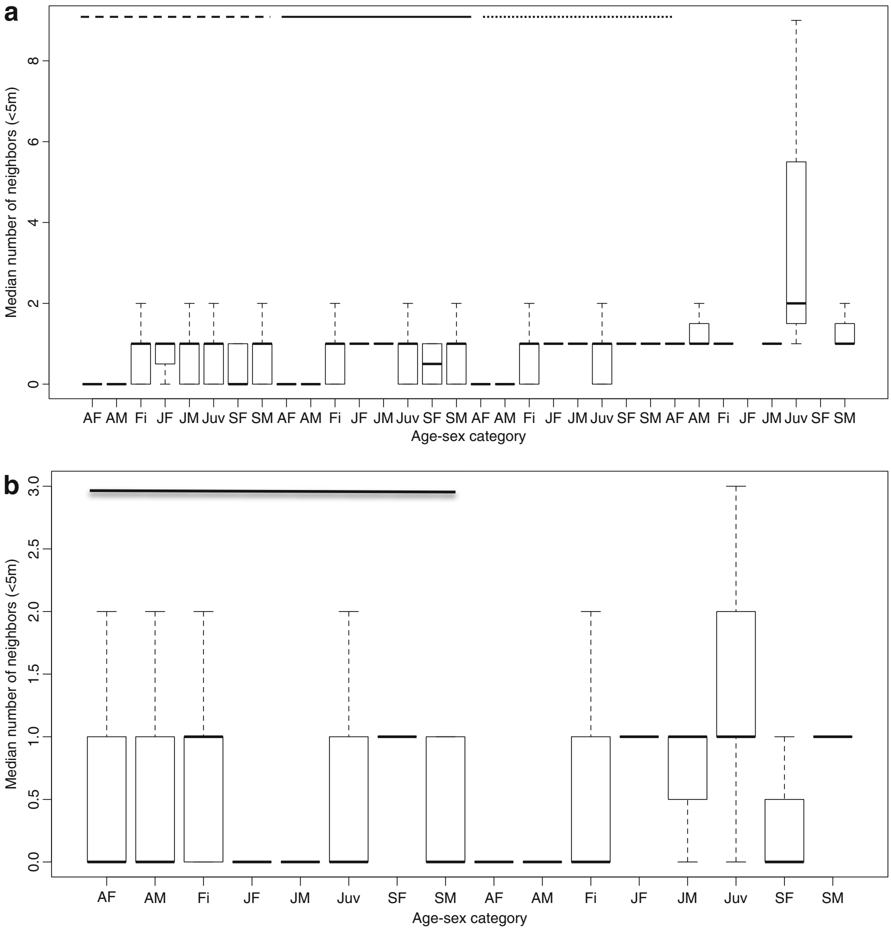


Fig. 3.8 Average number of neighbors (<5 m) by age–sex focal category discriminated by activity. (**a**) Major activities: interrupted *horizontal line*, feeding; *continuous line*, movement; *dotted line*, resting; no bar indicates social interaction. (**b**) Feeding categories: The *black horizontal line* indicates arthropod's consumption by focal, no bar indicates fruit consumption. Age–sex abbreviation categories as in previous figures

grooming (25 %) and the lowest mating rates (20 %). Similar play frequencies were obtained for the El Trueno and Guacharos populations (Fig. 3.9).

Kinship and Social Association

Given the social structure of woolly monkeys, low levels of interactions among adult females were expected. Since females disperse from group to group more often than males, they do not need to establish affiliative relationships among them, perhaps

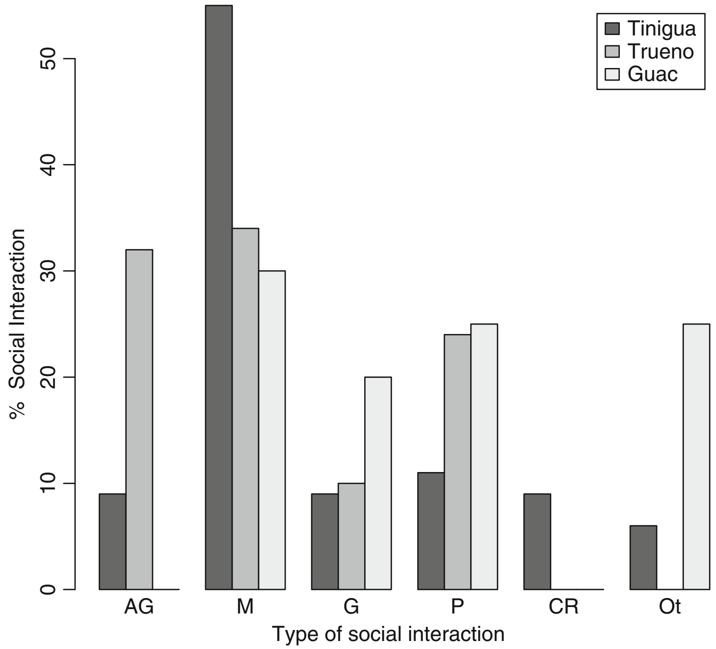


Fig. 3.9 Comparison of the percentage of social interactions in three study sites (*AG* aggression, *M* mating, *G* grooming, *P* play, *CR* chest rubbing, and *Ot* others)

because social status (in terms of the number of aggressions that females receive from males) is highly dependent on good relationships with males. Woolly monkey males are dominant over females (Nishimura 1990, 1994), potentially affecting the feeding rates of females (Stevenson et al. 1994, 1998; Stevenson 2006). According to the results of this study and previous observations (Stevenson 2006), females with infants seem to gain benefits from the association with particular adult males. Recurrent associations between particular females (both old and young adults) and adult males have been observed, which could be interpreted as relationships of parental care from males (which would imply that adult males have the possibility of recognizing their infants), generalized male care based on kin selection, or perhaps mother–offspring relationships (Nishimura 1994). It is also clear that these female–male associations are far from random. For instance, an adult female that gave birth to a female infant in 1990 (Madona) showed an association index of 12 with one of the four adult males (Tostao), four times larger than the association index with the other males (Stevenson 1998). Similarly, Nishimura (1994) reported a strong association between a particular pair in his study group. Nonetheless, these observations do not provide support for the idea of generalized male care, and molecular analyses are required to test whether these pairs represent mother–offspring or male–offspring relationships.

On the other hand, male–male associations, being the preponderant philopatric sex, are expected to show high affinity, but our proximity observations and results from other studies (Nishimura 1994; Di Fiore and Fleischer 2005) do not support this idea. Perhaps, male–male support during intergroup agonistic encounters should be a better social indicator (Stevenson 1998), but such events are rare and occur rapidly and interpretation is difficult. In addition, a potential way to maintain positive intragroup interactions among males is by avoiding proximity during foraging and mating contexts (Nishimura et al. 1992; Stevenson 1998; Di Fiore and Fleischer 2005), which also reduces the chance of male–male grooming bouts. Therefore, our current assessment of the strength of male–male intragroup social affiliations in woolly monkeys indicates low levels of interactions.

In Yasuni National Park at the Ecuadorian Amazon, several studies have been conducted on woolly monkeys' social behavior. In these studies, behavioral data from habituated groups of woolly monkeys have been collected using scan sampling and focal observations. For each sample, individual identity, behavior, and distance to their nearest conspecific were registered. These data were complemented with genetic information retrieved from noninvasive samples. Results from those studies showed similar association patterns in the female's bonding associations to the ones obtained by Di Fiore and Fleischer (2005). These associations were classified as tolerant, but without affiliative relationships. Results on male association patterns were also similar, since in Yasuni males were also reported to avoid frequent contact with other males (Di Fiore and Fleischer 2005). The lack of spatial proximity among *Lagothrix* males in comparison to the strong male associations found in other atelines (Nishimura 1990; Strier 1994b; Di Fiore and Fleischer 2004) is possibly caused by the degree of territoriality and intergroup conflicts, which so far are reported to have more drastic consequences in spider than in woolly monkeys (Link 2011). For instance, in spider monkeys, incursion of several group members (usually leaded by males) into the home range of neighboring groups has been reported to result in attacks causing severe wounds and even deaths. In contrast, such consequences have not been reported for woolly monkeys (although intergroup fights have been observed).

On the other hand, kinship is not the only way that could promote the association and proximity between group members. Even though it has been shown that cooperation is more likely among close maternal kin than either paternal kin or unrelated pairs (Langergraber et al. 2007), cooperation is also common among unrelated individuals (Muller and Mitani 2005). Additionally, in a study on chimpanzees, Gilby and Wrangham (2008) found that a high rate of association between females over a long period of time perhaps reflects their tendency to selectively range in the same area of the territory, instead of representing any particular social affinity between them. These findings support the idea that cooperation requires a "tolerant" relationship (Melis et al. 2006), which may be also affected by the environmental conditions.

Influences of Environmental Factors on Social Interactions

The frequency of social interactions found for the studied woolly monkey populations is within the reported ranges for other atelines (Di Fiore et al. 2010). Results from our study case are consistent with the previous reports, suggesting that despite commonly showing male philopatry, atelines possess high behavioral plasticity. This plasticity could be influenced by competition for resources within and between groups (van Schaik 1989; Strier 1994b). As established in socioecological models, habitat productivity and resource distribution are the most important factors determining relationships among individuals (Sterk et al. 1997; Isbell and Young 2002). Stevenson and coworkers (1994) proposed that arthropod consumption might enhance cohesion in groups of woolly monkeys, which is not a common trait of other atelines. If indeed arthropod foraging makes a relevant ecological difference, it is likely that resource defense is less efficient than in strictly herbivorous primates like the highly frugivorous *Ateles*, and this may be the explanation for a stronger role of male–male alliances in spider monkeys compared to woolly monkeys.

Despite the differences in space availability (forest extension and continuity) between the Tinigua and El Trueno study sites, similar association patterns were found for both populations (Fig. 3.6a, b). This suggests that woolly monkeys in the fragment forest at El Trueno patch still have enough resources (Zárate-Caicedo 2009), which allow them to behave in a similar way compared to undisturbed habitats. However, the highest rate of aggressive encounters in the fragment may be due to the combined effects of a high population density and a limited home range. On the other hand, if resource supply is affecting social interactions, woolly monkeys at the two sites with the highest forest productivity should have more energy for social interactions. In fact, we observed a tendency to find a higher frequency of social behaviors in Tinigua (producing 616 $kg.ha^{-1}.yr^{-1}$ of ripe fruits, Stevenson 2014) than in Guacharos, the least productive forest (327 $kg.ha^{-1}.yr^{-1}$, Cifuentes et al. 2013). However, the frequency of social interactions was also low at the fragment in El Trueno station, which showed high fruit productivity (685 $kg.ha^{-1}.yr^{-1}$, Zárate and Stevenson 2014). This could be explained by the low frequency of mating and chest rubbing in El Trueno, perhaps because many females were pregnant during the study period, and therefore, they were not sexually active. In fact, at the end of the study, 11 females gave birth (Table 3.1), supporting our argument.

In general, our results suggest that a higher availability of resources allows individuals to invest more time performing activities different from foraging (e.g., social interactions), but the overall rates of interactions depend mostly on the social environment. For instance, mating rates are higher when there are several estrous females than when all adult females have infants (Stevenson 1997), and the frequency of playing is also dependent on the number of playmates (as the chance of finding a playmate increases with the number of juveniles in the group). The fact that similar patterns of association among sex and age classes were obtained for the two sites with the highest densities and the presence of large groups (Tinigua NP and El

Trueno station) suggests that density may influence social interactions. However, the highest aggression rate was obtained for the El Trueno population (Fig. 3.9), which showed a similar density to Tinigua's, thus suggesting that aggression rates may not be only affected by population density but also on space requirements. Group size may be an additional factor affecting aggression rates and other social interactions; however, the variation in group size seems to be high in all the sites studied so far (Table 3.1), and the only pattern so far reported is that aggression rates increase as the density of individuals feeding in a patch also increases (as the maximum number of individuals feeding simultaneously in a feeding tree divided by the diameter at breast height of the tree; Stevenson et al. 1998).

Conclusions and Future Directions

Results from this study indicate that patterns of proximal spacing in woolly monkeys show resemblances among populations under similar ecological conditions. There were no strong differences in the interactions determined by proximity between females and males, contrary to what was expected from the female dispersal of woolly monkeys. However, we found differences when comparing the proximity patterns of adult males and adult females, which could be related to a strategy aimed at improving reproductive success. Finally, when comparing populations, it is worth noticing that woolly monkeys in fragments do not deviate from normal social interactions, at least when the patches show high productivity (Zárate and Stevenson 2014). Overall, differences between years and between populations are most likely caused by temporal changes in the composition and status of group members. For instance, the number of infants in one study group at El Trueno increased from 2 to 13 infants in a single year, abruptly changing the composition and status of many adult females within the group. This type of synchronization in births has been attributed to a response to resource productivity peaks (Di Bitteti and Janson 2000); however, resource availability does not usually vary much in the three study sites included in this study.

Results from the proximity analyses for each adult sex class showed differences only for the relationships of focal females with a dependent infant (Fig. 3.7c). These differences could be associated with a higher proximity between these females and adult males, which can directly improve reproductive success by increasing parental attention (Stevenson 2006). Although male parental care, such as infant caring has not been reported in woolly monkeys, it is likely that the presence of nearby males may reduce predation rates and the feeding rates of other individuals (perhaps mediated by biased aggression rates). Interestingly, when adult males are followed, they are not usually observed to be in close proximity to females with infants. An alternative explanation is that even in populations that have been habituated and followed for decades, it is possible that observers are perceived as danger for adult females carrying young infants, and when followed, they actively look for the protection of males (or the males may actively seek the protection of the females being followed). If true, it is likely that even what we observe in habituated populations could be biased by the presence of humans, and the best way to resolve the natural spacing patterns is by the use of GPS devices. Nevertheless, this hypothesis remains to be tested through comparisons between focal and GPS data from females.

We conclude that social interactions in groups of woolly monkeys are affected by many conditions that change over time, such as environmental (e.g., food availability) and social factors (e.g., variation in age and sex structure). In spite of some variation, there is a consistent pattern of interaction and proximity among age–sex classes in all populations. It is clear that the prevalent affiliative relationship corresponds to mother–offspring associations, followed by adult female–adult male interactions. For instance, females with infants seem to seek association with particular adult males. Even though proximity between adult males is quite infrequent (perhaps due to competition), their associations may play relevant roles in intergroup encounters. Similar to what has been found in previous studies, female associations were rarely observed and relationships could be defined as tolerant. This lack of associations can be explained by the female-biased dispersal that characterizes undisturbed populations of woolly monkeys. Although forest productivity and the temporal variation in sex–age structure could determine a particular scenario for each population, all populations studied so far fit the described pattern. Nevertheless, we suggest that at least agonistic interactions might be affected by space requirements.

Which environmental factors promote proximity among females? How can habitat disturbances affect female dispersal and their relationships? Is there some hormonal or genetic signal that enhances or diminishes female interactions? To address these questions and to find out how other factors affect interactions among female woolly monkeys, it is necessary to perform long-term studies in several populations with different environmental and ecological conditions for comparative purposes. In order to untangle the interactions among all the intervening factors, future works should integrate several technological and analytical tools like GPS devices and molecular data.

Acknowledgments We would like to thank the editors of this book for the invitation to participate and to the anonymous reviewers. Doctor Akisato Nishimura kindly provided information on group composition. Permits were provided by Unidad de Parques Nacionales of Colombia and Insituto Sinchi. This study was possible by the funds provided by Primate Conservation Inc., Woolly Monkey Foundation, Margot Marsh Biodiversity Foundation, Colciencias, Banco de La República, and Universidad de Los Andes.

References

Ahumada J (1989) Behavior and social structure of free ranging spider monkeys (*Ateles belzebuth*) in La Macarena. Field Stud New World Monk Macarena Colomb 2:7–31

Altmann J (1974) Observational study of behavior: sampling methods. Behaviour 49:227–267

Aureli F, Di Fiore A, Murillo-Chacon E et al (2013) Male philopatry in spider monkeys revisited. Am J Phys Anthropol 152:86–95

Bennett S (2003) Los Micos de Colombia. Instituto de Investigación de Recursos Biológicos Alexander von Humboldt & Fundación Tropenbos, Bogotá, p 206

Boesch C, Boesch-Achermann H (2000) The chimpanzees of the Taï Forest: behavioural ecology and evolution. Oxford University Press, Oxford

Bradley BJ, Doran-Sheehy DM, Lukas D et al (2004) Dispersed male networks in western gorillas. Curr Biol 14:510–513

Broquet T, Johnson CA, Petit E et al (2006) Dispersal and genetic structure in the American marten, *Martes americana*. Mol Ecol 15:1689–1697

Cifuentes EF, Ramirez M, León JJ, Galvis NF, Vargas S, Stevenson PR (2013) Dieta de los churucos colombianos (*Lagothrix lagothricha lugens*) en relación a la productividad de frutos en el Parque Nacional Cueva de los Guácharos. In: Defler TH, Stevenson PR, Bueno ML, Guzmán DC (eds) Primates Colombianos en Peligro de Extinción. Asociación Primatológica Colombiana, Bogotá, pp 271–289

Clobert J, Le Galliard J-F, Cote J et al (2009) Informed dispersal, heterogeneity in animal dispersal syndromes and the dynamics of spatially structured populations. Ecol Lett 12:197–209

Clutton-Brock T, Janson C (2012) Primate socioecology at the crossroads: past, present, and future. Evol Anthropol 21:136–150

Defler TR (1995) The time budget of a group of wild woolly monkeys (*Lagothrix lagotricha*). Int J Primatol 16(1):107–120

Defler TR (2010) Historia natural de los primates colombianos. Universidad Nacional de Colombia, Bogotá

Development Core Team R (2012) R: a language and environment for statistical computing. R Foundation for Statistical Computing, Vienna

Di Bitteti M, Janson CH (2000) When will the stork arrive? Patterns of birth seasonality in neotropical primates. Am J Primatol 50:109–130

Di Fiore A (1997) Ecology and behavior of lowland woolly monkeys (*Lagothrix lagotricha poeppigii*) in Eastern Ecuador. PhD dissertation, University of California Davis

Di Fiore A (2002) Molecular perspectives and dispersal in lowland woolly monkeys (*Lagothrix lagotricha poeppigii*). Am J Phys Anthropol S34:63

Di Fiore A, Fleischer RC (2004) Microsatellite markers for woolly monkeys (*Lagothrix lagotricha*) and their amplification in other New World primates (Primates: Platyrrhini). Mol Ecol Notes 4:246–249

Di Fiore A, Fleischer RC (2005) Social behavior, reproductive strategies, and population genetic structure of *Lagothrix poeppigii*. Int J Primatol 26:1137–1173

Di Fiore A, Rendall D (1994) Evolution of social organization: a reappraisal for primates by using phylogenetic methods. Proc Natl Acad Sci U S A 91:9941–9945

Di Fiore A, Rodman PS (2001) Time allocation patterns of lowland woolly monkeys (*Lagothrix lagotricha poeppigii*) in a neotropical terra firma forest. Int J Primatol 22(3):449–480

Di Fiore A, Link A, Schmitt CA, Spehar SN (2009) Dispersal patterns in sympatric woolly and spider monkeys: integrating molecular and observational data. Behaviour 146:437–470

Di Fiore A, Link A, Campbell C (2010) The atelines behavioral and socioecological diversity in the new world monkey radiation. In: Primates in perspective. Oxford University Press, Oxford, pp 155–188

Dobson F (1982) Competition for mates and predominant juvenile male dispersal in mammals. Anim Behav 30:1183–1192

Escobar-Páramo P (1999) Inbreeding avoidance and the evolution of male mating strategies. PhD dissertation, State University of New York at Stony Brook, Stony Brook, New York

Fedigan LM, Baxter MJ (1984) Sex differences and social organization in free-ranging spider monkeys (*Ateles geoffroyi*). Primates 25:279–294

Gilby IC, Wrangham R (2008) Association patterns among wild chimpanzees (*Pan troglodytes schweinfurthii*) reflect sex differences in cooperation. Behav Ecol Sociobiol 62:1831–1842

Gonzalez M, Stevenson PR (2010) Comparación de los patrones de movimiento diario, actividad y dieta, reportados para los micos churucos (*Lagothrix lagothricha*): Diferencias producto de la oferta de frutos y de la metodología usada. In: Nassar-Montoya F (ed) Primatología en Colombia: Avances al principio del milenio, Pereira-Bengoa V SPR, Bueno ML. Fundación Universitaria San Martin, Bogotá, pp 3–18

Goodall J (1986) The chimpanzees of Gombe: patterns of behavior. Harvard University Press, Cambridge, MA

Greenwood P (1980) Mating systems, philopatry and dispersal in birds and mammals. Anim Behav 28:1140–1162

Irwin M (2007) Living in forest fragments reduces group cohesion in diademed sifakas (*Propithecus diadema*) in eastern Madagascar by reducing food patch size. Am J Primatol 69:434–447

Isbell LA, Young TP (2002) Ecological models of female social relationships in primates: similarities, disparities, and some directions for future clarity. Behaviour 139:177–202

Izawa K (1976) Group sizes and compositions of monkeys in the upper Amazon basin. Primates 17:327–331

Izawa K, Nishimura A (1988) Primate fauna at the study site La Macarena Colombia. Field Stud New World Monk Macarena Colomb 1:5–11

Jack KM, Fedigan L (2004a) Male dispersal patterns in white-faced capuchins, *Cebus capucinus* Part 1: patterns and causes of natal emigration. Anim Behav 67:761–769

Jack KM, Fedigan L (2004b) Male dispersal patterns in white-faced capuchins, *Cebus capucinus* Part 2: patterns and causes of secondary dispersal. Anim Behav 67:771–782

Kappeler PM, Van Schaik CP (2002) Evolution of primate social systems. Int J Primatol 23:707–740

Koenig A (2002) Competition for resources and its behavioral consequences among female primates. Int J Primatol 23:759–783

Koenig A, Scarry CJ, Wheeler BC, Borries C (2013) Variation in grouping patterns, mating systems and social structure: what socio-ecological models attempt to explain. Philos Trans R Soc B 368(1618):20120348

Langergraber KE, Mitani JC, Vigilant L (2007) The limited impact of kinship on cooperation in wild chimpanzees. Proc Natl Acad Sci U S A 104:7786–7790

Link A (2011) Social and ecological determinants of ‘fission-fusion’ sociality and grouping strategies in the white bellied spider monkey (*Ateles belzebuth belzebuth*) in a lowland rainforest in Western Amazonia. PhD dissertation, New York University, New York

Maldonado A, Botero S (2009) Possible evidence of male dispersal in common woolly monkeys (*Lagothrix lagotricha*). Neotrop Primates 16:76–78

Melis AP, Hare B, Tomasello M (2006) Engineering cooperation in chimpanzees: tolerance constraints on cooperation. Anim Behav 72:275–286

Mitani J, Watts D, Pepper J, Merriwether DA (2002) Demographic and social constraints on male chimpanzee behaviour. Anim Behav 63:727–737

Muller MN, Mitani JC (2005) Conflict and cooperation in wild chimpanzees. Adv Stud Behav 35:275–331

Nishida T (1979) Social structure among wild chimpanzees of the Mahali Mountains. In: Hamburg D, McCown E (eds) The great apes. B. Cummings, Menlo Park, pp 72–121

Nishida T, Corp N, Hamai M, Hasegawa T, Hiraiwa-Hasegawa M, Hosaka K, Hunt KD, Itoh N, Kawanaka K, Matsumoto-Oda A, Mitani JC, Nakamura M, Norikoshi K, Sakamaki T, Turner L, Uehara S, Zamma K (2003) Demography, female life history, and reproductive profiles among the chimpanzees of Mahale. Am J Primatol 59:99–121

Nishimura A (1990) A sociological and behavioral study of woolly monkeys, *Lagothrix lagotricha*, in the upper Amazon. Sci Eng Rev Doshida Univ 31:87–121

Nishimura A (1994) Social interaction patterns of woolly monkeys (*Lagothrix lagotricha*): a comparison among the Atelines. Sci Eng Rev Doshida Univ 35:235–254

Nishimura A (2003) Reproductive parameters of wild female *Lagothrix lagotricha*. Int J Primatol 24:707–722

Nishimura A, Wilches AV, Estrada C (1992) Mating behaviors of woolly monkeys, *Lagothrix lagotricha*, at La Macarena, Colombia (III): reproductive parameters viewed from a long-term study. Field Stud New World Monk La Macarena Col 7:1–7

Oklander L, Kowalewski M, Corach D (2010) Genetic consequences of habitat fragmentation in black-and-gold howler (*Alouatta caraya*) populations from northern Argentina. Int J Primatol 31:813–832

Peres CA (1996) Use of space, spatial group structure, foraging group size of gray woolly monkeys (*Lagothrix lagotricha cana*) at Urucu, Brazil. In: Norconk MA, Rosenberger AL, Garber PA (eds) Adaptative variations of neotropical primates. Plenum Press, New York, pp 467–488

Perrin N, Mazalov V (2000) Local competition, inbreeding, and the evolution of sex-biased dispersal. Am Nat 155:116–127

Pusey A (1987a) Sex-biased dispersal and inbreeding avoidance in birds and mammals. Trends Ecol Evol 2:295–299

Pusey A (1987b) Dispersal and philopatry. In: Smuts BB, Cheney DL, Seyfarth RM (eds) Primate societies. University of Chicago Press, Chicago, pp 250–266

Shimooka Y, Campbell C, Di Fiore A et al (2008) Demography and group composition of *Ateles*. In: Campbell C (ed) Spider monkeys: behavior, ecology and evolution of the genus *Ateles*. The Cambridge University Press, Cambridge, pp 329–348

Soini P (1990) Ecología y dinámica poblacional del "Choro" (*Lagothrix lagothricha*, Primates) en Río Pacaya, Perú. La primatología en el Perú.- Investigaciones primatologicas (1973–1985). Lima, Perú. Galicia, pp 382–396

Sokal RR, Rohlf FJ (1995) Biometry. W. H. Freeman, New York

Sterck EH, Watts DP, Van Schaik C (1997) The evolution of female social relationship in nonhuman primates. Behav Ecol Sociobiol 41:291–309

Stevenson PR (1997) Notes on the mating behavior of woolly monkeys (*Lagothrix lagothricha*) at Tinigua National Park. Field Stud New World Monk Macarena Colomb 10:13–15

Stevenson PR (1998) Proximal spacing between individuals in a group of woolly monkeys (*Lagothrix lagotricha*) in Tinigua National Park, Colombia. Int J Primatol 19:299–311

Stevenson PR (2006) Activity and ranging patterns of Colombian woolly monkeys in north-western Amazonia. Primates 47:239–247

Stevenson PR (2007) Estimates of the number of seeds dispersed by a population of primates in a lowland forest in western Amazonia. In: Dennis AJ, Schupp EW, Green RJ, Westcott DW (eds) Seed dispersal: theory and its application in a changing world. CAB International, Wallingford, pp 340–362

Stevenson PR (2014) Potential determinants of the abundance of woolly monkeys in neotropical forests. In: Defler TH, Stevenson PR (eds) The woolly monkey: behavior, ecology, systematics, and captive research. Springer, New York, pp 207–226

Stevenson PR, Castellanos MC (2000) Feeding rates and daily path range of Colombian woolly monkeys as evidence for between and within group competition. Folia Primatol 71:399–408

Stevenson P, Link A (2008) *Lagothrix lugens*. In: IUCN 2011. IUCN Red list of threatened species. Version 2011.1. www.iucnredlist.org

Stevenson PR, Quiñones MJ (2004) Sampling methods used to quantify activity patterns and diet: a comparative example using woolly monkeys (*Lagothrix lagothricha*). Field Stud Fauna Flora La Macarena Colomb 14:21–28

Stevenson PR, Vargas IN (2008) Sample size and appropriate design of fruit and seed traps in tropical forests. J Trop Ecol 24:95–105

Stevenson PR, Quiñones MJ, Ahumada JA (1994) Ecological strategies of woolly monkeys (*Lagothrix lagotricha*) at Tinigua National Park, Colombia. Am J Primatol 32:123–140

Stevenson PR, Quiñones MJ, Ahumada JA (1998) Effects of fruit patch availability on feeding subgroup size and spacing patterns in four primate species at Tinigua National Park, Colombia. Int J Primatol 19:313–324

Strier K (1987) Demographic patterns in one group of muriquis. Primate Conserv 8:73–74

Strier KB (1991) Demography and conservation of an endangered primate, *Brachyteles arachnoids*. Conserv Biol 5:214–218

Strier KB (1994a) Myth of the typical primate. Am J Phys Anthropol 37:233–271

Strier KB (1994b) Brotherhoods among atelines: kinship, affiliation, and competition. Behaviour 130:151–167

Sugiyama Y (2004) Demographic parameters and life history of chimpanzees at Bossou, Guinea. Am J Phys Anthropol 124:154–165

Symington MM (1987) Sex ratio and maternal rank in wild spider monkeys: when daughters disperse. Behav Ecol Sociobiol 20:421–425

Terborgh J, Janson CH (1986) The socioecology of primate groups. Annu Rev Ecol Syst 17:111–136

Thierry B (2013) Identifying constraints in the evolution of primate societies. Philos Trans R Soc B 368:1618

UAESPNN (2005) Plan de Manejo PNN Cueva de los Guácharos 2005–2009. Unidad de Parques Nacionales Naturales, Bogotá

van Schaik CP (1989) The ecology of social relationships amongst female primates. In: Standen V, Foley RA (eds) Comparative socioecology: the behavioural ecology of humans and other mammals. Blackwell, Oxford, pp 195–218

Vargas S, Léon JJ, Ramírez MA, Galvis NF, Cifuentes E, Stevenson PR (2014) Population density and ecological traits of high land woolly monkeys at Cueva de los Guacharos National Park, Colombia. In: Krzton A, Gursky S, Grow NB (eds) High altitude primates, Developments in primatology. Springer, New York, pp 85–102

Whitlock M, Schluter D (2009) The analysis of biological data. Roberts and Co. Publishers. Greenwood Village, Colorado

Williams JM, Oehlert GW, Carlis JV, Pusey AE (2004) Why do male chimpanzees defend a home range? Anim Behav 68:523–532

Wrangham RW (1980) An ecological model of female-bonded primate groups. Behaviour 75:262–300

Zárate DA, Stevenson PR (2014) Ecological strategies of woolly monkeys (*Lagothrix lagothricha*) in a forest fragment (Guaviare, Colombia). In: Defler T, Stevenson PR (eds) The woolly monkey: behavior, ecology, systematics, and captive research. Springer, New York, pp 227–245

Zárate-Caicedo DA (2009) Primer estudio de estrategias ecológicas de monos churucos (*Lagothrix lagotricha*) en bosques fragmentados (Guaviare, Colombia). MSc. Thesis. Departamento de Ciencias Biológicas. Universidad de Los Andes, Bogotá

Part II
Dispersing Hominine Females

Chapter 4
Dispersal Patterns of Females in the Genus Gorilla

Andrew M. Robbins and Martha M. Robbins

Introduction

Two main theories have been proposed to explain the evolution of female dispersal in plural breeders (Lukas and Clutton-Brock 2011). The first theory is that females disperse to avoid inbreeding, particularly in species where the tenure length of dominant males is greater than the female's age of first reproduction (Clutton-Brock 1989; Clutton-Brock and Lukas 2012). The second theory is that females disperse to avoid the socioecological costs of predation, infanticide, and/or scramble competition for food, particularly in species that do not feed on clumped resources that could promote contest competition and nepotism within groups (Wrangham 1980; van Schaik 1989; Sterck et al. 1997). Inbreeding avoidance is typically considered an explanation for natal dispersal, whereas the socioecological factors can also apply to secondary dispersal. This chapter explores how both sets of theories apply to gorillas.

Gorillas are interesting species for studying these theories because philopatry, natal dispersal, and secondary dispersal are all common and because their populations span a wide range of socioecological conditions. In this chapter, we first provide background information about the socioecological similarities and differences among populations of gorillas. Then we summarize the proximate causes for natal and secondary dispersal, while also noting that females are sometimes forced to change groups when their current group fissions or disintegrates (involuntary transfers). Most of the analyses focus on potential benefits of dispersal, so we conclude by briefly considering some potential costs. The sections in this chapter are often divided into subsections for Background Information, Results, and Discussion.

A.M. Robbins • M.M. Robbins (✉)
Department of Primatology, Max Planck Institute of Evolutionary Anthropology,
Deutscher Platz 6, 04103 Leipzig, Germany
e-mail: robbins@eva.mpg.de

T. Furuichi et al. (eds.), *Dispersing Primate Females*,
Primatology Monographs, DOI 10.1007/978-4-431-55480-6_4

Overview of Gorillas

Gorilla habitat spans ten countries across central Africa (Fig. 4.1). The most numerous subspecies is the western gorilla (*Gorilla gorilla gorilla*), with 50,000–110,000 gorillas living in Angola, Cameroon, Central African Republic, Equatorial Guinea, Gabon, and the Republic of Congo. The most critically endangered subspecies is the Cross River gorilla (*G. g. diehli*) with only approximately 300 gorillas remaining in isolated pockets of Cameroon and Nigeria (Bergl and Vigilant 2007). Grauer's gorillas (*G. beringei graueri*) are found in the Democratic Republic of Congo, where their population has declined drastically to only 2,000–12,000 gorillas due to political instability and war (Mehlman 2007; Yamagiwa 2004). Although their populations have stabilized and even grown in recent years, mountain gorillas (*G. b. beringei*) still have only $\sim$900 individuals in two isolated populations (the Virunga Volcanoes Region and Bwindi Impenetrable National Park) in Rwanda, Uganda, and the Democratic Republic of Congo (Gray et al. 2013; Guschanski et al. 2009, unpublished data)

Gorillas eat leaves and herbaceous material that are high in protein and fruits that are high in soluble sugars (Robbins 2010). The degree of frugivory generally decreases as fruit availability declines at higher altitudes. Western gorillas and Grauer's gorillas both inhabit lowland tropical forests and consume fruit on an

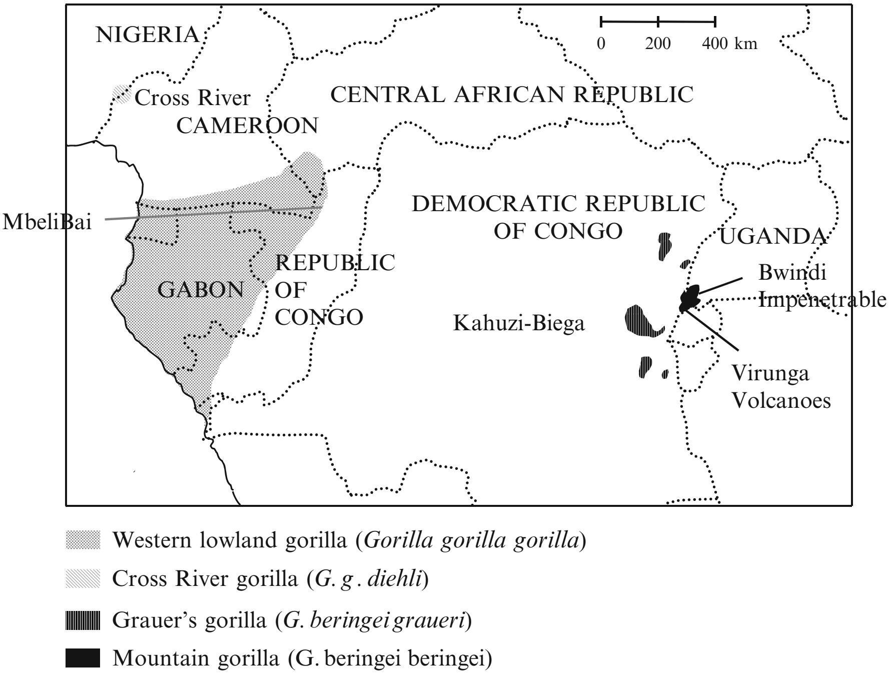


Fig. 4.1 Map of distribution of gorillas in Africa. The locations of major field sites discussed in the text are indicated (Taken from Robbins 2010)

almost daily basis (Doran and McNeilage 1999; Doran et al. 2002; Rogers et al. 2004; Yamagiwa et al. 2003). Bwindi mountain gorillas live in Montane forests at altitudes of 1,400–2,500 m and eat fruit on 60–80 % of days (Robbins and McNeilage 2003; Ganas et al. 2004). The Virunga mountain gorillas inhabit the highest altitudes (>2,500 m) and have almost no fruit in their diet (Fossey and Harcourt 1977; Watts 1984; McNeilage 2001).

Abundant and evenly distributed foliage is expected to lead to low levels of contest competition, negligible benefits of associating with other female kin, and minimal social and ecological costs of transferring to new groups and habitats (Watts 1984; Watts 1994a). The weak social relationships of folivorous female mountain gorillas are consistent with those expectations (Harcourt 1979; Watts 1994a; Robbins et al. 2005). Although growing evidence shows that generalizations can be too simplistic, fruit is generally considered to be a more clumped resource than foliage (e.g. Koenig et al. 1998). As a result, higher levels of frugivory are expected to lead to more within-group contest competition and more differentiated female-female social relationships that include linear agonistic dominance hierarchies (Doran and McNeilage 1998). In contrast with those latter expectations, however, observations at Mbeli Bai failed to show more differentiated social relationships among female western gorillas than mountain gorillas, despite their higher level of frugivory, but those results may be biased by observation conditions (Stokes 2004). Foliage remains a major part of gorilla diets at all locations, which may limit the effect that frugivory has on their social relationships (Robbins 2008).

Gorillas live in relatively cohesive groups that typically contain several adult females, their immature offspring, and at least one adult male (silverback) (Fig. 4.2). Females are rarely found in groups without a silverback, who provides protection against predators and infanticide by outsider males (Watts 1989; Watts 2000). Breeding groups of western gorillas and Grauer's gorillas typically contain only one silverback, but multimale groups are also common among mountain gorillas (Yamagiwa et al. 1993; Gatti et al. 2004; Kalpers et al. 2003; Parnell 2002). Gorillas may also form nonreproductive all-male groups, but most silverbacks are solitary when they have no potential mates. Extragroup copulations are exceedingly rare (Stoinski et al. 2009a). Both male and female gorillas may be philopatric or disperse (Harcourt et al. 1976). Females transfer directly to a solitary male or to another group, but they usually do not transfer with unweaned offspring because unrelated males may kill the infants (Watts 1989; Sicotte 2000; Yamagiwa and Kahekwa 2001; Stokes et al. 2003). Dispersing silverbacks typically become solitary.

Variability in the social system of gorillas arises from several group transitions (Fig. 4.3). Groups form when females transfer to lone silverbacks or when a multimale group fissions (Parnell 2002; Robbins and Robbins 2004; Yamagiwa et al. 2009). Nonbreeding groups become breeding groups when they acquire adult females or when immature females within the group become adults (Robbins 2001). One-male groups become multimale when their immature males become adults, but outsider silverbacks typically do not join or take over breeding groups (Watts 1989; Harcourt and Stewart 2007). Through death and dispersal, multimale groups can become one-male groups, breeding groups can become nonbreeding groups, and

Fig. 4.2 Adult female, infant, and silverback mountain gorilla resting together after rain (Photo by Martha M. Robbins)

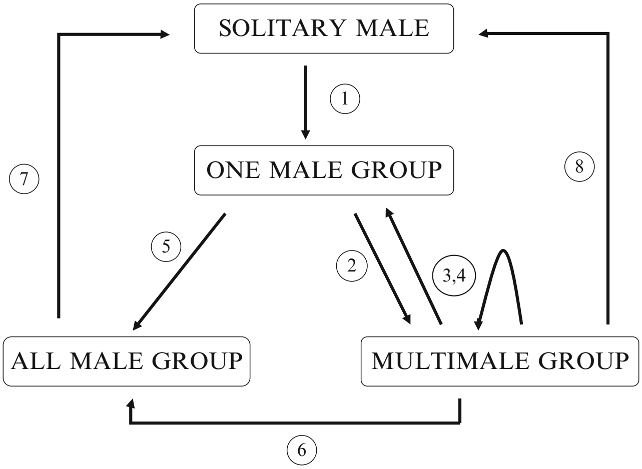


Fig. 4.3 Transitions between types of social units in mountain gorillas. (1) Solitary males acquire females to form one-male groups. (2) One-male groups become multimale when a maturing male becomes a silverback. (3) Multimale groups may become one-male when a silverback dies. (4) Fission of a multimale group leads to two groups that may be either one-male or multimale. (5,6) Males transfer into an all-male group from either a one-male or multimale group. (7,8) Males emigrate to become solitary (Taken from Robbins 2001)

dominant males can become lone silverbacks (Robbins 1995; Robbins et al. 2004). Multimale groups can also become one-male groups through fission (Robbins 2001; Yamagiwa et al. 2009). One-male groups typically disintegrate when the dominant silverback dies: the adult females join an outsider silverback who may kill their infants and evict the other immature males (Watts 1989; Yamagiwa and Kahekwa 2001; Breuer et al. 2010).

Transfers by female gorillas are generally considered voluntary because they are not evicted by resident females or abducted by outsider males (e.g., as in howler monkeys and hamadryas baboons Sicotte 2001). Only a few minutes are needed for females to travel from one group to the other during encounters. Females seem to make "sudden decisions to leave, and why they did not do so during a previous inter-unit encounter, or wait until another one is unknown" (Sicotte 2001, citing Harcourt 1978). Despite the apparent ease of such dispersal, it is not entirely free from outside influences.

One of the most likely causes for dispersal – infanticide protection – is an extreme example of coercion by males (Robbins 2009; Weingrill and van Schaik 2011). Sexual coercion is best defined as "the use by a male of force, or threat of force, that functions to increase the chances that a female will mate with him at the time when she is likely to be fertile, and to decrease the chances that she will mate with other males, at some cost to the female" (Smuts and Smuts 1993). Infanticide by an outsider male may increase the chances that the mother will leave her current group to join him, because the infanticide demonstrates that her current dominant male is unable to protect her offspring (Palombit 2012). Thus, such infanticide may give females a strong incentive to disperse, even though they are not forced to leave (Sterck 1997; Saj and Sicotte 2005).

Another potentially important influence on female dispersal during intergroup encounters is herding by resident males (Sicotte 1993). Herding is defined as "any aggressive behavior performed by a silverback and directed to one of his own females during an encounter" (Sicotte 1993). For example, a resident silverback can interfere with potential female transfers by positioning himself between the female and another group during an encounter and by driving her back toward his own group (Sicotte 1993). Herding has been significantly more frequent in multimale groups than one-male groups of the Virunga mountain gorillas, which may contribute to the lower rates of female emigration from multimale groups (Sicotte 1993, 2001; Robbins et al. 2009c). Females also receive aggressive displays from the dominant male at other times, which may reduce the need for herding by discouraging them from even attempting to transfer (Robbins 2003, 2009). If the risk of injury from herding and male coercion can represent a substantial cost of dispersal for female mountain gorillas, then they may not be able to transfer as freely as typically assumed for folivorous primates (Watts 1992; Sicotte 1994; Robbins 2009).

Aggressive interactions among male mountain gorillas are another potentially important influence on the decision of females to transfer. Harcourt (1978) suggested that aggression is the main tactic by a resident male against others to prevent their association with his females. Aggression during inter-unit encounters was common. Harcourt (1978) and Yamagiwa (1987) classified the social units into an established group, a newly formed group, and a solitary male and pointed out that inter-unit interactions including a newly formed group should be most antagonistic, because a silverback of a newly formed group is always willing to acquire females. By contrast, a silverback of an established group is relatively calm, because he may not prevent young females (his putative daughters) from emigration. So ratio of these three social units in the population may decide the inter-unit relationships. A silverback of a newly formed group tries to lure females away from the other group, but when inter-unit encounter lasts long, he also increases the opportunity to lose his females. A silverback of an established group may not follow young females who transferred into other groups because they are not his mates but his daughters.

Natal Transfers Versus Inbreeding

Background for Natal Dispersal

Natal dispersal is often attributed to inbreeding avoidance, even though theoretical calculations indicate that moderate inbreeding can be favorable (Moore and Ali 1984; Perrin and Mazalov 1999; Guillaume and Perrin 2006). If the costs of dispersal are negligible, then females should breed with relatives when $d(r) < r/(1 + r)$, where r is the relatedness between the female and her mate and $d(r)$ is the inbreeding depression for mating with a relative (Waser et al. 1986). Thus, a female should prefer mating with her father ($r = 0.5$) instead of non-relatives unless $d(0.5) > 1/3$, which is reportedly near the upper range for wild populations (Kokko and Ots 2006; Lehmann and Perrin 2003; Keller and Waller 2002). If the costs of dispersal are substantial, then higher levels of inbreeding become even more favorable in comparison (Waser et al. 1986). These potential benefits of *moderate* inbreeding should not be interpreted to suggest that *all* inbreeding is beneficial (Waser et al. 1986).

Empirical observations provide two slightly different perspectives on natal dispersal versus inbreeding. Among polygynous mammals, natal dispersal by females is typical when their average age at first conception is less than the average tenure of breeding males (Clutton-Brock 1989; Clutton-Brock and Lukas 2012). Those results suggest that natal females disperse to avoid inbreeding with their father. When female mountain gorillas mate with males within their group, it is more common for them to mate with half-brothers and even full brothers than to mate with males who are old enough to be their father (Harcourt 1981; Watts 1990b, 1991b; Harcourt and Stewart 2007; Stoinski et al. 2009a). If females can reproduce with moderately close relatives such as half-brothers (i.e., because such relatives are in the group and the dominant male does not prevent them from mating), then natal dispersal may not be necessary (Watts 1990b). Thus, the main threshold for female dispersal could be when they have any possibility of mating with their father (Clutton-Brock 1989) or only when they have no alternatives who are less closely related (Watts 1990b).

Results for Natal Dispersal

The average age at first conception among Virunga mountain gorillas is 9.1 ± 1.4 years, which is shorter than 14.3 years for the average tenure length of dominant males (Robbins et al. 2009b; Janson and van Schaik 2000). Thus, dispersal by female mountain gorillas is consistent with comparative studies of polygynous mammals (Clutton-Brock 1989; Clutton-Brock and Lukas 2012). Those comparative studies do not explicitly address conditional dispersal within species, however, and their criteria do not seem to explain which nulliparous female mountain gorillas make a natal transfer (Robbins et al. 2009a). Among 44 nulliparous female mountain gorillas observed in the Virungas, 46 % gave birth in their natal group and the other 54 % made a natal transfer. Those 44 nulliparous female mountain gorillas were not significantly more likely to transfer when their group contained a male who was old enough to be their father, even when the male was the dominant silverback and even if the male had already been dominant when they were born. Thus, the female mountain gorillas did not rely entirely upon dispersal to avoid any possibility of inbreeding with such males (Robbins et al. 2009a).

In the same study, 90–95 % of natal nulliparous females were with at least one such potential mate who was not old enough to be their father, so it was difficult to evaluate whether dispersal is significantly more common when such options are missing. Nonetheless, dispersal remained frequent when those options were available, so the Watts (1989) criteria did not seem to explain most of the observed transfers (Robbins et al. 2009a). As indicated above, the Watts criteria are that females may disperse when they have no options to mate with males who are not old enough to be their father (Watts 1990b).

The strongest evidence for inbreeding avoidance was that natal nulliparous females transferred more frequently than non-natal nulliparous females and parous females, who typically have less need to avoid inbreeding. Alternatively, however, those results may arise because non-natal females are less likely to leave a group that they have recently chosen to join (Robbins et al. 2009a, b). Female dispersal is considered a form of mate choice (Sicotte 2001), so most non-natal nulliparous females and parous females have chosen where to mate (via their previous transfers). Thus, natal nulliparous females may be less satisfied with their current group than non-natal nulliparous females and parous females. Natal nulliparous females may also transfer more frequently than non-natal nulliparous females and parous females because they have more time to encounter suitable destinations (See section "Background for Costs of Dispersal").

Among western gorillas at Mbeli Bai (Republic of Congo), natal dispersal was reported for all five preadolescent females that reached transferring age (Stokes et al. 2003). Western gorillas have almost exclusively one-male groups, so those results are similar to the Virunga mountain gorillas where natal nulliparous females were significantly more likely to leave one-male groups than multimale groups (Robbins et al. 2009a). The frequency of female philopatry versus natal dispersal has not been reported for Cross River gorillas, Grauer's gorillas, or Bwindi mountain gorillas due to lack of sufficient long-term demographic data.

Discussion About Natal Dispersal

The natal dispersal patterns of female mountain gorillas provide little support for the empirical models for inbreeding avoidance, and they seem more consistent with theoretical predictions that the consequences of moderate inbreeding may be minimal or even beneficial (Waser et al. 1986; Clutton-Brock 1989; Watts 1990b). Rather than proving that inbreeding does not affect the dispersal patterns of female mountain gorillas, however, the results may instead indicate that any influence is more subtle. For example, when female mountain gorillas are in their natal multimale group with a dominant silverback who could have been their father, their dispersal decisions may depend upon the extent to which he allows them to mate with less closely related subordinates. The costs of inbreeding are predicted to be higher for females than males, which may lead to intersexual conflicts over optimal reproductive strategies (Waser et al. 1986). If so, then differences between natal versus non-natal females may arise with respect to the likelihood that the dominant silverback interferes with subordinate mating attempts, the amount of coercion that females receive from dominant and subordinate silverbacks, and whether the male or the female is more likely to initiate the copulations. Subordinate silverbacks have sired 15 % of offspring born in multimale groups in the Virungas, but the correlations between relatedness, mating patterns, and dispersal of both sexes have not been fully established (Bradley et al. 2005; Stoinski et al. 2009a, b).

Some of the mountain gorilla study groups contained up to five to seven silverbacks, so the results may not apply to the one-male groups of western gorillas or even the rest of the Virungas (Robbins et al. 2009a). The common occurrence of both one-male and multimale groups makes mountain gorillas fairly unusual among primates, as does the prevalence of both natal dispersal and philopatry. Nonetheless, the dispersal patterns of natal female mountain gorillas may reflect a combination of the same factors that influence other primates. Therefore, we compare and contrast the mountain gorillas with three sets of species where one combination of conditions predominates: philopatry in multimale groups, natal dispersal from multimale groups, and dispersal from one-male groups.

Firstly, we compare and contrast mountain gorillas with species that have female philopatry in multimale groups. To some degree, the conditions faced by philopatric female mountain gorillas may resemble some female-bonded species, such as long-tailed macaques (*Macaca fascicularis*) and white-faced capuchin monkeys (Cebus capucinus, Jack 2003; Muniz et al. 2006). Despite frequent male transfers in those species, the male tenure sometimes exceeds the female age of first conception. The dominant male may sire up to 90 % of offspring by unrelated females, but subordinates can sire an even higher proportion of offspring by his daughters (ibid).

So selective mating enables those females to avoid inbreeding with their probable father, yet they do not disperse to avoid familiar males altogether (see also Alberts 1999; Honer et al. 2007). In those female-bonded species, cooperation among kin may be important during feeding competition (Sterck et al. 1997; van Schaik 1989; Wrangham 1980; Schulke and Ostner 2012), so females would probably remain philopatric even if it occasionally imposed some inbreeding costs (plus some subordinate males may be unrelated immigrants). In contrast with those species, however, female mountain gorillas gain little or no apparent benefit from cooperation among kin (because dispersal is common), and it seems less likely that they would accept any net fitness loss from inbreeding. Instead, such inbreeding may optimize their inclusive fitness, as proposed for some rodents and birds (Lehmann and Perrin 2003). Inbreeding depression may increase exponentially with relatedness (Keller and Waller 2002; Charlesworth and Charlesworth 1987), so those costs may not exceed the indirect fitness benefits when the potential mates are only moderately close relatives (Waser et al. 1986; Kokko and Ots 2006). The average fitness consequences among all female mountain gorillas are probably marginal, however, because philopatry and dispersal were both common.

Secondly, we compare and contrast mountain gorillas with species that have natal dispersal by females in multimale groups. Despite the possible benefits of moderate inbreeding, dispersal of natal females is near 100 % in some species with universal male philopatry and large multimale groups (Handley and Perrin 2007; Nagy et al. 2007). For example, in two populations of chimpanzees (*Pan troglodytes*), 90 % of nulliparous females have transferred from their natal group, even though those groups typically provide more mating options than gorilla groups, in which females can usually avoid breeding with close relatives, they sometimes engage in extragroup copulations, and they can suffer breeding delays during transfers (Stumpf 2007; Boesch and Boesch-Achermann 2000; Nishida et al. 2003; Pusey 1980; Constable et al. 2001). Nulliparous female bonobos also transfer from their natal group before they start to reproduce (Chap. 6). Chimpanzees and bonobos (*Pan paniscus*) could be more vulnerable to inbreeding depression than mountain gorillas, if their universal male philopatry leads to less gene flow and greater accumulation of mildly deleterious recessive mutations (Lukas et al. 2005; Guillaume and Perrin 2006; Langergraber et al. 2007; Schubert et al. 2011). Natal dispersal may also be more important for female chimpanzees (but not bonobos) to avoid mating with older males, if those males show more aggressive sexual interest than their mountain gorilla counterparts (Pusey 1980; Furuichi 2011). Even if female chimpanzees can often resist such interest, they may risk injury by doing so (Constable et al. 2001; Stumpf and Boesch 2006). Further study is needed to quantify how such factors may contribute to the benefits of natal dispersal in species with male philopatry and multimale groups.

Thirdly, we compare and contrast mountain gorillas with species that have female dispersal from one-male groups. Hypothetically, the higher frequency of dispersal by natal nulliparous female mountain gorillas in one-male groups (versus multimale groups) could be considered evidence for inbreeding avoidance, because females in one-male groups have fewer potential mates. Natal dispersal is also near 100 %

for other species with one-male mating systems and long male tenures, such as horses (*Equus caballus*, Monard and Duncan 1996; Monard et al. 1996), zebras (*Equus burchelli*, Rasa and Lloyd 1994) and Thomas langurs (*Presbytis thomasi*, Sterck et al. 2005). However, Clutton-Brock's (1989) comparative study showed that the influence of dominant male tenure did not depend on group type, and some natal nulliparous female mountain gorillas left one-male groups even when the silverback was not old enough to be their father. Additionally, natal nulliparous female mountain gorillas may leave one-male groups to avoid infanticide, which would also explain the higher rate of dispersal by parous females from those groups than from multimale groups (See section "Socioecological Influences").

Socioecological Influences

Background for Socioecological Influences

Socioecological models indicate that the abundance and distribution of food, predation pressures, and infanticide risks are the main influences upon the social system and dispersal patterns of primates (Wrangham 1980; Isbell 1991; van Schaik 1989; Sterck et al. 1997). One of the main aspects of social systems that those models address is the group size distribution (Steenbeek and van Schaik 2001). If habitat quality is held constant, feeding competition is expected to increase within groups as they get larger (Isbell 1991; Janson and Goldsmith 1995; Gillespie and Chapman 2001; Robbins et al. 2007). Conversely, larger groups may have advantages in feeding competition between groups (Sicotte 1993; Bermejo 2004; Harris 2006), as well as lower predation risks due to improved detection (Hill and Lee 1998; Rogovin et al. 2004). As a result of those contrasting costs and benefits, the optimal female reproductive success is expected to occur at an intermediate group size (Crockett and Janson 2000; Chapman and Pavelka 2005). The group sizes of some folivores are considered to be smaller than optimal, an apparent discrepancy which is known as the "folivore paradox" or the "original" folivore paradox (Steenbeek and van Schaik 2001; Robbins et al. 2009c).

While intermediate group sizes may represent the optimal trade-off between predation and feeding competition, such groups could also provide the worst conditions for infanticide risks. Infanticide often occurs when a group is taken over by outsider males who had little or no chance of siring its offspring (Hrdy et al. 1994; Janson and van Schaik 2000; Zhao et al. 2011). The probability of such takeovers may increase in one-male groups with a large number of females, so the optimal male reproductive strategies involve a trade-off between higher siring rates versus shorter dominance tenures in those groups (Dunbar 1984). When groups have a large number of females, they are increasingly likely to have more than one female in estrus at the same time, so it may become harder for one male to monopolize reproduction (Alberts et al. 2003; Altmann 1962). Thus, larger groups are more

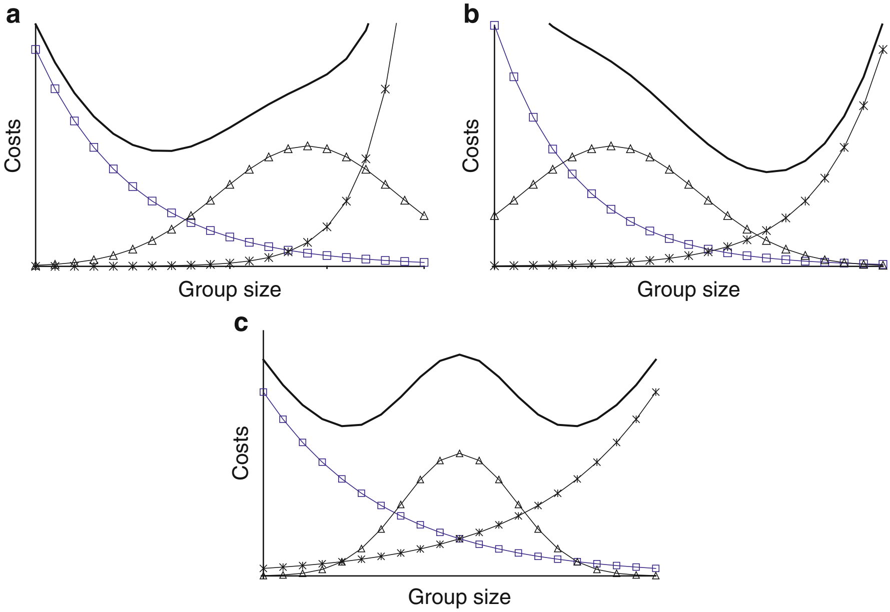


Fig. 4.4 Female reproductive costs versus group size. Costs of predation (*squares*), infanticide (*triangles*), and feeding competition (*asterisks*). The optimal group size occurs when the total cost (*dark solid line*) is minimized. The total cost equals the sum of the other three costs, plus a small fixed cost (independent of group size) is added for purposes of clarity (i.e., so the lines don't overlap). (**a**) Proposed solution to the original folivore paradox, because group size is limited by infanticide risk before feeding competition. (**b**) Potential scenario for a second folivore paradox, if observed group sizes are smaller than optimum, leading to extra infanticide risks even while feeding competition remains minimal. (**c**) Potential for two optimal group sizes under the same socioecological conditions (Adapted from Crockett and Janson 2000; Chapman and Pavelka 2005)

likely to be multimale groups, which typically have lower rates of infanticide than one-male groups (Janson and van Schaik 2000; Lindenfors et al. 2004). As a result of those combined influences, the risk of infanticide may be greatest at intermediate group sizes where the largest number of females can still be monopolized by a single male (Crockett and Janson 2000; Chapman and Pavelka 2005).

The relative importance of predation, feeding competition, and infanticide could have a variety of impacts upon group size and female transfer patterns. The group size of some species may be limited by the costs of infanticide risk more than feeding competition within groups, thus providing a potential explanation for the original folivore paradox (Fig. 4.4a). This explanation applies at an intermediate range of food abundance, which can accommodate some additional females, but not enough to consistently support multimale groups (Crockett and Janson 2000).

Alternatively, total reproductive costs could be minimized at larger sizes, as groups become primarily multimale (Fig. 4.4b). If observed groups were smaller than that optimum, it could be considered a "second" folivore paradox, because the trade-offs are slightly different than the original version. Both paradoxes ask why group sizes are not larger, when the constraints of feeding competition within groups are apparently missing. But whereas infanticide risks may be the constraint that resolves the original paradox with some species, it becomes the driving force for larger groups that creates the second paradox (Robbins et al. 2009c).

Theoretically, both the original folivore paradox and the second folivore paradox could operate under the same conditions, where total reproductive costs can be minimized in either smaller one-male groups or larger multimale groups (Fig. 4.4c). Thus, some populations could find two separate solutions to the same socioecological problems. The double paradox in Fig. 4.4c could lead to a bimodal distribution of group sizes within a population, although such patterns might be blurred by small-scale variability in ecological conditions, as well as other influences upon group size such as male quality. The bimodal effects in Fig. 4.4c might also explain why different species seem to have different social responses to the same (sympatric) ecological conditions (Chapman and Pavelka 2005).

Results for Socioecological Factors

The socioecological consequences of variations in group size have been examined from multiple perspectives. The most direct comparisons with Fig. 4.4 involve analyses of female reproductive success versus group size (Robbins et al. 2007; Stokes et al. 2003). If the costs of dispersal are small, however, then females may transfer as soon as a suboptimal group size begins to reduce their fitness (Gillespie and Chapman 2001; Dias and Strier 2003). If so, then studies of dispersal may provide a more sensitive measure of optimal group size than studies of female reproductive success (Watts 1990a, 1996; Robbins et al. 2009c). Activity budgets and daily travel distances may also be more sensitive to group size than female fitness, but the impact of such variables upon female fitness may not be straightforward (Watts 1988, 1998; Sterck et al. 1997). Finally, the optimal size may be inferred from the actual compositions of groups observed throughout each population.

Western Gorillas The population density of western gorillas has been higher in areas where their staple foods are more abundant (Rogers et al. 2004). Theoretically, the abundance of food can limit population density through scramble feeding competition between groups, if foraging efficiency suffers when multiple groups use the same area (van Schaik 1989). Such limitations can also intensify feeding competition within groups, potentially leading to lower reproductive success in larger groups (Isbell 1991; Robbins et al. 2007). Nonetheless, the birth rate and offspring survivorship to age one were not significantly correlated with the total number of gorillas per group or the number of adult females per group among western gorillas at Mbeli Bai (Stokes et al. 2003).

Although offspring survivorship to age one was not significantly correlated with group size, males with larger harems had significantly higher offspring survival to age four (Stokes et al. 2003; Breuer et al. 2010). The risk of predation may increase as infants get older and become more independent of their mother (Breuer et al. 2010). In contrast, the risk of infanticide may decrease as offspring approach weaning age, because males have less incentive to kill infants whose mother will soon resume cycling anyway (Hrdy 1977, 1979). Thus, the effects of harem size on offspring survival (at ages one versus four) were considered more consistent with the predictions for predation than for infanticide (Breuer et al. 2010). In addition, males with larger harems had significantly longer observed tenure lengths, which suggests that their infants were not at greater risk of infanticide from outside takeovers. Collectively, therefore, the results for offspring survival and dominance tenure length gave no indication that the optimal harem size might be limited by the risk of infanticide (Breuer et al. 2010).

Dispersing females at Mbeli Bai showed a preference for joining smaller groups following group disintegrations, but the overall rate of immigrations per year was not significantly correlated with group size, and groups with more females had more voluntary emigrations per year (Stokes et al. 2003). If group size does not influence the probability that a female will emigrate, then more emigrations will be expected in groups that have more potential emigrants (Harcourt and Stewart 2007). Therefore, the latter two results are both consistent with the hypothesis that group size does not influence female dispersal (Harcourt and Stewart 2007). Collectively, the analyses for female reproductive success and dispersal show little evidence of any influence from group size, and the two significant results are in opposite directions (males with larger harems have higher infant survival through age four, yet females prefer smaller harems after their group disintegrates).

Virunga Mountain Gorillas In the Virungas, no decline in female reproductive success was observed in larger groups, even as those groups became three to five times larger than average (Robbins et al. 2007). For example, group size accounted for less than 0.1 % of the variance in the average interbirth intervals of 39 females. Infant mortality was significantly higher in one-male groups than multimale groups, partly because infanticide occurs when one-male groups disintegrate after the dominant male dies. Infant survival was not significantly correlated with group size even after controlling for group type (Robbins et al. 2007). Thus, the analyses of reproductive success gave no indication of any socioecological limitations on group size. Analyses of activity budgets and daily travel distances also showed little or no costs for females living in larger groups (Watts 1988, 1998).

Analyses of female dispersal patterns in the Virungas may have reflected the temporal variations in relative proportions of solitary males, one-male groups, and multimale groups that the study groups were encountering. In the early phase, study groups encountered primarily one-male units, and transferring females preferred smaller newly formed units (Harcourt et al. 1981a). As the study groups began to encounter a higher proportion of multimale groups than before, an analysis of transfer destinations showed that females had a preference for multimale groups (Watts

2000). Most recently, the study groups (and the groups they encountered) became exclusively multimale, and dispersal patterns showed mixed results (Robbins et al. 2009c). Both parous and natal nulliparous females were significantly more likely to leave one-male groups than multimale groups, but differences in immigration rates were not significant. Transferring females joined multimale groups more frequently than expectations based on relative quantity of each group type, but not when based on how often females encountered each group type. The analyses of secondary dispersal also gave no indication of any socioecological limitations on group size (Robbins et al. 2009c).

Other Gorilla Populations Among the Bwindi mountain gorillas, infant mortality was not significantly higher in one-male groups than multimale groups, perhaps because no disintegrations occurred during the 49.8 group-years of the study so there was no opportunity for infanticide (Robbins et al. 2009d). Other aspects of female reproductive success and secondary dispersal have not been reported for the Bwindi mountain gorillas, Grauer's gorillas, or Cross River gorillas.

Discussion About Socioecological Influences

Paradoxical Gorillas

Although western gorillas are more frugivorous than the Virunga mountain gorillas, they might be a better example of the original folivore paradox. Western gorillas still have natural predators (unlike mountain gorillas), and their maximum group size seems to be more limited than mountain gorillas (Parnell 2002; Fay et al. 1995; Magliocca et al. 1999; Yamagiwa et al. 2003). The analyses of birth rates showed no significant evidence that feeding competition is limiting female fertility within larger groups (Stokes et al. 2003). Females preferred smaller groups after their previous group disintegrated, but other dispersal patterns showed no significant influence from group size (Stokes et al. 2003). If any costs of feeding competition are insignificant, then it is unclear why female western gorillas remain in smaller groups, despite predictions of higher predation risks in small groups than in large groups.

Data for female reproductive success, dispersal, and social system suggest that the second folivore paradox may apply to the Virunga mountain gorillas (Kalpers et al. 2003; Robbins et al. 2007, 2009c). One-male groups have significantly higher rates of infanticide and overall infant mortality than multimale groups (Fossey et al. 1984; Watts 1989; Robbins et al. 2007). The analyses of interbirth intervals showed no significant evidence that feeding competition is limiting female fertility, even as the study groups became three to five times larger than average (Robbins et al. 2007). Female dispersal patterns also showed no evidence of feeding competition within groups, and mixed results emerged regarding any preference for multimale groups (Robbins et al. 2009c). If any costs of feeding competition are insignificant, then it is unclear why 50–60 % of adult female mountain gorillas live in smaller one-male groups, despite the higher risk of infanticide.

Male Quality

The folivore paradox models do not explicitly account for one variable that could potentially explain the social system of both gorilla populations: variability in male quality. Indeed, variability in male quality may generally confound analyses of infanticide risks versus group size and group type, just as variability in habitat quality can confound analyses of feeding competition versus group size (e.g., Gillespie and Chapman 2001). For western gorillas, analyses have already shown that larger males have both higher infant survival and larger harems, which suggests that male quality could influence univariate analyses of infant survival versus harem size (Caillaud et al. 2008; Breuer et al. 2010, 2012). Even if infanticide risks increase in *each* individual group as it accumulates more females, those patterns may not be apparent from the *average* infanticide rates among all groups, if larger groups have males who can provide better protection (higher-quality males). Multivariate analyses (with larger sample sizes) are needed to evaluate group size and male quality simultaneously.

In contrast with western gorillas, measurements of male quality are not yet available for mountain gorillas, but a theoretical model has predicted that one-male groups can have lower infanticide risks than multimale groups, if their dominant male has exceptional strength (Pradhan and van Schaik 2008). The *average* infanticide rate has been significantly higher in one-male groups than multimale groups, but again, variability in male quality could give *some* one-male groups a lower infanticide risk than some multimale groups (Robbins et al. 2007). If so, then variability in male quality could explain the variability in social system of mountain gorillas (i.e., the prevalence of both one-male and multimale groups).

When subordinate silverbacks get fewer mating opportunities within a multimale group, they are more likely to emigrate, which increases the probability that the group will become one-male (Stoinski et al. 2009b). Reproductive skew within multimale groups is expected to depend upon the ability of the dominant male to monopolize reproduction, as well as his need to offer concessions to encourage subordinates to stay (Robbins and Robbins 2005; Bradley et al. 2005; Stoinski et al. 2009b). Dominant males with higher quality should have greater competitive ability to monopolize reproduction within groups and less need for help from subordinates to protect the group against outsider males. Therefore, it would not be surprising if the average quality of dominant males was higher in one-male groups than multimale groups.

Phylogenetic Inertia

Another potential explanation for the second folivore paradox is that the dispersal patterns and distribution of female mountain gorillas may not fully reflect the lower risk of infanticide in multimale groups. Mountain gorillas do not have some traits that are typical of species with multimale groups, such as large female sexual swellings, long estrous periods, and large testes size (Harcourt et al. 1981b; Nunn 1999; Harcourt and Stewart 2007). Those distinctions may indicate that multimale groups are a recent development in the evolutionary history of mountain gorillas (Harcourt and Stewart 2007; Robbins et al. 2009c). If so, then a female preference for multimale groups may not have fully evolved. Mixed results have emerged from assessments of phylogenetic constraints in macaques, lemurs, colobines, and other primates (Thierry et al. 2000; Korstjens et al. 2002; Ossi and Kamilar 2006; Chapman and Rothman 2009). A comparative study of infanticide rates may be most relevant (Janson and van Schaik 2000), because infanticide risks are the reason why females are predicted to prefer multimale groups. Janson and van Schaik (2000) found that the greatest variations in infanticide rates arose within species rather than among species, which suggests that phylogenetic constraints were not important.

Alternatively, if phylogenetic constraints are unimportant, and females can adjust quickly to changes in socioecological conditions within a population, then temporal variations in the dispersal patterns of the Virunga mountain gorillas might be consistent with the bimodal effects of the double folivore paradox (Fig. 4.4c). Following the first decades of observations, analyses showed that transferring females preferred smaller newly formed units, which is consistent with the minimum of reproductive costs on the left side of Fig. 4.4c, especially if predation costs are negligible (Harcourt et al. 1981a). As the distribution of encounters between different types of social units became more mixed, a preference emerged for multimale groups, which would start to push the groups toward the optimum on the right side of Fig. 4.4c (Watts 2000). In recent years, encounters were primarily with multimale groups, so it became harder to see any transfer bias toward them. Instead, the strongest result is that females within such groups had a lower frequency of emigration (Robbins et al. 2009c). A limit on group size is not yet apparent, which indicates a lack of feeding competition within groups, so the groups have not yet reached the right edge of Fig. 4.4c. The shift from one optimum to the other could arise from demographic stochasticity, even without an improvement in ecological conditions, or it could have been aided by an easing of human disturbances.

Further Study

As with many aspects of the socioecological model, further clarification of this paradox may emerge from more detailed analyses of its components (Schulke and Ostner 2012). Analyses of group size versus interbirth intervals, daily travel distances, and activity budgets may provide clearer evidence regarding feeding competition within groups of western gorillas. Analyses of group size versus rates of infanticide and predation would provide clearer evidence regarding the causes of infant (and adult female) mortality. Some of those components are admittedly difficult to measure, especially in a bai study that does not follow the gorillas all the time.

Closer evaluation of intergroup encounters may also help to explain why female gorillas transfer (Sicotte 1993; Caillaud et al. 2008; Robbins and Sawyer 2007; Bermejo 2004; Magliocca and Gautier-Hion 2004). Female transfers always occur during encounters with outsider males, and the encounters provide an opportunity for females to evaluate those males (Sicotte 2001). Females exhibit a strong preference to associate with at least one silverback (rather than ranging alone), and that preference could be based on a phylogenetically common tendency to rely on males for protection. From a very young age, females would recognize the protection that silverbacks provide, and they would be accustomed to relying upon such protection. In contrast, most female mountain gorillas would have little or no direct experience with disintegrations of one-male groups, and the infanticide that occurs during those disintegrations represents the most clear-cut incentive for females to prefer multimale groups. Females may not need direct experiences of group disintegrations if an inherent preference for multimale groups has already evolved in this population. Nonetheless, the scarcity of such direct experiences could impede the evolution of an inherent preference for multimale groups. Females might be more likely leave any group where protection is weak, regardless of how many silverbacks it contains. If so, then the outcome of male competition during intergroup encounters may have greater influence on female dispersal decisions than the probability of disintegration when the dominant male dies.

Involuntary Dispersal

This section describes two types of dispersal that may be considered involuntary because the female is forced to make a decision: group disintegrations and group fissions. Females almost always associate with a silverback for protection from predation and/or infanticide, so when a one-male group disintegrates after the dominant male dies, the resident females must find a replacement and their offspring are most vulnerable to risk of infanticide (Watts 1989; Yamagiwa and Kahekwa 2001). Similarly, when two silverbacks separate from each other in a multimale group, then females must choose to stay with one male or the other (Robbins et al. 2001). In most cases, the subordinate male emigrates without any other group members and becomes a lone silverback (considered a male dispersal, not a group fission), but in other cases immature males and/or adult females may leave with him (Stoinski et al. 2009b).

Group Disintegrations

Among western gorillas at Mbeli Bai, 8 of 27 cases of female dispersal (30 %) followed the death of the dominant silverback, which illustrates that involuntary transfers can represent a substantial portion of overall female dispersal (Stokes et al. 2003). In those eight cases, the remaining females and immature male gorillas traveled for up to 2 weeks before joining outsider silverbacks. In two cases (25 %), the outsider silverback did not kill a infant from the former group, and he allowed immature males to join his group too. In two other cases, an individual adult female joined an outsider silverback who (presumably) killed her infant (Stokes et al. 2003). While including those previous cases, a subsequent study showed that 9 of 11 infants (82 %) disappeared and were presumed killed following the death of the silverback in their group (Breuer et al. 2010).

Among the Virunga mountain gorillas, five group disintegrations following the death of the dominant silverback were reported from 1974 to 1985 (Fossey et al. 1984; Watts 1989). The remaining females and immature male gorillas traveled for up to 2 months before joining outsider silverbacks. The 5 group disintegrations led to 11 known or suspected cases of infanticide with no reported cases of infants surviving (Fossey et al. 1984; Watts 1989). The outsider silverback generally did not allow immature males to join his group, and most of them formed an all-male group which lasted for more than 12 years (Yamagiwa 1987; Robbins 1995). No subsequent group disintegrations were reported among the Karisoke groups through 2007, but the groups had become almost exclusively multimale for most of those subsequent years (Robbins et al. 2007; Robbins et al. 2009c). No disintegrations occurred during 49.8 group-years of observations reported for the Bwindi mountain gorillas (Robbins et al. 2009d).

Among Grauer's gorillas, no infanticide was reported following the deaths of eight silverbacks, despite the predominance of one-male groups (Yamagiwa et al. 2009). Following the deaths of two of those silverbacks, the remaining females and immature male gorillas traveled for up to 27 months before joining outsider silverbacks, and five infants were not killed (Yamagiwa and Kahekwa 2004). Indeed, no infanticide was observed in any context while two to four groups were monitored from 1972 to 1998, even though ten females had infants when they changed groups (Yamagiwa and Kahekwa 2001, Yamagiwa and Kahekwa 2004). In 2003, however, three infants were killed when their mother transferred, even though their putative father was still alive.

Collectively, these results show considerable variability in the rates of infanticide within and among gorilla populations, which is qualitatively consistent with the high variability within and among populations of other primates (Janson and van Schaik 2000; Palombit 2012). Possible causes for such variability within species include differences in the magnitude of human disturbances, differences in population density (particularly the proportions of young adult males), and genetic polymorphism (Butynski 1990; Janson and van Schaik 2000; Yamagiwa and Kahekwa 2004; Palombit 2012). Infanticide rates could also depend on how easily females can leave aging males with reduced ability to protect their offspring (Sterck et al. 2005). A comparative study among primates suggests that infanticide rates are higher in species with higher rates of dominant male replacements (deaths plus takeovers), in species with more one-male groups than multimale groups, and in species that are folivores rather than frugivores (Janson and van Schaik 2000).

Group Fissions

The most thoroughly documented group fission occurred in the Virungas when two subordinate silverbacks formed separate groups after the dominant male died (Robbins et al. 2001). The group had ten adult females and two subadult females before the fission, and those females generally chose to stay with the subordinate with whom they had greater proximity, more affiliative interactions, more aggressive interactions, and more copulations prior to the death of the dominant male. Female relatives were also likely to stay together after the fission, but the overall distribution illustrates the importance of male-female relationships in determining group compositions (Robbins et al. 2001).

From 2004 to 2007, six additional fissions occurred in multimale groups of Virunga mountain gorillas while the dominant male was still alive (Stoinski et al. 2009b). In each case, a subordinate silverback left the group along with one to three adult females. In four of those cases, the emigrating silverback lost the females within 2 months, but in the other two cases he maintained the group and sired offspring. No details were reported about the relationships among the silverbacks and the females leading up to the fissions (Stoinski et al. 2009b). The sudden increase in such fissions occurred as the groups became much larger than typical (with up to five to seven silverbacks). The Virunga mountain gorillas have been studied for more than 40 years, but many more group-years of study will be needed to understand the probabilities of rarely occurring events such as fissions and infanticides, which illustrates the value of maintaining long-term research even when primate populations are already relatively well studied (Clutton-Brock and Sheldon 2010; Kappeler et al. 2012).

A group of Bwindi mountain gorillas fissioned in 2002, forming a new one-male group with five adult females while the original group retained four silverbacks and six adult females (Robbins et al. 2009d). Subsequent genetic analyses indicated that the dominant male of the original group retained eight offspring that he sired (and their mothers), while the subordinate silverback left with two offspring of unknown paternity (Nsubuga et al. 2008). Those results again suggest that male-female relationships played an important role in determining group compositions.

Two fissions have also been observed among groups of Grauer's gorillas while the dominant male was still alive (Yamagiwa and Kahekwa 2001). The two emigrating silverbacks were 12–13 years old, which are both much younger than the range of 14–17 years for the six fissions in the Virungas (Yamagiwa and Kahekwa 2001; Stoinski et al. 2009b). Those age differences suggest that the maturation of males from blackbacks into silverbacks is a gradual process (Breuer et al. 2009), with variability both within and among populations, which is not fully represented by the dichotomous distinction between one-male versus multimale groups (often based solely on age of males). If so, then efforts to evaluate female preferences for multimale groups may be confounded by variability in the quality of subordinate silverbacks as well as the dominant males (See section "Male Quality").

Costs of Dispersal

Background for Costs of Dispersal

The potential costs of female dispersal include higher mortality and lower reproductive success due to greater predation risks and poorer foraging efficiency in unfamiliar environments (Koopman et al. 2000; Printes and Strier 1999; Williams et al. 2002). Predation risks can be minimized by transferring short distances (Dobson et al. 1998) or through associations with other species (Korstjens and Schippers 2003). Foraging efficiency can be maintained by transferring to other groups within the same habitat ("social" versus "locational" dispersal, Isbell and Van Vuren 1996). Even when transferring to a neighboring group, immigrants may face aggression from resident females (Isbell and Van Vuren 1996; McGraw et al. 2002; Payne et al. 2003). Dispersing females lose access to kin as potential coalition partners in the defense of resources, although some females may transfer in tandem. Aggression might also be reduced by visiting potential transfer destinations beforehand (Idani 1991), by choosing groups that contain familiar females (Monard and Duncan 1996), and/or by establishing alliances with males within the new group (Boesch and Boesch-Achermann 2000). Stress from such aggression has been implicated for breeding delays after direct transfers, even for nulliparous females (Berger 1987; Nishida et al. 2003; see also Crockett and Pope 1993; Pusey 1987). Females may also delay conception while waiting to encounter a suitable destination if they cannot disperse while pregnant or lactating due to the risk of infanticide (Sterck 1997).

Parous females in the Virungas may be potential candidates for breeding delays before transfers if they postpone conception while waiting to encounter a suitable destination (Robbins et al. 2009b). Intergroup encounters occur only about once a month which includes cases when the groups stay as far apart as 500 m (Sicotte 2001). Some adult males may avoid encounters with other groups to prevent females from transferring (Watts 1994b, 1998). Female mountain gorillas rarely transfer while pregnant or lactating, so after the death or weaning of an infant, parous females have only a few months when they can transfer before conceiving again (Watts 1990b; Harcourt et al. 1980). Thus parous female mountain gorillas may have limited opportunities to transfer (Robbins et al. 2009b). In contrast, the age of natal transfers by nulliparous females had a standard deviation of ±18 months, so they seem to have a much wider window of opportunity for dispersal (Robbins et al. 2009b).

Evidence is more limited to support any expectation that mountain gorillas might face breeding delays after dispersal. An initial study did not show significantly higher aggression toward immigrants than established females (Harcourt 1979), but immigrants received more aggression for at least three years after joining a larger group where some of the established females were closely related (Watts 1991a, 1994c). Only one minor example has been reported for females to face difficulties eating unfamiliar foods (Byrne 2001).

Results for Costs of Dispersal

Females who made a natal transfer did not have a significantly later age of first reproduction than those who gave birth in their natal group, which suggests that dispersal did not lead to breeding delays for nulliparous females (Robbins et al. 2009b). Analyses of parous females produced inconsistent results. Firstly, interbirth intervals of parous females with a surviving offspring were significantly longer when they transferred (than when they didn't transfer), which may suggest that the transfer led to breeding delays (Robbins et al. 2009b). Secondly, however, there was no significant evidence of breeding delays before dispersal for parous females, because transfers typically occurred at the time when other parous females would be conceiving their next offspring (Robbins et al. 2009b). Thirdly, there was no significant evidence of breeding delays after dispersal by parous females, because immigrants typically conceived within a few months just like parous females who did not transfer (Robbins et al. 2009b). Finally, females were more likely to transfer after an infant died, which suggested that dispersal might also be more likely when they have other reproductive difficulties that are harder to detect, such as lower fertility or miscarriages (Robbins et al. 2006, 2009b).

Discussion About Costs of Dispersal

Dispersal did not lead to breeding delays for nulliparous female mountain gorillas, which is similar to the results for Thomas's langurs but in contrast with data for chimpanzees (Nishida et al. 2003; Sterck et al. 2005; Robbins et al. 2009b). Like chimpanzees, immigrant female mountain gorillas can receive aggression from residents, and they may benefit from protection by males in the new group (Watts 1991a; Boesch and Boesch-Achermann 2000). If resident males take greater interest in protecting immigrants who are sexually active, then it may be safer for females to postpone dispersal until they reach sexual maturity (Boesch and Boesch-Achermann 2000; Field and Guatelli-Steinberg 2003). The period of adolescent sterility apparently gives female mountain gorillas enough time to find new groups while sexually active, without the risk of conceiving in their natal groups. Adolescent sterility has been reported for many female primates, but further study would be needed to determine whether it has special adaptive importance for species with female transfers (Knott 2001).

For parous female mountain gorillas, interbirth intervals were significantly longer when they contained a transfer, but the more detailed analyses did not provide significant evidence of delays either before or after dispersal (Robbins et al. 2009b). The main hypothesis was that females would postpone conception while waiting for encounters with suitable transfer destination, but the intervals before transfers were not significantly longer than females typically take to conceive. Furthermore, the longest apparent delays were linked to possible reproductive difficulties, such as lower fertility, miscarriages, and infant mortality. Thus, rather than concluding that dispersal leads to reproductive delays, it seems more likely that reproductive difficulties lead to dispersal. And indeed, the probability of transfer was higher following the death of an infant than when the offspring survives (Robbins et al. 2009b).

No analyses have been reported for reproductive delays or other costs of dispersal among gorilla populations beyond the Virungas. Breeding delays might be expected when Grauer’s gorillas travel for up to 27 months without an adult male in the group, but it was not reported whether any females were in estrus during such times (Yamagiwa and Kahekwa 2001). If western gorillas face greater constraints on group size than mountain gorillas (See section “Paradoxical Gorillas”), then female immigrants might face greater aggression which could lead to breeding delays after dispersal. The genetic structure of Cross River gorillas and Bwindi mountain gorillas indicate that the distribution of females is influenced by distance, altitude, and plant community composition, which suggest that those females prefer to remain in familiar habitats (Guschanski et al. 2008). Although intergroup encounters can enable a female to assess outsider males, she may have greater difficulty assessing the entire home range of a potential transfer destination. If so, then females may experience breeding delays after transferring to less familiar habitats, and the genetic structure might suggest that they eventually transfer back. In addition, females might be less likely to transfer when they are in relatively unfamiliar habitat within their home range (i.e., the fringes rather than the core), because any group they encounter in those areas could have more unfamiliar habitat throughout its home range. Further study is needed to show how female dispersal patterns contribute to the genetic structure of gorilla populations.

Conclusions

Although gorillas live in a wide range of habitats with varying degrees of frugivory, all of their populations exhibit the pattern of female dispersal that characterizes many non-female-bonded social groups of folivores. Natal dispersal is common for gorillas, as expected for species where their average age at first conception is less than the average tenure of breeding males. Nonetheless, such criteria for inbreeding avoidance did not explain conditional dispersal among the Virunga mountain gorillas (i.e., predicting which females would transfer versus give birth in their natal group). Analyses of female reproductive success and secondary transfers gave no indication that feeding competition limits the group size of western gorillas or mountain gorillas, although group size appears to be more constrained in western gorillas. As a result, western gorillas may be an example of the original folivore paradox: if any costs of feeding competition are insignificant, then why are females remaining in smaller groups, despite predictions of higher predation risks? Mountain gorillas no longer have natural predators, but they may be an example of a second folivore paradox: why do 50–60 % of females live in smaller one-male groups, despite a higher risk of infanticide? Transfers by female mountain gorillas did not show a consistent preference for multimale groups. A mathematical model and empirical results from western gorillas suggest that variability in male quality may resolve both paradoxes (Pradhan and van Schaik 2008; Caillaud et al. 2008; Breuer et al. 2010; Breuer et al. 2012). In addition, the influence of infanticide may vary considerably among gorilla populations. Preliminary analyses showed little evidence of any cost of dispersal by mountain gorillas in the Virungas. The lack of such costs may help to explain why dispersal is common among gorilla populations, even if the benefits are not yet fully apparent.

Acknowledgments We thank the many NGOs and governments for collaborating with us on various projects related to this book chapter. We thank Takeshi Furuichi, Juichi Yamagiwa, Filipo Aureli, and anonymous reviewers for their helpful comments. This project was funded by the Max Planck Society.

References

Alberts SC (1999) Paternal kin discrimination in wild baboons. Proc R Soc Lond Ser B Biol Sci 266:1501–1506

Alberts SC, Watts HE, Altmann J (2003) Queuing and queue-jumping: long-term patterns of reproductive skew in male savannah baboons, *Papio cynocephalus*. Anim Behav 65:821–840

Altmann SA (1962) A field study of the sociobiology of rhesus monkeys, *Macaca mulatta*. Annu Proc N Y Acad Sci 102:338–435

Berger J (1987) Reproductive fates of dispersers in a harem-dwelling ungulate: the wild horse. In: Chepko-Sade BD, Halpin ZT (eds) Mammalian dispersal patterns, the effects of social structure on population genetics. The University of Chicago Press, Chicago, pp 41–54

Bergl RA, Vigilant L (2007) Genetic analysis reveals population structure and recent migration within the highly fragmented range of the Cross River gorilla (*Gorilla gorilla diehli*). Mol Ecol 16:501–516

Bermejo M (2004) Home-range use and intergroup encounters in western gorillas (Gorilla g. gorilla) at Lossi Forest, north Congo. Am J Primatol 64:223–232

Boesch C, Boesch-Achermann H (2000) The chimpanzees of the Taï forest. Oxford University Press, Oxford

Bradley BJ, Robbins MM, Williamson EA, Steklis HD, Steklis NG, Eckhardt N, Boesch C, Vigilant L (2005) Mountain gorilla tug-of-war: Silverbacks have limited control over reproduction in multimale groups. Proc Natl Acad Sci U S A 102:9418–9423

Breuer T, Hockemba MBN, Olejniczak C, Parnell RJ, Stokes EJ (2009) Physical maturation, life-history classes and age estimates of free-ranging western gorillas – insights from Mbeli Bai, Republic of Congo. Am J Primatol 71:106–119

Breuer T, Robbins AM, Olejniczak C, Parnell RJ, Stokes EJ, Robbins MM (2010) Variance in the male reproductive success of western gorillas: acquiring females is just the beginning. Behav Ecol Sociobiol 64:515–528

Breuer T, Robbins AM, Boesch C, Robbins MM (2012) Phenotypic correlates of male reproductive success in western gorillas. J Hum Evol 62:466–472

Butynski TM (1990) Comparative Ecology of Blue Monkeys (*Cercopithecus-Mitis*) in High-Density and Low-Density Subpopulations. Ecol Monogr 60:1–26

Byrne RW (2001) Clever hands: the food processing skills of mountain gorillas. In: Robbins MM, Sicotte P, Stewart KJ (eds) Mountain gorillas: three decades of research at Karisoke. Cambridge University Press, Cambridge, pp 293–314

Caillaud D, Levrero F, Gatti S, Menard N, Raymond M (2008) Influence of male morphology on male mating status and behavior during interunit encounters in western lowland gorillas. Am J Phys Anthropol 135:379–388

Chapman CA, Pavelka MSM (2005) Group size in folivorous primates: ecological constraints and the possible influence of social factors. Primates 46:1–9

Chapman CA, Rothman JM (2009) Within-species differences in primate social structure: evolution of plasticity and phylogenetic constraints. Primates 50:12–22

Charlesworth D, Charlesworth B (1987) Inbreeding depression and its evolutionary consequences. Annu Rev Ecol Syst 18:237–268

Clutton-Brock TH (1989) Female transfer and inbreeding avoidance in social mammals. Nature 337:70–72

Clutton-Brock TH, Lukas D (2012) The evolution of social philopatry and dispersal in female mammals. Mol Ecol 21:472–492

Clutton-Brock T, Sheldon BC (2010) Individuals and populations: the role of long-term, individual-based studies of animals in ecology and evolutionary biology. Trends Ecol Evol 25:562–573

Constable JL, Ashley MV, Goodall J, Pusey AE (2001) Noninvasive paternity assignment in Gombe chimpanzees. Mol Ecol 10:1279–1300

Crockett C, Janson C (2000) Infanticide in red howlers: female group size, male membership, and a possible link to folivory. In: van Schaik C, Janson C (eds) Infanticide by males and its implications. Cambridge University Press, Cambridge, pp 75–98

Crockett CM, Pope TR (1993) Consequences of sex differences in dispersal for juvenile red howler monkeys. In: Pereira ME, Fairbanks LA (eds) Juvenile primates: life history, development, and behavior. Oxford University Press, New York, pp 104–118

Dias LG, Strier KB (2003) Effects of group size on ranging patterns in *Brachyteles arachnoides hypoxanthus*. Int J Primatol 24:209–221

Dobson FS, Smith AT, Gao WX (1998) Social and ecological influences on dispersal and philopatry in the plateau pika (Ochotona curzoniae). Behav Ecol 9:622–635

Doran DM, McNeilage A (1998) Gorilla ecology and behavior. Evolut Anthropol 6:120–131

Doran D, McNeilage A (1999) Diet of western lowland gorillas in south-west Central African republic: implications for subspecific variation in gorilla grouping and ranging patterns. Am J Phys Anthropol 28:121–121

Doran DM, McNeilage A, Greer D, Bocian C, Mehlman P, Shah N (2002) Western lowland gorilla diet and resource availability: new evidence, cross-site comparisons, and reflections on indirect sampling methods. Am J Primatol 58:91–116

Dunbar R (1984) Reproductive decisions: an economic analysis of Gelada baboon social strategies. Princeton University Press, Princeton

Fay JM, Carroll R, Peterhans JCK, Harris D (1995) Leopard attack on and consumption of gorillas in the Central-African-Republic. J Hum Evol 29:93–99

Field M, Guatelli-Steinberg D (2003) Dispersal and the inbreeding avoidance hypothesis. Primate Rep 67:7–60

Fossey D, Harcourt AH (1977) Feeding ecology of free-ranging mountain gorilla (*Gorilla gorilla beringei*). In: Clutton-Brock TH (ed) Primate ecology: studies of feeding and ranging behavior in lemurs, monkeys, and apes. Academic, London

Fossey D, Hausfater G, Hrdy S (1984) Infanticide in mountain gorillas (*Gorilla gorilla beringei*) with comparative notes on chimpanzees. In: Infanticide: comparative and evolutionary perspectives. Aldine, Hawthorne, New York, pp 217–236

Furuichi T (2011) Female contributions to the peaceful nature of bonobo society. Evolut Anthropol 20:131–142

Ganas J, Robbins MM, Nkurunungi JB, Kaplin BA, McNeilage A (2004) Dietary variability of mountain gorillas in Bwindi Impenetrable National Park, Uganda. Int J Primatol 25:1043–1072

Gatti S, Levrero F, Menard N, Gautier-Hion A (2004) Population and group structure of western lowland gorillas (Gorilla gorilla gorilla) at Lokoue, Republic of Congo. Am J Primatol 63:111–123

Gillespie TR, Chapman CA (2001) Determinants of group size in the red colobus monkey (*Procolobus badius*): an evaluation of the generality of the ecological-constraints model. Behav Ecol Sociobiol 50:329–338

Gray M, Roy J, Vigilant L, Fawcett K, Basabose A, Cranfield M, Uwingeli P, Mburanumwe I, Kagoda E, Robbins MM (2013) Genetic census reveals increased but uneven growth of a critically endangered mountain gorilla population. Biol Conserv 158:230–238

Guillaume F, Perrin N (2006) Joint evolution of dispersal and inbreeding load. Genetics 173:497–509

Guschanski K, Caillaud D, Robbins MM, Vigilant L (2008) Females shape the genetic structure of a gorilla population. Curr Biol 18:1809–1814

Guschanski K, Vigilant L, McNeilage A, Gray M, Kagoda E, Robbins MM (2009) Counting elusive animals: comparing field and genetic census of the entire mountain gorilla population of Bwindi Impenetrable National Park, Uganda. Biol Conserv 142:290–300

Handley LJL, Perrin N (2007) Advances in our understanding of mammalian sex-biased dispersal. Mol Ecol 16:1559–1578

Harcourt AH (1978) Strategies of emigration and transfer by primates, with particular reference to gorillas. J Compar Ethol 48:401–420

Harcourt AH (1979) Social relationships among adult female mountain gorillas. Anim Behav 27:251–264

Harcourt AH (1981) Intermale competition and the reproductive behavior of the great apes. In: Graham CE (ed) Reproductive biology of the great apes. Academic, New York, pp 301–318

Harcourt AH, Stewart KJ (2007) Gorilla society: conflict, compromise, and cooperation between the sexes. University of Chicago Press, Chicago

Harcourt AH, Stewart KS, Fossey D (1976) Male emigration and female transfer in wild mountain gorilla. Nature 263:226–227

Harcourt AH, Fossey D, Stewart KG, Watts D (1980) Reproduction in wild gorillas and some comparisons with chimpanzees. J Reprod Fertil 28:59–70

Harcourt AH, Fossey D, Sabaterpi J (1981a) Demography of *Gorilla gorilla*. J Zool 195:215–233

Harcourt AH, Harvey PH, Larson SG, Short RV (1981b) Testis weight, body-weight and breeding system in primates. Nature 293:55–57

Harris TR (2006) Between-group contest competition for food in a highly folivorous population of black and white colobus monkeys (Colobus guereza). Behav Ecol Sociobiol 61:317–329

Hill RA, Lee PC (1998) Predation risk as an influence on group size in cercopithecoid primates: implications for social structure. J Zool 245:447–456

Honer OP, Wachter B, East ML, Streich WJ, Wilhelm K, Burke T, Hofer H (2007) Female mate-choice drives the evolution of male-biased dispersal in a social mammal. Nature 448:798–801

Hrdy SB (1977) Infanticide as a primate reproductive strategy. Am Sci 65:40–49

Hrdy SB (1979) Infanticide among animals – review, classification, and examination of the implications for the reproductive strategies of females. Ethol Sociobiol 1:13–40

Hrdy SB, Janson C, van Schaik C (1994) Infanticide: let's not throw out the baby with the bath water. Evolut Anthropol 3:151–154

Idani G (1991) Social relationships between immigrant and resident bonobo females at Wamba. Folia Primatol 57:83–95

Isbell LA (1991) Contest and scramble competition: patterns of female aggression and ranging behavior in primates. Behav Ecol 2:143–155

Isbell LA, Van Vuren D (1996) Differential costs of locational and social dispersal and their consequences for female group-living primates. Behaviour 133:1–36

Jack K (2003) Males on the move: evolutionary explanations of secondary dispersal by male primates. Primate Rep 67:61–83

Janson CH, Goldsmith ML (1995) Predicting group size in primates – foraging costs and predation risks. Behav Ecol 6:326–336

Janson CH, van Schaik CP (2000) The behavioral ecology of infanticide by males. In: Janson CH, van Schaik CP (eds) Infanticide by males and its implications. Cambridge University Press, Cambridge, pp 469–494

Kalpers J, Williamson EA, Robbins MM, McNeilage A, Nzamurambaho A, Lola N, Mugiri G (2003) Gorillas in the crossfire: population dynamics of the Virunga mountain gorillas over the past three decades. Oryx 37:326–337

Kappeler PM, van Schaik C, Watts D (2012) The values and challenges of long-term field studies. In: Kappeler PM, Watts D (eds) Long-term field studies of primates. Springer, Berlin, pp 3–18

Keller LF, Waller DM (2002) Inbreeding effects in wild populations. Trends Ecol Evol 17:230–241

Knott C (2001) Female reproductive ecology of the apes. In: Ellison PT (ed) Reproductive ecology and human evolution. Aldine de Gruyter, New York, pp 429–464

Koenig A, Beise J, Chalise MK, Ganzhorn JU (1998) When females should contest for food – testing hypotheses about resource density, distribution, size, and quality with Hanuman langurs (*Presbytis entellus*). Behav Ecol Sociobiol 42:225–237

Kokko H, Ots I (2006) When not to avoid inbreeding. Evolution 60:467–475

Koopman ME, Cypher BL, Scrivner JH (2000) Dispersal patterns of San Joaquin kit foxes (*Vulpes macrotis mutica*). J Mammal 81:213–222

Korstjens AH, Schippers EP (2003) Dispersal patterns among olive colobus in Taï National Park. Int J Primatol 24:515–539

Korstjens AH, Sterck EHM, Noe R (2002) How adaptive or phylogenetically inert is primate social behaviour? A test with two sympatric colobines. Behaviour 139:203–225

Langergraber KE, Mitani JC, Vigilant L (2007) The limited impact of kinship on cooperation in wild chimpanzees. Proc Natl Acad Sci U S A 104:7786–7790

Lehmann L, Perrin N (2003) Inbreeding avoidance through kin recognition: choosy females boost male dispersal. Am Nat 162:638–652

Lindenfors P, Froberg L, Nunn CL (2004) Females drive primate social evolution. Proc R Soc Lond Ser B Biol Sci 271:S101–S103

Lukas D, Clutton-Brock TH (2011) Group structure, kinship, inbreeding risk and habitual female dispersal in plural-breeding mammals. J Evol Biol 24:2624–2630

Lukas D, Reynolds V, Boesch C, Vigilant L (2005) To what extent does living in a group mean living with kin? Mol Ecol 14:2181–2196

Magliocca F, Gautier-Hion A (2004) Inter-group encounters in western lowland gorillas at a forest clearing. Folia Primatol 75:379–382

Magliocca F, Querouil S, Gautier-Hion A (1999) Population structure and group composition of western lowland gorillas in north-western Republic of Congo. Am J Primatol 48:1–14

McGraw WS, Plavcan JM, Adachi-Kanazawa K (2002) Adult female *Cercopithecus diana* employ canine teeth to kill another adult female *C. diana*. Int J Primatol 23:1301–1308

McNeilage A (2001) Diet and habitat use of two mountain gorilla groups in contrasting habitats in the Virungas. In: Robbins MM, Sicotte P, Stewart KJ (eds) Mountain gorillas: three decades of research at Karisoke. Cambridge University Press, Cambridge, pp 265–292

Mehlman PT (2007) Current status of wild gorilla populations and strategies for their conservation. In: Stoinski TS, Steklis HD, Mehlman PT (eds) Conservation in the 21st century: gorillas as a case study. Springer, New York, pp 3–54

Monard AM, Duncan P (1996) Consequences of natal dispersal in female horses. Anim Behav 52:565–579

Monard AM, Duncan P, Boy V (1996) The proximate mechanisms of natal dispersal in female horses. Behaviour 133:1095–1124

Moore J, Ali R (1984) Are dispersal and inbreeding avoidance related? Anim Behav 32:94–112

Muniz L, Perry S, Manson JH, Gilkenson H, Gros-Louis J, Vigilant L (2006) Father-daughter inbreeding avoidance in a wild primate population. Curr Biol 16:R156–R157

Nagy M, Heckel G, Voigt CC, Mayer F (2007) Female-biased dispersal and patrilocal kin groups in a mammal with resource-defence polygyny. Proc R Soc Lond Ser B Biol Sci 274:3019–3025

Nishida T, Corp N, Hamai M, Hasegawa T, Hiraiwa-Hasegawa M, Hosaka K, Hunt KD, Itoh N, Kawanaka K, Matsumoto-Oda A, Mitani JC, Nakamura M, Norikoshi K, Sakamaki T, Turner L, Uehara S, Zamma K (2003) Demography, female life history, and reproductive profiles among the chimpanzees of Mahale. Am J Primatol 59:99–121

Nsubuga AM, Robbins MM, Boesch C, Vigilant L (2008) Patterns of paternity and group fission in wild multimale mountain gorilla groups. Am J Phys Anthropol 135:263–274

Nunn CL (1999) The evolution of exaggerated sexual swellings in primates and the graded-signal hypothesis. Anim Behav 58:229–246

Ossi K, Kamilar JM (2006) Environmental and phylogenetic correlates of Eulemur behavior and ecology (Primates: Lemuridae). Behav Ecol Sociobiol 61:53–64

Palombit RA (2012) Infanticide: male strategies and female counterstrategies. In: Mitani J, Call J, Kappeler PM, Palombit RA, Silk JB (eds) The evolution of primate societies. University of Chicago Press, Chicago, pp 432–468

Parnell RJ (2002) Group size and structure in western lowland gorillas (*Gorilla gorilla gorilla*) at Mbeli Bai, Republic of Congo. Am J Primatol 56:193–206

Payne HFP, Lawes MJ, Henzi SP (2003) Fatal attack on an adult female *Cercopithecus mitis erythrarchus*: implications for female dispersal in female-bonded societies. Int J Primatol 24:1245–1250

Perrin N, Mazalov V (1999) Dispersal and inbreeding avoidance. Am Nat 154:282–292

Pradhan GR, van Schaik C (2008) Infanticide-driven intersexual conflict over matings in primates and its effects on social organization. Behaviour 145:251–275

Printes RC, Strier KB (1999) Behavioral correlates of dispersal in female muriquis (Brachyteles arachnoides). Int J Primatol 20:941–960

Pusey AE (1980) Inbreeding avoidance in chimpanzees. Anim Behav 28:543–552

Pusey AE (1987) Sex-biased dispersal and inbreeding avoidance in birds and mammals. Trends Ecol Evol 2:295–299

Rasa OAE, Lloyd PH (1994) Incest avoidance and attainment of dominance by females in a cape mountain zebra (Equus-Zebra Zebra) population. Behaviour 128:169–188

Robbins MM (1995) A demographic analysis of male life history and social structure of mountain gorillas. Behaviour 132:21–47

Robbins MM (2001) Variation in the social system of mountain gorillas: the male perspective. In: Robbins MM, Sicotte P, Stewart KJ (eds) Mountain gorillas: three decades of research at Karisoke. Cambridge University Press, Cambridge, pp 29–58

Robbins MM (2003) Behavioral aspects of sexual selection in mountain gorillas. In: Jones CB (ed) Sexual selection and reproductive competition in primates: new perspectives and directions. American Society of Primatologists, Norman, pp 477–501

Robbins MM (2008) Feeding competition and agonistic relationships among Bwindi mountain gorillas. Int J Primatol 29:999–1018

Robbins MM (2009) Male aggression toward females in mountain gorillas: courtship or coercion? In: Muller MN, Wrangham R (eds) Sexual coercion in primates. Harvard University Press, Cambridge, pp 112–125

Robbins MM (2010) Gorillas: diversity in ecology and behavior. In: Campbell CJ, Fuentes A, MacKinnon KC, Bearder SK, Stumpf RM (eds) Primates in perspective. Oxford University Press, Oxford, pp 326–339

Robbins MM, McNeilage A (2003) Home range and frugivory patterns of mountain gorillas in Bwindi Impenetrable National Park, Uganda. Int J Primatol 24:467–491

Robbins MM, Robbins AM (2004) Simulation of the population dynamics and social structure of the Virunga mountain gorillas. Am J Primatol 63:201–223

Robbins AM, Robbins MM (2005) Fitness consequences of dispersal decisions for male mountain gorillas (*Gorilla beringei beringei*). Behav Ecol Sociobiol 58:295–309

Robbins MM, Sawyer SC (2007) Intergroup encounters in mountain gorillas of Bwindi Impenetrable National Park, Uganda. Behaviour 144:1497–1519

Robbins MM, Sicotte P, Stewart KJ (2001) Mountain gorillas: three decades of research at Karisoke. Cambridge University Press, Cambridge

Robbins MM, Bermejo M, Cipolletta C, Magliocca F, Parnell RJ, Stokes E (2004) Social structure and life-history patterns in western gorillas (*Gorilla gorilla gorilla*). Am J Primatol 64:145–159

Robbins MM, Robbins AM, Gerald-Steklis N, Steklis HD (2005) Long-term dominance relationships in female mountain gorillas: strength, stability and determinants of rank. Behaviour 142:779–809

Robbins AM, Robbins MM, Gerald-Steklis N, Steklis HD (2006) Age-related patterns of reproductive success among female mountain gorillas. Am J Phys Anthropol 131:511–521

Robbins MM, Robbins AM, Gerald-Steklis N, Steklis HD (2007) Socioecological influences on the reproductive success of female mountain gorillas (*Gorilla beringei beringei*). Behav Ecol Sociobiol 61:919–931

Robbins AM, Stoinski T, Fawcett K, Robbins MM (2009a) Leave or conceive: natal dispersal and philopatry of female mountain gorillas in the Virunga volcano region. Anim Behav 77:831–838

Robbins AM, Stoinski TS, Fawcett KA, Robbins MM (2009b) Does dispersal cause reproductive delays in female mountain gorillas? Behaviour 146:525–549

Robbins AM, Stoinski TS, Fawcett KA, Robbins MM (2009c) Socioecological influences on the dispersal of female mountain gorillas – evidence of a second folivore paradox. Behav Ecol Sociobiol 63:477–489

Robbins MM, Gray M, Kagoda E, Robbins AM (2009d) Population dynamics of the Bwindi mountain gorillas. Biol Conserv 142:2886–2895

Rogers ME, Abernethy K, Bermejo M, Cipolletta C, Doran D, McFarland K, Nishihara T, Remis M, Tutin CEG (2004) Western gorilla diet: a synthesis from six sites. Am J Primatol 64:173–192

Rogovin K, Randall JA, Kolosova I, Moshkin M (2004) Predation on a social desert rodent, *Rhombomys opimus*: effect of group size, composition, and location. J Mammal 85:723–730

Saj TL, Sicotte P (2005) Male takeover in Colobus vellerosus at boabeng-fiema monkey sanctuary, central Ghana. Primates 46:211–214

Schubert G, Stoneking CJ, Arandjelovic M, Boesch C, Eckhardt N, Hohmann G, Langergraber K, Lukas D, Vigilant L (2011) Male-mediated gene flow in patrilocal primates. PLoS One 6:e21514

Schulke O, Ostner J (2012) Ecological and social influences on sociality. In: Mitani J, Call J, Kappeler PM, Palombit RA, Silk JB (eds) The evolution of primate societies. University of Chicago Press, Chicago, pp 195–219

Sicotte P (1993) Intergroup encounters and female transfer in mountain gorillas – influence of group composition on male behavior. Am J Primatol 30:21–36

Sicotte P (1994) Effect of male competition on male-female relationships in bi-male groups of mountain gorillas. Ethology 97:47–64

Sicotte P (2000) A case study of mother-son transfer in mountain gorillas. Primates 41:93–101

Sicotte P (2001) Female mate choice in mountain gorillas. In: Robbins M, Sicotte P, Stewart K (eds) Mountain gorillas: three decades of research at Karisoke. Cambridge University Press, Cambridge, pp 59–88

Smuts BB, Smuts RW (1993) Male-aggression and sexual coercion of females in nonhuman-primates and other mammals – evidence and theoretical implications. Adv Stud Behav 22:1–63

Steenbeek R, van Schaik CP (2001) Competition and group size in Thomas's langurs (*Presbytis thomasi*): the folivore paradox revisited. Behav Ecol Sociobiol 49:100–110

Sterck EHM (1997) Determinants of female dispersal in Thomas langurs. Am J Primatol 42:179–198

Sterck EHM, Watts DP, van Schaik CP (1997) The evolution of female social relationships in nonhuman primates. Behav Ecol Sociobiol 41:291–309

Sterck EHM, Willems EP, van Hooff J, Wich SA (2005) Female dispersal, inbreeding avoidance and mate choice in Thomas langurs (*Presbytis thomasi*). Behaviour 142:845–868

Stoinski TS, Rosenbaum S, Ngaboyamahina T, Vecellio V, Ndagijimana F, Fawcett K (2009a) Patterns of male reproductive behaviour in multi-male groups of mountain gorillas: examining theories of reproductive skew. Behaviour 146:1193–1215

Stoinski TS, Vecellio V, Ngaboyamahina T, Ndagijimana F, Rosenbaum S, Fawcett KA (2009b) Proximate factors influencing dispersal decisions in male mountain gorillas, *Gorilla beringei beringei*. Anim Behav 77:1155–1164

Stokes EJ (2004) Within-group social relationships among females and adult males in wild western lowland gorillas (*Gorilla gorilla gorilla*). Am J Primatol 64:233–246

Stokes EJ, Parnell RJ, Olejniczak C (2003) Female dispersal and reproductive success in wild western lowland gorillas (*Gorilla gorilla gorilla*). Behav Ecol Sociobiol 54:329–339

Stumpf R (2007) Chimpanzees and bonobos: diversity within and between species. In: Campbell CJ, Fuentes A, MacKinnon KC, Panger M, Bearder SK (eds) Primates in perspective. Oxford University Press, Oxford, pp 321–344

Stumpf RM, Boesch C (2006) The efficacy of female choice in chimpanzees of the Taï Forest, Cote d'Ivoire. Behav Ecol Sociobiol 60:749–765

Thierry B, Iwaniuk AN, Pellis SM (2000) The influence of phylogeny on the social behaviour of macaques (Primates: Cercopithecidae, genus Macaca). Ethology 106:713–728

van Schaik CP (1989) The ecology of social relationships amongst female primates. In: Standon V, Foley RA (eds) Comparative socioecology: the behavioural ecology of humans and other mammals. Blackwell Scientific, Oxford, pp 195–218

Waser PM, Austad SN, Keane B (1986) When should animals tolerate inbreeding. Am Nat 128:529–537

Watts DP (1984) Composition and variability of mountain gorilla diets in the central Virungas. Am J Primatol 7:323–356

Watts DP (1988) Environmental influences on mountain gorilla time budgets. Am J Primatol 15:195–211

Watts DP (1989) Infanticide in mountain gorillas – new cases and a reconsideration of the evidence. Ethology 81:1–18

Watts DP (1990a) Ecology of gorillas and its relation to female transfer in mountain gorillas. Int J Primatol 11:21–45

Watts DP (1990b) Mountain gorilla life histories, reproductive competition, and sociosexual behavior and some implications for captive husbandry. Zoo Biol 9:185–200

Watts DP (1991a) Harassment of immigrant female mountain gorillas by resident females. Ethology 89:135–153

Watts DP (1991b) Mountain gorilla reproduction and sexual behavior. Am J Primatol 24:211–225

Watts DP (1992) Social relationships of immigrant and resident female mountain gorillas. 1. Male-female relationships. Am J Primatol 28:159–181

Watts DP (1994a) Agonistic relationships between female mountain gorillas (*Gorilla gorilla beringei*). Behav Ecol Sociobiol 34:347–358

Watts DP (1994b) The influence of male mating tactics on habitat use in mountain gorillas (*Gorilla gorilla beringei*). Primates 35:35–47

Watts DP (1994c) Social relationships of immigrant and resident female mountain gorillas. 2. Relatedness, residence, and relationships between females. Am J Primatol 32:13–30

Watts DP (1996) Comparative socioecology of gorillas. In: McGrew WC, Marchant LF, Nishida T (eds) Great ape societies. University of Cambridge, Cambridge, pp 16–28

Watts DP (1998) Long term habitat use by mountain gorillas (*Gorilla gorilla beringei*). 1. consistency, variation, and home range size and stability. Int J Primatol 19:651–680

Watts DP (2000) Causes and consequences of variation in male mountain gorilla life histories and group membership. In: Kappeler PM (ed) Primate males. Cambridge University Press, Cambridge, pp 169–180

Weingrill T, van Schaik C (2011) Sexual coercion in primates: evolutionary causes and counter-strategies of females. Z Sexualforsch 24:111–133

Williams JM, Pusey AE, Carlis JV, Farm BP, Goodall J (2002) Female competition and male territorial behaviour influence female chimpanzees' ranging patterns. Anim Behav 63:347–360

Wrangham RW (1980) An ecological model of female-bonded primate groups. Behaviour 75:262–300

Yamagiwa J (1987) Male life history and the social structure of wild mountain gorillas (*Gorilla gorilla beringei*). In: Kawano S, Connell J, Hidaka T (eds) Evolution and coadaptation in biotic communities. University of Tokyo Press, Tokyo, pp 31–51

Yamagiwa J (2004) Crisis of gorilla conservation in Kahuzi-Biega National Park. Primate Res 20:73–76

Yamagiwa J, Kahekwa J (2001) Dispersal patterns, group structure, and reproductive parameters of eastern lowland gorillas at Kahuzi in the absence of infanticide. In: Robbins MM, Sicotte P, Stewart K (eds) Mountain gorillas: three decades of research at Karisoke. Cambridge University Press, Cambridge, pp 89–122

Yamagiwa J, Kahekwa J (2004) First observations of infanticides by a silver-back in Kahuzi-Biega. Gorilla J 29:6–9

Yamagiwa J, Mwanza N, Spangenberg A, Maruhashi T, Yumoto T, Fischer A, Steinhauerburkart B (1993) A census of the eastern lowland gorillas Gorilla-gorilla-graueri in Kahuzi-Biega National-Park with reference to mountain gorillas G-G-beringei in the Virunga Region, Zaire. Biol Conserv 64:83–89

Yamagiwa J, Kahekwa J, Basabose AK (2003) Intra-specific variation in social organization of gorillas: implications for their social evolution. Primates 44:359–369

Yamagiwa J, Kahekwa J, Basabose AK (2009) Infanticide and social flexibility in the genus Gorilla. Primates 50:293–303

Zhao Q, Borries C, Pan W (2011) Male takeover, infanticide, and female countertactics in white-headed leaf monkeys (*Trachypithecus leucocephalus*). Behav Ecol Sociobiol 65:1535–1547

Chapter 5
Sex Differences in Ranging and Association Patterns in Chimpanzees in Comparison with Bonobos

Chie Hashimoto and Takeshi Furuichi

Introduction

More than 50 years have passed since studies on wild chimpanzees began in the 1960s. These studies revealed many aspects of chimpanzee sociality, such as their high degree of fission-fusion dynamics and female-biased dispersal patterns (Nishida 1968; Nishida and Kawanaka 1972; Pusey 1979; Goodall 1986). Many studies have focused on social relationships among males, reporting male dominance and strong male-male bonds (Goodall 1986; Nishida and Hiraiwa-Hasegawa 1987; Nishida and Hosaka 1996; Boesch and Boesch-Achermann 2000; Watts 2000; Arnold and Whiten 2003, Fig. 5.1). Male chimpanzees associate more with males than females do with females (Nishida and Hiraiwa-Hasegawa 1987; Newton-Fisher 1999). Grooming between males is more common than between males and females or between females, and reciprocity in male grooming and interchange of grooming for agonistic support have been reported (Goodall 1986; Takahata 1990b; Watts 2002; Arnold and Whiten 2003). In addition, pairs or trios of top-ranking males sometimes engage in cooperative mate guarding (Watts 1998). Duffy et al. (2007) reported that the alpha male selectively tolerates his allies mating in exchange for support in conflicts. Male chimpanzees maintain long-lasting and equitable social bonds whose formation is affected by maternal kinship and the quality of social relationships (Mitani 2009).

In contrast, few studies have focused on social relationships among female chimpanzees, possibly because social relationships among male chimpanzees are more prominent and because it is difficult to collect sufficient data on females

---

C. Hashimoto (✉) • T. Furuichi
Department of Ecology and Social Behavior, Primate Research Institute, Kyoto University,
41-2 Kanrin, Inuyama, Aichi 484-8506, Japan
e-mail: hashimoto.chie.2n@kyoto-u.ac.jp

T. Furuichi et al. (eds.), *Dispersing Primate Females*,
Primatology Monographs, DOI 10.1007/978-4-431-55480-6_5

Fig. 5.1 Affinitive relationships among male chimpanzees. Male chimpanzees often share meat among themselves

since they tend to range alone with their offspring. In the 2000s, however, several researchers started to study chimpanzee female-female relationships at various long-term study sites.

In this chapter, we examine the characteristics of chimpanzee sociality compared with that of bonobos. After reviewing the life history traits of female chimpanzees, we examine the patterns of female chimpanzee ranging and association by reviewing previous studies and analyzing our own data on the ranging patterns of chimpanzees in the Kalinzu Forest, Uganda, and bonobos at Wamba, Democratic Republic of the Congo. Finally, we discuss the flexibility in female chimpanzee social association and life history, in relation to the male-philopatric female-dispersal social structure.

Study Groups

We observed the M group of chimpanzees living in the Kalinzu Forest Reserve, which is located in western Uganda (0°17′S 30°07′ E, 0°17′ E) (Howard 1991; Hashimoto et al. 2001; Hashimoto and Furuichi 2006). In this chapter, we analyzed data from a period between September 2004 and August 2005. In this period, M group included 19 adult males, 4 adolescent males, 18 adult females, 5 adolescent females, and 17 immature individuals.

We observed the E1 group of wild bonobos living at Wamba, DR Congo (0°11′8″ N, 22°37′58″ E) (Furuichi 1987; Kano 1992; Furuichi et al. 2012) from November 2003 to October 2004. During this period, E1 group included 10 adult males, 5 adult females, 2 adolescent females, and 8 immature individuals.

During the chimpanzee study period, we followed an encountered party and recorded members of the party using the 1-h party method (Hashimoto et al. 2001). We recorded all individuals in sight at the beginning of each 1-h segment and continued recording individuals that appeared in sight until the end of that hour. While tracking a party, we recorded their position at 1-min intervals using a global positioning system (GPS) receiver. We obtained the position of the party in each hour by averaging the data of each minute within the hour.

For the bonobo study, we followed a party of bonobos and recorded its members using the same 1-h party method. We also recorded the position of the party at 30-min intervals using a GPS receiver.

Life History of Female Chimpanzees

Chimpanzees and bonobos live in multi-male/multi-female communities (Nishida 1968; Goodall 1986; Kano 1992). Their dispersal patterns are different from the typical mammalian dispersal pattern. Females in most mammal species tend to remain in their natal group for their whole life, whereas males leave their natal group at sexual maturity (Pusey 1987; Pusey and Packer 1987). However, male philopatry and female dispersal are the predominant patterns for chimpanzees and bonobos (Nishida and Kawanaka 1972; Goodall 1986; Kano 1992).

Female chimpanzees show their first maximal swelling in late adolescence (9–12 years old: Goodall 1986; Pusey 1990; Stumpf et al. 2009), by which time they begin to increase their distance from their mother (Pusey 1990; Stumpf et al. 2009). After about 1 year from the first maximal swelling, females emigrate from their natal group (Stumpf et al. 2009).

Although females generally leave their natal group during adolescence, the likelihood of female transfer varies between sites. In M group of Mahale Mountains National Park, Tanzania (Nishida et al. 2003), the north community of Taï National Park, Côte d'Ivoire (Boesch and Boesch-Achermann 2000), and Kanyawara community in the Kibale National Park, Uganda (Stumpf et al. 2009), the majority of females transfer to another group. However, in Kasakela community of Gombe National Park, Tanzania, only about half of all females transfer (Pusey et al. 1997). At Bossou, all individuals except one male disappeared before reaching 15 years old (Sugiyama 2004). Sugiyama (2004) suggested that at least some males and females emigrated from Bossou, although no emigrant from Bossou, male or female, has been confirmed alive in the adjacent chimpanzee habitat because observation there is difficult.

Little is known about female chimpanzees after they leave their natal group until their immigration into a new group. There is only a small difference between age at emigration from the natal group and age at immigration into a new group. Females emigrate from the natal group at 11 to 12 years (Kanyawara, 12.6 years old (Stumpf et al. 2009); Mahale, 11 years old (Nishida et al. 1990); Taï, 11.42 years old

Fig. 5.2 Females with infant often associate together

(Boesch and Boesch-Achermann 2000)) and immigrate into a new group at 10–13 years (Fig. 5.2; Gombe, 10–11 years old (Goodall 1986); Kanyawara, 13 years old (Stumpf et al. 2009); Taï, 11 years old (Boesch and Boesch-Achermann 2000)). When immigrant females appear in the new group, they are often in estrus (Nishida 1979; Pusey 1979; Goodall 1986).

Although only nulliparous females generally transfer, parous females may also transfer. Females at Bossou leave their natal group after giving birth for the first time (Sugiyama 2004). Nishida et al. (1985) reported that parous females of K group immigrated into M group at Mahale when K group became extinct. Emery Thompson et al. (2006) reported the immigration of more than five parous females with offspring into the study community at Budongo (in the study of chimpanzees, the terms “community” and “group” or “unit group” have the same meaning, as Van Elsacker et al. (1995) have explained in relation to bonobos).

There is a period of adolescent sterility for 2–3 years between the first maximal swelling and the first conception (Goodall 1986; Nishida et al. 1990; Wallis 1997; Boesch and Boesch-Achermann 2000). Females give birth for the first time when they are around 13–15 years old (Nishida et al. 1990; Wallis 1997; Boesch and Boesch-Achermann 2000). Females at Bossou start to give birth much earlier than females at other sites; the mean primiparous age at Bossou is 10.6 years (Sugiyama and Fujita 2011).

There is no evidence that menopause is a characteristic of chimpanzee life histories. Emery Thompson et al. (2007b) analyzed demographic data from six long-term chimpanzee study sites and compared fertility and mortality patterns with those of humans. They found that healthy female chimpanzees maintain high birth rates late into life.

Social Relationships Among Females

Female chimpanzees have fewer affiliative and agonistic social interactions than male chimpanzees. Grooming between females is less frequent than that of male-male dyads (Gombe: Goodall 1986; Mahale: Takahata 1990a, b; Ngogo: Watts 2000; Budongo: Arnold and Whiten 2003; Taï: Boesch and Boesch-Achermann 2000). Agonistic interactions among adult females occur infrequently (Gombe: Goodall 1986; Mahale: Nishida 1989; Kanyawara: Muller 2002; Taï: Wittig and Boesch 2003).

Linear hierarchies have not been documented at many study sites (Gombe: Goodall 1986; Williams et al. 2002; Mahale: Nishida 1989; Ngogo: Wakefield 2008) except at Taï (Wittig and Boesch 2003), although female dominance relationships are ordered in broad rank categories and alpha females can be identified (Gombe: Pusey et al. 1997; Kanyawara: Wrangham et al. 1992).

Characteristics of Females' Use of Space

Three models have been proposed to describe chimpanzee social organization (Fig. 5.3; Wrangham 1979; Boesch 1991). The male-only community model proposes that only male chimpanzees belong to the community and females are distributed evenly across the habitat in overlapping core areas independent of the males' range. The male-bonded community model assumes that females settle within the male-defended range but use individually distinct home ranges to minimize feeding competition (Wrangham 1979; Smuts and Smuts 1993). A third model proposes that both male and female chimpanzees occupy the same home range (Itani and Suzuki 1967). Wrangham (1979) referred to this third model as the "classic model," and Boesch (1991, 1996) termed it the "bisexually bonded community model."

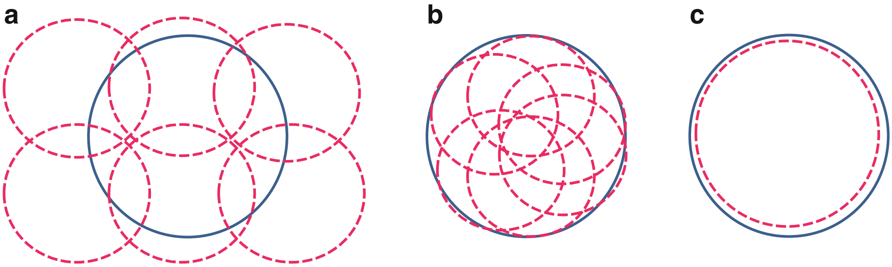


Fig. 5.3 The three models of fission-fusion society in chimpanzees (*blue lines* for males and *red lines* for females) originally proposed by Wrangham (1979) and modified by Boesch (1991), Williams et al. (2002), and Lehmann and Boesch (2005). (**a**) Male-only community model, (**b**) male-bonded community model, and (**c**) bisexually bonded community model

Studies of chimpanzees in Gombe have supported the male-bonded community model. Wrangham (1979) found that Gombe females occupied core areas dispersed within the community range, smaller than those of males in Gombe. He suggested that Gombe females ranged according to the male-only community model because three anestrous mothers occasionally associated peacefully with males from two communities. Pusey (1980) reported observations that males show unusually violent aggression to females in border areas as evidence for the male-bonded community model rather than the male-only community model. A recent study using a 10-year dataset showed that females spend most of their time in small overlapping core areas within the community range, supporting the male-bonded community model (Williams et al. 2002). Most core areas at Gombe cluster into two neighborhoods, north and south. Dominant females have higher site fidelity and smaller core areas than subordinates, and new immigrants use areas away from dominant females (Murray et al. 2007). High-ranking females use small core areas even during periods of food scarcity, while middle- and low-ranking females use much larger core areas. Because high-ranking females have more reproductive success than the other females (Pusey et al. 1997; Jones et al. 2010), there may be competition among females for areas of good quality (Murray et al. 2007).

Several other studies of chimpanzees at other sites in East Africa support the male-bonded community model. Chapman and Wrangham (1993) revealed that chimpanzee females of Kanyawara community have smaller core areas within the male home range and are dispersed relative to males within the defended area. Emery Thompson et al. (2007a) analyzed a 9-year dataset and found that the ranging patterns of Kanyawara chimpanzees agreed with the male-bonded community model. Like Gombe chimpanzees, Kanyawara females use the community range in a differentiated manner, forming distinct northern, central, and southern clusters. Females in neighborhoods containing more preferred foods have high reproductive success. There ought to be competition over where female chimpanzees settle within the home range, although dominance interactions are less frequent among females than among males (Emery Thompson et al. 2007a). Kahlenberg et al. (2008) examined aggression and dominance relationships among Kanyawara females using 10 years of data. The results supported Emery Thompson et al. (2007a) by showing that females occupying core areas high in foraging quality ranked highly overall and higher than expected for their ages, whereas females occupying low-quality core areas were lower ranking and ranked lower than expected for their ages.

Results from a study by Hasegawa (1990) in Mahale also supported the male-bonded community model, indicating that males used the community home range more evenly than females, who used some areas more preferentially.

In contrast, a recent study of chimpanzees of the Sonso Community in the Budongo Forest, Uganda, showed that female ranges fell within the area of male ranges and that there was no significant difference between male and female core areas, supporting the bisexually bonded community model (Fawcett 2000). Studies of West African chimpanzees also support the bisexually bonded community model. Boesch (1991, 1996) showed that female chimpanzees in Taï range extensively over the whole home range like males, irrespective of their estrous cycle. Recent analysis of a 5-year dataset on the ranging patterns of Taï chimpanzees also suggests that both male and female individual home ranges and core areas greatly overlap (Lehmann and Boesch 2005). A similar pattern was also reported for chimpanzees in Bossou, Guinea (Sugiyama 1988; Sakura 1994; Ohashi, personal communication).

We examined the ranging pattern of M group chimpanzees in the Kalinzu Forest, Uganda. Like Budongo and West African chimpanzees, the ranging pattern in Kalinzu supported the bisexually bonded community model (Fig. 5.4). Both male and female chimpanzees used almost the entire area of the group home range, although females used slightly smaller areas than males (95 % range for males, 8.8 ± 1.0 (SD) km^2, $n = 19$; for females, 6.3 ± 0.8, $n = 12$; Mann-Whitney U = 8.0,

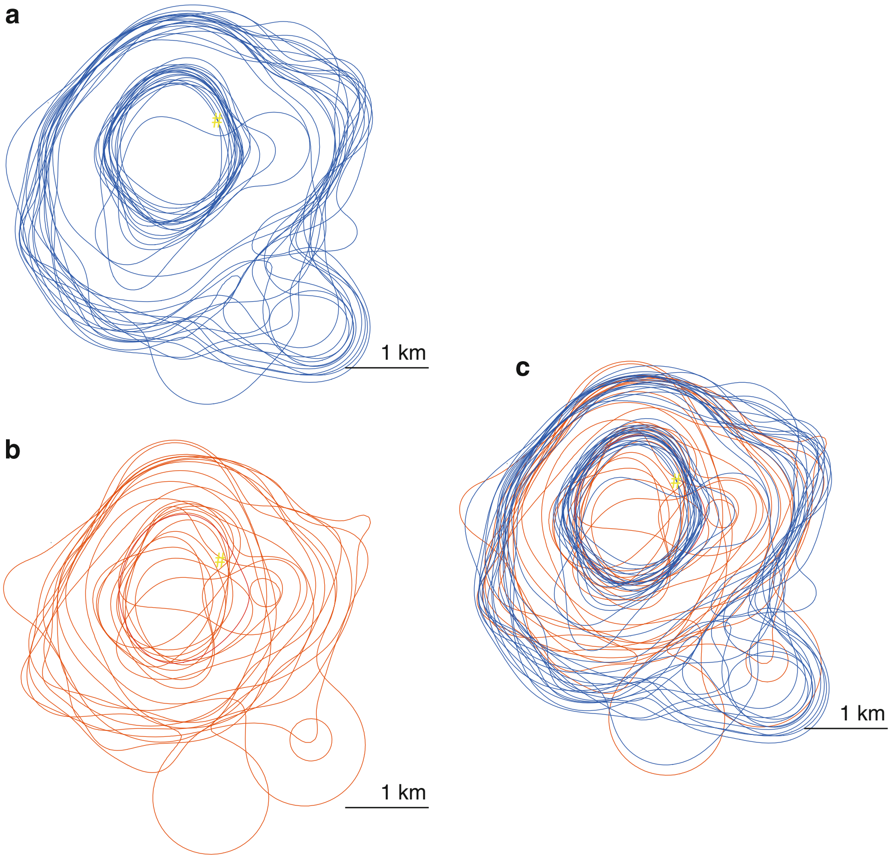


Fig. 5.4 Ranging patterns of M group chimpanzees in the Kalinzu Forest. Each line represents the ranging pattern of an individual (*blue lines* for males and *red lines* for females). (**a**) Ranging patterns of males, and (**b**) ranging patterns of females, (**c**) ranging patterns of males and females. We estimated individual areas (95 and 50 % of usage) using the fixed kernel density estimation method with Hawth's Tools and ArcGIS 9. We set the single parameter smoothing factor (h) for the kernel density estimation at 650

$p < 0.001$). Unlike Gombe and Kanyawara chimpanzees, Kalinzu females did not form clusters and most females used most of the community home range.

In summary, early studies suggested that chimpanzees in East Africa followed a male-bonded community model and that chimpanzees in West Africa followed a bisexually bonded community model. However, current evidence suggests that female ranging patterns vary among East African chimpanzees. However, one feature is common to all chimpanzee study sites: male ranges are larger than female ranges, which are incorporated into the male ranges.

There has been only one study of ranging patterns in bonobos, which showed that males and females have very similar ranging patterns (Waller 2011). We examined the ranging patterns of bonobos of E1 group at Wamba, DR Congo. Because there is a human village in the center of the E1 group range, each individual had two or three core areas (Fig. 5.5). The ranging patterns of most individuals except three (Nord, Jacky, and Yuki) were similar (Fig. 5.5). These three individuals probably joined E1 group from extinct groups (Hashimoto et al. 2008). Although the ranging patterns of these three immigrants were slightly different, there was no difference in the size of ranging areas between males and females (95 % range for males, 55.4 ± 1.8 (SD) km^2, $n = 19$; for females, 55.2 ± 2.5, $n = 6$; Mann-Whitney $U = 26$, n.s.; Fig. 5.5). That bonobos at Wamba have a much larger ranging area than chimpanzees at Kalinzu might be partly explained by the fact that neighboring groups disappeared

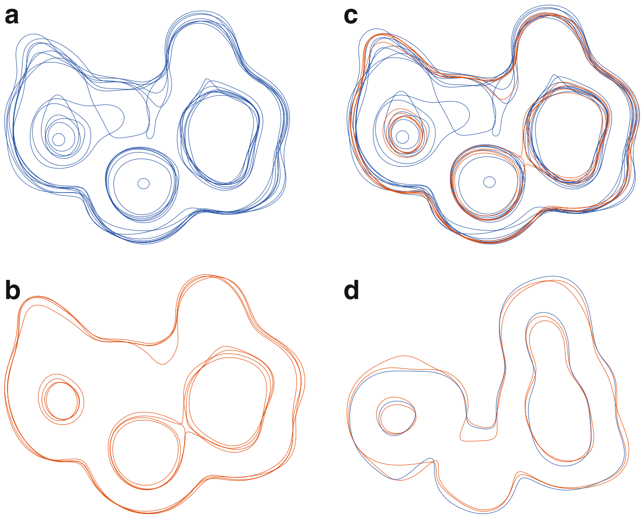


Fig. 5.5 Ranging patterns of bonobos of E1 group at Wamba. Each line represents the ranging pattern of an individual (*blue lines* for males and *red lines* for females). (**a**) Ranging patterns of males, (**b**) ranging patterns of females, (**c**) ranging patterns of males and females, and (**d**) ranging patterns of individuals that transferred into E1 group from an extinct group. We estimated individual areas (95 and 50 % of usage) using the fixed kernel density estimation method with Hawth's Tools and ArcGIS 9.x. We set the single parameter smoothing factor (h) for the kernel density estimation at 650

during the warfare at Wamba (chapter 6). Our findings agree with Waller's (2011) results, suggesting that the bisexually bonded community model explains bonobo behavior at these two study sites.

Association Among Females

Based on association patterns (in most studies, "association" is defined as two individuals observed in the same party), previous studies have revealed that males are more gregarious than females, although female gregariousness varies (Wrangham and Smuts 1980; Nishida et al. 1990; Pepper et al. 1999; Lehmann and Boesch 2005).

Goodall (1986) reported that males were more gregarious than females at Gombe, and Wrangham and Smuts (1980) found that females spent more than twice as much time alone as males. Females in the same neighborhood (in which a subset of females have overlapping core ranging areas in the same general part of their community's range) had levels of association stronger than the average female-female association. Low-ranking females associated more with other low-ranking females than with dominant females (Murray et al. 2006).

Pepper et al. (1999) found that anestrous chimpanzee females showed low gregariousness in Ngogo community in Kibale National Park, Uganda, whereas adult males and estrous females associated with each other significantly more than expected. Unlike at Gombe, anestrous females at Ngogo preferred each other as party members. Although Ngogo females were less gregarious than males, they spent a mean of 64 % of their time in association with ≥ 1 other female (Wakefield 2008). Females spent as much time ranging in all-female parties as they did alone and exhibited association preferences that extended beyond the dyadic level. They formed distinct association clusters termed "cliques," within which affiliative interactions occurred more than expected for female-female dyads (Wakefield 2008, 2013).

In the Sonso community at Budongo, female-female associations are weaker than male-male associations (Fawcett 2000). However, some female dyads showed levels of association stronger than the median level for male-male dyads. In addition, associations between females were stronger during rich food periods than during poor food periods. Associations of female chimpanzees were also weaker than those of males in the Kanyawara community at Kibale (Wrangham et al. 1992). Gilby and Wrangham (2008) analyzed 10 years of Kanyawara chimpanzee data and found the same results. A comparison of periods with different alpha males showed that the strength of association changed more frequently among males than among females; female association patterns appeared to be more a consequence of individual ranging behavior rather than a correlate of cooperation (Gilby and Wrangham 2008). Emery Thompson and Wrangham (2006) compared the gregariousness of chimpanzees in the Sonso and Kanyawara communities. In both communities, males were more gregarious than females, and this tendency was stronger when the party size was larger. The sex difference was more pronounced in the Kanyawara community, probably because peripheral females were more gregarious in the Sonso community than in the Kanyawara community.

Huffman (1990) compared the association index between old/prime males and female chimpanzees at Mahale. Old and prime adult males associated more with other males, and old and prime adult females associated more with young and prime adult females than with individuals of the opposite sex.

For West African chimpanzees, Boesch (1996) found a high percentage of mixed parties (parties involving both males and females) at Taï. Although female-female associations were about one third less strong than male-male associations, their associations were much higher than those in other chimpanzee populations (Wittig and Boesch 2003). Female-female association did not occur randomly: 84 % of adult females had at least one preferred partner, and 78 % of these preferences were maintained for at least three of four consecutive years (Lehmann and Boesch 2009).

We examined dyadic association patterns among Kalinzu chimpanzees. Because estrous females tend to associate with males (Hashimoto et al. 2001) and because the previous studies analyzed only anestrous female association patterns, we used a dataset from anestrous females. We calculated the dyadic association index (DAI, Nishida 1968; Martin and Bateson 2007): $\mathrm{DAI}_{\mathrm{AB}} = \sum \mathrm{A\ B}/(\sum \mathrm{A} + \sum \mathrm{B} - \sum \mathrm{AB})$, where $\sum$A is the amount of time that only A was observed in a party, $\sum$B is the amount of time individual B was seen in a party, and $\sum$AB is the amount of time individuals A and B were in the same party. Cluster analyses were performed employing the unweighted pair group method using arithmetic averages (UPGMA, Sneath and Sokal 1973). The association patterns of the whole community are shown in Fig. 5.6, which shows separate clusters for males and females. Although most females used almost the entire group range, levels of association among females were low (Fig. 5.7a). The mean dyadic association index (DAI) between males (0.093 ± 0.040 (SD), $\mathrm{n} = 231$) was significantly larger than that between males and females (0.020 ± 0.019, $n = 484$) and between females (0.023 ± 0.040, $n = 231$). There was no significant difference in the DAIs between males and females and those between females. One pair of females (*ga*-*mn*) formed the closest association in the group (Fig. 5.6). When we observed them for the first time in 2001, both of them were immature individuals (*ga* was an early adolescent (Goodall 1986) and *mn* was a juvenile) and ranged together without their mothers. Therefore, we presumed them to be sisters coming from another community. Our results therefore confirm that association among chimpanzee females is in general weaker than that among males. However, the level of female-female association varies considerably among sites.

Although there are only a few studies on bonobo associations, the pattern is different from that in chimpanzees. A review by Furuichi (2009) revealed that the mean relative party size (i.e., the percentage of individuals in the party from all individuals in the group: Boesch 1996) tends to be larger in bonobos than in chimpanzees (Wamba: Kuroda 1979; Furuichi 1989; Mulavwa et al. 2008; Lomako: White 1988; Hohmann and Fruth 2002; Hohmann et al. 2006). Although there was no significant difference, the presence ratio (i.e., the proportion of observation

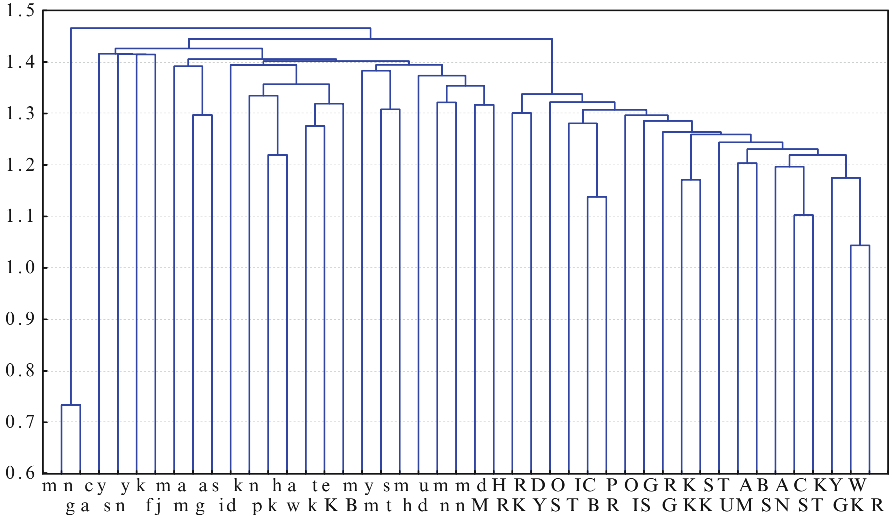


Fig. 5.6 Dendrogram based on the DAI of chimpanzees in Kalinzu drawn by UPGMA method. The names of females are written in small letters and those of males are written in capital letters

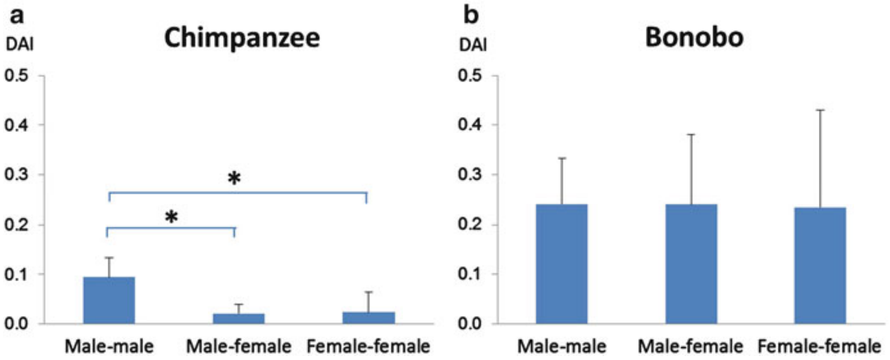


Fig. 5.7 Comparison of DAIs for (**a**) chimpanzees of M group in Kalinzu and (**b**) bonobos of E1 group in Wamba. A significant difference among dyads of different sex combinations was found for chimpanzees (one way ANOVA, $df = 2$, $F = 482.8$, $p < 0.01$), but not for bonobos ($df = 2$, $F = 0.02$, n.s.). (*Pairwise comparisons showed significant differences in the DAI between chimpanzee male-male and male-female dyads and between male-male and female-female dyads (Fisher's LSD test, $p < 0.01$))

days on which each individual was observed in a mixed party) was slightly higher between females than between males in E1 group at Wamba during a period in which bonobos were food provisioned (90.9 % for males and 92.1 % for females) (Furuichi 1989). This result was not due to the provisioning, as a study conducted long after the cessation of provisioning also found that the relative party size was slightly higher for females than for males (Mulavwa et al. 2008).

At Lomako, DR. Congo, White (1988) found that, on average, there were more females than males in parties in the Hedrons, Rangers, and Blobs communities. Association among females was the highest among all combinations, and cluster analysis showed that most subgroups included both males and females (White and Burgman 1990). Hohmann and Fruth (2002) analyzed dyadic association in the Eyengo community and found that dyadic association between community members (association time >25 %) occurred most frequently between females, followed by mixed-sex dyads and male-male dyads. Moreover, long-term association occurred between male-female dyads, while most female-female association did not last longer than one field season (Hohmann et al. 1999). Similarly, female-female pairs were more cohesive (based on the tendency of pairs of animals to be close together, measured by Jacobs' index) than male-male pairs or male-female pairs in the Eyengo and Splinter communities (Waller 2011).

We examined dyadic associations in the E1 group at Wamba (Fig. 5.8) using the same method we used for Kalinzu chimpanzees. Cluster analysis using the UPGMA method showed the strongest associations between the alpha male (TW) and some females. Remnants of a disappearing group who joined the E1 group in 2004 (ND, yk, jk) formed a separate cluster. A young adolescent female (me) that joined E1 group recently was most distant. The DAI was considerably higher than that in chimpanzees, and there was no significant difference among DAIs for male-male, male-female, and female-female dyads (Fig. 5.7b). Although Furuichi

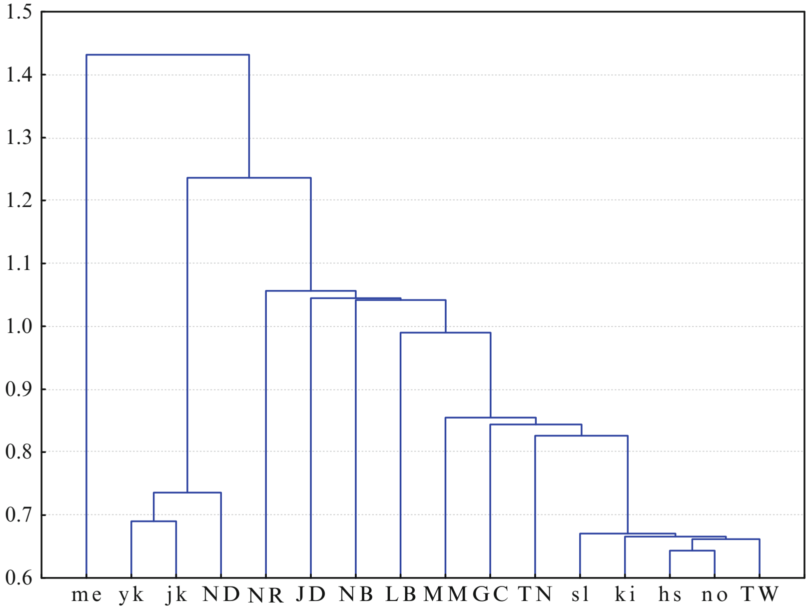


Fig. 5.8 Dendrogram based on the DAI of bonobos at Wamba drawn by the UPGMA method. The names of females are written in small letters and those of males are written in capital letters

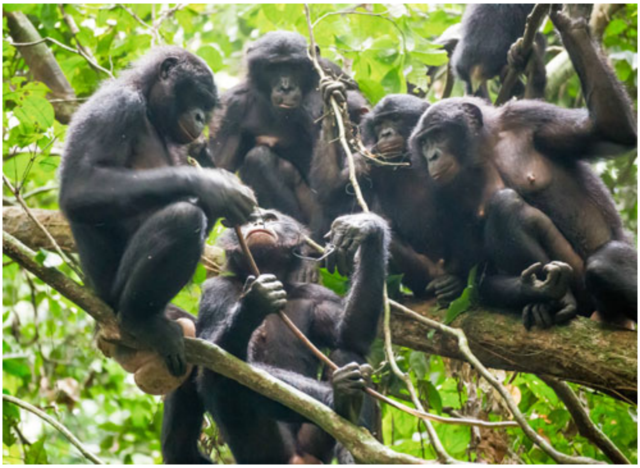


Fig. 5.9 Close association in female bonobos. Many females came together around the female whose fingers were caught by snares

(Furuichi 1989) showed that some mother-adult son pairs showed a high frequency of association, we did not find this tendency. The mother of the alpha male TW had already died. Although we assumed that ki and NB were mother and son from their facial characteristics and DNA analysis (Hashimoto et al. 2008), they did not show a close association during this period.

In summary, the association between female bonobos is stronger overall than that between males or that between males and females (Fig. 5.9).

Discussion

It has generally been assumed that East African female chimpanzees do not form close social relationships with one another. When we compared association data between our study groups, female chimpanzees were indeed less gregarious than female bonobos, which is consistent with previous studies (Stumpf 2011; Watts 2012). However, recent studies based on long-term data collection from several sites revealed a large variation in female-female associations across East African chimpanzees. While females in some communities do not form close associations, such as at Gombe, Kanyawara, and Kalinzu (Fig. 5.10; Goodall 1986; Wrangham et al. 1992; Emery Thompson and Wrangham 2006; this study), females in some communities, such as Ngogo and Sonso (Fawcett 2000; Emery Thompson and Wrangham 2006; Wakefield 2013), form close and consistent associations with at least some other females. Although many studies of chimpanzee social behavior have focused on male-male or male-female relationships, more studies on female-female relationships are needed to fully understand the social structure of chimpanzee communities.

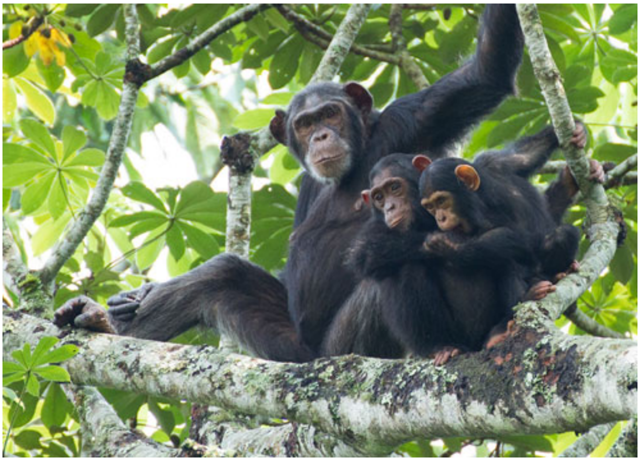


Fig. 5.10 Mother and her offspring. Female chimpanzees tend to forage in their mother's party

There seems to be a large variation in female chimpanzee dispersal patterns. Although it is well established that chimpanzees have a male-philopatric social organization, the proportion of female transfers varies among communities. While the majority of females leave their natal group during adolescence and transfer to other groups at sites like Mahale and Taï (Boesch and Boesch-Achermann 2000; Nishida et al. 2003; Stumpf 2011), nearly half of females remain in their natal group at Gombe (Pusey et al. 1997). Even transfer of parous females with offspring occurs at some sites (Mahale: Nishida et al. 1990, 2003: Sonso: Emery Thompson et al. 2006; Bossou: Sugiyama and Fujita 2011). Such variation in female transfer may be related to a range of reasons that change over time, such as inbreeding avoidance (Pusey 1990), availability of energy for dispersal (Stumpf et al. 2009), and the presence or absence of neighboring groups (Sugiyama 2004).

There is also great variation in female ranging and association patterns across communities, which seems to be related to social and/or ecological conditions. At Gombe and Kanyawara, females seem to compete with each other over high-quality areas with good food availability, resulting in higher-ranking females having higher-quality core areas and higher reproductive success than lower-ranking females (Emery Thompson et al. 2007a; Murray et al. 2007). At Sonso and Ngogo, food resources are abundant and stable (Chapman et al. 1999; Newton-Fisher et al. 2000), and female chimpanzees do not show either extensive overlap in space use or competition over core areas (Fawcett 2000; Wakefield 2008, 2013). Moreover, because of the huge size of the Ngogo community, associated travel costs may place an upper limit on party size, and female chimpanzees form cliques to maintain consistent social relationships among limited numbers of individuals to minimize any costs of gregariousness (Wakefield 2013). By contrast, traveling alone may be too risky for females at Taï because chimpanzees frequently encounter leopards and suffer a higher risk of predation than at other sites (Boesch 1991; Boesch and Boesch-Achermann 2000). This leads to higher gregariousness in Taï females.

Social factors may also affect association patterns. The size of the main study community at Taï decreased from 54 individuals in 1999 to a minimum of 34 individuals in 2006, and the number of females decreased from 19 to 11. Following this decline, party size and dyadic association between females decreased (Wittiger and Boesch 2013). By contrast, changes in male social dynamics did not affect female gregariousness at Kanyawara (Gilby and Wrangham 2008). A comparison of periods with different alpha males revealed that changes in the strength of association occurred more frequently among males, while patterns of female association were less sensitive to changes in the male hierarchy. Overall, these findings may indicate that associations among males and among females tend to be influenced by different social factors.

In female-philopatric primate species, variation in association among females seems to be limited compared with that among males. In Japanese macaques, for example, grooming cliques of female kin are found in many of the groups studied, whether of large or small size, provisioned or wild, or living in different environmental conditions (Mori 1975; Furuichi 1984). By contrast, the association among male Japanese monkeys, and their emigration rate, is generally different across groups. For example, in Takasakiyama, some males stay in the natal troops and obtain high dominance rank, while all males in Yakushima and Kikazan leave their natal group (Sprague et al. 1998). While female monkeys confine their grooming to kin in most of the populations studied, male-male grooming relationships are different among populations. For example, males frequently groom one another in Yakushima-M troop, while males rarely groom one another in Yakushima-Ko troop, from which the Yakushima-M troop fissioned (Furuichi 1985).

It should also be noted that both one-male groups and multi-male groups are found in the same species according to ecological or reproductive conditions. For example, in Hanuman langurs, both one-male groups and multi-male groups have been observed (Sugiyama 1964; Newton 1988). Patas monkeys and forest guenons usually form a one-male group throughout the year, and extra-group males enter the troop during some conceptive seasons to copulate with females (Cords 2000; Carlson and Isbell 2001). This suggests that the males of female-philopatric species, which typically do not have ties with kin, can change their association with other males rather freely according to the social and ecological conditions.

The variation in female chimpanzee association patterns may be understood in the same context. Because they do not in general depend on kin-based ties, females can more freely manage their associations according to the social and ecological conditions, by changing their associations with members of other groups (or communities) and transferring between groups. Wrangham (1979) reported that three anestrous mothers occasionally associated peacefully with males of both the northern and southern communities at Gombe. At Kalinzu, we observed two young adult females move back and forth between neighboring communities and associate peacefully with members of both communities. Nishida et al. (1985) reported female transfer during the process of group extinction. When the number of adult males in K group dropped to only two, many cycling females of K group began to additionally associate with the males of M group. When only one adult male remained in K group, all the fertile, cycling females of K group began to associate mostly with M group. Such varying patterns of female association and transfer may suggest that the "group" is not as important an entity for female chimpanzees as it is for males.

Bonobos seem to show even higher flexibility in female association with members of other groups or communities. Research at Wamba shows that when two groups encounter each other, not only do they forage together for several days, but females also mate with males of the other group (Idani 1990). Although DNA analysis showed that most infants were sired by resident males of the Eyengo community in Lomako (Gerloff et al. 1999), there is a possibility that relatedness among resident males is weaker in bonobos due to such extra-group copulation. It is interesting that bonobo males also show more flexible associations with males of other groups than do chimpanzee males. Hohmann (2001) reported that two strange males entered the Eyengo community and one of them stayed there for at least one year. At Wamba, we observed several cases in which adult males disappeared from the study group for several months, eventually coming back to the original group. Although those males were observed sometimes ranging alone, it is possible that they temporarily visited other groups (chapter 6). Moreover, Hashimoto et al. (2008) reported permanent transfer of male bonobos at Wamba. After the likely extinction of neighboring groups during warfare, two adult males and two adult females with dependent infants joined the E1 study group and became stable members (Hashimoto et al. 2008).

Variations in female transfer and association are also found in eastern gorillas (*Gorilla beringei*). Some females leave their natal group before sexual maturity, while others give birth in their natal group (Robbins et al. 2009; Robbins & Robbins, chapter 4). The pattern of intergroup transfer varies according to sites, subspecies, and the period of observations (Yamagiwa et al. 2011). Studies of associations among female chimpanzees have increased in recent years, but the number of study groups and study areas remains limited to fully understand the extent and implications of this variation. Furthermore, our knowledge of female bonobo associations is derived from only a few study groups. We need more long-term data from different sites for chimpanzees and bonobos to obtain a full picture of associations for both sexes and to understand the adaptive meaning of the variation of such associations in *Pan* species.

Conclusion

Previous studies reported that female East African chimpanzees spend most of their time in small overlapping core areas within the community range. In this chapter, we examined the ranging and association patterns of chimpanzees and bonobos at a variety of sites, including new data from chimpanzees of the Kalinzu Forest and bonobos at Wamba. We found that male chimpanzees utilize the whole community range and that the home range of chimpanzee males is larger than that of females. However, the ranging pattern of female chimpanzees varies among study sites. Female chimpanzees at Taï, Sonso, and Kalinzu utilize a whole community range, supporting the bisexually bonded community model. The ranging patterns of female chimpanzees at Gombe and Kanyawara support the male-bonded community model. The differences in female ranging patterns are not explained by subspecies differences. Our findings show that both male and female bonobos utilize the whole group range, supporting the bisexually bonded community model. The association patterns of female chimpanzees also vary among study sites, although females are less gregarious than males at all sites. At Gombe, Kanyawara, and Kalinzu, association between female chimpanzees is very weak. At Taï, Ngogo, and Sonso, female chimpanzees have specific female partners with whom they associate more than average. These differences in association patterns are not explained by subspecies differences either. Associations between female bonobos are stronger than those between male bonobos. The variation in female chimpanzee patterns of association and intergroup transfer show that, as they are free from kin ties in a male-philopatric society, they can change their behavior according to various factors, such as ecological and/or social conditions.

Acknowledgments We thank Dr. Mulavwa, the late Mr. K. Yangozene, Mr. M. Yamba-Yamba, and Mr. B. Motema-Salo of the Research Center for Ecology and Forestry (CREF) of DR Congo for their support in data collection. We thank Mr. Etwodu Levi of the National Forestry Authority of Uganda, Dr. Peter Ndemere of Uganda National Council for Science and Technology, Mr. I. Monkengo-mo-Mpenge of CREF, and Mr. F. Bukasa of the Ministry of Scientific Research and Technology of DRC for research permits and logistic support. We thank the research assistants and other workers in Bushenyi, Uganda, and Wamba, DR Congo, for collecting data and maintenance of the study sites. We thank members of the Department of Biology at Meiji-Gakuin University and Primate Research Institute (PRI), Kyoto University, Drs. T. Kano, the late T. Nishida, T. Matsuzawa, S. Kuroda, G. Idani, D. Kimura, H. Ihobe, Y. Tashiro, T. Sakamaki, and M. Isaji for various support and encouragement. This study was financially supported by Japan Ministry of the Environment Global Environment Research Fund (F-061 to Nishida; D-1007 to Furuichi), JSPS Grants-in-Aid for Scientific Research (17570193, 19405015, 40379011, to Hashimoto; 17255005, 22255007, 26257408 to Furuichi; 24255010 to Yamagiwa; 21255006, 25257409 to Ihobe; 25257407 to Yumoto), JSPS Asia-Africa Science Platform Program (2009–2011, 2012–2014 to Furuichi), JSPS HOPE project of the Primate Research Institute (PRI) of Kyoto University (to Matsuzawa), MEXT special grant "Human evolution," and JSPS Grant-in-Aid for Strategic Young Researcher Overseas Visits Program for Accelerating Brain Circulation (to PRI, Kyoto University).

References

Arnold K, Whiten A (2003) Grooming dynamics of male chimpanzees of the Budongo Forest, Uganda: tests of five explanatory models. Behaviour 140:519–552

Boesch C (1991) The effect of leopard predation on grouping patterns in forest chimpanzees. Behaviour 117:220–42

Boesch C (1996) Social grouping in Taï chimpanzees. In: McGrew WC, Marchant LF, Nishida T (eds) Great ape societies. Cambridge University, Cambridge, pp 101–113

Boesch C, Boesch-Achermann H (2000) The chimpanzees of the Täi Forest. Oxford University Press, New York

Carlson AA, Isbell LA (2001) Causes and consequences of single-male and multimale mating in free-ranging patas monkeys, *Erythrocebus patas*. Anim Behav 62:1047–1058

Chapman CA, Wrangham RW (1993) Range use of the forest chimpanzees of Kibale: implications for the understanding of chimpanzee social organisation. Am J Primatol 31:263–273

Chapman CA, Wrangham RW, Chapman LJ, Kennard DK, Zanne AE (1999) Fruit and flower phenology at two sites in Kibale National Park, Uganda. J Trop Ecol 15:189–211

Cords M (2000) The number of males in guenon groups. In: Kappeler PM (ed) Primate males: causes and consequences of variation in group composition. Cambridge University Press, Cambridge, pp 84–96

Duffy KG, Wrangham RW, Silk JB (2007) Male chimpanzees exchange political support for mating opportunities. Curr Biol 17:R586–587

Emery Thompson M, Wrangham RW (2006) Comparison of sex differences in gregariousness in fission-fusion species: reducing bias by standardizing for party size. In: Newton-Fisher NE, Notman H, Reynolds V, Paterson J (eds) Primates of Western Uganda. Springer, New York, pp 209–226

Emery Thompson M, Newton-Fisher NE, Reynolds V (2006) Probable community transfer of parous adult female chimpanzees in the Budongo Forest, Uganda. Int J Primatol 27:1601–1617

Emery Thompson M, Kahlenberg SM, Gilby IC, Wrangham RW (2007a) Core area quality is associated with variance in reproductive success among female chimpanzees at Kibale National Park. Anim Behav 73:501–512

Emery Thompson M, Jones JH, Pusey AE, Brewer-Marsden S, Goodall J, Marsden D, Matsuzawa T, Nishida T, Reynolds V, Sugiyama Y, Wrangham RW (2007b) Aging and fertility patterns in wild chimpanzees provide insights into the evolution of menopause. Curr Biol 17:2150–2156

Fawcett KA (2000) Female relationships and food availability in a forest community of chimpanzees. PhD thesis, University of Edinburgh

Furuichi T (1984) Symmetrical patterns in non-agonistic interactions found in unprovisioned Japanese macaques. J Ethol 2:109–119

Furuichi T (1985) Inter-male associations in a wild Japanese macaque troop on Yakushima Island, Japan. Primates 26:219–237

Furuichi T (1987) Sexual swelling receptivity and grouping of wild pygmy chimpanzee females at Wamba, Zaïre. Primates 28:309–318

Furuichi T (1989) Social interactions and the life history of female *Pan paniscus* in Wamba, Zaïre. Int J Primatol 10:173–97

Furuichi T (2009) Factors underlying party size differences between chimpanzees and bonobos: a review and hypotheses for future study. Primates 50:197–209

Furuichi T, Idani G et al (2012) 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. In: Kappeler PM, Watts DP (eds) Long-term field studies of primates. Springer, Berlin/Heidelberg, pp 413–433

Gerloff U, Hartung B, Fruth B, Hohmann G, Tautz D (1999) Intracommunity relationships, dispersal pattern and paternity success in a wild living community of bonobos (*Pan paniscus*) determined from DNA analysis of faecal samples. Proc R Soc Lond 266:1189–1195

Gilby IC, Wrangham RW (2008) Association patterns among wild chimpanzees (*Pan troglodytes schweinfurthii*) reflect sex differences in cooperation. Behav Ecol Sociobiol 62:1831–1842

Goodall J (1986) The chimpanzees of Gombe. Harvard University Press, Cambridge, MA

Hasegawa T (1990) Sex differences in ranging patterns. In: Nishida T (ed) The chimpanzees of the Mahale Mountains: sexual and life history strategies. University of Tokyo Press, Tokyo, pp 99–114

Hashimoto C, Furuichi T (2006) Frequent copulations by females and high promiscuity in chimpanzees in the Kalinzu Forest, Uganda. In: Newton-Fisher NE, Notman H, Paterson JD, Reynolds V (eds) Primates in Western Uganda. Springer, New York, pp 247–257

Hashimoto C, Tashiro Y, Furuichi T (2001) What factors affect the size of chimpanzee parties in the Kalinzu Forest, Uganda? Examination of fruit abundance and number of estrous females. Int J Primatol 22:947–959

Hashimoto C, Tashiro Y, Hibino E, Mulavwa M, Yangozene K, Furuichi T, Takenaka O (2008) Longitudinal structure of a unit-group of bonobos: male philopatry and possible fusion of unit-groups. In: Furuichi T, Thompson J (eds) The bonobos: behavior, ecology, and conservation. Springer, New York, pp 107–119

Hohmann, G. (2001) Association and social interactions between strangers and residents in bonobos (*Pan paniscus*). Primates 42:91–99

Hohmann G, Fruth B (2002) Dynamics in social organization of bonobos (*Pan paniscus*). In: Boesch C, Hohmann G, Marchant LF (eds) Behavioural diversity in chimpanzees and bonobos. Cambridge Univ Press, New York, pp 138–150

Hohmann G, Gerloff U, Tautz D, Fruth B (1999) Social bonds and genetic ties: kinship, association and affiliation in a community of bonobos (*Pan paniscus*). Behaviour 136:1219–1235

Hohmann G, Fowler A, Sommer V, Ortmann S (2006) Frugivory and gregariousness of Salonga bonobos and Gashaka chimpanzees: the abundance and nutritional quality of fruit. In: Hohmann G, Robbins M, Boesch C (eds) Feeding ecology in apes and other primates. Cambridge University Press, Cambridge, pp 123–159

Howard PC (1991) Nature conservation in Uganda's tropical forest reserves. IUCN, Gland

Huffman MA (1990) Some socio-behavioral manifestations of Old Age. In: Nishida T (ed) The chimpanzees of the Mahale Mountains; sexual and life history strategies. University of Tokyo Press, Tokyo, pp 235–255

Idani G (1990) Relations between unit-groups of bonobos at Wamba, Zaire: encounters and temporary fusions. Afr Stud Monogr 11:153–186

Itani J, Suzuki A (1967) The social unit of wild chimpanzees. Primates 8:355–381

Jones JH, Wilson ML, Murray C, Pusey A (2010) Phenotypic quality influences fertility in Gombe chimpanzees. J Anim Ecol 79:1262–1269

Kahlenberg SM, Emery Thompson M, Wrangham RW (2008) Female competition over core areas among Kanyawara chimpanzees, Kibale National Park. Uganda Int J Primatol 29:931–947

Kano T (1992) The last ape: pygmy chimpanzee behavior and ecology. Stanford University Press, Stanford

Kuroda S (1979) Grouping of the pygmy chimpanzees. Primates 20:161–83

Lehmann J, Boesch C (2005) Bisexually bonded ranging in chimpanzees (*Pan troglodytes verus*). Behav Ecol Sociobiol 57:525–535

Lehmann J, Boesch C (2009) Sociality of the dispersing sex: the nature of social bonds in West African female chimpanzees, *Pan troglodytes*. Anim Behav 77:377–387

Martin P, Bateson P (2007) Measuring behaviour: an introductory guide, 3rd edn. Cambridge University Press, Cambridge

Mitani JC (2009) Male chimpanzees form enduring and equitable social bonds. Anim Behav 77:633–640

Mori A (1975) Signals found in the grooming interactions of wild Japanese monkeys of the Koshima troop. Primates 16:107–140

Mulavwa M, Furuichi T, Yangozene K, Yamba-Yamba M, Motema-Salo B, Idani G, Ihobe H, Hashimoto C, Tashiro Y, Mwanza N (2008) Seasonal changes in fruit production and party size of bonobos at Wamba. In: Furuichi T, Thompson J (eds) The bonobos: behavior, ecology, and conservation. Springer, New York, pp 107–119

Muller MN (2002) Agonistic relations among Kanyawara chimpanzees. In: Boesch C, Hohmann G, Marchant LF (eds) Behavioural diversity in chimpanzees and bonobos. Cambridge University Press, Cambridge, pp 112–124

Murray CM, Eberly LE, Pusey AE (2006) Foraging strategies as a function of season and rank among wild female chimpanzees (*Pan troglodytes*). Behav Ecol 17:1020–1028

Murray CM, Mane SV, Pusey AE (2007) Dominance rank influences female space use in wild chimpanzees, *Pan troglodytes*: towards an ideal despotic distribution. Anim Behav 74:1795–1804

Newton PN (1988) The variable social organization of hanuman langurs (Presbytis entellus), infanticide, and the monopolization of females. Int J Primatol 9:59–77

Newton-Fisher NE (1999) Association by male chimpanzees: a social tactic? Behaviour 136:705–730

Newton-Fisher NE, Reynolds V, Plumptre AJ (2000) Food supply and chimpanzee (*Pan troglodytes schweinfurthii*) party size in the Budongo Forest Reserve, Uganda. Int J Primatol 21:613–628

Nishida T (1968) The social group of wild chimpanzees in the Mahale Mountains. Primates 9:167–224

Nishida T (1979) The social structure of chimpanzees of the Mahale Mountains. In: Hamburg DA, McCown ER (eds) The great apes. Benjamin/Cummings, Menlo Park

Nishida T (1989) Social interactions between resident and immigrant female chimpanzees. In: Heltne PG, Marquardt LA (eds) Understanding chimpanzees. Harvard University Press, Cambridge, MA, pp 68–89

Nishida T, Hiraiwa-Hasegawa M (1987) Chimpanzees and bonobos: cooperative relationships among males. In: Smuts BB, Cheney DL, Seyfarth RM, Wrangham RW, Struhsaker TT (eds) Primate societies. University of Chicago Press, Chicago, pp 165–177

Nishida T, Hosaka K (1996) Coalition strategies among adult male chimpanzees of the Mahale Mountains, Tanzania. In: McGrew WC, Marchant LF, Nishida T (eds) Great ape societies. Cambridge University Press, Cambridge, pp 114–134

Nishida T, Kawanaka K (1972) Inter-unit-group relationships among wild chimpanzees of the Mahali Mountains. Kyoto Univ Afr Stud 7:131–169

Nishida T, Hiraiwa-Hasegawa M, Hasegawa T, Takahata Y (1985) Group extinction and female transfer in wild chimpanzees in the Mahale National Park, Tanzania. Z Tierpsychol 67:284–301

Nishida T, Takasaki H, Takahata Y (1990) Demography and reproductive profiles. In: Nishida T (ed) The chimpanzees of the Mahale Mountains – sexual and life history strategies. University of Tokyo Press, Tokyo, pp 63–97

Nishida T, Corp N, Hamai M, Hasegawa T, Hiraiwa-Hasegawa M, Hosaka K, Hunt KD, Itoh N, Kawanaka K, Matsumoto-Oda A, Mitani JC, Nakamura M, Norikoshi K, Sakamaki T, Turner L, Uehara S, Zamma K (2003) Demography, female life history, and reproductive profiles among the chimpanzees of Mahale. Am J Primatol 59:99–121

Pepper JW, Mitani JC, Watts DP (1999) General gregariousness and specific social preferences among wild chimpanzees. Int J Primatol 20:613–632

Pusey AE (1979) Inter-community transfer of chimpanzees in Gombe National Park. In: Hamburg D, McCown E (eds) The great apes. Benjamin/Cummings, Menlo Park, pp 465–479

Pusey AE (1980) Inbreeding avoidance in chimpanzees. Anim Behav 28:543

Pusey AE (1987) Sex-biased dispersal and inbreeding avoidance in birds and mammals. Trends Ecol Evol 2:295–299

Pusey AE (1990) Behavioural changes at adolescence in chimpanzees. Behaviour 115:203–246

Pusey AE, Packer C (1987) Dispersal and philopatry. In: Smuts BB, Cheney DL, Seyfarth RM, Wrangham RW, Struhsaker TT (eds) Primate societies. University of Chicago Press, Chicago, pp 250–266

Pusey AE, Williams JM, Goodall J (1997) The influence of dominance rank on the reproductive success of female chimpanzees. Science 277:828–831

Robbins AM, Stoinski T, Fawcett K, Robbins MM (2009) Leave or conceive: natal dispersal and philopatry of female mountain gorillas in the Virunga volcano region. Anim Behav 77:831–838

Sakura O (1994) Factors affecting party size and composition of chimpanzees (*Pan troglodytes verus*) at Bossou, Guinea. Int J Primatol 15:167–183

Smuts BB, Smuts RW (1993) Male aggression and sexual coercion of females in nonhuman primates and other mammals - evidence and theoretical implications. Adv Stud Behav 22:1–63

Sneath PHA, Sokal RR (1973) Numerical taxonomy. W.A. Freeman, San Francisco

Sprague DS, Suzuki S, Takahashi H, Sato S (1998) Male life history in natural populations of Japanese macaques: migration, dominance rank, and troop participation of males in two habitats. Primates 39:351–363

Stumpf RM (2011) Chimpanzees and bonobos: Inter- and intra-species diversity. In: Campbell CJ, Fuentes A, MacKinnon KC, Bearder SK, Stumpf RM (eds) Primates in perspective, 2nd edn. Oxford University Press, Oxford, pp 340–356

Stumpf RM, Thompson ME, Muller MN, Wrangham RW (2009) The context of female dispersal in Kanyawara chimpanzees. Behaviour 146:629–656

Sugiyama (1964) Group composition, population density and some sociological observations of Hanuman langurs (*Presbytis entellus*). Primates 5:7–37

Sugiyama Y (1988) Grooming interactions among adult chimpanzees in Bossou, Guinea, with special reference to social structure. Int J Primatol 9:393–407

Sugiyama Y (2004) Demographic parameters and life history of chimpanzees at Bossou, Guinea. Am J Phys Anthropol 124:154–165

Sugiyama Y, Fujita S (2011) The demography and reproductive parameters of Bossou chimpanzees. In: Matsuzawa T, Humle T, Sugiyama Y (eds) The chimpanzees of Bossou and Nimba. Springer, Tokyo/Dordrecht/Heidelberg/London/New York, pp 23–34

Takahata Y (1990a) Adult males' social relations with adult females. In: Nishida T (ed) The chimpanzees of the Mahale Mountains: sexual and life history strategies. University of Tokyo Press, Tokyo, pp 133–148

Takahata Y (1990b) Social relationships among adult males. In: Nishida T (ed) The chimpanzees of the Mahale Mountains: sexual and life history strategies. University of Tokyo Press, Tokyo, pp 149–170

Van Elsacker L, Vervaecke H, Verheyen RF (1995) A review of terminology on aggregation patterns in bonobos (*Pan paniscus*). Int J Primatol 16:37–52

Wakefield ML (2008) Grouping patterns and competition among female chimpanzees (*Pan troglodytes schweinfurthii*) at Ngogo, Kibale National Park. Int J Primatol 29:907–929

Wakefield ML (2013) Social dynamics among females and their influence on social structure in an East African chimpanzee community. Anim Behav 85:1303–1313

Waller MT (2011) The ranging behavior of bonobos in the Lomako Forest. PhD thesis, University of Oregon, xvii, 149 p

Wallis J (1997) A survey of reproductive parameters in the free-ranging chimpanzees of Gombe National Park. J Reprod Fertil 109:297–307

Watts DP (1998) Coalitionary mate guarding by male chimpanzees at Ngogo, Kibale National Park, Uganda. Behav Ecol Sociobiol 44:43–55

Watts DP (2000) Grooming between male chimpanzees at Ngogo, Kibale National Park, Uganda. II. Male rank and priority of access to partners. Int J Primatol 21:211–238

Watts DP (2002) Reciprocity and interchange in the social relationships of wild male chimpanzees. Behaviour 139:343–370

Watts DP (2012) The apes: taxonomy, biogeography, life histories, and behavioral ecology. In: Mitani JC, Call J, Kappeler PM, Palombit RA, Silk JB (eds) The evolution of primate societies. Cambridge University Press, Cambridge, pp 113–141

White F (1988) Party composition and dynamics in *Pan paniscus*. Int J Primatol 9:179–93

White FJ, Burgman MA (1990) Social organization of pygmy chimpanzee (*Pan paniscus*): multivariate analysis of intracommunity associations. Am J Phys Anthropol 83:193–201

Williams JM, Pusey AE, Carlis JV, Farm BP, Goodall J (2002) Female competition and male territorial behaviour influence female chimpanzees' ranging patterns. Anim Behav 63:347–360

Wittig RM, Boesch C (2003) Food competition and linear dominance hierarchy among female chimpanzees of the Taï National Park. Int J Primatol 24:847–867

Wittiger L, Boesch C (2013) Female gregariousness in Western Chimpanzees (*Pan troglodytes verus*) is influenced by resource aggregation. Behav Ecol Sociobiol 67:1097–1111

Wrangham RW (1979) Sex differences in chimpanzee dispersion. In: Hamburg DA, McCown ER (eds) The great apes. Benjamin/Cummings, Menlo Park, pp 480–489

Wrangham RW, Smuts B (1980) Sex differences in behavioural ecology of chimpanzees in Gombe National Park, Tanzania. J Reprod Fertil Suppl 28:13–31

Wrangham RW, Clark AP, Isabirye-Basuta G (1992) Female social relationships and social organization of Kibale Forest chimpanzees. In: Nishida T, McGrew WC, Marler P (eds) Topics in primatology, vol 1, Human Origins. University of Tokyo Press, Tokyo, pp 81–98

Yamagiwa J, Basabose AK, Kahekwa J, Bikaba D, Ando C, Matsubara M, Iwasaki N, Sprague DS (2011) Long-term research on Grauer's gorillas in Kahuzi-Biega National Park, DRC: life history, foraging strategies, and ecological differentiation from sympatric chimpanzees. In: Kappeler PM, Watts DP (eds) Long-term field studies of primates. Springer, New York, pp 385–412

Chapter 6
Intergroup Transfer of Females and Social Relationships Between Immigrants and Residents in Bonobo (*Pan paniscus*) Societies

Tetsuya Sakamaki, Isabel Behncke, Marion Laporte, Mbangi Mulavwa, Heungjin Ryu, Hiroyuki Takemoto, Nahoko Tokuyama, Shinya Yamamoto, and Takeshi Furuichi

Introduction

Bonobos (*Pan paniscus*) form multi-male and multi-female unit groups (community) that regularly divide into temporary parties (Kuroda 1979; Kano 1982; White 1988). Although such fission–fusion dynamics occur to some extent in the social systems of most other species (Aureli et al. 2008), bonobo societies are unique in their tendency toward bonding among female nonrelatives, scarcity of male bonding despite male residence, and relative absence of males outranking females (Kano 1992; White 1996; Furuichi 2011). This is in striking contrast with another of our closest living relatives, chimpanzees (*Pan troglodytes*); chimpanzee males form a coalition network, females are less social than are males, and female and immature individuals offer submissive greetings to adult males. However, both *Pan* species

---

T. Sakamaki (✉) • H. Ryu • H. Takemoto • N. Tokuyama • T. Furuichi
Department of Ecology and Social Behavior, Primate Research Institute, Kyoto University,
41-2 Kanrin, Inuyama, Aichi 484-8506, Japan
e-mail: sakamaki.tetsuya.8v@kyoto-u.ac.jp

I. Behncke
Department of Experimental Psychology, University of Oxford, Oxford, UK

M. Laporte
Laboratoire EthoS Ethologie Animale et Humaine, UMR 6552, Université de Rennes 1, France

M. Mulavwa
Research Center for Ecology and Forestry, Ministry of Scientific Research and Technology,
Mabali, Equateur, Democratic Republic of the Congo

S. Yamamoto
Graduate School of Intercultural Studies, Kobe University, Kobe, Japan

Wildlife Research Center, Kyoto University, Kyoto, Japan

T. Furuichi et al. (eds.), *Dispersing Primate Females*,
Primatology Monographs, DOI 10.1007/978-4-431-55480-6_6

show strong tendencies toward female dispersal and male residence (Nishida 1979; de Waal 1982; Goodall 1986; Wrangham 1986; Nishida and Hiraiwa-Hasegawa 1987; Furuichi 1989; Kano 1992).

Itani(1977, 1985) argued that female or male philopatry is a phylogenetically stable social feature. However, there have been several reports of exceptions to male philopatry and female transfer in chimpanzees and bonobos. In some cases involving chimpanzees at Gombe and Mahale in Tanzania, females remained and gave birth in their natal group (Goodall 1986; Nishida et al. 2003). Both male and female chimpanzees seemed to emigrate from their natal group at Bossou in Guinea (Sugiyama 1999, 2004), although the emigration of those animals to other unit groups has not been confirmed. Possible male immigration was reported in a bonobo society at Lomako in the Democratic Republic of the Congo (DRC; Hohmann 2001). Immigration of adult males and adult females with offspring, which was considered a result of a group fusion, was observed in a bonobo group at Wamba in DRC (Hashimoto et al. 2008; Furuichi et al. 2012; see below for details). It is important to understand the circumstances under which such exceptional cases occur when examining the evolutionary models used to explain sex-biased dispersal patterns.

Sex-biased dispersal is an almost ubiquitous feature of the life history of mammals, and many articles have attempted to explain the diversity of sex-biased dispersal patterns (Handley and Perrin 2007), such as the avoidance of inbreeding (Itani 1972; Pusey 1987; Clutton-Brock 1989; Chap. 9, this volume), competition for local resources (Clark 1978; Greenwood 1980; Waser 1985), and competition for local mates (Hamilton 1967; Dobson 1982; Moore and Ali 1984). Cooperation among kin may also play an important role in sex-biased dispersal (Perrin and Lehmann 2001; Le Galliard et al. 2006).

Long-term studies regarding a particular bonobo group based on individual identification can provide valuable data for the evaluation of the factors that facilitate and the evolutionary explanations for female dispersal. In this paper, we begin by reexamining the tendencies toward female dispersal in the E1 group at Wamba by reviewing the data from 1976 to 2013. Data regarding intergroup transfer in the E1 group until 2006 have already been published (Furuichi 1989; Kano 1992; Hashimoto et al. 2008), and we add data obtained between 2007 and the end of 2013 in this paper. We then review the patterns of female transfer between unit groups, such as the ages at transfer and the role of intergroup encounters. Although the manner in which immigrant females establish their social position in a new group is an important issue related to the formation of female bonding and dominance relationships between females and males, only three cases of social interactions of immigrant females with resident individuals have been reported (Furuichi 1989; Idani 1990). In the third section, we describe the social interactions of two new immigrant females with resident individuals from their time of immigration to their first birth. We focus on the social associations, dominance relationships, and affiliative interactions of the two new immigrants. Finally, in the last two sections, we summarize the tactics of immigrant females and discuss which of the traditionally proposed factors best explain why female bonobos transfer between unit groups.

Study Subjects and Observation

Bonobos at Wamba

The bonobos at Wamba in the northern sector of the Luo Scientific Reserve in DRC have been studied since 1973 (Kano 1992; Hashimoto et al. 2008; Furuichi et al. 2012). Researchers identified all members of the main study group, “E,” by 1976. Two subgroups (a southern one and a northern one) have been present in the E group since the beginning of the study, and they were known by researchers as two independent groups (“E1” and “E2,” respectively) until 1984. The primary focus of our study was the E1 group, which refers both to the southern subgroup of E group and to E1 group itself. Although artificial provisioning was initially used for detailed behavioral observations, this practice was abolished in 1996 when civil war prevented research in this area. Observations of E1 group resumed in 2003 and have since been conducted under natural conditions. When research resumed, we found that the previously adjacent B and K groups that had ranged in E1’s eastern areas had disappeared, probably because of poaching.

Although we had also studied a western adjacent group, “P,” until 1996, we resumed intensive habituation and daily following of this group in September 2010. We then named one adjacent group “Pe” and another “Pw,” as the latter ranged in the western part of the area ranged by the Pe group. All the individuals in the Pe group were identified by August 2011. As described in detail below, the E1 group had gradually been expanding its home range toward the east at least since 2003, and the E1 group encountered the eastern adjacent group in 2008, probably for the first time. We named this the “Iy” group; members have not been habituated or identified.

Since 2003, the researchers and trained local assistants who had identified all the bonobos in E1 group have usually followed the largest party from one sleeping site (around 0600 h) to the next (around 1700 h). We recorded individual attendance on a daily basis, and the *ad libitum* behaviors of bonobos were directly observed while we followed them. Age groups were defined as follows (Hashimoto 1997): infants (<4 years old), juveniles (4 to <8 years old), adolescents (8 to <15 years old), and adults (15 years or older). When adolescent females gave birth to their first infant, they were considered adults.

Two New Immigrant Females

We analyzed the social interactions of two nulliparous immigrant females, Fuku and Otomi, based on observational data collected by one of the authors (TS) with support from local assistants. In April 2008, while the E1 group ranged to the west and encountered the Pe group (and probably the Pw group as well), a young nulliparous female (probably Fuku) started to range with the E1 group. In June 2008, while the E1 group ranged within the eastern part of their home range, another young nulliparous female (probably Otomi) that may have been from the Iy group started to range with this group. When the E1 group traveled away from the adjacent groups after this encounter, other unknown individuals that had been observed in the E1 group returned to their groups. However, the two young females mentioned above continued to range with the E1 group. These two females were named Fuku and Otomi on October 14, 2008. At that time, we estimated Fuku to be 10 years old (born in 1998) and Otomi to be 11 years old (born in 1997). After about 2.5 years, on January 6, 2011, and January 11, 2011, we confirmed the first infants born to Fuku and Otomi, respectively.

Behavioral data regarding Fuku and Otomi were collected during four periods between their immigration and their first birth: period 1 (P1) lasted from August 28, 2008, to January 6, 2009; period 2 (P2) from July 4, 2009, to November 23, 2009; period 3 (P3) from June 19, 2010, to August 8, 2010; and period 4 (P4) from October 21, 2010, to February 14, 2011. The observations made during P1 were collected over 574.8 h spread across 76 days, those during P2 covered 447.1 h spread across 65 days, those in P3 were made in 47.4 h spread across 5 days, and those made in P4 were made in 188.3 h spread across 22 days. Observation time was limited in P3 because a researcher (TS) started a survey on other groups at Wamba and in another adjacent population in 2010.

Definitions and Measurements

Daily Social Association and Association Rate

Daily social association (DSA) refers to instances in which group members were observed following the party at least once on a given day. We calculated the DSA values of adult individuals relative to the total number of adult members of the E1 group. The calculation of this DSA ratio included only data collected on days in which we followed the bonobos for almost the entire day or from one sleeping site to the next (whole-day data).

We also calculated the association rates (ARs) of Otomi and Fuku within the observation party. When we directly observed that a target (i.e., Otomi or Fuku) engaged in an association at least once while following a party on a given day, we counted the day as an "association day" for the target. We used only the whole-day data in these calculations. The AR of a target was calculated by dividing the number of her association days by the number of days for which whole-day data were available.

Agonistic Interactions

Agonistic interactions have aggressive components and submissive components; Aggressive components involve *attacking*, *hitting*, *kicking*, *charging*, *chasing*, *charging displays*, *threats*, *dragging branches*, *leaping*, *running*, *shaking branches*, *bending shrubs*, and *contest hooting*. Submissive components include *fleeing*, *grinning*, *screaming*, *peep yelping*, *other submissive vocalizations*, and *avoiding* (see de Waal 1988 and Nishida et al. 1999 regarding italicized terms).

We classified agonistic interactions into three types. The first type included interactions in which dominance was clear due to the aggressive and/or submissive behaviors involved. The second type included agonistic interactions in which dominance was unclear. For example, individual *A* rapidly attacked, charged, or enacted a charging display toward another individual, *B*, but *B* did not flee or engage in avoidance, or individual *A* engaged in a charging display (e.g., dragging a branch close to *B*), but *B* did not flee or show submission even though *B* moved a few meters away. The third type involved agonistic interactions that reflected an equal relationship between the participants. For example, individual *A* charged toward or pretended to chase another individual, *B*, and even if *B* initially fled, *B* immediately returned to chase or charge *A*.

It was sometimes difficult to identify the participants in agonistic interactions, especially when the bonobos were in high trees. Therefore, our data were not sufficient to evaluate the frequency of the agonistic interactions involving each individual. The observational data from P3 were not suitable for comparison with those of other periods (P1, P2, and P4) because of reduced observation time during this phase.

Frequency of Affiliative Interactions

We focused on four types of affiliative interactions: social grooming, social play, genito-genital (GG) rubbing, and copulation. First, we divided our continuous observations into 1-h observation units (OUs). Data from OUs that included less than 40 min of actual observations were excluded from the analyses. When a researcher visually observed an individual, *A*, at least once in one OU, we counted the OU as one for individual *A* (OU-*A*). Table 6.1 presents the number of OUs for each adult and adolescent individual.

Second, in terms of social grooming and social play, if a researcher observed an individual, *A*, engaging in a social interaction X (i.e., social grooming or social play) at least once in one OU, we counted the OU as an OU-*A* of social interaction X (OU-*A*-X). Social interactions between a mother and her own infant (<4 years old) were excluded from the analysis. The frequency with which *A* engaged in interaction X (freq-*A*-X) was calculated by dividing the number of OU-*A*-Xs by the number of OU-*A*s. The frequencies are presented in terms of hundreds (Figs. 6.1 and 6.2). With respect to GG rubbing and copulation, a researcher counted the number of Y events (Y is GG rubbing or copulation). Multi-mounting copulations and multiple GG rubbings were also observed. In such cases, if two or more successive events involving the same participants occurred in a <3-min interval, these events were

Table 6.1 Number of 1-h observation units (OUs) of all adult and adolescent individuals during each study period

		Study period			
		P1 [Oct. 14, 2008, to Jan. 4, 2009]	P2 [July 8, 2009, to Nov. 19, 2009]	P3 [June 28, 2010, to Aug. 6, 2010]	P4 [Oct. 28, 2010, to Feb. 7, 2011]
Total observations (#OU)		334	425	46	177
Female (abbreviation)					
Nao	(No)	90	201	26	119
Kiku	(Ki)	134	223	29	128
Hoshi	(Hs)	125	201	34	116
Sala	(Sl)	198	210	34	136
Yuki	(Yk)	128	201	21	95
Jacky	(Jk)	142	279	32	82
Nova	(Nv)	128	189	10	79
Otomi	(Ot)	108	175	19	83
Fuku	(Fk)	109	237	15	77
Male (abbreviation)					
Ten	(TN)	97	184	28	109
Tawashi	(TW)	0	121	24	106
Mori	(MM)	121	49	–	–
Loboko	(LB)	87	128	26	90
Gauche	(GC)	112	119	12	30
Nobita	(NB)	122	235	33	126
Jeudi	(JD)	94	151	12	43
Nord	(ND)	150	244	–	–
Dai	(DI)	99	150	23	84
Jiro	(JR)	133	240	33	88

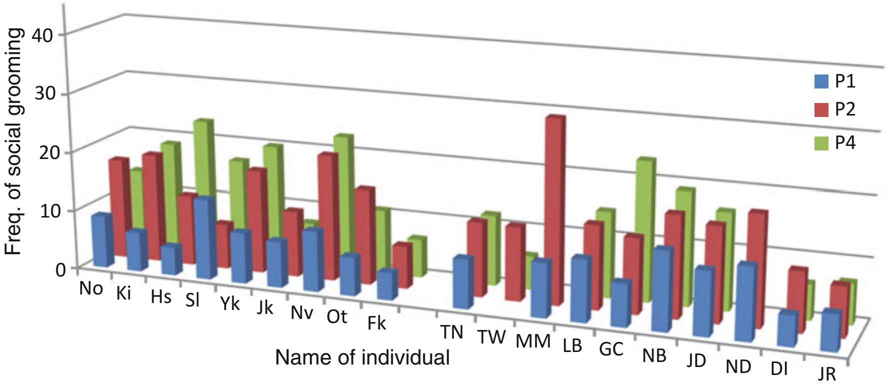


Fig. 6.1 Frequency of social grooming of each adult and adolescent individual during each period (see the text for additional details about the frequency)

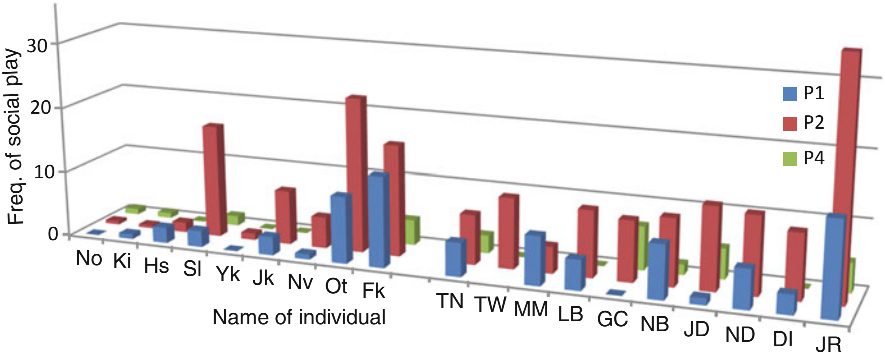


Fig. 6.2 Frequency of social play of each adult and adolescent individual during each period (see the text for additional details about the frequency)

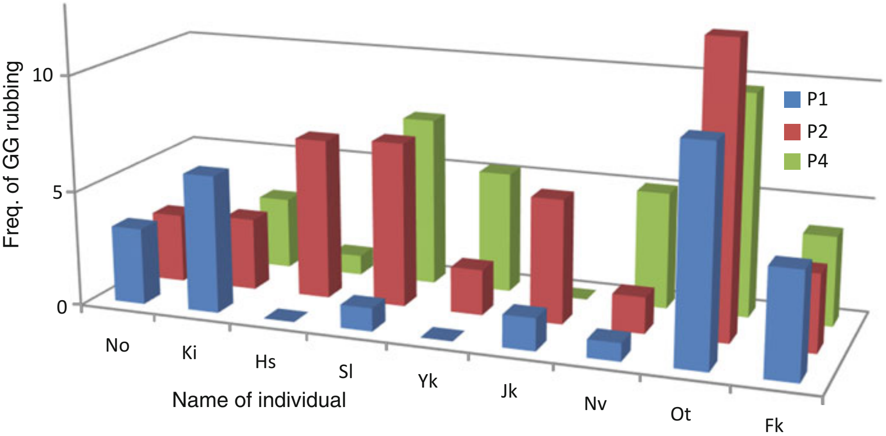


Fig. 6.3 Frequency of GG rubbing of each adult and adolescent female during each period (see the text for additional details about the frequency)

counted as one event. The frequency with which *A* engaged in event Y (Freq-*A*-Y) was calculated by dividing the number of Y acts observed in *A* by the number of OU-*A*s. The frequencies are presented in terms of hundreds (Figs. 6.3 and 6.4). We excluded data from infants and juveniles from the analyses of frequencies.

Sex-Biased Dispersal

Our observational data regarding bonobos at Wamba reflect strong tendencies toward female dispersal during the entire study period. Tables 6.2 and 6.3 present data regarding the life history of the females and males, respectively, in the E1

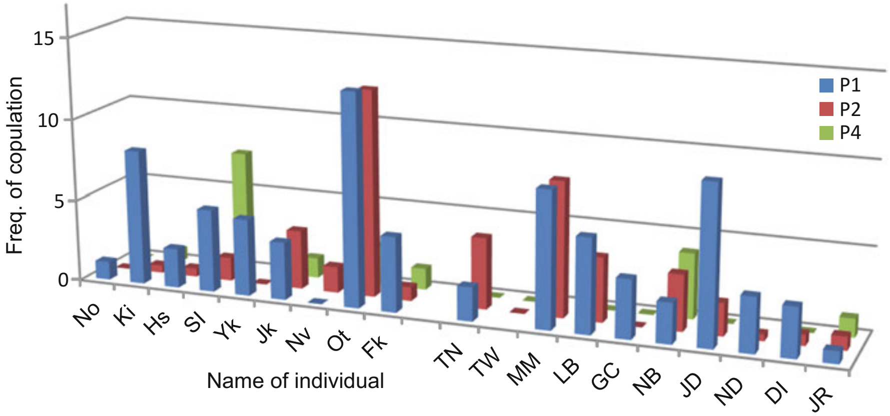


Fig. 6.4 Frequency of copulation of each adult and adolescent female during each period (see the text for additional details about the frequency)

group from 1976 to the end of 2013. The data for the period until the end of 2006 were obtained from Furuichi (1989), Idani (1990), Furuichi et al. (1999), Hashimoto and Furuichi (2001), and Hashimoto et al. (2008) (see also the genetic evidence in Hashimoto et al. 1996). Because observations were not continuous, the data contain gaps regarding births, ages, and the presence of targets. Observations were also interrupted from August 1991 to February 1994 (except during a short visit in August 1992) because of political instability and from June 1996 to August 2003 because of two wars in DRC. Several records maintained by local assistants while the researchers were absent are also included in Tables 6.2 and 6.3.

Identification of the E1 Group and Possible Group Fusion

Eight females and ten males, including immature individuals, belonged to the E1 group when the members of this group were identified before or during 1976. When we resumed our study of the E1 group in 2003, we reidentified members by both direct observation and mitochondrial DNA sequences from fecal samples (Hashimoto et al. 2008; see Tables 6.2 and 6.3). In 2003, the presence of four original members, two females (Nao, Kiku) and two males (Ten, Tawashi), was confirmed. An additional four females and seven males, including immature individuals, were newly identified. The results of DNA analysis suggested that Noire and Nobita were the former Mao and Kikuo, respectively, and that Mori or Jeudi was probably the former Bio (Hashimoto et al. 2008). Further observations of Nobita's relationship with his mother, Kiku, strongly suggested he was Kikuo, but the other identities were not confirmed, as the mothers of Mao and Bio had already disappeared.

Table 6.2 Life histories of females in the E1 group

			Immigration		Disappearance		
Name	Birth	Mother	Time	Age (years)	Time	Age (years)	Presumed cause
1976–1996							
Kame	1945–1950*	?	(Initial member in 1976)		Mar.–Sept. 1990	40–45*	Death by old age
Sen	1945–1950*	?	(Initial member in 1976)		Sept. 1992–Feb. 1994	42–49*	Death by old age
Mitsu	1950–1955*	?	(Initial member in 1976)		Sept. 1992–Feb. 1994	37–44*	Death by old age
Halu	1957*	?	(Initial member in 1976)		1996–2003	39–46*	?
Shiro	1957*	?	(Initial member in 1976)		Aug. 1991–Sept. 1992	34–35*	?
Bihi	1964–1967*	?	Oct.–Nov. 1978	11–14*	1996–2003	29–39*	?
Mayu	1966*	?	(Initial member in 1976)		July 1995–Feb. 1996	29–30*	?
Iku	1971*	?	(Initial member in 1976)		May 1980–Oct. 1981	9–10*	Emigration
Junko	1971*	?	(Initial member in 1976)		May 1980–Oct. 1981	9–10*	Emigration
Nao	1970–1972*	?	Nov. 1983[a]	11–13*	–		–
Miso	1973–1974*	?	Jan. 1984[a]	9–10*	1996–2003	22–30*	?
Kiku	1974*	?	Dec. 1984[a]	10*	–		–
Shiko	Oct.–Nov. 1978	Shiro	(Native)		Oct. 1987	8	Emigration
Kameko	Mar. 1980	Kame	(Native)		Dec. 1981	1	Death at a young age
Biko	Jan. 1981	Bihi	(Native)		Aug.–Sept. 1989	8	Emigration
Mako	Jan.–Oct. 1981	Mayu	(Native)		Dec. 1988	7	Emigration
Shin	1982*	?	Sept. 1992–Sept. 1994	10–14*	(Alive? Different name after 2003?)[b]		
Balu	1982	Halu	(Native)		Feb.–Sept. 1988	5–6	Emigration or death
Toshi	Mar.–Oct. 1984	Kame	(Native)		Sept. 1992–Feb. 1994	7–9	Emigration
Naomi	Jan. 1985	Nao	(Native)		Feb.–Aug. 1985	0	Death at a young age
Bibi	May 1986	Bihi	(Native)		Sept. 1992–Feb. 1994	6–7	Emigration
Miki	Aug.–Oct. 1986	Miso	(Native)		Sept. 1992–Feb. 1994	5–7	Emigration

(continued)

Table 6.2 (continued)

			Immigration		Disappearance		
Name	Birth	Mother	Time	Age (years)	Time	Age (years)	Presumed cause
Nasa	Sept. 1987	Nao	(Native)		July 1995–Feb. 1996	7–8	Emigration
Miho	Apr. 1990	Miso	(Native)		Sept.–Dec. 1992	2	Death at a young age
Nako	Mar.–Dec. 1993	Nao	(Native)		July–Dec. 1995	1–2	Death at a young age
Midori	Mar.–Dec. 1993	Miso	(Native)		1996–2003	3–10	?
Kino	Mar.–Apr. 1994	Kiku	(Native)		1996–2003	2–9	?
Bina	Jan.–Feb. 1996	Bihi	(Native)		1996–2003	0–7	?
After the resumption of study in 2003							
Hoshi	1981–1985*	?	(Identified in 2003)		–		–
Sala	1991–1992*	?	(Identified in 2003)		–		–
Kirara	1998*	?	(Identified in 2003)		May 2006–Aug. 2007	8–9*	Emigration
Nana	2000*	?	(Identified in 2003)		Sept. 2006–Aug. 2007	6–7*	Emigration
Moseka	1995*	?	(Identified in 2004)		Sept. 2007	12*	Emigration
Yuki	1981–1985*	?	Apr. 2004^{c}	19–23*	–		–
Jacky	1986–1990*	?	Apr. 2004^{c}	14–18*	–		–
Yukiko	2002–2003*	Yuki	Apr. 2004^{c}	1–2*	July 2011	8–9*	Emigration
Nachi	Mar.–Apr. 2005	Nao	(Native)		Feb. 2013	7	Emigration
(No name)	Apr. 2005	Hoshi	(Native)		Apr. 2005	0	Death at a young age
Hina	Feb.–Mar. 2007	Hoshi	(Native)		Dec. 2008	1	Death by flu-like disease^{d}
Nova	1994–1995*	?	Aug. 2007	12–13*	–		–

Fuku	1998*	?	Apr. 2008	10*	–		–
Otomi	1997*	?	June 2008	11*	–		–
Nadir	Sept. 2008	Nova	(Native)		–		–
Natsuko	May 2009	Nao	(Native)		–		–
Yume	Oct. 2009	Yuki	(Native)		–		–
Fua	Jan. 2011	Fuku	(Native)		–		–
Otoko	Jan. 2011	Otomi	(Native)		–		–
Zina	2001*	?	Oct. 2011	10*	–		–
Jolie	Jan. 2012	Jacky	(Native)		–		–
Puffy	2003*	(Pao[e])	Oct. 2013	10*	–		–

*Age estimated

[a] See Furuichi (1989) and Idani (1991)

[b] See Hashimoto et al. (2008) for details

[c] Possible group fusion occurred (Hashimoto et al. 2008)

[d] See Sakamaki et al. (2009) for details

[e] Pao is an adult female in the adjacent Pe group

Table 6.3 Life histories of males in the E1 group

				Disappearance		
Name	Birth	Mother	Time of identification	Time	Age (years)	Supposed cause
1976–1996						
Kake	1945–1950*	?	1976 (initial member)	Jan. 1989	39–44*	Death by old age
Kuro	1950–1955*	?	1976 (initial member)	Aug. 1991–Sept. 1992	36–42*	Death by old age
Hata	1955–1960*	?	1976 (initial member)	June 1991	31–36*	Death by old age
Ika	1960–1962*	?	1976 (initial member)	1996–2003	34–43*	?
Ibo	1962*	Kame	1976 (initial member)	Jan.–Oct. 1987	25*	?
Mon	1967*	Kame	1976 (initial member)	1996–2003	29–36*	?
Goro	1968*	Mitsu	1976 (initial member)	Aug. 1984	16*	Death by poaching
Ten	1970*	Sen	1976 (initial member)	–		–
Tawashi	1974*	Kame	1976 (initial member)	–		–
Mitsuo	1975*	Mitsu	1976 (initial member)	July 1991–Sept. 1992	16–17*	?
Haluo	Nov. 1977	Halu	(Native)	Mar.–July 1989	11	?
Senta	Apr. 1980	Sen	(Native)	Sept. 1992–Feb. 1994	12–13	?
Haku	1982	Shiro	(Native)	2002	20	Killed by a soldier[a]
Matsu	Mar.–Oct. 1984	Mitsu	(Native)	Feb.–Sept. 1988	4	Death at a young age
Hayato	Apr. 1986	Halu	(Native)	1996–2003	10–17	?
Mao	Aug.–Oct. 1986	Mayu	(Native, probably identical to Noire in 2003)[b]			–
Shijimi	Feb.–Sept. 1988	Shiro	(Native)	1996–2003	8–15	?
Kikuo	Feb.–Sept. 1988	Kiku	(Native, probably identical to Nobita in 2003)[b]			–
Bio	Feb.–Mar. 1990	Bihi	(Native, probably identical to Mori or Jeudi in 2003)[b]			–
Haze	Mar. 1990	Halu	(Native)	1996–2003	6–13	?
Maro	May 1990	Mayu	(Native)	July 1995–Feb. 1996	5	?

After the resumption of study in 2003						
Hokuto	2002*	Hoshi	2003	Aug. 2004	2*	Death at a young age
Gauche	1986–1990*	?	2003	–		–
Noire	1986–1990*	?	2003 (probably identical to Mao)[b]	Jan.–May. 2006	16–20*	?
Mori	1991–1996*	(Bihi?)	2003	Aug. 2009	13–18*	Death due to serious injury
Nobita	1988*	Kiku	2003 (probably identical to Kikuo)[b]	–		–
Loboko	1991–1996*	?	2003	–		–
Jeudi	1991–1996*	(Bihi?)	2003	–		–
Nord	1985*	?	Apr. 2004[c]	Feb. 2010	25*	?
Dai	1975*	?	Sept. 2004[c]	–		–
Jiro	2001–2002*	Jacky	Apr. 2004[c]	–		–
Kitaro	Feb. 2004	Kiku	(Native)	–		–
Shiba	Nov. 2004	Sala	(Native)	–		–
Joe	Sept. 2006	Jacky	(Native)	–		–
Kyota	July 2009	Kiku	(Native)	–		–
Hachiro	Aug. 2009	Hoshi	(Native)	–		–
Seko	Dec. 2011	Sala	(Native)	–		–
Nimba	July 2013	Nova	(Native)	–		–

*Age estimated

[a] See Furuichi et al. (2012)

[b] See Hashimoto et al. (2008)

[c] Possible group fusion occurred (Hashimoto et al. 2008)

A fusion of unit groups between the E1 group and the formerly adjacent B and/or K groups probably occurred. When we resumed our field study in 2003, we found that most members of the formerly adjacent B and K groups had disappeared, probably because of poaching during periods of political instability and war (Tashiro et al. 2007; Idani et al. 2008; Furuichi et al. 2012). Two adult females and their offspring (Yuki with Yukiko, Jacky with Jiro) and two adult males (Nord, Dai) were initially observed in the E1 group in 2004, when the group ranged in the eastern area, which had been the areas of the formerly adjacent B and K groups. By 2006, they had gradually become stable members of the E1 group. They were thought to be the remnants of the former B and/or K groups (Hashimoto et al. 2008).

Individuals That Disappeared and Newcomers

Three elderly females (Kame, Sen, Mitsu) and three elderly males (Kake, Kuro, Hata) probably died due to old age. Five infant females (Kameko, Naomi, Miho, Nako, Hina) and two infant males (Matsu, Hokuto) disappeared, probably due to death. The carcass of Kameko was confirmed (Kano 1992). Hokuto was an infant that seemed to be skinny and underdeveloped before his disappearance. Hina disappeared during the epidemic of a flu-like disease (Sakamaki et al. 2009).

Among the other females, five adults (Halu, Shiro, Bihi, Mayu, Miso) disappeared for unknown reasons during the researchers' absence. They were stable members with offspring. Because there were no records of the permanent transfer of parous females (see the next section), we assumed that they had died. Three immature females (Midori, Kino, Bina) also disappeared for unknown reasons during the researchers' absence between 1996 and 2003. They may have reached the age of potential emigration by 2003. An additional 15 native females (Iku, Junko, Shiko, Biko, Mako, Balu, Toshi, Bibi, Miki, Nasa, Kirara, Nana, Moseka, Yukiko, Nachi) disappeared from the E1 group before having their first child. We presumed that they had emigrated from the natal group. Nine cases of immigration by females were recorded (Bihi, Nao, Miso, Kiku, Shin, Nova, Fuku, Otomi, Zina). Another young female (Puffy) immigrated in October 2013 and was still present at the end of 2013. All were young nulliparous females when they immigrated to the E1 group. Several strange females with clinging infants were observed in the E1 group when the group encountered or traveled near the adjacent unit groups, but they stayed in the E1 group for a short period of time (see the next section and Table 6.4).

Of the other males, Goro died in August 1984 as a result of poaching, and Haku was killed by soldiers in 2002. Mori disappeared in August 2009, immediately after sustaining a serious injury when he accidentally fell from a tree while performing a charging display. His death must have been a consequence of this serious injury (Behncke and Sakamaki, unpublished data). Six adult males (Ika, Ibo, Mon, Mitsuo, Noire, Nord) and six adolescent males (Haluo, Senta, Hayato, Shijimi, Haze, Maro) disappeared for unknown reasons. Several disappeared during the researchers' absence. Nord seemed to have no health problems before disappearing in February

Table 6.4 Females that temporarily visited the E1 group

		Immigration			
Name	Birth	Time	Estimated age (years)	Period of stay in E1	Accompanying infant
Atsu[a]	1974–1975*	Oct. 1983	8–9	ca. 1 week	None
Mini[a]	1975–1976*	Oct. 1983	7–8	ca. 1 week	None
Kisu[a]	1976–1977*	Aug. 1985	8–9	ca. 1 month	None
Suga[a]	1958–1963*	Sept. 1985	22–27	ca. 2–3 weeks	Yes
Yuki[a,b]	1971–1972*	Dec. 1985	13–14	ca. 3 weeks	None
Elu[a]	1960–1965*	Dec. 1985	20–25	ca. 1 week	Yes
Yasa[a]	1956–1961*	Jan. 1986	25–30	ca. 1 week	Yes
Viki[a]	1979–1980*	Jan. 1988	8–9	ca. 1 week	None
Fuku[a,b]	1979–1980*	Feb. 1988	8–9	ca. 1 week	None
(No name)[c]		Feb. 1985	(Adolescent)	1 day	None
Shiwa[c]	1979–1980*	Nov. 1988	8–9	ca. 1–2 weeks	None
Pino	2000–2001*	Aug. 2007	6–7	ca. 1 week	None
Zolo	2000–2001*	Aug. 2007	6–7	ca. 3 months	None
Kasa	1985–1990*	Sept. 2008	18–23	ca. 1–2 weeks	Yes
Ana	2001*	Feb. 2011	10	ca. 5–6 months	None
Ana[d]		Aug. 2013		ca. 2–3 months	None

*Age estimated

[a] See Furuichi (1989)

[b] Note that these two individuals (Yuki, Fuku) differed from the individuals with the same name in Table 6.2

[c] See Idani (1991)

[d] This was Ana's second visit

2010. These males were not found in other unit groups. With the exception of the possible group fusion mentioned above, there are no records of the immigration of strange males into the E1 group.

Other Study Sites

Among the other study sites with wild bonobos, descriptions of intergroup transfer were found in the previous reports about Lomako. Two nulliparous females immigrated to the "Hedon" group and gave birth by 1991, and one nulliparous female that had been very peripheral in 1985 had become a central parous female in the "Ranger" group by 1991 (White 1996). Between 1993 and 1998, one adult female immigrated to and four adolescent or adult females without infants temporarily visited the "Eyengo" (same as the Ranger) group (Hohmann 2001). Two strange adult males entered the Eyengo group in 1997, and at least one of them remained in the group for at least 11 months, until the end of the study period (Hohmann 2001). During the study period, the number of adult males decreased, whereas the group size and the number of adult females remained relatively stable. In summary, bonobos at Lomako tended toward a pattern of female dispersal (see also genetic evidence: Gerloff et al. 2011), and our data also suggested that male transfer can occur under certain social or ecological conditions (Hohmann 2001).

Patterns of Female Transfer

In this section, we describe several patterns of female intergroup transfer in terms of ages at emigration and immigration, temporary visits, intergroup encounters as opportunities for transfer, second transfers by parous females, and time from immigration to first birth.

Ages at Intergroup Transfer

We assumed that 15 females emigrated from the E1 group (Table 6.2) because they were in a good health during the observations prior to their disappearance, although the immigration of these females to other groups was not confirmed. These individuals ranged from 5 to 12 years at emigration. The oldest émigré was Moseka, who was identified in 2004 after the long interruption in our study, and her age may have been overestimated. If we exclude Moseka, the oldest age at emigration was 9–10 years (Iku, Junko; both ages were estimated). The youngest émigrés, who were 5 years of age, were two females (Balu, Miki). Thus, we estimated that most emigration occurred between 6 and 9 years of age and that this practice was most common at 5–10 years of age. Although these results are consistent with previous reports (Furuichi 1989; Hashimoto and Furuichi 2001; Hashimoto et al. 2008), these ages are younger than those of emigrating chimpanzees (Mahale, range = 9.7–14.0 years, median = 11, Nishida et al. 2003; Kibale (Kanyawara), 10.4–15.7 years; Gombe, 12–13 years, Emery Thompson 2013).

Older juvenile and adolescent females sometimes remain on the periphery of a ranging party (Hashimoto et al. 2008). One young female, Puffy, sometimes remained on the periphery of the gathering while in her native Pe group in 2012, and she immigrated to the E1 group in October 2013. In contrast, Yukiko and Nachi, who were assumed to emigrate from the E1 group in 2011 and 2013, respectively, did not exhibit a clear tendency to stay on the periphery of a gathering before their emigration. Prior to their departure, the E1 group ranged away from adjacent groups and rarely encountered such groups (e.g., no visual encounters for the nearly 2 years beginning in September 2008). These conditions may have affected their spatial positions in the ranging parties.

Nine females immigrated to the E1 group from other unit groups (Table 6.2). Their estimated age at immigration was between 9 and 14 years. It is sometimes difficult to estimate the age of young females because of individual variations in body size and in the shape of the genital area. However, females aged 6–9 years (ages at emigration) are childlike and small, and their genital area is also obviously small even though it is swollen (Fig. 6.5). We found a gap of a few years between the age at emigration (6–9 years) and that at immigration (9–14 years).

Temporary Visits

In view of the gap between the age at emigration and that at immigration, young females appear to visit several unit groups after leaving their natal group before they finally settle in a new group. Kano (1992) reported that at least 30 young females of other unit groups had contact with the E group from 1976 to 1985, and 25 of these individuals disappeared after intermittent stays of various lengths of time (no data were presented on the lengths of time). The other five females gave birth to their first infants in the E group and became fairly stable group members. In 2013, we observed that one nulliparous adolescent female (Nara) sometimes ranged with the Pe and with the adjacent Pw groups.

Table 6.4 presents data regarding females that temporarily visited the E1 group, usually for about 1 week. The data for the period until about 1988 were drawn from Furuichi (1989) and Idani (1991). These short temporary visits usually occurred when the E1 group encountered or ranged near the adjacent unit groups. The number of females listed in Table 6.4 is limited because not all the temporary visitors were identified. We also confirmed the presence of other unknown individuals in the E1 group when adjacent unit groups encountered and ranged near the E1 group (Kano 1982, 1992; Idani 1990; this study).

Fig. 6.5 *Upper left*: a temporary visitor, Zolo, on September 7, 2007. *Upper right*: Fuku on November 25, 2008. *Lower left*: Fuku and her first infant on August 29, 2011. *Lower right*: Fuku on August 29, 2011

Although most of the females listed in Table 6.4 were nulliparous and young, four had clinging infants (Suga, Elu, Yasa, Kasa). They were observed in the E1 group for 1–3 weeks. When the E1 group ranged away from adjacent groups, they returned to the adjacent groups. With the exception of Yuki and Jacky (during the possible group fusion), there were no records of parous females immigrating to and settling with the E1 group.

The cases of Zolo and Ana differed from those of other temporary visitors in terms of the length of their stay, as they remained in the E1 group for a relatively long duration, a few months or more. Zolo joined the E1 group when it encountered the Pe group in August 2007, and she continued to stay in the group when it ranged away from the Pe group. She disappeared from the E1 group in December 2007. Ana stayed in the E1 group for 5.5 months, beginning in February 2011. She was probably from the Iy group, as we first confirmed her presence in the eastern area of the range of the E1 group. She disappeared from the E1 group but returned to the group after about 1 year. After an approximately 2-month stay in the E1 group, she disappeared again. [Her return to E1 was again confirmed in 2014, although this study presents only data gathered until the end of 2013.]

Opportunities for Transfer

Intergroup transfer usually occurs when two unit groups encounter and range closely to each other. Therefore, the opportunity for transfer increases when bonobos range in an area that overlaps with that of adjacent groups. In this sense, overlap supports the maintenance of the social structure (Kano 1982, 1992; Idani 1990).

Because the E1 group has been in a special situation since the resumption of our study in 2003, our observations provide important information about the relationship between intergroup encounters and female transfer. After the extinction of the adjacent B and K groups, the E1 group markedly expanded its home range toward the east and changed the area it frequently ranged (Tashiro et al. 2007; Idani et al. 2008; Sakamaki et al. unpublished data). As a result, opportunities for intergroup encounters have decreased. For example, the E1 group had not encountered adjacent groups during the approximately 22 months from September 2008 to July 2010. During this period, we did not observe any newcomers enter E1 group. Although the bonobos of E1 group exchanged vocalizations (but not visual contact) with the Iy group on August 31 and September 17–18 of 2009 in an area farther to the east, we did not confirm the presence of any unfamiliar bonobos in the E1 group. This very rare case at Wamba shows that young females do not travel alone to an adjacent group in distant area.

Second Transfer

There has been no evidence of a second transfer between unit groups by parous females at Wamba. After giving birth to their first infants in the E1 group (Bihi, Nao, Miso, Kiku, Nova, Fuku, Otomi), immigrant females became fairly stable members of that group. The presence and first birth of another immigrant nulliparous female (Shin) were not confirmed because of the researchers’ long absence during the war. Before 1991, when political disorder began, no parous female, except for Kame, who probably died of old age, was noted. Sen and Mitsu, who disappeared during the researchers' absence from 1992 to 1994, may have died of old age. Parous Bihi and Miso disappeared during the researchers' long absence between 1996 and 2003.

From Immigration to First Birth

The median time between immigration and first birth was 30 months (range = 12–45 months). The first births of eight of nine immigrant females were confirmed (Table 6.5). At least Miso and Kiku seemed to sometimes visit other unit groups between immigrating and their first birth (Idani 1990). The data regarding these 30 months are similar to those of chimpanzees (approx. 2–3 years; in review, Emery Thompson 2013).

Two New Cases of Immigrant Females

This section describes the social interactions of two new immigrant females, Otomi and Fuku. Their behaviors were observed from the time of their immigration to their first birth. The first part focuses on their DSA rate, and the next describes dominance relationships between the new immigrant females and resident individuals. In the third part, we present the data regarding their affiliative interactions, social grooming, social play, GG rubbing, and copulation.

Associational Patterns of New Immigrants

At first, Otomi and Fuku almost always associated with most of the resident individuals in the main party of the E1 group. The two bars on the left-hand side of each period represented in Fig. 6.6 show the DSA rates of adult individuals (white and light-gray bars indicate adult males and adult females, respectively). More than 80 % of the adults in the E1 group were observed on most days, with the exception of P1b. This means that almost all members of the E1 group usually ranged together; even if they were scattered to some degree, they were probably within earshot (Fig. 6.7). During P1b, many individuals showed symptoms of a flu-like disease, and they divided into small parties for approximately 3 weeks in December 2008 (Sakamaki et al. 2009). The two bars on the right-hand side in each period depicted in Fig. 6.6 show the AR in the observation party (dark-gray and black bars indicate Otomi and Fuku, respectively). When the DSA rate was high, Otomi and Fuku were observed primarily in the observation party. When the AR was low (in P1b), the DSA rate was also low. During this time, Otomi and Fuku probably ranged alone or with other members that had separated from the observation party.

Table 6.5 Period between immigration and first birth

Name	Time of immigration	Time of first birth	Name of first offspring	Period (months) until the first birth
Bihi	Oct.–Nov. 1978	Jan. 1981	Biko	26–27
Nao	Nov. 1983	Jan. 1985	Naomi	14
Miso	Jan. 1984	Aug.–Oct. 1986	Miki	31–33
Kiku	Dec. 1984	Feb.–Sept. 1988	Kikuo	38–45
Nova	Aug. 2007	Sept. 2008	Nadir	12–13
Fuku	Apr. 2008	Jan. 2011	Fua	33
Otomi	June 2008	Jan. 2011	Otoko	31

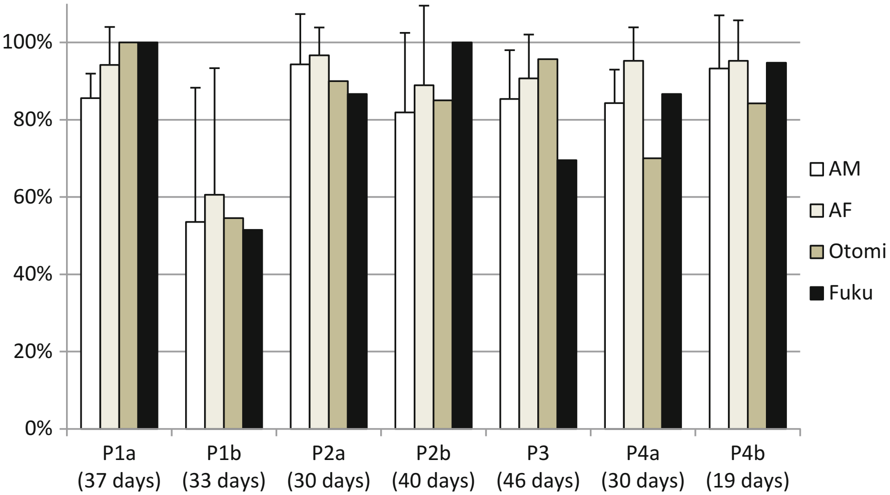
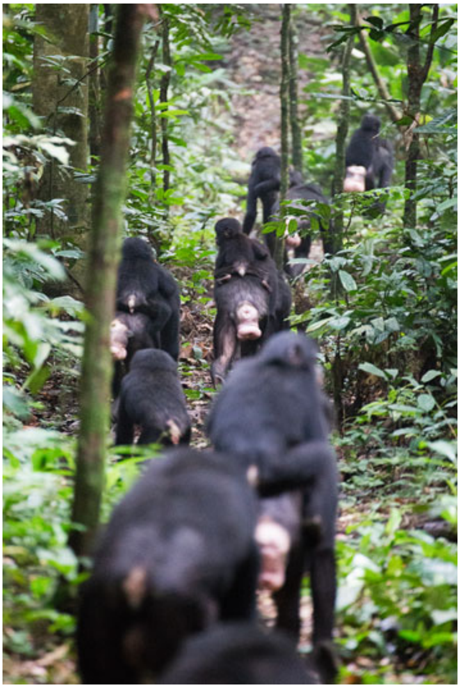


Fig. 6.6 Mean and *SD* of the daily social association (DSA) value relative to the total adult members of the E1 group (the two bars on the left side, *white* and *light–gray bars*, indicate adult males (AMs) and adult females (AFs), respectively) and association rate (AR) of Otomi and Fuku in the observation party (the two bars on the right, *dark-gray* and *black*, indicate Otomi and Fuku, respectively). The numbers in *parentheses* indicate the number of the days in each period. We analyzed only the days on which the bonobos were followed for almost the entire day

Fig. 6.7 Females walking with their offspring



Otomi and Fuku rarely visited other unit groups during the approximately 2.5 years from their immigration to their first birth. However, they may have visited other unit groups before we identified them in 2008. There were four periods in which Otomi or Fuku was absent from the large observation party for several successive days. First, Fuku was absent when most E1 members were observed on August 5–10, 2009. As noted above, an adult male, Mori, was seriously injured on August 4, 2009, and disappeared. All other members were observed during every day. Fuku may have ranged alone or with the injured Mori. Second, Fuku was absent while almost all E1 members were observed from January 27 to February 5, 2010. Immediately before and after this period, the E1 group separated into relatively small parties. Thus, Fuku may have ranged with another small party. Third, Fuku was absent when almost all E1 members ranged together from July 23 to August 4, 2010. During this time, the E1 group repeatedly encountered the Iy group. Another adult female, Nova, was also absent during this period, and we suspected that Fuku and Nova ranged with individuals from the Iy group. Fourth, Otomi was absent when we followed a relatively large party from November 25 to December 4, 2010. During this period, a few other individuals, including Fuku, were only intermittently present in the observation party. Otomi may have ranged with others in separate small parties.

Dominance Relationships Between Immigrants and Residents

In bonobo societies, the dominance relationship between males and females is equivocal or characterized by equality, and females seem to be dominant over males in the context of feeding (White and Wood 2007; Furuichi 2011). Because new immigrant females are usually observed on the periphery of a gathering and do not have high social status at the beginning, the process by which immigrant females establish their social position in a new group is of great interest. We examine this process based on our observations of Otomi and Fuku.

Figure 6.8a–c shows the direction of three types of agonistic interactions during P1, P2, and P4, respectively. As mentioned above, our observational data were not sufficient for estimating the frequency of agonistic interactions because only some of the participants in the interactions were identified. However, agonistic interactions including Otomi and Fuku were observed primarily during P2. Some, but not all, adult females exerted dominance over Otomi and Fuku, but not vice versa. In contrast, males exerted dominance over Otomi and Fuku in some interactions, but Otomi and Fuku also exerted dominance over males in other interactions. In other words, Otomi and Fuku were subordinate to resident females, whereas they were equal to or had equivocal relationships with resident males.

We observed several cases in which Otomi and Fuku appeared to challenge adult males. Interestingly, they behaved playfully in such instances. In the scene described below, we observed both an aggressive attitude and a playful mood.

a P1

Aggressor		Receiver																									
		NB	MM	ND	TN	GC	JD	DI	LB	TW	JR	Kitaro	Shiba	Joe	No	Ki	Hs	Sl	Yk	Jk	Nv	Ot	Fk	Yukiko	Nachi	Hina	Nadir
AM	NB	X	ΔΔ	Δ	EO	OΔΔ ΔOO	OOΔ OO	O			O																
AM	MM		X	O	Δ!Δ	Δ!O	O!		O																		
AM	ND			X		O	O!	OO																			
AM	TN	E			X	O		O	Δ																		
AM	GC					X		O	O		Δ																
AM	JD						X	O	O																		
AM	DI							X	O																		
AM	LB				O			O	X																		
AM	TW									X																	
JM	JR										X																
JM	Kitaro											X															
I-JM	Shiba												X														
IM	Joe													X													
AF	No		O						OOO						X												
AF	Ki		O					O	O!O!O OOOO							X											
AF	Hs						O		O!O!								X										
AF	Sl										O							X					O				
AF	Yk				O				O!OO!										X								
AF	Jk								O!											X							
AF	Nv																				X						
SF	Ot																					X					
SF	Fk																						X				
JF	Yukiko																							X			
IF	Nachi																								X		
IF	Hina																									X	
IF	Nadir																										X

Fig. 6.8 (continued)

b P2

		Receiver																												
Aggressor		NB	TN	MM	GC	JD	ND	LB	DI	TW	JR	Kitaro	Shiba	Joe	Kyota	Hachiro	No	Ki	Hs	Sl	Yk	Jk	Nv	Ot	Fk	Yukiko	Nachi	Hina	Nadir	Yume
AM	NB	X	Δ	O	OOO																									
AM	TN		X				OO			OO														O						
AM	MM			X	OOO O																									
AM	GC				X			ΔO																						
AM	JD					X	EOO		ΔO													Δ								
AM	ND					EO	X		OΔΔ OO																					
AM	LB							X	O	OΔ													E	OO						
AM	DI								X															EE						
AM	TW									X	Δ									E				E	Δ					
SM	JR										X																			
JM	Kitaro											X																		
JM	Shiba												X																	
IM	Joe													X																
IM	Kyota														X															
IM	Hachiro															X														
AF	No																X							O	OO					
AF	Ki							O										X												
AF	Hs									O	Δ								X											
AF	Sl	O				O		O	O	EO										X				OO	OOO OOO					
AF	Yk						O				OO										X			OO	OOO OOO					
AF	Jk																					X			Δ					
AF	Nv							ΔE															X		OO					
SF	Ot						O		EE	EO				O										X	O					
SF	Fk						O																		X	OO				
JF	Yukiko																									X				
JF	Nachi																										X			
IF	Hina																											X		
IF	Nadir																												X	
IF	Yume																													X

Fig. 6.8 (continued)

c P4

Aggressor		Receiver																										
		NB	TN	DI	GC	TW	LB	JD	JR	Kitaro	Shiba	Joe	Kyota	Hachiro	No	Ki	Hs	Sl	Yk	Jk	Nv	Ot	Fk	Yukiko	Nachi	Hina	Nadir	Yume
AM	NB	X		ΔO	O!				OO!									Δ										
AM	TN		X	O	O!O	Δ		O		O																		
AM	DI			X	O			O	O													O						
AM	GC				X																							
AM	TW					X	O																					
AM	LB						X	O																	O			
AM	JD							X	O													Δ						
SM	JR								X																			
JM	Kitaro									X																		
JM	Shiba										X																	
IM	Joe											X																
IM	Kyota												X															
IM	Hachiro													X														
AF	No						O								X									O				
AF	Ki								O!							X												
AF	Hs																X								O			
AF	Sl					ΔO	O	O										X							O			
AF	Yk																		X									
AF	Jk																			X		O!	O!					
AF	Nv																				X	O						
SF	Ot																					X						
SF	Fk																						X					
JF	Yukiko																							X	O			
JF	Nachi																								X			
IF	Hina																									X		
IF	Nadir																										X	
IF	Yume																											X

Fig. 6.8 Dominance relationships based on the direction of behaviors in agonistic interactions (see the text for further details). Panels (**a**–**c**) are during P1, P2, and P4, respectively. "O" indicates agonistic interactions in which dominance was clear due to aggressive and/or submissive behaviors. If two or more aggressors or two or more receivers participated in the agonistic interactions, "O!" was coded (e.g., when two aggressors attacked one receiver, two cells were marked). "Δ" indicates the agonistic interactions in which dominance was unclear. "E" indicates the agonistic interactions that reflected equality between/among participants (i.e., in such cases, both cells are marked for each participant). "AM" and "AF" indicate adult male and female, respectively (15 years or older). "SM" and "SF" indicate adolescent male and female, respectively (8 to <15 years old). "JM" and "JF" indicate juvenile male and female, respectively (4 to <8 years old). "IM" and "IF" indicate infant male and female, respectively (<4 years old)

Scene 1 (August 19, 2009)

Beginning at 0703 h, a large party (seven adult males, four adult females, Otomi, Fuku, and immature individuals) remained in a clearing created by felled trees. Several dyads were engaged in grooming. At 0736 h, Otomi charged toward one adult male (Dai), and he fled. At 0737 h, Dai emitted a contest-hooting utterance and charged toward Otomi, and she fled. Dai continued contest hooting and sometimes engaged in charging displays. At 0740 h, Dai issued a contest-hooting utterance and engaged in a charging display, and Otomi charged toward Dai, who then fled to a tree. At 0742 h, while Dai continued contest hooting and engaging in charging displays, a juvenile female (Yukiko) approached him as if inviting him to play. At 0744 h, Yukiko, another juvenile female (Nachi), and a juvenile male (Shiba) approached Dai while playing with one another, although Dai emitted contest-hooting utterances and repeatedly engaged in charging displays. At 0746 h, another adult male (Nord) approached to groom Dai, but Dai moved away from him and sat 5 m from Nord. At 0748 h, Otomi approached Nachi, who was playing with Yukiko and Shiba. At 0749 h, Dai again issued contest-hooting utterances and engaged in a charging display, and Otomi chased Dai. Several adult individuals continued grooming, and immature individuals continued playing.

In this scene, many bonobos were resting in a clearing. Several adults engaged in social grooming, and immature individuals played with one another. During this period, Dai exhibited aggressive intentions, as evidenced by behavior such as charging, charging displays, and contest hooting. In response to such aggression, Otomi sometimes fled and sometimes charged toward Dai. Otomi's behaviors in this context seemed to be playful rather than serious. Other immature individuals also behaved playfully and appeared to enjoy chasing and wrestling with one another. During this time, Dai was the only individual that attempted to show his dominance over others. Although Genty et al. (2014) argued that bonobos at the "Lola ya Bonobo" sanctuary used contest hooting in two opposite contexts, agonistic and friendly, Dai's behaviors in this scene were clearly aggressive and contrasted with the playful behaviors of other individuals. Thus, immature individuals, including Otomi, reacted playfully to the aggression exhibited by Dai in this scene.

Social play also sometimes escalates into aggression. Such aggressiveness in playful interactions was also observed. For example, during P2, we observed increasingly aggressive behaviors by Sala (adult female) against Otomi and Fuku while they actively engaged in chasing play. In such scenes, we sometimes observed dominance relationships between participants. Again, it was sometimes difficult to distinguish aggressive from playful behaviors in such situations.

In this way, actual dominance relationships in bonobos appeared not only in clear-cut agonistic interactions but also in prolonged playful interactions. These playful interactions indicate that their dominance relationships are ambiguous rather than rigid. First, wrestling and chasing, in which participants change roles (e.g., chasing and fleeing), are frequent forms of play. Second, when a larger, older, or dominant individual plays with a smaller, younger, or subordinate individual, the former does not use his/her full strength but matches his/her strength to that of the

Social grooming

	Adult females									Adult males									
Ot	No	Ki	Hs	Sl	Yk	Jk	Nv	Ot	Fk	TN	TW	MM	LB	GC	NB	JD	ND	DI	JR
P1	1	1	0	0	1	1	0	X	0	0	--	0	0	0	0	0	0	0	1
P2	0	0	0	1	1	3	2	X	3	0	0	0	4	0	0	2	1	1	1
P4	1	0	0	1	2	0	0	X	1	1	0	--	0	0	2	1	--	1	0
Fk																			
P1	0	0	1	0	1	0	0	0	X	1	--	0	0	0	0	0	0	0	0
P2	2	0	1	0	0	0	1	3	X	0	0	0	0	0	1	1	2	0	0
P4	0	0	0	0	0	0	0	1	X	0	0	--	2	0	1	1	--	0	0

GG rubbing

	Adult females								
Ot	No	Ki	Hs	Sl	Yk	Jk	Nv	Ot	Fk
P1	2	3	0	2	0	0	0	X	0
P2	2	0	4	4	0	2	1	X	4
P4	0	0	1	4	1	0	0	X	2
Fk									
P1	0	4	0	0	0	0	0	0	X
P2	0	0	0	1	1	1	0	3	X
P4	0	0	0	1	0	0	0	2	X

Copulation

	Adult males									
Ot	TN	TW	MM	LB	GC	NB	JD	ND	DI	JR
P1	1	--	4	1	2	0	1	0	2	0
P2	2	0	0	4	0	4	2	1	1	1
P4	0	0	--	0	0	0	0	--	0	0
Fk										
P1	1	--	1	0	0	0	1	1	0	0
P2	0	0	2	0	0	0	0	0	0	0
P4	0	0	--	0	0	0	0	--	0	0

Fig. 6.9 Social grooming and GG rubbing and copulation involving Otomi and Fuku during each period. The number of events observed is presented in each cell

latter. Such a tactic while playing is called "self-handicapping" (Fagen 1981; Hayaki 1985; Enomoto 1990). Therefore, social play consists of a kind of reciprocal and symmetrical interaction, and this feature leads to relatively benign and ambiguous dominance relationships among participants.

Affiliative Interactions

The frequency with which every adult and adolescent engaged in affiliative interactions (i.e., social grooming, social play, GG rubbing, and copulation) in each period (except for P3, because of the brief period of observation) is presented in Figs. 6.1, 6.2, 6.3, and 6.4. Otomi's and Fuku's partners in social grooming, GG rubbing, and copulation are presented in Fig. 6.9.

All adult and adolescent individuals engaged in social grooming to some extent (Fig. 6.1). Otomi and Fuku engaged in social grooming, which is among the most common social behaviors among bonobos and contributes to the maintenance of social bonds (Kano 1992; Sakamaki 2013), during each period. However, their partners in social grooming seemed to change from P1 to P2 (Fig. 6.9). Otomi and Fuku groomed primarily with adult females in P1 but rarely did so with adult males. Their engagement in social grooming with adult males started in earnest during P2.

Otomi and Fuku engaged in social play more frequently than other adult individuals did (Fig. 6.2), whereas an adolescent male (Jiro) also did so frequently. Figure 6.2 shows that more adult males than adult females engaged in social play on a frequent basis, although Sala and Jacky frequently engaged in social play during P2. Because we did not maintain records of all the immature individuals that engaged in social play, Fig. 6.2 presents the data for only adolescent and adult individuals. However, juveniles frequently engaged in social play (Fagen

Fig. 6.10 Adult and adolescent females grooming

1981; de Waal 1988; Kano 1992), and we sometimes observed many individuals simultaneously involved in social play.

Otomi engaged in GG rubbing more frequently than Fuku did during each period (Fig. 6.3), although Fuku also engaged in this activity. Additionally, the frequency with which adult females engaged in this activity differed across periods. For example, Hoshi, Sala, and Jacky engaged in GG rubbing more frequently during P2 than during P1. Although more studies are needed before conclusions can be drawn, this may be related to the ages of their infants and their reproductive status. Otomi also engaged in copulation more frequently than did Fuku (Fig. 6.4), and Otomi had more partners in GG rubbing and copulation than did Fuku (Fig. 6.9). No copulation with adult males was observed during P4, probably because of their pregnancy. Copulation with juvenile males was observed during P4.

In summary, during the initial stage of immigration, Otomi and Fuku engaged in social grooming with resident females but rarely did so with adult males. At the beginning, they appeared to regard social bonding with resident females as more important than bonding with males (Fig. 6.10). Copulation is a main medium through which immigrant females can interact with adult males immediately following their arrival. Otomi was more active in regard to copulation and GG rubbing than was Fuku. Indeed, there may be consistent individual differences in sexual and sociosexual activities. Additional research is needed regarding the effects of such differences on future social positions. Otomi and Fuku engaged in social play more frequently than did resident adults, indicating that females at the age of immigration remain childlike in some respects. Given its commonality, social play serves an important role in establishing social bonds between immigrant females and resident individuals.

Tactics of Immigrant Females

What is the cost of immigration for immigrant females? In chimpanzee societies, aggression perpetrated by resident females is costly to immigrant females; however, although severe aggression sometimes occurs, males are effective in protecting immigrant females (Nishida 1989; Kahlenberg et al. 2008a, b; Pusey et al. 2008). The establishment of close relationships with particular resident females is an effective strategy with which immigrant chimpanzee and bonobo females improve their social position in a new group (Furuichi 1989; Idani 1991; Nishida 2012). In what follows, we first summarize the dominance relationships and associations of Otomi and Fuku with particular females. Next, we underscore the importance of social play for immigrant females. Finally, we discuss the absence of a second transfer among parous females.

Dominance Relationships with Residents

Aggression by resident females toward Otomi and Fuku was observed, especially during P2, suggesting conflict between resident and immigrant females. As a result of these agonistic interactions, Otomi and Fuku assumed a low position among the adult females of the new group. Interestingly, no agonistic interactions were observed among resident adult females during the study periods, although such interactions were sometimes observed between adult females and males. In bonobo society, dominance relationships among adult females are rarely manifested in agonistic interactions, whereas the subordination of immigrant females to resident females is manifested in agonistic interactions.

Instances of copulation between immigrant females and adult males were observed from the arrival of the former. Copulation is an important way to establish tolerance and bonding between immigrant females and resident males (Idani 1990). On the other hand, no male protection of immigrant females from aggression perpetrated by resident females was observed. This may be related to the dominance relationship between males and females, as adult males cannot easily overcome adult females (White and Wood 2007; Furuichi 2011).

Our observations showed that dominance relationships between immigrant females and resident males were sometimes unclear or equivocal (Fig. 6.8). In *Scene 1*, an immigrant female, Otomi, exhibited a competitive attitude toward an adult male, Dai, while Dai persistently tried to show his dominance over Otomi. However, Otomi responded to this aggression with a playful attitude. Neither Dai nor Otomi lost. The relative absence of males outranking females is a conspicuous feature of a bonobo society that contributes to the establishment of the social position of immigrant females in a new group.

Association with Particular Females

Female bonding is a key feature of bonobo society. Previous studies have shown that immigrant females frequently approached, followed, and engaged in affiliative interactions with a specific senior female (SSF) (Furuichi 1989; Idani 1991). We did not find clear an SSF for Otomi and Fuku, but our data may be lacking in this regard, as we did not record behavioral data in the same way as we had in previous studies (i.e., focal animal sampling). However, we did not observe a close association between Otomi or Fuku and a particular female that lasted for at least a few days. Some immigrant females are closely associated with an SSF for a relatively long period of time (Furuichi 1989; Idani 1991), suggesting that individual differences may affect the extent to which immigrant females rely on particular resident females.

Otomi and Fuku appeared to engage in social interactions with most resident females. Social association with resident individuals may be essential for immigrant females to establish affinitive bonds in a new group. The relatively high DSA rates and ARs indicate that Otomi and Fuku ranged with most members of the E1 group almost every day. These activities offered opportunities for them to engage in various interactions with resident individuals, and they frequently played with immature individuals. Most playmates were offspring of resident females. Moreover, GG rubbing between immigrant and resident females was observed from the beginning of the arrival of the immigrants. Frequent GG rubbing occurs at feeding sites, as bonobos become excited in response to large quantities of ripe fruits, leading females to engage in GG rubbing with each other. This reduces their tension, and they then eat together. GG rubbing enables female bonobos to tolerate and peacefully coexist with one another in potentially conflictual situations to a greater extent than males are able to do (Hohmann and Fruth 2000; Ryu et al. 2014).

Social Play

We now focus on the role of social play as a tactic for immigrant females. First, the female bonobos that transferred between unit groups were younger than the chimpanzees that did so. Second, Otomi and Fuku engaged in social play more frequently than did adult individuals. Generally, juveniles engage in social play much more frequently, and younger immigrant females are more likely to engage in social play (Fagen 1981; de Waal 1988; Kano 1992). Because immigrant females are still childlike at the time of their immigration (Fig. 6.5), they frequently play with immature individuals in a new group. At times, many individuals are simultaneously involved in social play. Thus, social play accounts for a relatively large part of the social interactions between immigrant females and resident individuals in a new group.

Dominance relationships are sometimes observed in social play, and this can escalate into aggression. We also observed an immigrant female exhibiting a competitive but playful attitude toward an aggressive adult male. Dominance relationships in such playful interactions may also be related to the mild and simple forms of aggression among bonobos (Kuroda 1980). Adult bonobos appear to engage in social play more than do adult chimpanzees (Enomoto 1990; Palagi 2006). It is also important to note that social play consists of reciprocal and symmetrical interactions; that is, participants sometimes change roles (e.g., chasing and fleeing) and self-handicap during social play. Reciprocal and symmetrical interactions contribute to the establishment of symmetrical or equal relationships among participants. It is also important to note that GG rubbing is a kind of symmetrical interaction. Socially symmetrical relationships are the basis for the egalitarianism of bonobo society (Enomoto 1990; Palagi 2006). During the process of establishing their social positions in a new group, childlike immigrant females appear to embody the typical features of bonobo society.

Absence of Second Transfer

With the exception of a case of group fusion and despite the risk of mother–son incest and the absence of infanticide, there is no evidence of second transfer by parous females. Intergroup encounters present opportunities to transfer between unit groups. Adult females with clinging infants sometimes enter another unit group and may stay for a week, but they return to their own group when the two unit groups range far from each other. The absence of a second transfer by parous females may be related to the practice of intimate female bonding. Once a female acquires her social position in a new group, she may want to maintain a close association with other females in the group. Furthermore, mother–son relationships are related to the absence of parous female transfer in that mothers can increase the number of their grandsons if they can provide effective support for their sons (Furuichi 1997; Surbeck et al. 2011).

Why Do Female Bonobos Transfer Between Groups?

Our observations of bonobos at Wamba from 1976 to 2013 revealed a typical male-philopatric and female-dispersal society. This pattern did not differ according to whether data were collected before or after the interruptions in our research or to the abandonment of artificial provisioning.

Thus, questions about why female bonobos transfer between unit groups and males remain in their natal group arise. As mentioned in the Introduction, there may be several reasons for this pattern, including the avoidance of inbreeding (Itani 1972; Pusey 1987; Clutton-Brock 1989), competition for local resources (Clark 1978;

Greenwood 1980; Waser 1985), and competition for local mates (Hamilton 1967; Dobson 1982; Moore and Ali 1984). The need for cooperation among kin may also be important in this regard (Perrin and Lehmann 2001; Le Galliard et al. 2006).

Intragroup Competition and Kin Cooperation

In one exceptional case involving chimpanzees at Mahale, four females remained in their natal group without transferring during a period in which the size of the study group decreased by half. Although the reasons for this behavior remain unknown, it suggests that the lower density reduced the competition for local resources or intragroup feeding and increased the benefits of remaining in the natal group. Because some adult males also disappeared during this period, the inbreeding risk or the possibility of father–daughter and sister–half-brother incest also decreased (Nishida et al. 2003; Nishida 2012). In contrast, the consistent tendency of females in the E1 group at Wamba to transfer, which has been evident since 2003, when the E1 group substantially expanded its home range (Tashiro et al. 2007; Idani et al. 2008), suggests that competition over local resources was not an important contributor to the transfer of female bonobos between unit groups. The lower population density seemed to reduce the intragroup feeding competition in the E1 group even after some remnants of the extinct groups were integrated into that group, which had occurred by 2006.

Competition for local mates (Hamilton 1967; Dobson 1982; Moore and Ali 1984) is also an unlikely explanation of the dispersal of female bonobos. Males that live in one-male units must encounter a high level of competition for local mates, but several species exhibit female-biased dispersal (e.g., hamadryas baboons, gorillas). Bonobos live in multi-male, multi-female groups, and it is assumed that there is less competition for local mates among males. Moreover, the prolonged sexual swelling of female bonobos would be expected to reduce the competition among males for mates (Thompson-Handler et al. 1984; Furuichi 1987; Kano 1992). Females are able to find mates in their natal group, although the possibility of father–daughter and sister–half-brother incest remains. The absence of second transfer by parous females indicates low intragroup competition among females for mates.

The issue of whether cooperation among male kin functions to protect females in estrus and/or mothers and offspring remains controversial with regard to bonobos. On the one hand, bonobos show tolerance for members of neighboring groups; although males are more aggressive than are females in intergroup encounters, copulation between members of different groups occurs (Idani 1990; our unpublished data). On the other hand, one genetic study showed that dominant males achieved high levels of success with regard to paternity, but issues related to extra-group paternity remain unclear (Gerloff et al. 2011).

If female bonobos remain in their natal groups, they may benefit from cooperating with kin, such as mother and sisters. However, the need for kin cooperation does not seem to prevent them from transferring between unit groups, because they succeed in establishing cooperative bonds with unrelated females. The close associations and intimate bonding among females are key elements of bonobo society; that is, the less agonistic temperament of males, their priority of access to the food of females, the absence of infanticide, and intergroup tolerance (Nishida and Hiraiwa-Hasegawa 1987; Kano 1992; White 1996; White and Wood 2007; Furuichi 2011) are advantageous to female bonobos. Therefore, female bonobos are unlikely to pay extra costs for leaving their kin in their natal group or for unstable and risky social relationships with the resident individuals in a new group.

Avoidance of Inbreeding

The traditional view of inbreeding avoidance (Itani 1972; Pusey 1987; Clutton-Brock 1989) may explain part of the evolutionary basis of female transfer. However, as discussed in detail in Chap. 9, inbreeding in the natal group is not necessarily associated with serious disadvantages, especially when the inbreeding involves half-siblings. Additional research regarding the proximate causes of emigration and the mate choices by females in natal and new groups is needed to examine how inbreeding avoidance leads females to leave their natal groups.

One significant risk associated with remaining in one's natal group may be mother–son and father–daughter incest. The former would be less risky because both a mother and her son recognize their kin relationship and avoid incest (Kano 1992). The latter is more risky among bonobos, because paternity is ambiguous due to promiscuous mating patterns. The emigration of young females from their natal group reduces the possibility of father–daughter incest in a male-residence society.

Male bonobos remain in their natal group until the end of their life despite the low level of male bonding. We sometimes observed that adult males ranged alone for a month or more, but they ultimately returned to their original group (our unpublished data). For example, an adult male, Tawashi, had not been observed in the E1 group for about 5 months, from August 2008 to January 2009. During this time, villagers sometimes saw and heard a lone bonobo in the forest and near the crop fields. Tawashi seemed to have lived alone in the range of the E1 group. Males live alone for a variety of reasons. In the case of Tawashi, he lost the position of alpha male before his disappearance. After his return, he had clearly lost his previous vigor and vitality and may have contracted a disease. Despite the occurrence of such temporary disappearances, we have no records of unknown males entering or approaching the periphery of the E1 group, which suggests a strong tendency toward male philopatry.

In contrast to chimpanzees, male bonobos do not ally with other males in agonistic interactions. Therefore, male residence would not be needed to promote male bonding. Instead, lifelong mother–son bonding, which is a characteristic of bonobos, may be among the factors promoting male residence, because this pattern may offer benefits to both mothers and sons (Kano 1992; Furuichi 1997; Surbeck et al. 2011). The absence of a second transfer by parous females may support this notion. However, no evidence of intergroup transfer by orphan males is available.

In conclusion, bonobos show a strong tendency toward male philopatry and female dispersal despite the rarity of male bonding and the frequency of intimate female bonding. It is unlikely that intragroup competition for food and mates explains this tendency. Although future studies on issues such as extra-group paternity and mate choices by females are needed, cooperation among male kin, a relic of the common ancestry of bonobos and chimpanzees (Furuichi and Ihobe 1994), may be advantageous when male kin cooperate to protect relatively scattered females. Therefore, male residence and the risk of father–daughter incest may encourage female transfer in bonobos. Based on this tendency, females would have developed tactics to promote close association and intimate bonding with nonrelatives and to reduce the cost of male aggression. Female transfer at a young age may promote smooth integration into a new group and reduce the cost of transfer via frequent engagement in social play. Frequent social play would be also related to other paedomorphic characteristics of bonobos (e.g., the ventral position of female genitals, which enables GG rubbing between females) and to the high tolerance for other individuals (e.g., mother–son bonds) (Shea 1983; Kuroda 1989). It is intriguing that a type of social structure that differs from that of chimpanzees has developed in societies that show a consistent tendency toward female dispersal.

Acknowledgments This study was financially supported by the Japan Ministry of the Environment Global Environment Research Fund (F-061 to Nishida; D-1007 to Furuichi), Japan Society for the Promotion of Science (JSPS) Grants-in-Aid for Scientific Research (21255006 to Ihobe; 22255007 to Furuichi), JSPS Asia–Africa Science Platform Program (2009–2011, 2012–2014 to Furuichi), JSPS HOPE project of the Primate Research Institute (PRI) of Kyoto University (to Matsuzawa), US Fish and Wildlife Service Assistance Award (96200-0-G017 to the African Wildlife Foundation), Ministry of Education, Culture, Sports, Science & Technology in Japan special grant ("Human Evolution"), and JSPS Grants-in-Aid for Strategic Young Researcher Overseas Visits Program for Accelerating Brain Circulation (to PRI, Kyoto University). We thank Mr. I. Monkengo and Dr. N. Mwanza of the Research Center for Ecology and Forestry; Mr. F. Bukasa of the Ministry of Scientific Research and Technology in the DRC for research permits and logistical support; Mrs. B. Luunga, B. Bokamba, I. Bafanande, B. Likombe, N. Isoluka, E. Besao, and other workers and villagers at Wamba for collecting data and cooperating with our study; members of the Department of Biology of Meiji Gakuin University and PRI of Kyoto University; and the late Drs. T. Nishida, T. Matsuzawa, S. Kuroda, G. Idani, H. Ihobe, D. Kimura, C. Hashimoto, Y. Tashiro, and Y. Tsuji for support and encouragement.

References

Aureli F, Schaffner CM, Boesch C, Bearder SK, Call J, Chapman CA, Connor R, Di Fiore A, Dunbar RIM, Henzi SP, Holekamp K, Korstjens AH, Layton R, Lee P, Lehmann J, Manson JH, Ramos-Fernandez G, Strier KB, van Schaik CP (2008) Fission–fusion dynamics: new research frameworks. Curr Anthropol 49:627–654

Clark AB (1978) Sex ratio and local resource competition in a prosimian primate. Science 201:163–165

Clutton-Brock TH (1989) Female transfer and inbreeding avoidance in mammals. Nature 337:70–71

de Waal FBM (1982) Chimpanzee politics: power and sex among apes. Harper & Row, New York de Waal FBM (1988) The communicative repertoire of captive bonobos (*Pan paniscus*), compared to that of chimpanzees. Behaviour 106:183–251

Dobson FS (1982) Competition for mates and predominant juvenile male dispersal in mammals. Anim Behav 30:1183–1192

Emery Thompson M (2013) Reproductive ecology of female chimpanzees. Am J Primatol 75:222–237

Enomoto T (1990) Social play and sexual behavior of the bonobo (*Pan paniscus*) with special reference to flexibility. Primates 31:469–480

Fagen R (1981) Animal play behavior. Oxford University Press, New York

Furuichi T (1987) Sexual swelling, receptivity, and grouping of wild pygmy chimpanzee female at Wamba, Zaire. Primates 28:309–318

Furuichi T (1989) Social interactions and the life history of female *Pan paniscus* in Wamba, Zaïre. Int J Primatol 10:173–197

Furuichi T (1997) Agonistic interactions and matrifocal dominance rank of wild bonobos (*Pan paniscus*) at Wamba, Zaire. Int J Primatol 18:855–875

Furuichi T (2011) Female contributions to the peaceful nature of bonobo society. Evol Anthropol 20:131–142

Furuichi T, Ihobe H (1994) Variation in male relationships in bonobos and chimpanzees. Behaviour 130:211–228

Furuichi T, Hashimoto C, Idani G, Ihobe H, Tashiro Y, Kano T (1999) Current situation of studies of bonobos (*Pan paniscus*) at Wamba, D. R. Congo. Primate Res 15:115–127 (in Japanese with English summary)

Furuichi T, Idani G, Ihobe H, Hashimoto C, Tashiro Y, Sakamaki T, Mulavwa MN, Yangozene K, Kuroda S (2012) 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. In: Kappeler PM, Watts DP (eds) Long-term field studies of primates. Springer, Berlin, pp 413–433

Genty E, Clay Z, Hobaiter C, Zuberbühler K (2014) Multi-modal use of a socially directed call in bonobos. PLoS ONE 9(1):e84738. doi:10.1371/journal.pone.0084738

Gerloff U, Hartung B, Fruth B, Hohmann G, Tautz D (2011) Intracommunity relationships, dispersal pattern and paternity success in a wild living community of bonobos (*Pan paniscus*) determined from DNA analysis of faecal samples. Proc R Soc B Biol Sci 266:1189–1195

Goodall J (1986) The chimpanzees of Gombe: patterns of behavior. Harvard University Press, Cambridge

Greenwood PJ (1980) Mating system, philopatry and dispersal in birds and mammals. Anim Behav 28:1140–1162

Hamilton WD (1967) Extraordinary sex ratios. Science 156:477–488

Handley LJL, Perrin N (2007) Advances in our understanding of mammalian sex-biased dispersal. Mol Ecol 16:1559–1578

Hashimoto C (1997) Context and development of sexual behavior of wild bonobos (*Pan paniscus*) at Wamba, Zaire. Int J Primatol 18:1–21

Hashimoto C, Furuichi T (2001) Intergroup transfer and inbreeding avoidance in bonobos. Primate Res 17:259–269 (in Japanese with English summary)

Hashimoto C, Furuichi T, Takenaka O (1996) Matrilineal kin relationship and social behavior of wild bonobos (*Pan paniscus*): sequencing the D-loop region of mitochondrial DNA. Primates 37:305–318

Hashimoto C, Tashiro Y, Hibino E, Mulavwa M, Yangozene K, Furuichi T, Idani G, Takenaka O (2008) Longitudinal structure of a unit-group of bonobos: male philopatry and possible fusion of unit-groups. In: Furuichi T, Thompson J (eds) The bonobos: behavior, ecology, and conservation. Springer, New York, pp 107–119

Hayaki H (1985) Social play of juvenile and adolescent chimpanzees in the Mahale Mountains National Park, Tanzania. Primates 26:343–360

Hohmann G (2001) Association and social interactions between strangers and residents in bonobos (*Pan paniscus*). Primates 42:91–99

Hohmann G, Fruth B (2000) Use and function of genital contacts among female bonobos. Anim Behav 60:107–120

Idani G (1990) Relations between unit-groups of bonobos at Wamba, Zaire: encounters and temporary fusions. Afr Study Monogr 11:153–186

Idani G (1991) Social relationships between immigrant and resident bonobo (*Pan paniscus*) females at Wamba. Folia Primatol 57:83–95

Idani G, Mwanza N, Ihobe H, Hashimoto C, Tashiro Y, Furuichi T (2008) Changes in the status of bonobos, their habitat, and the situation of humans at Wamba in the Luo Scientific Reserve, Democratic Republic of Congo. In: Furuichi T, Thompson J (eds) The bonobos: behavior, ecology, and conservation. Springer, New York, pp 291–302

Itani J (1972) A preliminary essay on the relationship between social organization and incest avoidance in nonhuman primates. In: Poirier FR (ed) Primate socialization. Random House, New York, pp 165–171

Itani J (1977) Evolution of primate social structure. J Hum Evol 6:235–243

Itani J (1985) The evolution of primate social structures. Man 20:593–611

Kahlenberg SM, Emery Thompson M, Wrangham RW (2008a) Female competition over core areas in *Pan troglodytes schweinfurthii*, Kibale National Park, Uganda. Int J Primatol 29:931–947

Kahlenberg SM, Emery Thompson M, Muller MN, Wrangham RW (2008b) Immigration costs for female chimpanzees and male protection as an immigrant counterstrategy to intrasexual aggression. Anim Behav 76:1497–1509

Kano T (1982) The social group of pygmy chimpanzees (*Pan paniscus*) of Wamba. Primates 23:171–188

Kano T (1992) The last ape: pigmy chimpanzee behavior and ecology. Stanford University Press, Stanford

Kuroda S (1979) Grouping of the pygmy chimpanzees. Primates 20:161–183

Kuroda S (1980) Social behavior of the pygmy chimpanzees. Primates 21:181–197

Kuroda S (1989) Developmental retardation and behavioral characteristics. In: Heltne PG, Marquardt LA (eds) Understanding chimpanzees. Harvard University Press, Cambridge, pp 184–193

Le Galliard J-F, Gundersen G, Andreassen HP, Stenseth NC (2006) Natal dispersal, interactions among siblings and intrasexual competition. Behav Ecol 17:733–740

Moore J, Ali R (1984) Are dispersal and inbreeding avoidance related? Anim Behav 32:94–112

Nishida T (1979) The social structure of chimpanzees of the Mahale Mountains. In: Hamburg DA, McCown ER (eds) The great apes. Benjamin/Cummings Publishing, Menlo Park, pp 73–121

Nishida T (1989) Social interactions between resident and immigrant female chimpanzees. In: Heltne PG, Marquardt L (eds) Understanding chimpanzees. Harvard University Press, Cambridge, pp 68–89

Nishida T (2012) Chimpanzees of the Lakeshore: natural history and culture at Mahale. Cambridge University Press, Cambridge

Nishida T, Hiraiwa-Hasegawa M (1987) Chimpanzees and bonobos: cooperative relationships among males. In: Smuts BB, Cheney DL, Seyfarth RM, Wrangham RW, Struhsaker TT (eds) Primate societies. University of Chicago Press, Chicago, pp 165–177

Nishida T, Kano T, Goodall J, McGrew WC, Nakamura M (1999) Ethogram and ethnography of Mahale chimpanzees. Anthropol Sci 107:141–188

Nishida T, Corp N, Hamai M, Hasegawa T, Hiraiwa-Hasegawa M, Hosaka K, Hunt KD, Itoh N, Kawanaka K, Matsumoto-Oda A, Mitani JC, Nakamura M, Norikoshi K, Sakamaki T, Turner L, Uehara S, Zamma K (2003) Demography, female life history, and reproductive profiles among the chimpanzees of Mahale. Am J Primatol 59:99–121

Palagi E (2006) Social play in bonobos (*Pan paniscus*) and chimpanzees (*Pan troglodytes*): implications for natural social systems and interindividual relationships. Am J Phys Anthropol 129:418–426

Perrin N, Lehmann L (2001) Is sociality driven by the costs of dispersal or the benefits of philopatry? A role for kin-discrimination mechanisms. Am Nat 158:471–483

Pusey AE (1987) Sex-biased dispersal and inbreeding avoidance in birds and mammals. Trends Ecol Evol 2:295–299

Pusey A, Murray C, Wallauer W, Wilson M, Wroblewski E, Goodall J (2008) Severe aggression among female *Pan troglodytes schweinfurthii* at Gombe National Park, Tanzania. Int J Primatol 29:949–973

Ryu H, Hill DA, Furuichi T (2014) Prolonged maximal sexual swelling in wild bonobos facilitates affiliative interactions between females. Behaviour. doi:10.1163/1568539X-00003212

Sakamaki T (2013) Social grooming among wild bonobos (*Pan paniscus*) at Wamba in the Luo Scientific Reserve, DR Congo, with special reference to the formation of grooming gatherings. Primates 54:349–359

Sakamaki T, Mulavwa M, Furuichi T (2009) Flu-like epidemics in wild bonobos *(Pan paniscus)* at Wamba, the Luo Scientific Reserve, Democratic Republic of Congo. Pan Afr News 16:1–4

Shea BT (1983) Paedomorphosis and neoteny in the pygmy chimpanzee. Science 222:521–522

Sugiyama Y (1999) Socioecological factors of male chimpanzee migration at Bossou, Guinea. Primates 40:61–68

Sugiyama Y (2004) Demographic parameters and life history of chimpanzees at Bossou, Guinea. Am J Phys Anthropol 124:154–165

Surbeck M, Mundry R, Hohmann G (2011) Mothers matter! Maternal support, dominance status and mating success in male bonobos (*Pan paniscus*). Proc R Soc B 278:590–598

Tashiro Y, Idani G, Kimura D, Bongori L (2007) Habitat changes and decreases in the bonobo population in Wamba, Democratic Republic of the Congo. Afr Study Monogr 28:99–106

Thompson-Handler N, Malenky RK, Badrian N (1984) Sexual behavior of *Pan paniscus* under natural conditions in the Lomako Forest, Equateur, Zaire. In: Susman RL (ed) The pygmy chimpanzee: its evolutionary biology and behavior. Plenum Press, New York, pp 347–368

Waser PM (1985) Does competition drive dispersal? Ecology 66:1170–1175

White FJ (1988) Party composition and dynamics in *Pan paniscus*. Int J Primatol 9:179–193

White FJ (1996) *Pan paniscus* 1973 to 1996: twenty-three years of field research. Evolut Anthropol 5:11–17

White FJ, Wood KD (2007) Female feeding priority in bonobos, *Pan paniscus*, and the question of female dominance. Am J Primatol 69:837–850

Wrangham RW (1986) Ecology and social relationships in two species of chimpanzees. In: Rubenstein DL, Wrangham RW (eds) Ecological aspect of social evolution. Princeton University Press, Princeton, pp 352–378

Chapter 7
Human Female Dispersal and Social Organization: A Case of Central African Hunter-Gatherers

Naoki Matsuura

Introduction

Modern hunter-gatherer societies are not necessarily characterized by female dispersal but have flexible residence patterns. Traditionally, human society was regarded as exhibiting female dispersal in the patrilineal-patrilocal band model (Radcliffe-Brown 1930–1931; Steward 1955; Sahlins 1959; Service 1962; Owen 1965). The patrilineal-patrilocal band model was suggested in studies of hunter-gatherer societies in the first half of the twentieth century. Radcliffe-Brown (1930–1931) described Australian aboriginal people's societies that were composed of the horde, the primary land-owning group based on an exogamous patrilineal clan. Cultural ecological studies discussed patrilineal bands as being formed because of the necessity for men to be familiar with the land and cooperate with their kin for hunting activities (Steward 1955; Sahlins 1959; Service 1962). It has also been claimed that there were benefits of patrilineal-patrilocal bands for defending food resources and/or females from other bands (Steward 1955; Sahlins 1959; Service 1962).

However, the patrilineal-patrilocal band model was challenged by subsequent empirical studies based on fieldwork observing contemporary hunter-gatherer societies. Many ethnographic reports on hunter-gather societies having composite and flexible local groups were presented in the first international conference on hunting and gathering societies in 1966, Man the Hunter. This empirical evidence led to the conclusion that the patrilocal band is not the universal form of hunter-gatherer group structure (Lee and DeVore 1968). Since then, the view that hunter-gatherer societies are typically bilocal, where a married couple alternates their residence between that

---

N. Matsuura (✉)
School of International Relations, University of Shizuoka, Yada 52-1, Suruga-ku, Shizuoka 422-8526, Japan
e-mail: n-matsuura@u-shizuoka-ken.ac.jp

T. Furuichi et al. (eds.), *Dispersing Primate Females*,
Primatology Monographs, DOI 10.1007/978-4-431-55480-6_7

of the wife's and husband's group, has risen to prominence. This social organization pattern has been described with terms such as flux, flexibility, and fluidity (Barnard 1983; Kelly 1995).

Nevertheless, hunter-gatherer social organization has continued to prompt scholarly debate. Ember (1975, 1978) statistically analyzed data from the *Ethnographic Atlas* (Murdock 1967) and challenged earlier views that the gathering is the most important subsistence activity and that women contribute substantially more to subsistence than men (Lee and DeVore 1968). She suggested again that hunter-gatherer societies are typically patrilocal because men contribute relatively more to subsistence than women and because of frequent warfare, which reinforces male bonds in many hunter-gatherer societies (Ember 1975, 1978). In human evolution studies, researchers tend to emphasize the similarities between male philopatry of African great apes and human patrilocal bands to characterize hominoid social organization as exhibiting female dispersal (Wrangham 1987; Foley and Lee 1989; Rodseth et al. 1991; Furuichi 2006). However, these studies were criticized because they failed to take early ethnographies' inaccurate data into account and did not consider residence changes which occur throughout the duration of marriage (Barnard 1983; Kelly 1995; Alvarez 2004; Marlowe 2004).

Kelly (1995) criticized the unilineal evolutionism, the idea that all human societies pass through the same evolutionary stages by improving their moral and mental capacities, and renounced generalizations that mask this underlying variability. He emphasized the diversity of hunter-gatherer societies' structures and of human behavior by giving an account of varying factors such as subsistence activities, mobility, trade, sharing, territoriality, demography, and sociopolitical organization. Alvarez (2004) reexamined ethnographies in the *Ethnographic Atlas* that Ember (1975, 1978) cited and concluded that strategic flexibility in female dispersal and male kinship alliances are clearly indicated among modern hunter-gatherers. She claims that "the concepts of patrilineage and patrilocality, as applied to the evolution of human sociality, have focused attention away from the actual, strategically varying behavior of individuals, and fostered erroneous ideas about the social organization of hunter-gatherers" (Alvarez 2004: 421).

Marlowe (2004) compared residential patterns of 36 foraging societies using the Standard Cross-Cultural Sample (SCCS). SCCS includes ethnographic data of 186 societies that have been chosen to create an unbiased sample with respect to geographic region, language family, and cultural area, accounting for many variables. His analysis shows that there is a significant difference in residential patterns between foragers (hunting-gathering and fishing societies in his definition) and nonforagers; foragers have greater residential flexibility than nonforagers. He also pointed out other key differences. One is that early residence among foragers is biased less toward patrilocality because bride service (work or services done by a groom for his bride's family) is often provided in many forager societies while bride price (the money or goods given by a groom to his bride's family) is more common in nonforager societies. Another is the difference in reckoning kinship. Foragers bond more closely to both mothers' and fathers' kin and interact bilaterally, while nonforagers are more patrilineal. Foragers are also less patrilocal and more multilocal than nonforagers because they form significantly smaller local groups which require that people find mates outside their camp. They have a lower frequency of warfare as they do not have much wealth or defensible home ranges due to a hunting-dependent lifestyle, which targets more mobile food resources (Marlowe 2004).

Hill et al. (2011) analyzed coresidence patterns among 32 present-day hunter-gatherer societies and showed that bisexual philopatry and dispersal are typical among them, resulting in frequent adult brother-sister affiliation. They hypothesize that "monogamous pair bonding, paternal recognition within cooperatively breeding social units, and bisexual dispersal facilitate frequent and friendly intergroup relations and migration and low group genetic relatedness of band co-residents" (Hill et al. 2011: 1288). They discuss how large social networks of genetically unrelated adults helped humans evolve capacities for social learning that may have resulted in cumulative cultural evolution (Hill et al. 2011). In their statistical analysis of band composition, they emphasize the importance of actual residence rather than cultural rules.

Recently, there have been many ethnographic studies on residence patterns, marriages, and child rearing among foragers (e.g., the Ju/'hoansi of Namibia and Botswana, Hames and Draper 2004; Ache in Paraguay, Hill and Hurtado 2009; Hadza in Tanzania, Marlowe 2010 and Wood and Marlowe 2011; Pumé in Venezuela, Kramer and Greaves 2011). Kramer and Greaves (2011) noted that cross-cultural studies have limitations because they use ethnographic databases, which depend primarily on interviews rather than observation and emphasize the importance of focused individual-level longitudinal data. Using detailed data spanning 25 years, they demonstrate that the Pumé have strong natalocality (where both partners remain within their natal community after marriage and bilateral affiliations are maintained), although they have been characterized as matrilocal based on cultural norms (Kramer and Greaves 2011).

Although further data from field studies is needed, we should also be cautious about the use of data on contemporary hunter-gatherers as analogs for human ancestors. This problem had been discussed since the early studies of these societies. Service (1962) claimed that the observed bilocal or multilocal bands were the collapsed or reconstructed form of originally patrilocal bands influenced by strong outside pressure. There has long been controversy over the "authenticity" or "pureness" of hunter-gatherers (Headland and Reid 1989; Wilmsen 1989; Lee 1992; Kelly 1995; Kent 1996). Early ethnographies on hunter-gatherer societies were criticized by "revisionists" because of their ignorance of history and political economy. Revisionists described how hunter-gatherers have been integrated into large regional and international structures of political power and economic exchange. It is doubtless that we should consider hunter-gatherer social organization carefully in the context of much broader social and economic systems, even though it is hard to say that all hunter-gatherer societies are figments of scholars' imaginations. In particular, remote hunter-gatherer communities are interconnected with external forces in today's globalizing world, and their social structures have been dramatically influenced by surrounding peoples, modern political and economic systems, state policies, and international trends (Schweitzer et al. 2000; Kent 2002; Widlok and Tadesse 2005).

In this chapter, I analyze the ethnographic data of a group of central African hunter-gatherers obtained from my continuous fieldwork since 2003 to demonstrate the flexibility of actual hunter-gatherer residential patterns and social organization. I also demonstrate where and to what extent there is impact from the outside world by considering the context of globalization. I focus especially on the interethnic relationships with neighboring farmers and women's choice of marriage partner and postmarital residence. Finally, I discuss whether it is reasonable to utilize contemporary hunter-gatherer societies for an evolutionary perspective.

Residential Patterns of Central African Hunter-Gatherers

Central African hunter-gatherers, Pygmies, have inhabited tropical rainforests in the Congo basin for no less than 10,000 years. The Pygmy is not an ethnic group and there is no Pygmy language, but there are about 20 diverse local Pygmy groups categorized ethnolinguistically; for example, the Baka group in northern Gabon and southeastern Cameroon and northwestern Congo, Aka in southern Central African Republic and northern Congo, Babongo in southern Gabon and Congo, Mbuti in eastern Democratic Republic of the Congo (DRC), and Twa in Uganda (Hewlett 1996; Bahuchet 2012) (Fig. 7.1). In spite of ethnolinguistic diversity, there are many

Fig. 7.1 Baka Pygmies of south eastern Cameroon in a forest camp (Photo by H. Yasuoka)

commonalities among them, such as short stature, seminomadic hunting-gathering lifestyle, and cultural practices deeply tied with forest environments such as singing and dancing performances (Turnbull 1965; Ichikawa 1978; Bahuchet 1992, 2012; Hewlett 1996). Many Pygmies have come to live sedentarily along the road and practice agriculture since the mid-twentieth century partly due to implementation of a sedentarization policy by the governments and the construction of roads (Sato 1992; Kitanishi 2003; Knight 2003; Matsuura 2006; Soengas 2009).

Social anthropological theories regarding Pygmy residential patterns have also been the topic of controversy for decades, as mentioned above. At first, there were classical studies on the Mbuti in the Ituri Forest of the eastern DRC in the early twentieth century by P. Schebesta, a missionary from Silesia, and P. Putnam, an American anthropologist. Based on the long-term field study, both of them illustrated Mbuti residential patterns as patrilineal-patrilocal in which closely related males form the core of band composition (Schebesta 1933; Putnam 1948). However, C. Turnbull, a British-born anthropologist, denied the existence of the patrilineal extended family. He claimed that "the band as a whole in no way and at no time resembles a patrilineage in its composition" (Turnbull 1965: 99). Hart (1978) also noted that there are no rigid affiliations with particular lineages.

However, some ecological anthropological studies on the Mbuti residential patterns and social organization suggest that the band is strongly based on a core patrilineal group, as Schebesta (1933) and Putnam (1948) described (Harako 1976; Tanno 1976; Ichikawa 1978; Terashima 1983). They regarded the Epulu band, which Turnbull studied, as an exception in that the population is highly dense because it contains "the Putnam Camp," which includes a shop, restaurant, hotel, hospital, etc. Mosko (1987) pointed out that there are some descriptions by Turnbull himself that show that the Epulu's patrifilial subband is a salient unit of the band (Turnbull 1965). The patrilineal-patrilocal social system is also observed among the Aka and the Baka in Central African Republic (Hewlett 1989; Bahuchet 1992). Hewlett (1996) compared kinship, marriage, and descent patterns of four Pygmy groups (Mbuti, Efe, Aka, and Baka) and found that they are remarkably similar. Although he recognized the flexibility of patrilineages and postmarital residences among Pygmy groups, he concluded that they practice patrilocal residence where related men hunt together (Hewlett 1996).

On the other hand, Bahuchet (1985) described the Aka as multilocal. Following the debate of historical revisionism versus traditionalism about hunter-gatherer authenticity in the 1980s and 1990s, many ethnographers have come to regard Pygmy bands as having fluid social structures and support the flexible ecological model rather than the patrilineal-patrilocal model. In fact, when we focus on residence changes throughout life and individual practices, the residential patterns are not rigid but dynamic. The Aka live matrilocally for several years during bride service and move to a patrilocal residence afterward (Hewlett 1991; Kitanishi 1998; Hill et al. 2011). H. Terashima conducted field research on the Mbuti in 1978 and claimed that the patrilineal-patrilocal model fit well with his study group (Terashima 1983). However, when he visited them again in 1983, he found that the membership of the band had changed considerably and the patrilineal-patrilocal model was no longer applicable (Terashima 1985, 2013). Instead of considering marriage and residential rules, he analyzed individuals' status and revealed that social relationships among members of a residence group are simply classified into three categories: (1) staying with patrilateral kin, (2) staying with affinal relatives (relatives by marriage), and (3) staying with matrilateral relatives (Terashima 1985, 2013). Terashima pointed out that patrilocality is not a rule or institution one must obey, but a matter of personal choice that occurred in a certain socioeconomic contexts (Terashima 1985).

Among socioeconomic factors, Terashima (1985) considered that the symbiotic relationship with neighboring farmers is the most important factor influencing patrilocality. Every Pygmy group has established long-term mutually dependent symbiotic relationships based upon economic exchanges, pseudo-kinship, shared ceremonies, and/or friendships (Bahuchet and Guillaume 1982; Joiris 2003; Rupp 2011; Bahuchet 2012; Takeuchi 2014). Pygmies are generally absorbed into the farmers' social systems, and the relationships range from patron-client relationships (of the farmers and Pygmies, respectively) to quasi-equality, to the point of sharing the same clan system and establishing close affiliations due to farmers' social characteristics (Bahuchet 2012). While characterizing four Pygmy groups as patrilineal-patrilocal, Hewlett (1996) pointed out that these characteristics resemble the patterns of farmers (Hewlett 1996: 231). He mentioned that it is unclear whether the patterns existed before farmer-Pygmy relations were established or whether Pygmies adopted the farmers' social organization forms and modified them (Hewlett 1996: 231). Referring to examples of many other African hunter-gatherers' flexible residential patterns, Terashima pointed out that the strong patrilocal tendency in the Mbuti is rather exceptional (1985: 116). Patrilocality is not rigid and there are some traits of bilaterality. Thus, he hypothesized that the Mbuti once had a more flexible and bilateral tendency but shifted to patrilocality through their symbiotic relationship with farmers (Terashima 1985: 116–117). Although further historical studies are needed to determine the actual process of social change, it is doubtless that Pygmy residential patterns are considerably influenced by the farmers' existence.

Today, there are few ethnographic studies on Pygmy residential patterns, probably because many ethnographers think it no longer important or even possible to study, as significant social changes have occurred among them. Rather, many contemporary studies focus on the dynamics of globalization. Little basic data are available about Pygmies' most recent residential patterns, and recent cross-cultural studies still refer to Turnbull's classic ethnography (Alvarez 2004; Marlowe 2004; Hill et al. 2011). However, it is doubtful that only such a classical description of a particular group represents Pygmy characteristics in general or is comparable with other hunter-gatherer societies. Even among the Mbuti, there is considerable variation (Turnbull 1965; Ichikawa 1978; Terashima 1985). In addition, it might be difficult to apply the models used in the 1960s and 1970s to various contemporary Pygmy groups because social situations are considerably different. Therefore, I present the most recent residential patterns and marriage cases of the Babongo Pygmies in Gabon. Focusing on the group that is supposed to have undergone the most significant social changes, I will discuss diachronic and interregional commonalities among Pygmy groups.

The Babongo Pygmies in Southern Gabon

Ethnographic Background

The Babongo is a group of Pygmies living in areas of central to southern Gabon and southwestern Congo. There are approximately 20,000 Pygmy people in Gabon, where several Pygmy groups exist (Massandé 2005), but there is no available statistical data for only the Babongo. The research site for this study is Boutoumbi Village in the Ogoulou Department, Ngounié Province, in southern Gabon (Fig. 7.2). There is a Bantu farmer group, Massango (Bantu B42: Guthrie 1967–1971), other than the Babongo in this area. While there are 100–200 persons, including Babongo and Massango, living without spatial separation in this area's villages, Boutoumbi Village is unique in that there are only approximately 30 Babongo living there alongside close relatives (Fig. 7.3). The uniqueness of Boutoumbi Village is thought

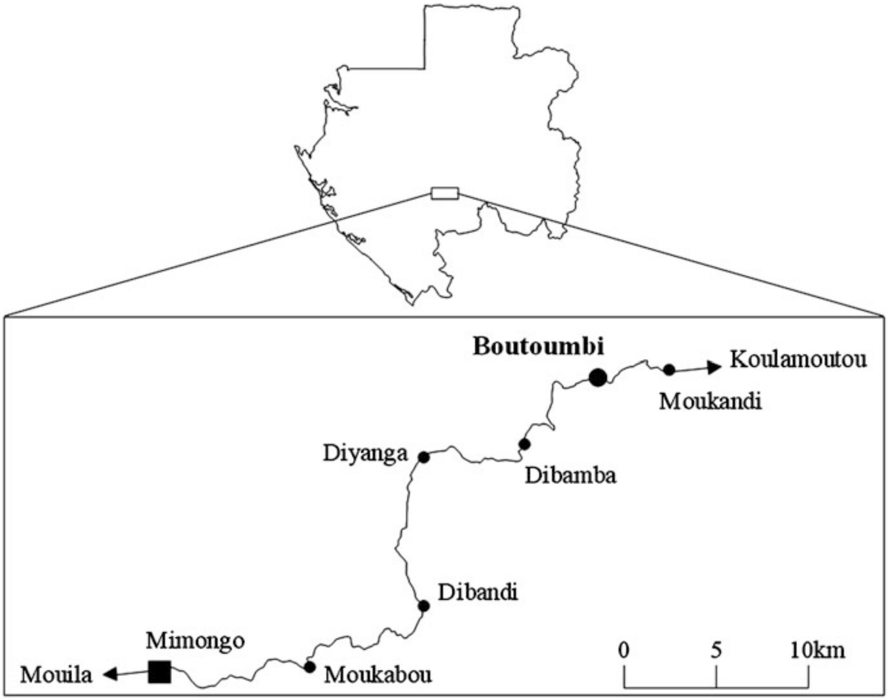


Fig. 7.2 Research site

Fig. 7.3 Sedentary village of the Babongo in southern Gabon

to be derived from historical processes (Matsuura 2006, 2009, 2011). Boutoumbi was integrated into the adjacent village, Moukandi, by the Gabonese regroupment policy in the 1960s, but the Babongo originally from the Boutoumbi area and those from the Moukandi area were unable to peacefully coexist. Consequently, an extended Babongo family moved away from Moukandi and resettled in Boutoumbi. However, this does not mean that the Boutoumbi people are socially isolated. The Boutoumbi people have kept close relationships with others through marriage, mutual visits, and ritual practices (Matsuura 2006, 2009, 2011).

The Babongo in Boutoumbi are highly sedentarized. While they sometimes go on hunting and gathering camping trips lasting from a few days to a week in the forest far from the village, they spend many days in the village (Matsuura 2006). In addition, people in Boutoumbi visit neighboring villages and towns frequently and vice versa (Matsuura 2009). Their principal subsistence activity is shifting cultivation, and they depend heavily on agricultural products such as the cassava and plantain banana for their calorie intake (Matsuura 2006). Commercial activities are rarely carried out in the village, and cash income is quite limited. There are few opportunities to sell forest products such as bushmeat and wild plants to visitors passing through in cars.

The interethnic relationship between the Babongo and Massango is unique when comparing it with many other Pygmy-farmer relationships in that it is quasi-equal rather than patron-client (Matsuura 2006, 2009, 2011). The Babongo have in principle adopted the Massango's matrilineal descent system and the patrilocal residence rules and share language, clanship, and rituals with the Massango. While intermarriage is strongly avoided or rare between other Pygmy groups and farmers, there are frequent intermarriages between the Babongo and Massango (Matsuura 2006, 2011). Although there are some examples of frequent intermarriage cases in other regions, they are limited to marriage between farmer men and Pygmy women and generally occur not as a result of personal choices but rather due to socioeconomic reasons (Terashima 1987; Hewlett 1996; Bahuchet 2012; Takeuchi 2014). On the contrary, there are intermarriages not only between Massango men and Babongo women but also between Babongo men and Massango women as the ethnic distinction is less important among them (Matsuura 2006, 2011). In addition to social bonds through intermarriage, it is thought that other social practices such as naming, mutual visits, rituals, and daily social interactions make the ethnic boundary between the Babongo and their neighboring farmers more and more ambiguous (Matsuura 2006, 2009, 2011; Bonhomme et al. 2012). Because of ethnic intermixture, it is difficult to assume a pure Babongo community. Boutoumbi Village, composed only of the Babongo close relatives in a small population, is thus ideal for examining Babongo social characteristics in order to compare them with other Pygmy bands and assess overall female dispersal patterns.

Kinship, Marriage, and Residential Patterns

I have conducted field research during ten different periods in Boutoumbi Village since 2003, approximately two and a half years in total. I collected basic information and quantitative data about population composition and social relations in July–October 2003, December 2004–February 2005, May–August 2005, and January–March 2007. I visited the village during a short period and verified population changes due to birth, death, marriage, and other immigration and migration cases in September 2008, January 2010, and August 2012.

There were 32 people (14 males and 18 females) including children in Boutoumbi Village in August 2003 (Fig. 7.4, Tables 7.1 and 7.2). As shown in Fig. 7.4, villagers were mainly composed of siblings (M1, M2, M4, M5, M6, and F2) and their spouses (M3, F3, F4, and F5). The male kin members occupied a central role in the village. There was also a tendency toward female dispersal. All daughters between M5 and F3, between M3 and F2, and F5 have married out to their husbands' places of residence. Their sons (M8, M9, and M10) were not married, despite being of adult age in 2003. While such patrilocal tendencies were observed, brother-sister associations after marriage existed. F2 continued to stay in her natal village through a sister-exchange marriage, a simultaneous marriage of a brother-sister pair from two different family groups (M3-F2, M4-F4). M11 came to live in Boutoumbi with his older sister (F8) after she married a man in Boutoumbi (M7).

Matrilineal clanship also influences residential patterns. F5's children came to live in Boutoumbi with her mother who remarried a Boutoumbi man (M6) after her former husband's death. Two women (F6 and F9) came back to Boutoumbi after

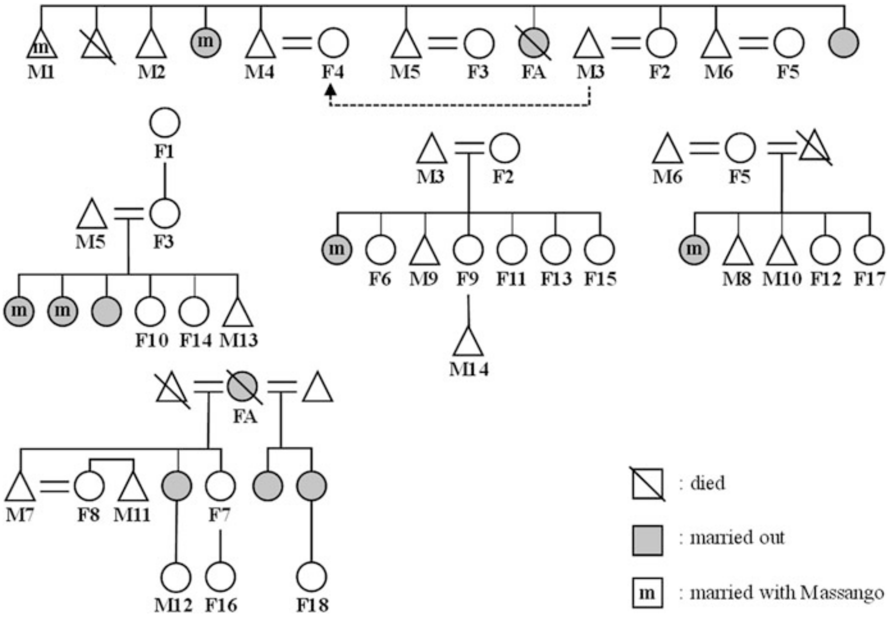


Fig. 7.4 Inhabitants of Boutoumbi and their relations in Aug. 2003

Table 7.1 Profile of Boutoumbi males and residence in 2003 and 2012

No.	Birth year	Residence In 2003	 In 2012
M1	1940s	Boutoumbi	Moukandi
M2	1940s	Boutoumbi	Died
M3	1940s	Boutoumbi	Boutoumbi
M4	1950s	Boutoumbi	Boutoumbi
M5	1950s	Boutoumbi	Boutoumbi
M6	1960s	Boutoumbi	Boutoumbi
M7	1960s	Boutoumbi	Boutoumbi
M8	1970s	Boutoumbi	Boutoumbi
M9	1980s	Boutoumbi	Other village
M10	1980s	Boutoumbi	Town
M11	1990s	Boutoumbi	Other village
M12	1999	Boutoumbi	Boutoumbi
M13	1999	Boutoumbi	Boutoumbi
M14	2000	Boutoumbi	Boutoumbi
M15	1980s	Town	Boutoumbi
M16	2004	–	Boutoumbi
M17	2007	–	Boutoumbi
M18	2009	–	Boutoumbi
M19	2011	–	Boutoumbi

Table 7.2 Profile of Boutoumbi females and residence in 2003 and 2012

No.	Birth year	Residence	
		In 2003	In 2012
F1	1930s	Boutoumbi	Moukandi
F2	1950s	Boutoumbi	Boutoumbi
F3	1950s	Boutoumbi	Boutoumbi
F4	1960s	Boutoumbi	Boutoumbi
F5	1960s	Boutoumbi	Boutoumbi
F6	1970s	Boutoumbi	Other village
F7	1970s	Boutoumbi	Town
F8	1970s	Boutoumbi	Boutoumbi
F9	1980s	Boutoumbi	Other village
F10	1990s	Boutoumbi	Moukandi
F11	1990s	Boutoumbi	Boutoumbi
F12	1990s	Boutoumbi	Moukandi
F13	1990s	Boutoumbi	Town (Libreville)
F14	1990s	Boutoumbi	Moukandi
F15	1990s	Boutoumbi	Town (Libreville)
F16	2000	Boutoumbi	Town
F17	2000	Boutoumbi	Other village
F18	2001	Boutoumbi	Boutoumbi
F19	1940s	Dibamba	Boutoumbi
F20	2003	–	Boutoumbi
F21	2004	–	Boutoumbi
F22	2004	–	Boutoumbi
F23	2006	–	Boutoumbi
F24	2007	–	Boutoumbi
F25	2009	–	Boutoumbi
F26	2009	–	Boutoumbi

their divorce; F6 did not have any children, but F9 brought her son. A daughter of FA (F7) lived in Boutoumbi with her daughter (F16) because her husband worked at a logging base for wage labor. The other two daughters of FA had already married out to neighboring villages, but they brought their small children (M12 and F18) to stay with their relatives in Boutoumbi despite living elsewhere. Being separated from their mothers, children are taken care of by their grandparents, uncles, and aunts on the mother's side for several months or years.

The kinship relations extend beyond the ethnic boundary between the Babongo and Massango through intermarriage (Matsuura 2006, 2009, 2011). M1 continued a close relationship with a Massango patron he had formed when he had seminomadic lifestyle in his youth. He had neither wife nor children until he married a Massango woman, his patron's widow in Moukandi Village, after the patron's death. They had lived separately (M1 in Boutoumbi and his wife in Moukandi), but M1 moved to his wife's place around 2010. His younger sister married a Massango man in a neighboring village, Dibamba. After the death of her husband, she remarried his

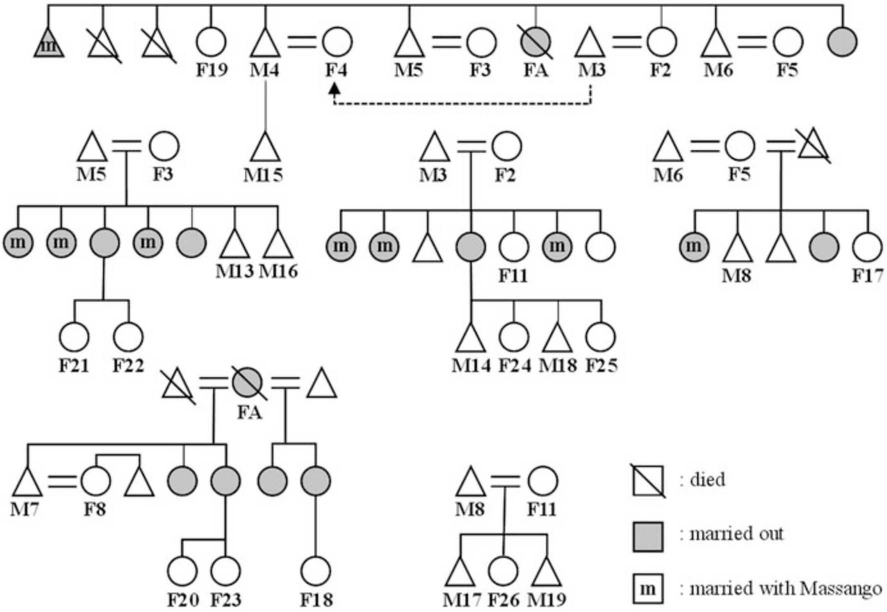


Fig. 7.5 Inhabitants of Boutoumbi and their relations in Aug. 2012

younger brother. Recently, younger women who marry Massango men tend to leave Boutoumbi. For example, two daughters of M5 and F4 live in a departmental capital, Mimongo, approximately 50 km to the west of Boutoumbi. However, their kinship ties with relatives in Boutoumbi are maintained. I observed that two daughters of M5 and F4 visited Boutoumbi with their children and Massango husbands, staying for several weeks (Matsuura 2009).

According to data collected in August 2012, there were 29 people (14 males and 15 females) including children in Boutoumbi (Fig. 7.5, Tables 7.1 and 7.2). When comparing 2003 and 2012 data, there is slight decrease in the total population and a remarkable change in membership. While core members of sibling relationships in the age range of 50s to 60s are stable, many young people have migrated. Three young men (M9, M10, and M11) have gone to look for labor opportunities. Five young women (F6, F10, F12, F13, and F14) have newly married out. Four of them (F6, F10, F12, and F14) have gone to neighboring villages, and F13 has gone to Libreville, a Gabonese capital, with her younger sister (F15). F7 has moved to the place where her husband works for a logging company. F9 found a new partner in a neighboring village. However, there was only one marriage occurring within the village during this period (M8 and F11). As there are only a small number of people in Boutoumbi and most of them are in kinship relations, it can be difficult to find a spouse. Opportunities for wage labor are also limited. Therefore, there is a strong tendency, especially among young people, to leave the village.

While the number of young people decreased, children under the age of 12 increased. One reason is that there were new births (M16, M17, M19, and F26) among Boutoumbi inhabitants. In addition, some females of Boutoumbi origin, who have already married out, brought their children (M18, F21, F22, F24, and F25) to stay with their relatives in Boutoumbi. F7 had left, as mentioned above, with her oldest daughter (F16), but she left behind her two little children (F20 and F23). As I mentioned above, children do not always live with their parents but often with grandparents and/or uncles and aunts in the research area, sometimes spending several years apart from their parents. This is partly because parents want to reduce the burden of childcare. It is also assumed that women maintain a relationship with their parents after marriage through childcare.

There were also movements of older people. M1, a man in his 70s, has gone to a neighboring village, Moukandi, where his Massango wife lives. F1, a woman in her 80s, has also gone to Moukandi because her sister and niece live there. On the other hand, F19, a sister of core members, came back from Dibamba because her husband died.

Intermarriage with Massango occurred frequently. Three out of six women (F6, F10, F11, F12, F13, and F14) who were newly married are with Massango men. Based on the data of marriage cases in three research villages including Boutoumbi, I demonstrated that about one third of the total marriages were between the Babongo and Massango (Matsuura 2006). I also pointed out that the intermarriage rate increased considerably for those born after the 1960s because the Babongo adopted a sedentary lifestyle, and interactions with Massango have increased since then (Matsuura 2011). It has been shown that such trends are clearer during this period. While marriage cases between Babongo men and Massango women exist, opposite patterns are much more frequent.

Women's Choice of Spouse and Postmarital Residence

To understand women's spousal choices and postmarital residences, I examined the life histories of two women, whom I have followed since they were children. F11 and F13 are sisters and grew up in Boutoumbi. Both of them have been accustomed to living the village lifestyle, shifting cultivation combined with hunting and gathering as means of daily subsistence. While F11 has lived with her parents (M3 and F2), F13 has lived with her uncle (M4) and aunt (F4) because M4 and F4 did not have children. They went to an elementary school in Moukandi Village for several years but did not graduate. In her late teenage years, F11 married a Babongo man in Boutoumbi Village and continues to live in Boutoumbi. She had three children as of August 2012. On the other hand, F13 married a Massango man in Moukandi Village who was her childhood friend. Because her husband was working at a logging company, she left Boutoumbi to go to Libreville with her husband. A younger sister (F15) of F11 and F13 also followed F13 to live with her. In August

2012, F13 gave birth to two children and was living in Libreville with her husband's relatives.

This example shows that the Babongo women can choose their spouse among both Babongo and Massango men as well as their postmarital residence, depending on their husband's lifestyle. Some Babongo women continue to live in their native village and continue a traditional hunting and gathering lifestyle, but others leave the village and adopt a life in town. Despite F11 and F13 having a similar life history until their later teenage years, they have an entirely different lifestyle today. Although it is not easy for the Babongo to live in town because they are not used to the lifestyle and do not have many relatives there, marriage with Massango men makes it possible for Babongo women to live in town. Given that intermarriage between Massango and Babongo becomes more frequent, it is assumed that the number of Babongo women who want to live in town is increasing. The Babongo women's marriage and residence choices are much wider today, and they are able to adopt a new lifestyle in a flexible way.

Discussion

I demonstrated that there is a strong patrilocal tendency among the people in Boutoumbi Village, which is composed only of a small population of Babongo Pygmies. Core village members are composed of male siblings and their spouses. Postmarital female dispersal is often observed. However, patrilocality is not a strict social rule. From the viewpoint of each individual's behavior, there are three types of residence: staying with patrilateral kin, staying with affinal relatives, and staying with matrilateral relatives, as shown by Terashima (1985, 2013) in the Efe society. Both patrilateral and matrilateral kin are important for social life. For example, while M4, M5, and M6 live in their native village and married women from other villages, F3 continues to stay in her native village after marriage. Thus, her husband lives with his affinal relatives, and her children stay with their matrilateral relatives.

When considering residence change throughout the life of a marriage (Marlowe 2004, 2010; Kramer and Greaves 2011), it is also suggested that their residential patterns are fairly flexible and that patrilocality is merely a result of each individual's personal choice in each life stage. Brother-sister associations are important even after marriage; many married-out women keep close ties with their relatives because they are helpful in reducing childcare burdens. Some children stay in Boutoumbi, separated from their mothers for a long period, and their mothers visit Boutoumbi frequently to see them (Matsuura 2009). After these children reach maturity, they go outside to look for labor opportunities and/or spouses. Other children come to live in Boutoumbi in their place. For Boutoumbi residents, these children are important because they can help with housework and subsistence activities starting when they are about 10 years old.

Although the Babongo are not "classical hunter-gatherers" due to sedentarization since the 1960s and the influence of globalization (Matsuura 2011), the flexible band model, which has long been discussed in Pygmy studies (Turnbull 1965; Terashima 1985; Bahuchet 1992) and hunter-gatherer studies in general (Lee and DeVore 1968; Kelly 1995), is partly applicable in explaining their residential patterns. It is supposed that the Babongo maintain the social practices of hunter-gatherers despite lifestyle changes. While subsistence patterns and residential places can change easily, two or three generations are not enough to change their social rules and organizations. Therefore, the flexibility in residential places that was observed in the Babongo may reflect the commonality of social characteristics of other hunter-gatherers to some extent. At the same time, of course, it must be noted that diverse influences from the outside world strongly affect Babongo residential patterns. Many ethnographic studies of Pygmies indicated a number of factors that influence their lifestyle: sedentarization policies and road construction (Sato 1992; Knight 2003; Soengas 2009), bushmeat trade (Hart 1978; Ichikawa 1983; Auzel and Wilkie 2000; Yasuoka 2006), logging and mining operations (Burnham 2000; Lewis 2005), oil-drilling operations (Kenrick 2005), rural development projects (Wæhle 1999; Pemunta 2013), civil wars (Pottier 2007), nature conservation policies (Schmidt–Soltau 2003, 2004; Ichikawa 2014), and indigenous people movements (Kenrick and Lewis 2004; Pelican 2009).

Among these factors, the most important and broadly observed concern the interethnic relationships with neighboring farmers. The Pygmies have established longtime symbiotic relationships with farmers (Joiris 2003; Rupp 2011; Bahuchet 2012; Takeuchi 2014). They belong to the same social system. Because farmers are generally superior to Pygmies politically and economically, Pygmies have adopted farmers' social norms, descent system, clanship, rituals, and language (Rupp 2011; Bahuchet 2012; Takeuchi 2014). Therefore, the interethnic relationships strongly reflect farmers' social characteristics. For example, the Aka in the Republic of Congo are integrated into the local social hierarchical system and socially discriminated against because their neighboring farmers have highly hierarchical ideology (Takeuchi 2014). Each regards the other as animallike, and there is no intermarriage between them (Takeuchi 2014). A patrilineal-patrilocal tendency is observed among the Mbuti because there is a close partnership between the Mbuti and farmers, which is passed down from father to son on both sides (Terashima 1985). The Babongo also share the social system of the Massango, and their strong tendency toward patrilocality seems to be largely influenced by Massango land-use patterns. In general, it is thought that Pygmies adopt the residential patterns of their neighboring farmers through longtime coexistence. This might be possible because of their considerable social flexibility. Controversy over Pygmies' residential patterns is in and of itself the positive evidence of Pygmies' social flexibility because it indicates that Pygmies have adapted their lifestyle differently according to the different social and ecological situation in each region.

The uniqueness of the quasi-equal interethnic relationship between the Babongo and Massango is also explained in part by the Massango social system. In their matrilineal descent system, ethnic categories are less important and the primacy of clan allegiance goes beyond ethnic boundaries (Vansina 1990; Gray 2002; Mayer 2002). This is why there are no rigid pseudo-kinship, social relationships simulate biological ones (consanguinity or affinity), and/or partnership relations between the Babongo and Massango (Matsuura 2006, 2009, 2011). It is also supposed that such social characteristics make frequent bidirectional intermarriages possible (Matsuura 2006, 2009, 2011). Concerning residential patterns, frequent movements and fluidity of membership among the Babongo are possible results of their decreased territoriality and wide social networks on both paternal and maternal sides.

In conclusion, the data demonstrate that residential patterns of the Babongo Pygmies in southern Gabon are fundamentally flexible, even if the group is experiencing dynamic social changes toward sedentarization in today's globalizing world. It is of possible value to discuss human residential patterns in the evolutionary context, even based on ethnographic studies of contemporary hunter-gatherer societies. However, we should also note that it is meaningless to use the word *evolution* for a coarse generalization without ample consideration of the complex socioeconomic context. The present study demonstrates that the Babongo have been strongly influenced by many external factors, particularly the social characteristics of neighboring farmers. Hunter-gatherer societies have no distinguishable essential nature that eliminates influence from the outside world. We should always be mindful of the contemporary sociopolitical situation and account for hunter-gatherer social characteristics based on ethnographic evidence.

Acknowledgments This study was financially supported by a Grant-in-Aid for Scientific Research from the Ministry of Education, Science, and Culture, Japan. I would like to express my gratitude to Prof. Juichi Yamagiwa, my graduate study supervisor, for his continuous support and encouragement. I gratefully thank Prof. Takeshi Furuichi and Prof. Filippo Aureli, editors of this book, for giving me a valuable opportunity to write the chapter and their useful comments. I also thank Dr. Hirokazu Yasuoka for providing an impressive picture. Finally, I would like to thank the people of my research village who supplied me with much information and offered me great help in the field.

References

Alvarez H (2004) Residence groups among hunter-gatherers: a view of the claims and evidence for patrilocal bands. In: Chapais B, Berman CM (eds) Kinship and behavior in primates. Oxford University Press, Oxford, pp 420–442

Auzel P, Wilkie DS (2000) Wildlife use in northern Congo: hunting in a commercial logging concession. In: Robinson JG, Bennet EL (eds) Hunting for sustainability in tropical forests. Columbia University Press, New York, pp 413–454

Bahuchet S (1985) Les pygmees Aka et la foret Centrafricaine. SELAF, Paris

Bahuchet S (1992) Dans la forêt d'Afrique centrale; les Pygmées Aka et Baka. SELAF, Paris

Bahuchet S (2012) Changing language, remaining pygmy. Hum Biol 84(1):11–43

Bahuchet S, Guillaume H (1982) Aka-farmer relations in the northwest Congo Basin. In: Leacock E, Lee R (eds) Politics and history in band societies. Cambridge University Press, Cambridge, pp 189–211

Barnard A (1983) Contemporary hunter-gatherers: current theoretical issues in ecology and social organization. Annu Rev Anthropol 12:193–214

Bonhomme J, De Ruyter M, Moussavou GM (2012) Blurring the lines. Ritual and relationships between Babongo Pygmies and their neighbours (Gabon). Anthropos 107(2):387–406

Burnham P (2000) Whose forest? Whose myth? Conceptualisations of community forests in Cameroon. In: Abramson A, Theodossopoulos D (eds) Land, law and environment: mythical land, legal boundaries. Pluto Press, London, pp 31–58

Ember CR (1975) Residential variation in hunter-gatherers. Cross-Cult Res 10:199–227

Ember CR (1978) Myths about hunter-gatherers. Ethnology 17(4):439–448

Foley RA, Lee PC (1989) Finite social space, evolutionary pathways, and reconstructing hominid behaviour. Science 243:901–906

Furuichi T (2006) Evolution of the social structure of hominoids: reconsideration of food distribution and the estrus sex ratio. In: Ishida H, Tuttle R, Pickford M, Ogihara N, Nakatsukasa M (eds) Human origins and environmental backgrounds. Springer, New York, pp 235–248

Gray CJ (2002) Colonial rule and crisis in equatorial Africa: Southern Gabon, ca.1850–1940. University of Rochester Press, Rochester

Guthrie M (1967–1971) Comparative Bantu: an introduction to the comparative linguistics and prehistory of the Bantu languages, 4 vol. Gregg International Publishers, Farnborough

Hames R, Draper P (2004) Women's work, child care, and helpers-at-the-nest in a hunter-gatherer society. Hum Nat 15:319–342

Harako R (1976) The Mbuti as hunters: a study of ecological anthropology of the Mbuti Pygmies. Kyoto Univ Afr Stud 10:37–99

Hart JA (1978) From subsistence to market: a case study of the Mbuti net hunters. Hum Ecol 6:32–53

Headland TN, Reid LA (1989) Hunter-gatherers and their neighbors from prehistory to the present. Curr Anthropol 30(1):27–43

Hewlett BS (1989) Multiple care among African Pygmies. Am Anthropol 91:270–276

Hewlett BS (1991) Intimate fathers: the nature and context of Aka pygmy paternal infant care. University of Michigan Press, Ann Arbor

Hewlett BS (1996) Cultural diversity among African pygmies. In: Kent S (ed) Cultural diversity among twentieth-century foragers: an African perspective. Cambridge University Press, New York

Hill KR, Hurtado AM (2009) Cooperative breeding in South American hunter-gatherers. Proc R Soc B Biol Sci 276(1674):3863–3870

Hill KR, Walker RS, Božičević M, Eder J, Headland T, Hewlett B, Hurtado AM, Marlowe F, Wiessner P, Wood B (2011) Co-residence patterns in hunter-gatherer societies show unique human social structure. Science 331:1286–1289

Ichikawa M (1978) The residential groups of the Mbuti Pygmies. Senri Ethnol Stud 1:131–188

Ichikawa M (1983) An examination of the hunting-dependent life of the Mbuti Pygmies, eastern Zaire. Afr Study Monogr 4:55–76

Ichikawa M (2014) Forest conservation and indigenous peoples in the Congo basin: new trends toward reconciliation between global issues and local interests. In: Hewlett B (ed) Hunter-gatherers of the Congo Basin: culture, history and biology of African Pygmies. Transaction Publishers, New Brunswick

Joiris DV (2003) The framework of central African hunter-gatherers and neighbouring societies. Afr Study Monogr 28(Suppl):57–79

Kelly RL (1995) The foraging spectrum: diversity in hunter-gatherer lifeways. Smithsonian Institution, Washington, DC

Kenrick J (2005) Equalising processes, processes of discrimination and the forest people of Central Africa. In: Widlok T, Tadesse W (eds) Property and equality vol 2: encapsulation, commercialization, discrimination. Berg, Oxford, pp 104–128

Kenrick J, Lewis J (2004) Indigenous peoples' rights and the politics of the term 'indigenous'. Anthropol Today 20(2):4–9

Kent S (ed) (1996) Cultural diversity among twentieth-century foragers: an African perspective. Cambridge University Press, New York

Kent S (ed) (2002) Ethnicity, hunter-gatherers, and the other: association or assimilation in Africa. Smithsonian Institution Scholarly Press, Washington, DC

Kitanishi K (1998) Food sharing among the Aka hunter-gatherers in northeastern Congo. Afr Study Monogr 25(Suppl):3–32

Kitanishi K (2003) Cultivation by the Baka hunter-gatherers in the tropical rain forest of central Africa. Afr Study Monogr 28(Suppl):143–157

Knight J (2003) Relocated to the roadside: preliminary observations on the forest peoples of Gabon. Afr Study Monogr 28(Suppl):81–121

Kramer KL, Greaves RD (2011) Postmarital residence and bilateral kin associations among hunter-gatherers: Pumé foragers living in the best of both worlds. Hum Nat 22:41–63

Lee RB (1992) Art, science, or politics? The crisis in hunter-gatherer studies. Am Anthropol 94(1):31–54

Lee RB, DeVore I (eds) (1968) Man the hunter. Aldine, Chicago

Lewis J (2005) Whose forest is it anyway? Mbendjele Yaka pygmies, the Ndoki Forest and the wider world. In: Widlok T, Tadesse W (eds) Property and equality vol 2: encapsulation, commercialization, discrimination. Berg, Oxford, pp 56–78

Marlowe FW (2004) Marital residence among foragers. Curr Anthropol 45:277–284

Marlowe FW (2010) The Hadza: hunter-gatherers of Tanzania. University of California Press, Berkeley

Massandé D (2005) Organisation Territoriale du Gabon Démographie Chiffres Des Peuples Autochtones Pygmées de Gabon. ADCPPG report, 30 June 2005

Matsuura N (2006) Sedentary lifestyle and social relationship among Babongo in southern Gabon. Afr Study Monogr 33(Suppl):71–93

Matsuura N (2009) Visiting patterns of two sedentarized central African hunter-gatherers: comparison of the Babongo in Gabon and the Baka in Cameroon. Afr Study Monogr 30(3):137–159

Matsuura N (2011) Historical change in land use and interethnic relations of the Babongo in southern Gabon. Afr Study Monogr 32(4):157–176

Mayer R (2002) Histoire de la famille gabonaise. Editions du LUTO, Libreville

Mosko MS (1987) The symbols of "Forest": a structural analysis of Mbuti culture and social organization. Am Anthropol 89(4):896–913

Murdock GP (1967) Ethnographic atlas. The University of Pittsburgh Press, Pittsburgh

Owen RC (1965) The patrilocal band: a linguistically and culturally hybrid social unit. Am Anthropol 67(3):675–690

Pelican M (2009) Complexities of indigeneity and autochthony: an African example. Am Ethnol 36(1):52–65

Pemunta NV (2013) The governance of nature as development and the erasure of the Pygmies of Cameroon. GeoJournal 78(2):353–371

Pottier J (2007) Rights violations, rumour, and rhetoric: making sense of cannibalism in Mambasa, Ituri (Democratic Republic of Congo). J R Anthropol Inst 13(4):825–843

Putnam P (1948) The pygmies of the Ituri forest. In: Coon CS (ed) A reader in general anthropology. Henry Holt, New York, pp 322–342

Radcliffe-Brown AR (1930–1931) The social organization of Australian tribes. Oceania 1:34–63

Rodseth L, Wrangham RW, Harrigan AM, Smuts B (1991) The human community as a primate society. Curr Anthropol 32(3):221–254

Rupp S (2011) Forest of belonging. Identities, ethnicities and stereotypes in the Congo River Basin. University of Washington Press, Washington, DC

Sahlins MD (1959) The social life of monkeys, apes and primitive man. Hum Biol 31(1):54–73

Sato H (1992) Notes on the distribution and settlement pattern of hunter-gatherers in northwestern Congo. Afr Study Monogr 13(4):203–216

Schebesta P (1933) Among Congo Pygmies. Hutchinson and Co., London

Schmidt–Soltau K (2003) Conservation-related resettlement in central Africa: environmental and social risks. Dev Chang 34(3):525–551

Schmidt–Soltau K (2004) The local costs of rainforest conservation: local responses towards integrated conservation and development projects. J Contemp Afr Stud 22(1):93–117

Schweitzer PP, Biesele M, Hitchcock RK (eds) (2000) Hunters and gatherers in the modern world: conflict, resistance, and self-determination. Berghahn Books, New York

Service ER (1962) Primitive social organization: an evolutionary perspective. Random House, New York

Soengas B (2009) Preliminary ethnographic research on the Bakoya in Gabon. Afr Study Monogr 30(4):187–208

Steward JH (1955) Theory of culture change: the methodology of multilinear evolution. University of Illinois Press, Urbana

Takeuchi K (2014) Inter-ethnic relations between Pygmies and farmers. In: Hewlett B (ed) Hunter-gatherers of the Congo Basin: culture, history and biology of African Pygmies. Transaction Publishers, New Brunswick

Tanno T (1976) The Mbuti net-hunters in the Ituri forest, eastern Zaire. Kyoto Univ Afr Stud 10:101–135

Terashima H (1983) Mota and other hunting activities of the Mbuti archers: a socio-ecological study of subsistence technology. Afr Study Monogr 3:71–85

Terashima H (1985) Variation and composition principles of the residence group (band) of the Mbuti Pygmies. Afr Study Monogr 4(Suppl):103–120

Terashima H (1987) Why Efe girls marry farmers?: Socio-ecological backgrounds of inter-ethnic marriage in the Ituri forest of central Africa. Afr Study Monogr 6(Suppl):65–83

Terashima H (2013) From the "here and now group" to the "distant group": hunter–gatherer bands. In: Kawai K (ed) Groups: the evolution of human sociality. Trans Pacific Press, Melbourne

Turnbull CM (1965) Wayward servants: the two worlds of African pygmies. The Natural History Press, New York

Vansina J (1990) Path in the rainforests: toward a history of political tradition in equatorial Africa. The University of Wisconsin Press, Madison

Wæhle E (1999) Introduction. In: Biesbrouck K, Elders S, Rossel G (eds) Challenging elusiveness: central African hunter-gatherers in a multidisciplinary perspective. CNWS, Universiteit Leiden, Leiden, pp 3–17

Widlok T, Tadesse W (eds) (2005) Property and equality vol 2: encapsulation, commercialization, discrimination. Berg, Oxford

Wilmsen EN (1989) Land filled with flies: political economy of the Kalahari. University of Chicago Press, Chicago

Wood BM, Marlowe FW (2011) Dynamics of postmarital residence among the Hadza. Hum Nat 22:128–138

Wrangham RW (1987) The significance of African apes for reconstructing human social evolution. In: Kinzey WG (ed) The evolution of human behavior: primate models. State University of New York Press, Albany, pp 51–71

Yasuoka H (2006) The sustainability of duiker (*Cephalophus* spp.) hunting for the Baka hunter-gatherers in southeastern Cameroon. Afr Study Monogr 33(Suppl):95–120

Chapter 8
Life History and Sexual Relationships of Female Kalahari Hunter-Gatherers

Kaoru Imamura

Introduction

I would like to describe a female's life history among the Kalahari hunter-gatherers, the |Gui and ||Gana, from the viewpoint of sexual relationships in this chapter. In comparing humans with other nonhuman primates, an understanding of the hunter-gatherers' way of life is important because humans were hunter-gatherers until the beginning of the Holocene. There are three approaches to studying the life history of hunter-gatherers. One is via the sociological sphere, investigating postmarital co-residence patterns. The second is using biological and demographic research, which consists of birth rate, age at menarche, age at marriage, and mortality. The third is the intensive collection of individual oral histories by interview.

Postmarital residence in humans is often assumed to reflect female dispersal and male philopatry. Anthropologists have long debated which marital residence pattern is most prevalent among hunter-gatherers. Many have argued that hunter-gatherers are predominantly virilocal, that is, married couples live in the same camps as the husband's parents (Ember 1975; Rodseth et al. 1991; Foley and Lee 1989). This concept is derived from a patrilineal-patrilocal band model (Radcliffe-Brown 1930; Steward 1955; Service 1962; Owen 1965). Service (1962) concluded that patrilocality would be an adaptation for male cooperation in defense of hunting territories. Recently Chapais (2008) proposed the ancestral male kin group hypothesis based on two assumptions: firstly, the patrilocal band model was a basic tenet and, secondly, male philopatry in apes and humans was considered to be a homologous trait.

K. Imamura (✉)
Faculty of Contemporary Social Studies, Nagoya Gakuin University, 1-25, Atsutanishimachi, Atsuta-ku, Nagoya, Aichi 456-8612, Japan
e-mail: kaoru.imamura@gmail.com

T. Furuichi et al. (eds.), *Dispersing Primate Females*,
Primatology Monographs, DOI 10.1007/978-4-431-55480-6_8

However, a number of scholars have argued that hunter-gatherers tend to have a more flexible and bilocal pattern, where couples choose to reside near the kin of the husband or the wife. In the first conference on hunting and gathering societies in 1968, many researchers, including Turnbull on the Mbuti pygmies, Lee on the San, and Meggitt on Australian aborigines, reported the occurrence of composite and flexible local groups (Turnbull 1968; Lee and DeVore 1968; Meggitt 1968). More recently there have been many studies which conclude that bilocality or multilocality, rather than patrilocality, is the major residence pattern among modern hunter-gatherer societies (Alvarez 2004; Marlowe 2004; Hill et al. 2011; Kramer and Greaves 2011). Many foraging societies practice situational flexibility regarding the kin with whom an individual or family lives.

The characteristic features of small-scale hunter-gatherers are as follows (Lee and Daly 1999; Kelly 1995; Hewlett and Hewlett 2012): (1) High mobility and frequent movement of camps. (2) Camps consisting of 25–30 individuals. (3) Flexibility in camp composition. (4) Gender and age egalitarianism and lack of central authorities. (5) Extensive sharing and giving. (6) Low population density, high fertility, and mortality. In an ecological context Marlowe (2004) claims that hunting is more linked with bilateral descent than sedentism, probably because mobile resources such as game require large home ranges. Actually, African hunter-gatherers' home ranges are much larger than those of non-foragers and also larger than those of apes. While a hunting and gathering way of life favors greater mobility, their home ranges are too large to protect exclusively by male kin groups. So they disperse into small residential groups (camps) and share land use with other members of their camp. The relationship between the members of camps can be bilateral descent relatives, relatives by marriage (affinity), or even just friends. In relation to the issue of male violence, Knauft (1991) argued that the fact patrilocality is not ubiquitous in human societies, and is not the norm among hunter-gatherers, may appear incompatible with the idea that patrilocality is homologous to ape philopatry. Knauft noted that as far as patterns of aggressive competition are concerned, apes have much more in common with "middle-range" (or prestate) human societies than with hunter-gatherer societies. He concluded that the egalitarian nature of hunter-gatherers would reveal the phylogenetic gap separating apes and middle-range human societies.

In the case of the Central Kalahari San, consisting of |Gui and ||Gana, they traditionally led a nomadic life around Xade area, which was about 4,000 km^2 (Tanaka 1980). Under the linguistic groups, i.e., |Gui and ||Gana, there were several large clusters of families. Each cluster had their familiar land; people called this land simply "our land," being the land where they grew up and which they knew intimately, every nook and cranny. This land is a kind of home range but does not show territoriality at all, because hunter-gatherers in general do not have exclusive rights to resources. |Gui and ||Gana insisted that they could follow and hunt big antelopes with bows and arrows or spears in other people's land; however, it was not allowed to set traps outside it; only the "owners" could set snares or traps for small animals. Their ownership is still open because everyone, irrespective of bilateral descent relative, spouse, or just friend, could be accepted as a camp member. The constant nomadic way of life is accompanied by fission and fusion of camps, membership shift, and frequently by imprecise group boundaries.

The second approach, i.e., biological and demographic research on hunter-gatherers, is sparse because it is difficult to accurately determine the ages of people when they do not know their ages or dates of birth themselves, nor do they use numbers over three in their own language. There have been a few demographic investigations, such as Howell (1979) on the !Kung San in Botswana and Namibia, Blurton Jones et al. (1992) and Marlowe (2010) on the Hadza in Tanzania, and Hill and Hurtado (1996) on the Ache in Paraguay.

According to Howell's most precise and complete demographic study, an overview of the life history of !Kung San women is as follows: the mean age at menarche is 16.6 years and the mean age at first childbirth is 18.8 years. First births are tightly clustered between the ages of 17 and 20, when two-thirds of women give birth. The mean length of birth intervals is 4.12 years and the total fertility rate is 4.69. The oldest birth observed was at age 46, the mean age for a final birth is 34.35, the median is 37.00, and the mode is 34.00.

Concerning their marital histories, the first marriage is generally arranged by the parents of the two spouses, the bride is between 13 and 20 and the husband between 22 and 30, the mean difference in age of spouses for first marriage is 9.3 years. Marriages that end in divorce are frequent. Among women who have married, about 62 % of them remarry and the maximum marriage number for women is five. Among men who have married, about 61 % of them remarry and the maximum marriage number for men is six. Marriages tend to be short, as 65 % of marriages ended with the death of the husband or in divorce within 5 years. The expectation of life at birth falls within the range between 37.5 and 50 years. The adult survival rate, which is the proportion of 15-year-olds who survive to age 50, is 0.55.

The third approach to life history is the intensive collection of individual oral histories by interview. Ethnographic life narratives are very few, represented only by Shostak's (1981) work on !Kung women and the research on Aka Pygmy and Ngandu Bantu women by Hewlett (2013). In this chapter, I will focus on explaining the marital system and extramarital sexual relationships among the |Gui and ||Gana, through the oral histories recounting their lives in traditional times, before settlement.

Residential Pattern of the San

The San belong to the Khoi-San linguistic group, which is distributed in the southern part of Africa and consists of more than ten different linguistic groups. The Khoi or Khoikhoi are pastoral people, and the San are hunter-gatherers. The group composition among the San in the Kalahari Desert is extremely fluid (the Central Kalahari San by Tanaka (1969, 1976, 1980); the !Kung San by Lee (1968, 1979)). The membership of the residential groups, which includes relatives and friends, often changes during the frequent shift of campsites because of their food-gathering

Table 8.1 Residential pattern of four San groups

Rainfall	San linguistic groups	Dry season	Rainy season
↑ Much	Nharo	+	+
	!Kung	+	−
	Central Kalahari	−	+
↓ Little	!Ko	−	−

From Ichikawa (1986)
+ = aggregation
− = dispersal

activities. The residential group has neither a territory nor a fixed membership, and its size varies from one family to some 20 families with dozens of people. Lee (1968) and Tanaka (1969) called these residential groups simply "camps" instead of "bands," the usual name for the hunter-gatherer residential groups.

However, recent studies have revealed that not all the San have such fluid group compositions as the !Kung and the Central Kalahari San. Heinz (1972, 1979) claims the !Ko San has a band which is composed of fixed members and strict territory. It was reported that some 100 Nharo, who inhabit a relatively rich environment, had stayed near a particular water site for 3 years (Barnard 1985).

Barnard (1979, 1985) proposed an ecological explanation of the diversity of San society. The climate significantly changes every year in the Kalahari Desert. The Central Kalahari San splits into small groups composed of a few families in the dry season, from April to September, because they cannot get water due to the long drought. In the wet season, from October to March, they gather at a water site and form a large group, because they can easily collect food and water. When there was a lot of rain and a large pool of water appeared, hundreds of people would live together until the pool water was finished. This could be for as long as 3 months.

On the other hand, the !Kung San, who inhabit the northern Kalahari, where they have more rainfall, show the reverse pattern. They split into small groups in the wet season, as they can get water anywhere, while they form a large group at a permanent water site in the dry season. The Nharo, who inhabit the area where they have the most rainfall, maintain large coherent groups in both seasons. Furthermore, the !Ko, who inhabit the area with the most severe environment, split into small groups all through the year. The grouping patterns of these four societies correspond with four patterns of dispersal/concentration triggered by the availability of water resource (Table 8.1).

The Life of |Gui and ||Gana Women

The Central Kalahari San consists of |Gui and ||Gana people. |Gui and ||Gana are dialects, either group can understand each other, and they intermarry. The |Gui and ||Gana used to live a self-sufficient life, hunting and gathering in the Kalahari Desert until the 1970s (Tanaka 1980). In general, women collected plant-based foods and men hunted game, but men also gathered wild vegetables and fruit and women procured, or even hunted, small animals using their digging sticks (Imamura 1997).

A foraging unit, called a camp, is a temporal residential group, and it moved camp site frequently, staying in one place for from a few days to 3 months. The migrations involved frequent fission and fusion of groups. One camp consisted of between just one to around ten nuclear families. They shared food, work, and information within family. A camp moved and changed size to adapt to the natural resources. Plant resources were the most important because people got water from plant roots and the game animals also moved to places rich in vegetation. The membership of a camp might also be split to solve social conflict such as a quarrel or a fight with other members about food sharing (Fig. 8.1).

In recent times the |Gui and ||Gana started to settle down around boreholes with a diesel engine. These were installed in 1979 by the Botswana Government (Tanaka 1987). Since 1988 I have been conducting research in Xade, in the central part of the Republic of Botswana, where a complete village was formed. The methods of this study are participant observations, interview of particular subjects, and narrative studies.

In 1994, I took a census in Xade. There were 384 men and 388 women, a total of 772 people. Their ethnic groups were 376 |Gui, 279 ||Gana, six Nharo, and 111 Kgalagadi, who are Bantu agropastoral people (Table 8.2). When I started the research, around 20 years had passed since they had settled down. But still their residential pattern remained flexible, with frequent fission and fusion of groups.

Fig. 8.1 Women go gathering food together

Table 8.2 Population composition in Xade

		San		Kgalagadi	Total
	|Gui	||Gana	Nharo		
Man	172	146	3	63	384
Woman	204	133	3	48	388
Total	376	279	6	111	772

There were 37 San camps of mainly |Gui and ||Gana (651 people), and minorities of Nharo (three men and three women) and Kgalagadi (five men), and five Kgalagadi camps of mainly Kgalagadi (106 people) and a small number of |Gui women (two) and ||Gana women (two). The mean size of a San camp was 17.9 persons, ranging from four to 53. The average number of couples, which develop into nuclear families, per San camp was 3.8. I checked the co-resident pattern, whether they were living with the wife's relatives or the husband's relatives, and, on average, 1.14 couples lived with the wife's parents, 1.62 with the wife's sibling, 1.00 with the husband's parents, and 1.08 with the husband's siblings. So the |Gui and ||Gana's postmarital residential pattern is apparently bilocal.

Among the San camps, adult San women numbered 189 and adult men 154. Among the adults there were 132 marital couples: 123 couples were monogamous, eight couples were polygamous (one husband and two wives), and one couple was polyandrous (one wife and two husbands).

In 1994, I concentrated on recording |Gui and ||Gana's life history. I asked 12 elderly |Gui and ||Gana, four men and eight women, to talk about "what they did from their childhood to today." Their narration was first tape-recorded and transcribed in the |Gui and ||Gana language. Then I translated it into Japanese. The total length of the recording was more than 30 h.

Based on this research I attempt to reconstruct the traditional life of |Gui women before the settlement, especially focusing on their sexual experiences, according to the narration of a woman named Giocue, who was born in around 1936. Compared with the other seven women, I believe Giocue's life history is typical of |Gui women. Using her life narrative, I will present and discuss how the San's women establish relations with unrelated males and females and how their entire life is strongly affected by sexual relationships.

Though the San do not count ages, they are aware of the relative age between two individuals, such as which person is older. In addition to that, the subjects' ages were estimated based on several key events (e.g., the smallpox outbreak in 1951). Giocue's chronological table, with important events in her life, is shown in Table 8.3. For publication, I have edited the original narration and omitted some heavy repetition. Also, when the speaker referred to a specific child and said "a child around his/her age," I have used expressions such as "a seven-year-old," guessing from the age of the child mentioned.

Table 8.3 Life history of Giocue

Year[a]	Age[a]	Event
1936	0	Born
1943–1944	7–8	Began to gather food with women
1946	10	Death of her father
1950	14	Lived with her fiancé (a Kgalagadi man)
1950	14	Lived with her fiancé (a |Gui man named Goikua)
1951	15	Prevalence of smallpox
1952	16	Got her first period and married her fiancé
1954	18	Her first childbirth (Koakoaxo)
1958	22	Death of her husband (Goikua) and her son (Koakoaxo)
1960	24	Got remarried to |Xou
1963	27	Gave birth to first daughter (Keresie)
1967	31	Began *zaa-ku* relationship
1968	32	Gave birth to second son (Qawasie)
1971	35	Canceled the *zaa-ku* relationship
1974	36	Gave birth to second daughter (Kaba), her last child
1979	43	Settled down in Xade

[a] Year and age are both estimated

Hardship in Childhood

> I am the first child of my father and mother. I am the one who saw the sun first.
>
> Days and months passed and passed and passed, and I nursed and nursed and nursed and nursed, and a younger sister was born when I grew up. My younger sister was a girl who pushed me out and stayed in my mother's belly when I became about five years old. She was a girl who was inside my mother when I stopped nursing. Her name was Haena. But Haena died when she was three or four years old, and my mother gave birth to a boy after Haena. (Giocue, recorded on August 28, 1994).

Giocue was the first child, and she had a younger sister and a younger brother. However, both of them died young.

In the |Gui expression, the first child is often called "the one who saw the sun first" and the youngest, "the one who finished up the breast milk." The mother abruptly quits breast-feeding if she becomes pregnant with the next child while still breast-feeding the older child because the pregnancy is believed to change breast milk into something bad which has a deadly effect on both the older child and the unborn baby.

Because of this belief, the older child is forced to experience the hardship of being pulled away from the breast milk which he/she has become deeply attached to. This leads to the expression "a child who pushed me out and stayed in my mother's belly" referring to the next child.

There are further hardships to bear in childhood. Infants usually sleep in the same hut as their parents but move their sleeping place to their grandparents' on reaching the age of reasoning. |Guari, another |Gui woman estimated to be born in 1938, talked about this as follows:

> When her parents go to sleep, a child feels sad because she is left alone.
>
> |Gui parents hide their sexual intercourse from their children. Hide it very much. Parents lie down facing each other and their child is sleeping behind the mother's back. When parents overlap their blankets (metaphor for sexual intercourse), they eventually pull up the child's part of blanket. The child starts crying because it's cold. They don't want it to happen, so the father says to the child, "Go to grandmother's place and sleep there. We two are going to use the blankets in here." |Gui say this kind of thing to their children. Children who are three or four years old come to learn they must not sleep in their parents' hut and go to their grandmother's place to sleep. (|Guari, recorded on September 2, 1994)

It has already been described that |Gui and ||Gana frequently repeat patterns of grouping together and breaking up. They often visit another camp and stay there for a few days up to a few months. Consequently, camp members are in constant flux. Even children sleep in different places from day to day. They may sleep in their parents' hut for a few days, then in their grandmother's hut on the next day, and then spend another day in their aunt's hut in another camp.

When they become 7 or 8 years old, boys sleep only with boys and girls sleep only with girls. They may use a vacant hut or build a small hut by themselves. For boys, a "youth hut" where only unmarried men stay is often prepared. For young men, despite the name "hut," it usually just means a place under the shade of a large tree or a planked-in area at the most. It is not a hut with a roof.

Girls live together in a hut called "||*game* hut." ||*game* hut originally meant "a hut where several families live together," but often there are elderly couples and girls, widows and girls, or only girls living together.

|Gui children are not expected to help with the family occupation or to babysit, so they spend the day by themselves in a pretty easygoing way. There is no worry about meals because although any dish cooked in any hut is first eaten by adults, the leftovers are shared among any children who happen to be around. After age 7 or 8, boys and girls do not mix when they play. Groups of boys, or girls, hang around by themselves until dark in and around a camp, sometimes even going out into the bush.

Childhood Life and Play

Girls at age 7 or 8 followed adults when they went collecting foods or fetching water:

> When I became about seven years old, I often said, "No. Don't leave me. I'm going with you," when older women were leaving to go collecting, and I cried hard. Adults said, "Look how hard she's crying. This child will get lost in the bush if we leave her like that. We should take her with us." So, I went collecting with adults. I dug out food, watched adults digging, and dug again. That was how I learned collecting. (Giocue, recorded on August 28, 1994)
>
> When I was seven or eight, I began going out to fetch water and poured water into a carton. I went for water with the adult women. We women fetched water and carried it back

> to the camp. The water was put in ostrich eggs and adult women put them in leather net, set a rope on their forehead and carried them on their back, and we came back. (|Guari, recorded on September 9, 1994)

Children sometimes helped adults work in this way, but at other times they "played house" by themselves. The following story is a memory of this sort of "playing house." The |Gui term "*!kaa?o*" is translated as "play house" here. "*!kaa?o*" originally means "picnic." It is a word for playing outside a camp and spending time in cooking:

> Children who are around seven play house in the bush. When I was little, I often played house, too. I was just absorbed in playing house, nothing else. We played house away from the camp where adults were.
>
> The children built a small hut. We built a small hut, went in, came out, walked around it, visited other huts, and played house.
>
> Girls made a fire and played house. Like adults do in the camp, we cooked, ate and played house.
>
> Then we returned when it became dark. We came back to the camp. We came back to our parents' place. We used to spend many hours playing house in the bush. Yeah, we really did play a lot. We are |Gui. Children always sang, danced and played house.
>
> If there was a boy, he did *sie-ku* (marriage) with a girl and played house. It wasn't a real *sie-ku*, we just imitated it and played. Long, long time ago, I *sie*-ed (married) a cousin. I *sie*-ed him, and he and I built a tiny small hut and went inside together. The two of us did what we were supposed to do in the hut. We did things people do in *sie-ku* together. Yeah, we imitated *sie-ku*.
>
> Even if one boy *sie* two girls, there was no jealousy. It was a good *sie-ku*. Because it was just imitated *sie-ku*. We only imitated *sie-ku* of adults.
>
> When we become about ten years old, we stop playing house. Boys and girls begin to play separately. When they play, boys shoot an arrow at a bird or set a trap to get a turtle. They walk around in the bush doing useful things. They catch a turtle in the bush and play boys' house. They break the turtle shell to open it, cut the meat into pieces with a knife and eat the meat. Then they come back to the camp.
>
> Girls went collecting. We dug *cyoon* (a lily family plant, the root is eaten), collected *qan* (a kind of wild melon), and picked up thin twigs. Then, we made a fire in the place where we always played house, steam-roasted *cyoon* and *qan*, dug them out of hot sand and ate them. (Giocue, recorded on August 28, 1994)

The term "*sie*" in the story is a verb which means "to take," but it also means "to marry (take a spouse)." It can also mean "to have intercourse." The word "*sie-ku*," combined with a suffix which indicates mutuality "*ku*," means "to marry (take a spouse with each other)."

Children imitated what adults were doing in their everyday life, for example, hunting and collecting, cooking, hut-building, singing and dancing, marrying, and so on and used them to "play house."

Fiancé Selected Before the First Menstruation

> I lived with a man (my first husband) when I was a girl before having my first period. I boiled food and put it on a plate for him. I knew cooking when I was about 15 years old. I

> went collecting and came back carrying food and twigs on my head. I was living with my husband. But I didn't have my first period yet.
>
> When I grew a little older, adult women mentioned *sie-ku* (marriage). "*Sie* (Take) this man." I refused him and refused and refused. Adult women said, "No, no, *sie* him. *Sie* your man (husband). You don't know anything yet. You only give us trouble and make us tired. *Sie* him." So, I *sie*-ed my cousin at last. My husband's name was Goikua.
>
> He was a young man. He hadn't *sie*-ed any other women yet. He was very young. Goikua lived near my camp. He was the son of my aunt, so I *sie*-ed him. Because he was my aunt's son, he and I were cousins. So, I *sie*-ed him.
>
> At first, Goikua came visiting me, visited me, and we *sie*-ed. Because I hadn't had my first period, we *sie*-ed only a little.
>
> After my menstruation started, we had treatment of mixing our blood (performed the marriage ritual). So, we really *sie*-ed each other. (Giocue, recorded on August 28, 1994)

It was common until the early 1970s for a girl to have a future husband, or "fiancé," already selected for her before her first menstrual period. As far as my research discovered, a woman estimated to be born in 1958 was the last person to have a fiancé arranged before the onset of menstruation, following their custom. She had her first period around 1973. It is the girl's parents and relatives who choose a husband. They select an appropriate man from the girl's cousins.

In the case of Giocue, her first proposed fiancé was an old Kgalagadi man. She disliked him because he was too old and ugly (she said). She refused that man. So her mother arranged another fiancé, a young |Gui man, who was her cross-cousin (explained later).

The traditional |Gui and ||Gana's marital system is that a girl starts to live with her fiancé at around 15 years old, even if she has not yet had her first period. The fiancé is arranged by her parents and relatives. Cross-cousins are advisable for her husband, and a girl sometimes marries a relative. But often marriages are arranged outside the kindred and dialect group and even outside the ethnic group (such as when a |Gui or ||Gana girl marries a Kgalagadi man). When a girl reaches menarche, she undergoes rituals for this, and at the same time marriage rituals are held.

Concerning the postmarital residential pattern, in many cases, young |Gui and ||Gana couples stay with the wife's family at first. This is because the wife is so young and also bride service is expected from the husband or fiancé. Bride service in |Gui and ||Gana society is the sharing of meat, caught by the husband, with the wife's parents. In particular the neck meat of a big antelope must be given to the hunter's wife's parents.

Marlowe (2004) insists that early residence among foragers is biased less toward virilocality because bride service should be provided in many forager societies, while bride price is more common in non-forager societies. Foragers bond more closely with both mother's and father's kin and interact bilaterally, while non-foragers are more patrilineal (Marlowe 2004).

When a young wife has her first child, she needs help from other women. Her mother is the preferred helper, but other relatives, such as her aunts or grandmother, would also be available. Her husband's mother may also help, especially as she would also often be aunt to the new mother (usually her father's sister), as many couples are cousins. A few years after marriage, when their baby is growing up, the couple may choose to stay with the husband's family, if there would be more opportunity to get meat with hunting. In traditional times, they migrated so frequently with the fission and fusion of camps that sometimes a couple would stay with wife's relatives and at other times with husband's relatives.

|Gui and ||Gana people divide cousins into two types, parallel and cross, according to whether the pair of linking kin are same-sex siblings or opposite-sex siblings. Children whose parents are same-sex siblings are classified as parallel cousins, while those whose parents are opposite-sex siblings are classified as cross-cousins. |Gui and ||Gana also classify relatives of their own generation into two categories, *uo* and *ǂgua?o*, and these two categories make up an avoidance/joking dichotomy. The cross-cousins are the key members of the *ǂgua?o* category, whereas parallel cousins and siblings are a member of *uo*. Marriage between *uo* (siblings and parallel cousins) is avoided, while marriage between *ǂgua?o* (cross-cousins) is encouraged. |Gui and ||Gana tend to avoid marrying close relatives, but with the low opportunities to meet others in the broad Kalahari Desert, it would have been difficult to find a spouse. So members of the kinship category *ǂgua?o* were seen as desirable marriage partners. Marital relationships between another dialect group (|Gui and ||Gana) or other ethnic groups (e.g., San and Kgalagadi) were also established and sometimes even recommended.

The arrangement of marriages by parents or close kin is prevalent among hunter-gatherers, while in other societies, marriage is a nonchalant affair with limited regulation in courtship marriages (Apostolou 2007). It suggests that the regulated exchange of mates and resources may lead to human meta-group social structures with coalitions and alliances spanning across multiple residential communities (Walker et al. 2011).

The |Gui and ||Gana have a particular view concerning young girls and sexual intercourse. Girls sometimes lived in the camp of her "fiancé" (expressed as "her man" in the |Gui language, just like husband, as there is no special word for it) and at other times lived in her parents' camp with the fiancé. It was also mentioned that a girl and her fiancé sometimes slept in the same hut and had sex. Since the sexual intercourse of a girl prior to her first menstrual period is considered *gonaha* (meaning "useless" originally but "futile and harmless" here) in their community, no importance is attached to it.

Girls' sex is "futile and harmless" until menstruation begins, even when they become otherwise well developed, and adults do not attempt to control their sexual behavior. This is because a girl's sexual activity does not bring the "benefit" of childbirth nor does it lead to the "harm" of causing "disease" to her sexual partner. Thus, if a young man visits a "||*game* hut," where girls who have not had their first menstrual period live together, and has sex, it is not considered immoral. Naturally, women's virginity is never an issue.

The women's opinions about their first marriage were typically negative: "I didn't want to get married yet, but my mother and aunts were persistent in pushing me, so I reluctantly complied." In fact, many women had a husband selected by adults in their early girlhood, and the man was often much older (a man aged around 30 for a 14- or 15-year-old girl), so every woman talked about her first marriage in a negative way.

The First Menstruation Ritual

> When I had my first menstrual period, I lived in a place called Goagi. When I had my first period, Qemagi (mother's second husband) lived with us. Qemagi was the man who sewed my hat for the first menstruation ritual. My husband didn't do it for me. My husband was not good at trap hunting. He was good at arrow hunting. So, my father-in-law caught a bush duiker and made a hat from its skin. When I had my first period, I was living with my husband, my parents, and my husband's parents.
>
> My aunts sang. Then, adult women who lived together came and danced. Women from another camp visited us, danced and danced. Women came for a visit in the morning and danced and danced, and went back in the afternoon. I was lying covered with a leather robe from head to feet. I stayed still and lay in the hut.
>
> I was feeling happy during the first menstruation ritual. I wasn't afraid and I didn't get tired of lying down for a long time. My aunts said, "Listen carefully." The women said, "Listen carefully." So, as told, I closed my mouth shut and listened carefully. I did that and I was never bored. My body didn't hurt either. I was quietly lying down and the women lifted my body and massaged me. And then, they kindly bent my legs. I kept quiet and sat up. The women massaged my legs and arms again and bent my legs.
>
> "Male eland" (the first part of the first menstruation ritual) was over, but we didn't move to another camp. We stayed in the same camp and "female eland" (the second part of the first menstruation ritual) came back. We lived in the old camp for a long time and "female eland" returned. It was a rainy season, you know. I tell you, we don't move so soon in a good year. (Giocue, recorded on August 28, 1994)

It was estimated that Giocue got her first menstrual period around 1952. Giocue said that she had her first period in the year following the disappearance of the smallpox outbreak (1951).

|Gui and ||Gana carry out a series of rituals at the onset of a girl's first menstruation. For instance, if a girl notices an unexpected change in her body while out collecting in the bush, she squats down on the spot and the ritual begins at that moment. The girl pulls a leather robe over her head and an aunt carries the girl on her back. Other women surround them and they return to the camp. Back in the camp, a new hut is quickly built, and the girl is secluded inside for about 3 weeks. During the seclusion, she just quietly lies down covered with a blanket over her head and must follow various forms of ritual as instructed by her aunt.

This seclusion is again conducted when the girl has her second period. Furthermore, she has to keep the ritual hat (a pillbox-style hat without brim) on for over 6 months until it starts raining.

Despite such restrictions on activities and behavior, many people describe the experience of the first menstruation ritual as "happy," because, they say, suddenly they were the focus of attention from adults and became valued. Before then, they were ignored and considered "futile and harmless" by adults.

Women from nearby camps visit the girl and dance "eland" to celebrate her. Eland is the large antelope that lives in Kalahari. It is a meaty animal with a lot of fat. It also represents the ideal female figure among |Gui and ||Gana. Both the first menstruation ritual and the dance which is performed only during this ritual are called "eland."

The girl's parents, if they can afford it, serve the women who came to dance eland sweet fruit and liquor made by fermenting corn flour. When the girl comes out of the hut of seclusion, her aunts and women of the same generation gather to put makeup on her and lend her their valuable necklaces. The girl's fiancé and uncles sew a special leather hat for her. It is a definite rule that a meal, no matter how little, is served in the first house that the girl visits after seclusion.

As they are taken care of and treated with courtesy by adults, girls gradually feel their responsibility as an adult.

In the days when girls had a fiancé before the onset of the first menstruation, there was a ritual to "mix blood" with the fiancé on the morning of the day when the girl comes out of the hut. Undergoing this ritual meant that the girl had married her fiancé.

The First Childbirth

> I got married, days and months passed and passed, and I gave birth to his child. When I gave birth to a child, my mother and his aunt helped me with delivery. That day, I was out collecting wild melon. And I came back to the camp.
>
> It became dark and I gave birth to a child in the hut. I had a baby in my hut in the camp. I wasn't afraid of giving birth to a child. Two older women helped with delivery. They cut the navel cord of the newborn baby, wiped his body, straightened his backbone, and then handed me the baby. And I slept with the baby (boy). I wasn't afraid of the baby, because I knew I was going to raise the child. (Giocue, recorded on August 28, 1994)

Giocue gave birth to her first child around 1954 when she was estimated to be 18 years old. She had the baby in her own hut. As the following story describes, however, it seems common that women had a baby in the bush in the olden days. Her mother went all the way to the bush to give birth to a baby. At the time of childbirth, female relatives took care of the mother and the newborn baby. Collecting firewood and cooking meals were also done by women around the new mother:

> Because I was big enough, I saw my mother give birth to my little brother. Mother was calm. Mother felt and felt labor pain, and it became noon, and when it was still light, now, now, my mother went out of the hut by herself, and gave birth to my little brother in the bush a little away from the camp.
>
> My father said, "My woman, my wife, went out just now." Aunts ran after my mother and reached her. Yeah, in the bush. Mother gave birth to my little brother in the bush. Aunts supported my mother from both sides and came back to the camp with my mother.
>
> I rubbed mother. Then I carried firewood. The firewood mother had brought and placed before giving birth to a baby. I used it to make a fire and sat with mother. Then, people brought firewood to us. Mother gave birth to a baby and had a terrible pain in her lower back. (Giocue, recorded on August 28, 1994)

In the following story, |Guari, who is another |Gui woman born in around 1938, describes the sex life of a couple who have a small child and then criticizes the short interval between childbirths of today's young couples:

> “||*ankamaxa*” is that you give birth to a child and sleep alone. And it means your husband sleeps in a hut over there or in another camp.
>
> After having a baby in the bush, the mother comes back to the camp and rests in her hut. The husband sleeps in a different hut. Soon, there comes the day when they cut the baby’s hair with a razor (a ritual performed around three weeks after birth). So, the husband comes back to the hut where the mother and the baby stay. But the father sleeps alone and the mother sleeps with the child separately from him.
>
> And two months after birth, in the morning, the parents cut their bodies, mix blood, and treat the child. But the father and the mother still sleep in different blankets. Days and months pass and the child becomes able to sit by himself, and walk, and when the child becomes four or five years old, finally the parents share the same blanket.
>
> In |Gui, if you are |Gui, the father never looks for another woman even when he sleeps alone. He has a wife, only her, and cares for the child. When the child grows up and becomes healthy, the husband comes to the wife. In the |Gui way, the child becomes very sick if the parents have sex when the child is about two years old. People hate to see it happen. The parents finally share the same blanket when the child becomes four or five years old.
>
> A woman doesn’t have her period for a long time after giving birth to a child. She gets her period back when the child becomes two or three years old. When breast-feeding is finished, menstruation begins. But she still doesn’t have sex with the husband. And she has a period, another period, and doesn’t have sex with the husband, and days and months pass that way, but she doesn’t have sex with the husband. After having her periods and when the child becomes four or five years old, one day he and she overlap their blankets and sleep under it.
>
> Like this, |Gui people do it rightfully. If he doesn’t care for the child, if he tries to jeopardize the child, if he fathers a next one when the child is still little. If they do that, both the first child and the next child become weak and unhealthy.
>
> This is how it is today. They have a child. When the child is barely sitting up, the wife is already pregnant. And when the child is beginning to walk, the second child is born. This is what people do today. This is not good. They don’t care for their children. (|Guari, recorded on September 3, 1994)

After giving birth, the mother and the baby stay in the hut for about 3 weeks. The husband eats and sleeps in a different place during this time. Even after the mother and the baby come out of retreat, back to normal life, it was considered not appropriate for the couple to have sex until the child reached 4 or 5 years old.

People say that a mother doesn’t have a period until weaning, when the child is 2 or 3 years old. However, menstruation may resume even during the lactation period. When a mother becomes pregnant with the next baby, she must stop breast-feeding because people believe that “the pregnancy changes breast milk into something bad which has a deadly harmful effect on both the older child and the unborn baby.” The older child misses his/her mother’s breast milk so much he/she becomes stressed.

During those years, the husband abstains from sex if he sleeps in the same hut or goes to another hut to spend the night. By keeping abstinence in such a manner, they say the |Gui tried to have at least 5 years between childbirths in traditional times.

!Kung have long birth intervals, of which the mean length is 4.12 years (Howells 1979). Blurton Jones and Sibly (1978) and Blurton Jones (1986) proposed the back-loaded model in which four-year inter-birth intervals optimize the fitness of !Kung women because the weight mothers had to carry on foraging trips increased dramatically as intervals decreased from 4 years, although Pennington and Harpending (1993) criticized his data interpretation. On the other hand, Konner and Worthman (1980) found suppressed reproductive function in lactating !Kung women. But, at best, the study correlated nursing behavior with about 2 years of lactational infertility. The causes of further impaired reproductive functioning and 4-year inter-birth intervals are not explained.

Nevertheless, |Gui and ||Gana have the concept that the birth interval should be extended to 5 years. They tried to prolong birth intervals by keeping abstinence. Elderly women chastised young couples who produced children in consecutive years after the 1980s.

Death of the First Husband

Giocue married Goikua and had a boy, but Goikua was killed by a lion in around 1958. In the same year, her son also died of an illness:

> It's the lion. The lion was the one that killed my husband.
>
> My husband and Tougoma went hunting. My husband took down a female eland. He shot an arrow into the eland and the eland fell down. My husband and Tougoma cut its meat and cut it into pieces in the spot. It became dark and they made a fire, and they were sitting by the fire.
>
> They didn't realize there was a lion coming close up, and the lion got its claws into my husband's shoulder and attacked him. Tougoma stood up and shot his spear into the lion.
>
> Tougoma's spear stabbed the lion. In the moment when the lion let go of my husband, the two of them ran. They ran away. They feared the lion and ran away, ran, ran, ran, ran, and reached an old abandoned hut and they escaped in there.
>
> Then they tried to make a fire and blew and blew into a small fire. Before the fire flamed up, the lion came into the hut and caught my husband. The lion attacked my husband, held him between its teeth and finally bit him to death.
>
> It's the lion that killed my husband. My husband never came back to my camp. Because he died there.
>
> My cousin Tougoma came back alone. But he was also injured by the lion. His head was attacked and his face was half gone. He came back with his neck quivering and swaying. He told us they were attacked by a lion. And he just said to me, "Your husband is virtually gone," and lay down in the hut. He survived, remained, and was lying there in the hut on the brink of death. He was lying almost dead. And he never came to me. Eventually, he died.
>
> Goikua died and my child died. Goikua died when the god died. Goikua died, and in the same year, my child died.
>
> I was very sad. I cried and cried and cried and cried and cried loudly. I was sad and devastated. I was sad and cried and cried. People buried my husband and child in the sand. I cried and cried, all parts of my body hurt, and it was so hard and I cried. Then I moved. I threw out lots of bitter things and I relocated. (Giocue, recorded on August 29, 1994)

It is a terrible and sad story. She lost both her husband and child in the same year. What is more shocking is that another person told in their story how it was believed that Goikua was attacked by a lion because of a curse by Giocue (Sugawara 2010). Giocue suspected her husband was seeing another woman, became mad with jealousy, and made a curse: "A lion shall attack you." The belief says that it caused Goikua to die. If this was truly believed, Giocue certainly blamed herself and tortured herself with desperate sorrow.

Remarriage and Conflict with a Co-wife

> Days and months passed and passed and passed. Days and months passed after Goikua died, and I met my man, |Xou. I met him in Kaucue near my land.
>
> Goikua died, my child died, and I was alone and feeling lost every day. Then, |Xou came and *sie*-ed me. I lived with my relatives. |Xou came to my camp and persistently said to me, "I'm going to *sie* you." I said, "Oh, my, fool! I can't *sie* you." I refused and refused and refused and refused and refused him. I said, "You may *sie* me, but you'll never *sie* for a long time," and I refused. He wouldn't listen to me and *sie*-ed me.
>
> I refused him because |Xou had *sie* with another woman, Oatsaa. I was afraid of jealousy. I feared jealousy and refused and refused and refused. |Xou said, "I'm going to *sie* you, but I want to keep *sie* with Oatsaa." He said that and *sie*-ed me. And I complied with him. By that time, I came to like him. He put the two of us women together.
>
> My camp was located near his camp, and he came visiting me. After agreeing with |Xou, I moved to |Xou's camp. He built two huts next to each other. |Xou slept in Oatsaa's hut one day and slept in my hut on another day. Oatsaa would not accept me. Because she was jealous, she fiercely refused. She continued to refuse for a long time. She was the very woman that abandoned her husband.
>
> And for a long time, she remains away from him. So, now I'm with my husband. Oatsaa lives apart by herself. But when he gets something, my husband gives her some of it. She, too, gives it to |Xou when she gets something. Maybe, Oatsaa still likes |Xou. She lives nearby and wouldn't move to another camp. (Giocue, recorded on August 29, 1994)

In about 1960, Giocue was proposed to by a man named |Xou (estimated to be born in 1927), but |Xou already had a wife named Oatsaa and a son. Though it is not uncommon for a man to have two wives in the |Gui and ||Gana community, often one of the women breaks up the marriage and leaves, saying "I'm afraid of jealousy." However, it sometimes happens that both women accept each other. Once in a while there are unusual cases when polygamous wives (wives who share the same husband) become friends from the beginning.

Another woman, |Guari, describes her relationship with a co-wife in the following story:

> I lived with Buacirem||gae (name of a co-wife) for a short time. I got my first menstrual period and I married my husband, and the three of us slept together. The two of us women got together in that year, two years passed, and she left in the third year. Because of jealousy.
>
> The three of us slept in one hut. Our husband was in the middle and two women slept on both sides. When the husband goes under one blanket with one wife, the other wife sleeping alone thinks to herself, "Uh, the two of them are sleeping together. They're doing it in one blanket," and becomes angry. She is full of jealousy and it breaks her heart. (|Guari, recorded on September 2, 1994)

|Guari married a man who already had a wife, as his second wife. However, his first wife left him in the third year.

In |Gui and ||Gana society, divorce and remarriage is easy because their property is so scant. Some women divorced within a few years of marriage and freely choose a new spouse by themselves. In the case of polygamy, a wife needs to get on well with the co-wives. A unique practice of the |Gui and ||Gana society is that of extramarital sexual relationships. Married people sometimes have sexual relationships with people other than their husbands or wives. This is called *zaa-ku*.

To practice *zaa-ku* they must get the agreement of their spouse. Sometimes two couples swap spouses. They say this *zaa-ku* includes plural marriages, so it is like a big marriage and a big family. *Zaa-ku* relationships link plural families.

Although sexual conduct is regarded as something to conceal from other people in |Gui and ||Gana communities, sometimes plural couples sleep in the same hut because what the couple beside you is doing is supposed to be none of your business as long as they are one blanket away. The rule has been established that you did not see or hear anything the other couple does across a blanket. It follows that you are supposed to have no concern with other couples who do not share your blanket when multiple couples sleep in the same hut (called ||*game* hut) in *zaa-ku* (extramarital sexual relationship, described further below).

There is no public or formal ceremony for marriage, and there is no separate ritual that distinguishes a marriage from other sexual relationships within their community. They view marriage as just one kind of sexual relationship, not special. They believe that a sexual relationship causes a disease called "stain" (Imamura 2001a). So the bride and the groom must perform the ritual of bleeding and mixing their blood in order to get rid of the "stain" from their blood and prevent contracting this disease.

If a woman marries as a second wife, three people – the husband, the first wife, and the second wife – all bleed and mix their blood. Since children are thought to also contract "stain," all their children participate in this ritual and get small scars when they are cut with a razor, and the blood of the adults is put into the cuts.

Giocue started living with |Xou in this way, but the conflict with his co-wife, Oatsaa, continued. Oatsaa slept alone in her hut for as long as my field study continued from 1988 to 1998, but she stayed in the same camp as |Xou and Giocue. People around them told me that Oatsaa and |Xou "can be considered married as well as broken up."

Giocue described the conflict with Oatsaa over 30 years as below:

> When there are two women, they quarrel with the husband. Soon, the two women begin to fight and they bite each other. Then, people pull them apart. People say, "Stop. Both of you, leave the other alone. Leave her alone," and so the women stop fighting and each of them goes back to her own hut. They retreat into their own hut and leave the other alone, you know. Surely, they know what to do. They have a human heart. They probably fight with each other only once because they are jealous. Then days and months pass, and they quarrel only one more time and stop. After that, they will never fight. (Giocue, recorded on September 9, 1994)

Zaa-ku: Extramarital Sexual Relationship

After remarrying with |Xou, Giocue gave birth to a baby girl in around 1963. Then for about 4 years, from around 1967 to 1971 (Fig. 8.3), three sets of couples engaged in an extramarital sexual relationship called "*zaa-ku*" (Imamura 2001b).

|Gui and ||Gana community permits extramarital sexual relationships. Especially "*zaa-ku*" among multiple couples, expressed as "sharing a hut" or "enormous *zaa-ku*," is regarded as ideal *zaa-ku*. However, the person who wants to start *zaa-ku* must persuade his/her spouse to agree.

Giocue and |Xou entered a *zaa-ku* relationship with a ||Gana couple, Nosho and Anchuu. At about the same time, Oatsaa, |Xou's other wife, entered *zaa-ku* with a couple, Ginasie and !Qai. These seven people in total maintained a sexual relationship called "enormous *zaa-ku*." During these 4 years, three of the women each gave birth to a child. Giocue had a baby boy named Qawasie in 1968:

> After that, I gave birth to Qawasie. We were *zaa-ku*. The ||Gana man and |Xou got together and had Qawasie. Nosho (male), |Xou (male), Anchuu (female) and Giocue (story teller, female), all of us, did *zaa-ku*. We invited Oatsaa (|Xou's other wife, co-wife to Giocue) to *zaa-ku*.
>
> I knew I did a bad thing. I said, "What's wrong with us? Can we, this many (and she held up five fingers), this many, so many of us really do *zaa-ku*?" and I objected. "We include !Qai (female) and Ginasie (male) too, and so many of us (seven people) do *zaa-ku*. We are wrong. Wrong. Wrong." I refused and refused.
>
> There was no one specific to start *zaa-ku*. Everybody started. Everybody, everybody, they were all starting *zaa-ku*. I was the only one disgusted with such *zaa-ku* and I refused and refused. I said, "All of you wouldn't listen to me, so I'll die."
>
> At that time, we lived in Kaucue. Nosho was visiting us, leaving Anchuu in their camp. Because Anchuu was a ||Gana, she lived near Gyom. Nosho came and I had that child. I had Qawasie.
>
> When people started "sharing a hut" (meaning *zaa-ku*), I was, I was afraid of Nosho. But other people were doing fine sleeping with their partner. I was afraid of Nosho. When he came to me, I refused and refused and said I hated it as if this mouth of mine burned. He loved me and wanted me, but I hated him. Those men would not listen. Nosho came into my hut.
>
> |Xou slept with Anchuu, he was at her place. |Xou went to Anchuu's place, slept, and Nosho came here and slept at my place. Because Nosho said he's going to "*sie* wisely." So my son was named "Qawa-sie (wisely take)". (Giocue, recorded on September 2, 1994)

When *zaa-ku* began, the seven people performed "the ritual of mixing blood" just as they do at marriage. The children of the three couples, who were already born, were also made to participate in the ritual. The purpose was to prevent and treat a disease called "stain" which was believed to infect men and women in a sexual relationship and their children (Imamura 2001a).

Then, who would become the father of a child born in *zaa-ku*? Giocue explains about father in the following story:

> The father of Qawasie was Nosho and |Xou. There comes a child of theirs where the two of them got together, you know. Qawasie has two kinds of blood. The two men, |Xou and Nosho, gave birth to Qawasie. (Giocue, recorded on September 2, 1994)

Giocue says that their *zaa-ku* was a good one. It is because they were on good terms, shared food, and helped one another. Generally, |Gui and ||Gana people evaluate it as a "right" or "beautiful" *zaa-ku* if they agree and help one another:

> We gave to other people. For a long time, we gave to others and shared and it was *zaa-ku*.
>
> Days and months passed and passed and |Xou had Tsaine with Anchuu. |Xou left my camp and went far to the land of ||Gana people. And he reached there and had Tsaine.

> The four of us liked one another in those days. Just as in the right |Gui way, we liked one another, and |Xou went to Anchuu's place and had Tsaine. Even so, we lived without having a quarrel.
>
> We liked one another and lived together. We shared food. Nosho was good with traps. He caught animals with traps and gave them to Anchuu and me. When the man of us two women (meaning |Xou) shot an animal with an arrow and he gave meat to the two of us. We ate.
>
> The four of us shared like this. We happily gave and shared. I refused him at first, but gradually I came to like him and gave and gave food. (Giocue, recorded on September 2, 1994)

Love and Jealousy

To conclude this section "The life of |Gui and ||Gana women," here are examples from Giocue's story expressing feelings of love and what |Gui women do when suffering with sorrow or jealousy:

> When a man sees a woman he likes, his heart dances and vibrates. But when a woman sees a man she likes, her heart stays and calms down. If she doesn't see him, she becomes bewildered and wonders in her mind, "How is he doing?" But when she sees him, her heart is now peaceful. (Giocue, recorded on September 9, 1994)
>
> A woman goes out to the bush when she feels sad. Quietly she goes to the bush and walks around in the bush. Then she comes back, makes many things in the hut, makes them, but her mind is still not cleared. But she gives to her husband. Although her mind is not cleared, she cooks food and gives it to her husband.
>
> Like this, she strokes her own chest and calms her mind. When her mind recovers a little, she feels something like joy just a little bit and makes this and makes that. She cooks food and gives it to her husband. She gives it to her children. The husband eats it and sleeps. (Giocue, recorded on September 9, 1994)

Discussion

Sexual Relationships and Society

The |Gui and ||Gana have sexual relations without being married. By contrast, the !Kung, another San group, are reported to rarely have sexual relations outside marriage for reasons including a lack of privacy and, importantly, a social prohibition on such affairs (Marshall 1976; Shostak 1981).

Unlike the "illicit loves" seen in other societies, extramarital sexual relations among the |Gui and ||Gana, *zaa-ku*, are socially approved (Tanaka 1989; Sugawara 2004). *Zaa-ku* functions socially by creating social relationships between people other than the specific individuals and families involved in any particular marriage. Tanaka (1989) suggests that:

> … while the San maintain a system of simple marriage, they often practice divorce, remarriage, polygamous marriage and even the *zaa-ku* relationship … the San are making great efforts to maintain their society by utilizing the complex network of inter-personal relationships.

Zaa-ku relationships differ from the socially regulated extramarital sexual relationships generally seen in African pastoral societies, almost all of which are patrilineal, in that particular relationships are not always completely approved. For example, Sato reports on the existence of the *dumassi*, or love relationship outside of marriage, among the Rendille of northern Kenya. In Rendille society, "married women may live a comparatively free sexual life within the regulations of the *dumassi* institution (open-lover institution)" (Sato 1998). The sexual freedom of married women is restricted to *dumassi*, a socially regulated relationship between specific age-sex categorized groups. Thus, Rendille sexual relationships outside marriage are institutionally controlled.

The |Gui and ||Gana culture is flexible, so that particular relationships become socially accepted or approved by becoming common knowledge, although such relationships may be based on individual feelings of love. In addition, among the |Gui and ||Gana, it is commonly accepted that a stable *zaa-ku* is ideal, supporting the existence of diverse sexual relationships.

Sie-ku (Marriage)

In discussing *zaa-ku*, I want to make clear what marriage consists of among the |Gui and ||Gana. In |Gui and ||Gana society, although men are expected to pay women something at their wedding, this convention is not necessarily upheld in many cases. No property changes ownership, either at marriage or on divorce. A rite is held at the beginning of a marriage, but they do not invite people to the rite and never hold a wedding reception. Neither do they register marriages with a chief, although the Kgalagadi, a neighboring agropastoralist group, do so.

It is thus difficult to define what |Gui and ||Gana marriage is, at least in a strictly formal sense. Nevertheless, marriage certainly exists among the |Gui and ||Gana and is socially sanctioned. A man and woman live in the same hut, have sexual intercourse, earn their living together, divide food between themselves, and raise their children together. The couple is recognized as a married couple by everyone, so it can be said this state represents their typical style of marriage. However, beside the typical style of marriage, there are diverse associations between men and women which involve varying sexual relationships.

Zaa-ku Relationship

The term *zaa-ku* derives from the verb *zaa*, meaning "to make a person one's sweetheart," combined with the suffix *ku*, meaning "mutuality." It refers to the state in which a couple has repeated sexual intercourse despite not being married or to the relationship itself. Recently the word *zaa-ku* has extended to include all sexual relationships outside marriage, such as romances between young people and secret love affairs. *Zaa-ku* is also used to refer to "an intimate friend" without any sexual relationship being involved.

However, the typical meaning of *zaa-ku* is that a married man or woman has a sexual relationship with someone other than his/her spouse but with the permission of the latter. Importantly, the typical *zaa-ku* is a fairly open relationship with the permission of one's spouse. When such permission is obtained, the spouse's relationship to the lover, that of a husband to his wife's lover or of a wife to her husband's lover, is called *!naa-ku*, a mutually permitted relationship (Fig. 8.2). It is important that in *zaa-ku* relations the bond is not only man-to-woman but also man-to-man and woman-to-woman.

The |Gui and ||Gana regard the ideal type of *zaa-ku* as that in which two couples exchange partners, that is, partner swapping. They call this state "enormous *zaa-ku*" or "sharing huts." In enormous *zaa-ku*, two or more couples form a close community which extends beyond a nuclear family, sharing their food as well as their sexual partners. It is said that in the past, when the |Gui and ||Gana lived a traditional nomadic life, there were actually several cases in which two couples formed "enormous *zaa-ku*" relationships.

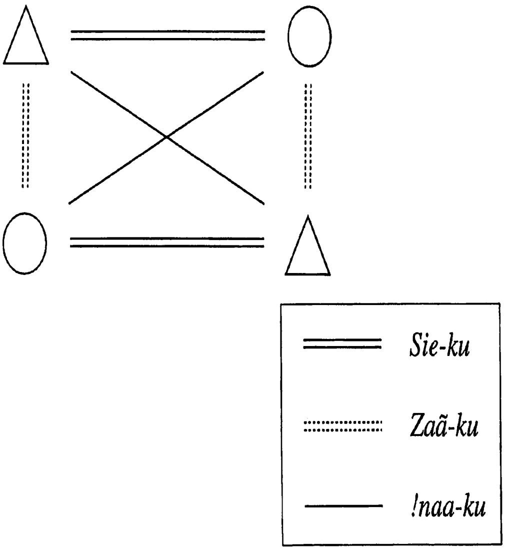


Fig. 8.2 *Zaa-ku* relationship

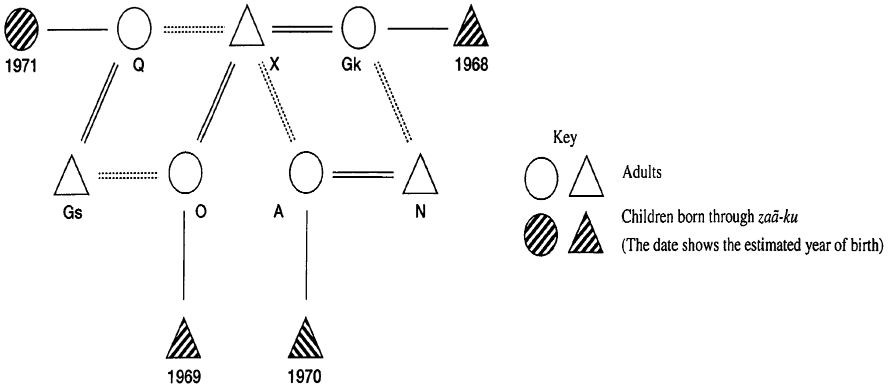


Fig. 8.3 An example of a *zaa-ku* relationship among seven people

More recently, three couples formed an "enormous *zaa-ku*" for about 5 years from 1967 to 1971 (Fig. 8.3). That is the case of Giocue, on whom I described above. The three couples comprised seven persons in total, a man (X) with two wives (Gk and O) and two men with one wife each (Gs was married to Q, and N was married to A). X had *zaa-ku* relations with Q and A; Gs with O and N with Gk were also *zaa-ku*. X, Gk, O, Gs, and Q are |Gui, and N and A are ||Gana. X and Gs are categorical siblings and used to live in the same land at that time. The three families lived separately, with about 30 km between X and Gs and more than 80 km between X and N.

The men were the main visitors between the *zaa-ku* families, which exchanged food (including meat) and sex. *Zaa-ku* refers to relationships not only between two people but also between whole groups of people connected by sexual intercourse. So it is often said, for example, that "We seven people were *zaa-ku*."

Enormous *zaa-ku* can be said to be "another style of marriage." Some people even say "enormous *zaa-ku* is superior to marriage, because *zaa-ku* includes marriage." In |Gui and ||Gana society, sexual relations are not restricted to married couples. Traditional sharing practices include not only the sharing of food but also sharing of work, information, amusement, and also sexual intercourse. Although a stable sexual relationship between two couples is the ideal in |Gui and ||Gana society, few "enormous *zaa-ku*" have occurred recently. The reason is that it is difficult to continue such relationships without jealousy. Today almost all of the extramarital sexual relationships occurring in |Gui and ||Gana society take place between married women or men without their spouses' permission. In fact, in most cases, spouses reluctantly accept the existence of lovers as time goes by. Therefore, the love affairs of married men and women are socially permitted as a form of *zaa-ku* in the broadest sense of the term. The conspicuous feature of *zaa-ku* relationship is an active choice on the part of women. In actuality husbands seem to have mostly given up making any effort to control their wives' sexual activity (Sugawara 2004).

Quite a lot of children are born as a result of *zaa-ku* relations. I asked 55 mothers about the situation under which they gave birth. Of 172 children born since the 1960s, 131 children were born through their mother's *sie-ku* (marriage), while 41 children were born through *zaa-ku*. That is, almost one quarter of the children (23.8 %) were born through *zaa-ku*. (But the true paternity of those children is not certain.)

When a married women bears a child following sexual relations outside marriage, the pater (social father) of the child is the husband of the child's mother: the man who married (*sie*) her. But how is the biological father (genitor), who is thought by the people to give the child life, decided? Given the |Gui and ||Gana folk-interpretation of human reproduction, a child is born through the mixing of male and female water. Male water is "semen"; female water is called "love juice" or "amniotic fluid." Frequent sexual intercourse causes male water to eventually accumulate in the woman's womb, and when the womb fills with water, an embryo will finally start to form. According to the |Gui and ||Gana interpretation, there exists no moment of fertilization. That is, they believe lives are created in an analogical way, not a digital one.

When a wife has a lover and becomes pregnant, the situation is explained as follows: she becomes pregnant with the mixture of the two male waters. In this case, the genitors of the child are both the wife's husband and her lover. The genitor is not limited exclusively to one person. The |Gui and ||Gana say "two men have met at the baby" or "two men bore a baby together." Of course, there is a tendency for people to try to identify a particular person as the genitor of a child born through *zaa-ku* by speculating about who the child resembles. However, there remains the possibility the husband is a genitor of the child.

The main theme of marital systems in almost all human societies is to determine the father of a new baby. A baby has a pater according to the marital system of each society. Many societies try to ensure the pater and genitor are one and the same, which is also why many societies have double standards about sexual behavior between women and men. But in |Gui and ||Gana society, people do not have to control women's sexuality, because by their folk-interpretation of human reproduction, a husband can be always a pater and a genitor of his wife's baby, even if his wife has a sexual relationship other than him.

Although gender egalitarianism is the feature of small-scale hunter-gatherers, there are still male dominance and sexual asymmetry in hunter-gatherers societies. For example, extramarital sexual relationship is prohibited especially for women, but not for men among the !Kung. Compared with the situation in most other societies, however, |Gui and ||Gana are tolerant of married women having sexual relations outside marriage, and their gender relations are more symmetrical than in other societies. About zaa-ku relation people said that it was difficult to overcome jealousy. Nevertheless "enormous zaa-ku" was thought to be ideal in traditional |Gui and ||Gana society, because they could share land use, meat and food, children, and lives. The relationships mediated by "sex" contribute to a more refined integration in a society of repeating fission and fusion.

Female Dispersal and Social Strategy

The |Gui and ||Gana are mostly monogamous with some polygamous men and their wives and a few polyandrous men and their wives. Typically, a girl starts to live with her fiancé even if she has not yet had her first period. When she reaches menarche, marriage rituals are held. In many cases young couples stay with the wife's family at first. But in traditional times, their residential groups frequently underwent fission and fusion. So the couple may sometimes choose to stay with the husband's family. Their postmarital residence shows non-sex-biased, bilocality, or multilocality pattern.

Central Kalahari hunter-gatherer women share a lot of common features with females of other female-dispersing primate species in that they have no consistent support from their natal kin, that they need to establish relations with unrelated males and females, and that their entire life is strongly affected by sexual relationships.

A unique practice of the |Gui and ||Gana society is that of extramarital sexual relationships. This is called *zaa-ku*. Sometimes two couples swap spouses. They say that this *zaa-ku* includes plural marriages. I would like to emphasize that in *zaa-ku* relations, the bond is not only man-to-woman but also man-to-man and woman-to-woman. And in the case of polygamy, a wife needs to get on well with the co-wives.

|Gui and ||Gana women often go to gather food in the bush in groups. They offer frequent help to one another in daily activities: gathering food, collecting fire wood, fetching water, cooking and repairing huts, etc. They also share the cooked food beyond the household. The food is distributed on a reciprocal basis according to the closeness of the relationship (Imamura 1993; Imamura-Hayaki 1996) (Fig. 8.4). The intimate closeness means not kinship but friendship within non-kindred. Often

Fig. 8.4 Lying down together, sharing one shade

women go gathering food and then share food not with sisters, even though they live together, but with close friends. Their social relationship is maintained not by formal rules such as kin but by face-to-face interaction.

In any society of humankind, a sexual relationship is considered a kind of possession. The *zaa-ku* practice does not displace another's possession but shares in it. And in this, men and women are on an equal footing. Despite this equality, every woman still comes into some conflict with her husband, her lovers, and her husband's lovers. Throughout their lives, |Gui and ||Gana women experience various sexual relationships. They struggle to manage these and also build many bonds and ties with other women.

Acknowledgements I am deeply grateful to |Gui and ||Gana friends in Botswana. I would like to express my gratitude to my family for their support and warm encouragement. Finally, I would like to thank JSPS KAKENHI Grant numbers 63041072, 07041012, and 22101001; these made it possible to complete this study.

References

Alvarez H (2004) Residence groups among hunter-gatherers: a view of the claims and evidence for patrilocal bands. In: Chapais B, Berman CM (eds) Kinship and behavior in primates. Oxford University Press, Oxford, pp 420–442

Apostolou M (2007) Sexual selection under parental choice: the role of parents in the evolution of human mating. Evol Hum Behav 28:403–409

Barnard A (1979) Kalahari Bushman settlement patterns. In: Burnham P, Ellen R (eds) Social and ecological systems. Academic, London

Barnard A (1985) Rethinking Bushman settlement and territoriality. Paper presented at the international symposium: African Hunter-gatherers, 3–5 January, Cologne

Blurton Jones NG (1986) Bushman birth spacing: a test for optimal interbirth intervals. Ethol Sociobiol 7:91–105

Blurton Jones N, Sibly R (1978) Testing adaptiveness of culturally determined behaviour: do Bushman women maximize their reproductive success by spacing births widely and foraging seldom? In: Blurton Jones N, Reynolds V (eds) Human behaviour and adaptation. Taylor and Francis, London, pp 135–155

Blurton Jones NG, Smith LC, O'Connell JF, Hawkes K, Kamuzora C (1992) Demography of the Hadza, an increasing and high density population of savanna foragers. Am J Phys Anthropol 89:159–181

Chapais B (2008) Primeval Kinship: how pair-bonding gave birth to human society. Harvard University Press, Cambridge

Ember CR (1975) Residential variation in hunter-gatherers. Cross-Cult Res 10:199–227

Foley RA, Lee PC (1989) Finite social space, evolutionary pathways, and reconstructing hominid behaviour. Science 243:901–906

Heinz HJ (1972) Territoriality among the Bushmen in General and the !Ko in particular. Anthrops 67:405–416

Heinz HJ (1979) The nexus complex among the !Ko Bushmen of Botswana. Anthrops 74:465–480

Hewlett BL (2013) Listen, here is a story: ethnographic life narratives from Aka and Ngandu women of the Congo Basin, Issues of globalization: case studies in contemporary anthropology. Oxford University Press, Oxford

Hewlett BL Hewlett BS (2012) Hunter-gatherer adolescence. In: Hewlett BL, (ed) Adolescent identity: evolutionary culture and developmental perspectives, Routledge studies in anthropology. Routledge, New York, pp 73–101

Hill K, Hurtado AM (1996) Ache life history. Aldine de Gruyter, New York

Hill KR, Walker RS, Božičević M, Eder J, Headland T, Hewlett BS, Hurtado AM, Marlowe F, Wiessner P, Wood B (2011) Co-residence patterns in hunter-gatherer societies show unique human social structure. Science 331:1286–1289

Howell N (1979) Demography of the Dobe !Kung. Academic, New York

Ichikawa M (1986) Flexibility in the African hunter-gatherer social organization. In: Itani J, Tanaka J (eds) Anthropology of nature-dependent societies. Academia Shuppankai, Kyoto, pp 279–311 (in Japanese)

Imamura K (1993) Cooperation and sharing among the Central Kalahari San: from the viewpoint of subsistence activities of women. Afr Kenkyuu 42:1–25 (in Japanese)

Imamura K (1997) Technical aspects of gathering among the Central Kalahari San. J Nagoya Gakuin Univ, Soc Sci 34(1):173–186

Imamura K (2001a) Water in the desert: rituals and vital power among the Central Kalahari hunter-gatherers. Afr study Monogr 27(Suppl):125–163

Imamura K (2001b) The folk-interpretation of human reproduction among the |Gui and ||Gana and its implications for father-child relations. In: Keen I, Yamada T (eds) Identity and gender in hunting and gathering societies, vol 56, Senri ethnological studies. National Museum of Ethnology, Osaka, pp 185–194

Imamura-Hayaki K (1996) Gathering activity among the Central Kalahari San. Afr Study Monogr 22(Suppl):47–66

Kelly RL (1995) Foraging spectrum. Percheron Press, Clinton Corners/Cambridge

Knauft BM (1991) Violence and sociality in human evolution. Curr Anthropol 32:391–428

Konner M, Worthman C (1980) Nursing frequency, gonadal function, and birth spacing among !Kung hunter-gatherers. Science 207:788–791

Kramer KL, Greaves RD (2011) Postmarital residence and bilateral kin associations among hunter-gatherers: Pumé foragers living in the best of both worlds. Hum Nat 22:41–63

Lee RB (1968) What hunters do for a living, or how to make out on scarce resources. In: Lee RB, Devore I (eds) Man the hunter. Aldine, New York, pp 30–38

Lee RB (1979) The !Kung San: men, women, and work in a foraging Society. Cambridge University, Cambridge

Lee RB, Daly R (1999) The Cambridge encyclopedia of hunters and gatherers. Cambridge University Press, Cambridge

Lee RB, DeVore I (1968) Problems in the study of hunters and gatherers. In: Lee RB, Devore I (eds) Man the hunter. Aldine, New York, pp 4–12

Marlowe FW (2004) Marital residence among foragers. Curr Anthropol 45:277–284

Marlowe FW (2010) The Hadza: hunter-gatherers of Tanzania. University of California Press, Berkeley

Marshall L (1976) The !Kung of Nyae Nyae. Harvard University Press, London

Meggitt MJ (1968) "Marriage classes" and demography in Central Australia. In: Lee RB, Devore I (eds) Man the hunter. Aldine, New York, pp 176–184

Owen RC (1965) The patrilocal band: a linguistically and culturally hybrid social unit. Am Anthropol 67(3):675–690

Pennington R, Harpending H (1993) The structure of an African pastoralist community: demography, history, and ecology of Ngamiland Herero, Research monographs on human population biology. Clarendon, Oxford

Radcliff-Brown AR (1930) The social organization of Australian tribes. Oceania I

Rodseth L, Wrangha RW, Harrigan AM, Smuts B (1991) The human community as a primate society. Curr Anthropol 32(3):221–254

Sato S (1998) The Rendille and the adaptive strategies of east African pastoralists. In: Kurimoto E, Simonse S (eds) Conflict, age & power in north east Africa. James Curry/Ohio University Press, Oxford/Athens, pp 206–226

Service ER (1962) Primitive social organization: an evolutionary perspective. Random House, New York

Shostak M (1981) Nisa: the life and words of a !Kung woman. Harvard University Press, Cambridge

Steward JH (1955) Theory of culture change: the methodology of multilinear evolution. University of Illinois Press, Urbana

Sugawara K (2004) Possession, equality and gender relations in |Gui discourse. In: Widlok T, Tadesse W (eds) Property and equality vol 1: ritualization, sharing, egalitarianism. Berghahn Books, Oxford, pp 105–129

Sugawara K (2010) Article of Lion. In: Tanaka J, Sugawara K (eds) An encyclopedia of |Gui and ||Gana culture and society. Laboratory of Cultural Anthropology, Graduate School of Human and Environmental Studies, Kyoto University, Kyoto, p 72

Tanaka J (1969) The ecology and social structure of Central Kalahari Bushmen: a preliminary report. Kyoto University African Studies vol 3:1–26. The Committee of the Kyoto University Africa Primatological Expedition, Kyoto University, Japan

Tanaka J (1976) Subsistence ecology of Central Kalahari San. In: Lee RB, Devore I (eds) Kalahari hunter-gatherers: studies of the !Kung San and their neighbors. Harvard University Press, Cambridge, pp 98–119

Tanaka J (1980) The San, hunter-gatherers of the Kalahari: a study in ecological anthropology. University of Tokyo Press, Tokyo

Tanaka J (1987) The recent changes in the life and society of the Central Kalahari San. Afr Study Monogr 7:37–51

Tanaka J (1989) Social integration of the San society from the viewpoint of sexual relationships. Afr Study Monogr 9:153–165

Turnbull CM (1968) The importance of flux in two hunting societies. In: Lee RB, Devore I (eds) Man the hunter. Aldine, New York, pp 132–137

Walker RS, Hill KR, Flinn MV, Ellsworth RM (2011) Evolutionary history of hunter-gatherer marriage practices. PLoS ONE 6–4:1–6

Part III
Evolution of Female Dispersal

Chapter 9
Complexities of Understanding Female Dispersal in Primates

Phyllis C. Lee and Karen B. Strier

Introduction

The heuristic model for the evolution of primate social organisation that has been used for the past 35 years has been based on the proposition that "ecological" factors generate costs and benefits for animals forming and then maintaining groups (Clutton-Brock and Janson 2012; Kappeler et al. 2013). In these models, predation risk and food characteristics are the key ecological predictors of the type of grouping. However, layered onto these ecological drivers and managing or moderating their effects are social factors internal and external to groups – the nature and degree of interindividual and intergroup competition for either food or reproductive opportunities (Isbell and Young 2002; Sterck et al. 1997; Thierry 2008). What we observe as flexibility in social organisation and social structure stems at least in part from variation in local ecology, but much also derives from the local internal dynamics of different groups in the same population (Strier et al. 2011).

Another classical statement about social organisation is: "Males disperse more regularly and over longer distances than females do in most mammalian taxa" (Silk 2009; pg. 540). This form of dispersal produces female philopatry and therefore a predominance of evolutionary explanations for the existence of female kin–male dispersing sociality, especially among the primates. But given how widespread female dispersal is among some primate taxa (colobids, apes, atelids, lemurids),

---

P.C. Lee (✉)
Behaviour and Evolution Research Group, Psychology, School of Natural Sciences,
University of Stirling, Stirling, FK9 4LA, UK
e-mail: phyllis.lee@stir.ac.uk

K.B. Strier
Department of Anthropology, University of Wisconsin–Madison, 1180 Observatory Drive,
Madison, WI 53706, USA

T. Furuichi et al. (eds.), *Dispersing Primate Females*,
Primatology Monographs, DOI 10.1007/978-4-431-55480-6_9

we can ask what social or behavioural traits underlie this phenomenon. Furthermore we can ask "when females do disperse, how far do they move?"

In a comprehensive review of philopatry and dispersal in mammals, Lukas and Clutton-Brock (2011) suggested that the underlying causal determinant of habitual female dispersal was the need to find unrelated mates. In their comparative analysis across a variety of mammalian taxa, Lukas and Clutton-Brock (2011) demonstrated that when a female's mean age at first reproduction was younger than the average duration of male tenure or residence in a group with his daughters, females rather than males disperse. Females thus disperse prior to commencing reproduction in order to avoid mating with males who had been in their group for long enough to be those females' father. Dispersal prior to breeding is both geographical (away from the natal range and resources) and genetic (away from close kin). Thus, the nature of reproductive skew – how much breeding is dominated by one or a small number of individuals – affects tendencies for dispersal, while site-specific local competition for resources among mothers and daughters tends to promote dispersal by daughters (Clarke 1978; Silk 1984). As such, with high intrasexual reproductive skew, closely related males as potential mates, or where opportunities for successful breeding are constrained by female–female local resource competition, females move to new groups or ranges (Clutton-Brock 1989; Lawson and Perrin 2007; Nagy et al. 2013).

There are a number of intriguing questions about the differences between habitually female-resident and habitually female-dispersing societies among primates. Is there a relationship between reproductive skew and steep hierarchical status or dominance differentials in reproductive rates and philopatry (e.g. Thierry 2013)? Since kin are expected to avoid competition, does a lack of kinship result in little cooperation (e.g. Sterck et al. 2005)? Or does a need for social embeddedness and cooperation, for example, in infant care, underlie female reproductive success (e.g. Silk et al. 2009) irrespective of kinship? Cooperation need not depend on kinship, but rather cooperation and association can be at least temporarily based on shared interests such as the presence of same-aged infants (e.g. cetaceans, Möller and Harcourt 2008; orang-utans, van Schaik 1999). In addition, in a context where females mate with multiple males over successive reproductive events, as is common in group-living multi-male primate societies, average relatedness among offspring and thus within the group may actually be quite low (Lukas et al. 2005; Rubenstein 2012) even with female philopatry. Relatedness alone is therefore not sufficient as a causal factor for philopatry versus dispersal. And finally, the question of interest is that of living with kin versus living near kin. Kin compete (sometimes intensely) so the benefits of living in close social proximity with related individuals may not always result in the reduced competition that is typically theoretically associated with kinship (Clutton-Brock 2009; West et al. 2002).

Behavioural traits associated with kin co-residence are characteristically associated with support in the context of competition from non-kin either in the same or in neighbouring groups (e.g. Isbell 1991). If, however, animals are able to manage conflicts of interest and their needs for cooperation through alterations in how they maintain cohesion rather than through manipulating within-group degree of relatedness, then there may be specific anticompetitive benefits to fission–fusion dynamics as one such mechanism to manage living with other females (e.g. Aureli et al. 2008), especially if females are unrelated. This final observation suggests that female dispersal in primates might be more commonly associated with fission–fusion dynamics rather than with stable, cohesive groups. These issues will be considered in this chapter, along with various controversies about the nature of female dispersal.

How Common Is Female Dispersal in Primates?

As is illustrated throughout this volume, female dispersal from the natal social unit is the predominant dispersal mode for modern *Homo* (Mace and Alvergne 2012), *Pan* (Pusey 1980; Nishida et al. 2003), gorilla (Harcourt et al. 1976; Watts 1990; Stokes et al. 2003), several colobids (Sterck et al. 1997; Qi et al. 2009) and many of the atelids (Crockett 1984; Strier 1994). The question of how female dispersal is distributed across primate taxa raises the notion of phylogenetic constraints on social systems, which have been adequately addressed elsewhere (Di Fiore and Rendall 1994; Strier 1994; Shultz et al. 2011). In terms of lineages rather than species, female dispersal is widespread across all the major groups of anthropoid primates (Fig. 9.1). It is however rare in a twig-tip species count within lineages. Lineages with male dispersal appear to have done well in terms of recent speciation while the overall pattern shows very little switching or alternation of dispersal mode (defined as predominately male dispersal, predominately female dispersal or both sexes disperse) between species within a lineage (see also Shultz et al. 2011). Why might it be rare to find within-lineage switching and why might it also be rare to find female dispersal at the twig tips of a phylogeny?

Moore and Ali (1984) argued that females were more prone to dispersal in interpopulation comparisons than was indicated by species-level explorations, and they therefore suggested that which sex disperses was not a fixed social state. We use the term social states (sensu Lee 1994) here to synthesise three dimensions of sociality – associations between females, those between males and associations between males and females – all as a function of relatedness. As a minimal descriptor of associations within and between sexes within social groups, each social state is thus a basal representation of group composition and kinship. Whether females or males, or indeed both sexes, disperse from one group compared to another group of the same species can be suggested to be a response to local conditions such as demography in terms of number of non-kin males which are locally available as mates. The monopolisation of groups of females over very long male tenures in the absence of competitors (e.g. Karisoke gorillas: Williamson 2014) may accelerate rates of female departure, while limited opportunities for dispersal may result in closely related females ending up in the same groups (e.g. northern muriquis, Strier et al., Chap. 1; chimpanzees, Pusey 1980). In combination with local energetic influences on the rate of maturation among females, opportunities for and a necessity to disperse for outbreeding may both result in high levels of

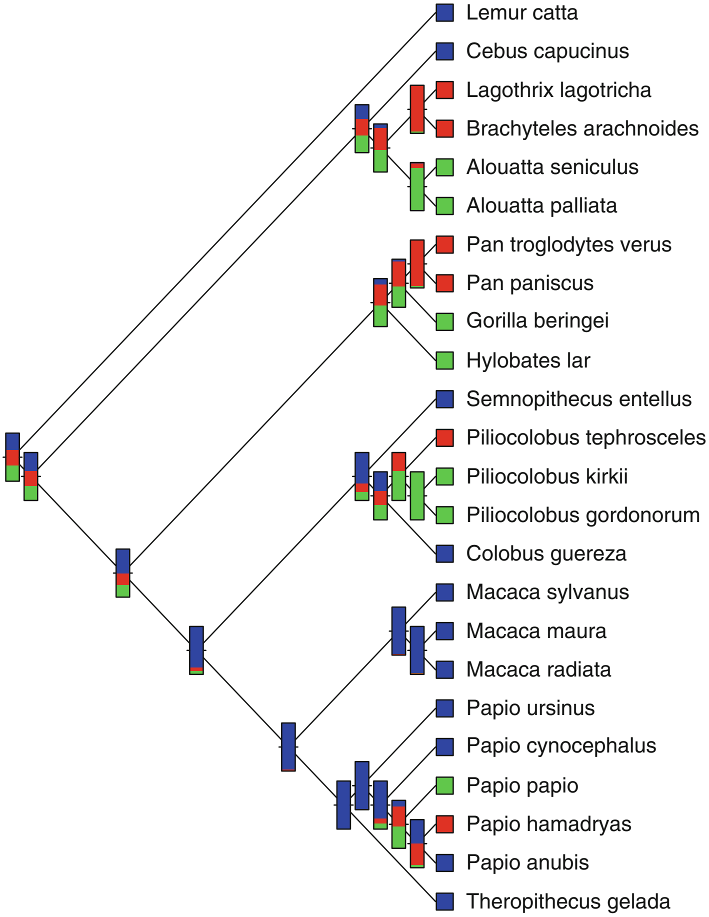


Fig. 9.1 Phylogenetic signal in dispersal from a sample of species with long-term observations (From Strier et al. 2014). The dispersal modes are coded as *blue* = male dispersal, *green* = both sexes disperse, and *red* = female dispersal. The colour proportions in the bars at the ancestral nodes give the expectation that the ancestor had the corresponding dispersal mode. These expectations were calculated using ancestral character estimation with the programme ACE in the R package APE (Paradis et al. 2004). A likelihood ratio test comparing the phylogenetic pattern of dispersal to a non-phylogenetic pattern demonstrated statistically significant phylogenetic signal ($P = 0.045$). The phylogeny was generated from the 10kTrees Website (Arnold et al. 2010)

local variation in dispersal modes among groups (e.g. black and white colobus: Harris et al. 2009). We therefore suggest that locally high energy availability and consequent rapid growth which accelerates female age at maturation, combined with long male tenure, might also result in females that simply move to avoid mating with their fathers irrespective of the species-level dispersal mode (e.g. Clutton-Brock 1989). Local variation does not, however, appear to produce marked species-level shifts in dispersal sex, but rather, this variation exists within the species-typical patterns. One important question then is just how common are evolutionary state shifts in dispersal modes?

Males have other options to avoid inbreeding such as secondary dispersal when daughters mature (Jack and Fedigan 2004). Alternatively, as Tennenhouse (2014) states, there can be clear fitness advantage for males who use a mating strategy that targets unrelated females within their groups (e.g. Charpentier et al. 2005; Setchell et al. 2010). Thus mechanisms of mate choice could be sufficient to minimise inbreeding, again, without necessarily producing species-level shifts in dispersal mode. As a further option, females can avoid the risks of inbreeding with their fathers while retaining the benefits of proximity to female kin by engaging in high rates of extra-group mating (e.g. callitrichids, Goldizen 2003; guenons, Cords 2000; langurs, Borries 2000).

The phylogenetic signal (e.g. Kamilar and Cooper 2013) in dispersal mode among primate species has not yet been assessed in a full set of comparative data across all taxa, although recent analyses of a subset of long-term studies across a range of species suggest that such a signal is present (Strier et al. 2014). What has long been clear is that female dispersal, either females only or when both sexes disperse, is present in many primate lineages (Fig. 9.1), and at a subfamily level female dispersal is as common as male dispersal (Strier 1994). Another interesting point is that female dispersal remains typical of the great apes, a lineage in which the vast majority of species went extinct by the late Miocene only to be subsequently "replaced" by lineages with more consistent male dispersal (e.g. papionines, cercopithecines) (Andrews 1981; Potts 2004). While we can only speculate on the ancestral dispersal mode, cladistic analysis suggests that the shift was from female or both sex dispersal to male dispersal at the origin of the cercopithecids (Foley and Lee 1989). That apes (large and small) and many colobids retain both sex or female dispersal suggests a later evolution of female philopatry in the lineage leading to cercopithecids. Was the evolution of female philopatry in the cercopithecid radiation associated with the observed shift to a more rapid life history as we detail below or the result of a need to monopolise lower quality foods in the face of interspecific competitors (e.g. Macho 2013) or both in the context of global habitat changes in the late Miocene? An evolutionary state analysis of this shift that can incorporate some of the Miocene apes might go some way to resolving this question for catarrhines. However, among the lemurs, a diversity of dispersal types exists in the absence of any replacements in evolutionary time or ecological space (Kappeler and Heymann 1996; van Schaik and Kappeler 1996; Takahata et al. 2014), while in the platyrrhines, we see a similar degree of diversity in dispersal modes (Strier 1999). Indeed, all of the evidence is consistent with previous proposals that the so-called rarity of female dispersal in primates is simply a result of sample biases towards the African and Asian cercopithecoid monkeys (Moore 1984; Di Fiore and Rendall 1994; Strier 1994).

The Push and Pull of Food Energy on Sociality

Sterck et al. (1997) suggested that female gregariousness was a key trait of diurnal primates and used the nature of female–female dominance relationships to describe variation in this trait (see also Thierry 2008). In their model, two key features were associated with female reproductive success: food intake and energy expenditure. Irrespective of any dominance or competitive mechanism affecting these two factors, their model emphasised the female need for sustaining some maximal energy balance in order to reproduce successfully. Reproductive energetics have been fundamental to models of primate sociality since the 1970s (e.g. Goss-Custard et al. 1972) but are less frequently assessed or related to the nature or dynamics of within- versus between-group competition, even though reproductive energetics and energetic constraints have long been linked to female philopatry or at least to a proposed need for female kinship in primate groups (Sterck et al. 1997; Isbell and Young 2002).

If, as is generally proposed, female reproductive success is limited by energy availability and males by opportunity, can we move beyond constraints such as infanticide (van Schaik and Janson 2000) for predicting the structure underlying primate sociality? We suggest that an understanding of reproductive costs, care allocation and infant survival probabilities in relation to female gregariousness alongside the genetic structuring to female–female relationships that results from dispersal will contribute to linking dispersal modes with reproductive strategies. Recent studies have attempted to assess the direct energy costs of maintenance and reproduction among female primates (reviewed by Emery Thompson 2013; Pontzer et al. 2014; baboons, Rosetta et al. 2011; and callitrichids, Tardif and Ross 2009). Despite a general observation that females in energy-poor environments or with low energy balance have reduced reproductive performance, the actual per kilogram costs of gestation and lactation for most primates are low by comparison to many birds as well as small- and even some medium-sized mammals. What female primates are “playing with” in models of energy and reproduction is time, rather than kilocalories (Altmann and Samuels 1992; Rosetta et al. 2011). We might thus need to reappraise our concepts of gregariousness and how this arises via dispersal in order to understand how female primates can use social strategies to minimise specifically the time allocated to reproductive events.

Trade-offs between the time allocated for infant care – lactation, sustaining growth, protection and support – and the time available for reproduction within a lifespan may underlie social strategies equally if not more than social or competitive trade-offs with respect to energy intake. It can be suggested that care is on average a more important determinant of infant survival than is food, as only during extremes of energy constraint does infant mortality increase (see Lycett et al. 1998). However, at this point, discussions of these energetic trade-offs in relation to infant survival are merely speculations; we need to be able to assess infant mortality as a consequence of variation in social strategies alongside the mortality risks due to care allocation strategies (e.g. Isler and van Schaik 2012) before we can evaluate the implications of time versus energy limitations on the reproductive strategies that emerge from various dispersal modes.

Female groups thus serve many more functions than simply managing food or reproductive competition with conspecifics; for example, females form active alliances against infanticidal males which can be equally effective between female kin or non-kin (Packer and Pusey 1979, 1983). When infants become expensive due to a combination of slow developmental rates and high energy costs associated with protection, carrying or provisioning (Key and Aiello 2000; Lee 2012; Bell et al. 2013), additional help from allomothers, grandmothers or fathers can secure infant survival. Although paternal care may be more readily available with monogamy (Opie et al. 2013), monogamy is by no means a prerequisite to male protection of infants (e.g. baboons, Huchard et al. 2010). Monogamy of course arises only when there is dispersal by both sexes, which clearly links this reproductive option to dispersal. Adding unrelated females to existing pairs through female dispersal could further aid in infant care, but this can be suggested to be a rare strategy seen in marmosets (Hilário and Ferrari 2010), lemurs (Huchard et al. 2012) and gibbons (Reichard et al. 2012). Such a strategy may be constrained in other primate taxa due to social instability resulting from conflicts of interest between the additional females (e.g. Silk 2009). Similarly, while grandmothering requires female kin derived through female philopatry (Hawkes and Coxworth 2013), allocare can also come from unrelated individuals who gain selfish benefits such as tolerance within a group. Shared care can also be reciprocally exchanged, and female kinship is unnecessary for reciprocated care (Bell et al. 2013; Whitten 1983).

Risks in Relation to Dispersal

Considering the influences of energetics and time on reproduction and the nature of sex-specific infant care and mating strategies, which impact on infant survival probabilities, the individual risks associated with dispersal may influence which sex disperses and over what distance. In all explanatory models of dispersal, some costs to dispersal (risk of predation, illness or injury during dispersal, rejection from a new group) are thought to operate, and yet these costs may not differ greatly between the sexes. The costs of movement might be greater for males who typically disperse several times over their lifespan and who may have little social support from females and juveniles when attempting to enter a new group as well as encountering direct hostility from resident males (Alberts and Altmann 1995; van Noordwijk and van Schaik 2001). By contrast, females may receive positive support and encouragement from resident males during their attempts to move into a group, although females too can encounter same-sex hostility during transfers (Williams et al. 2002; Sommer and Reichard 2000). Risks of dispersal due to predation or encounters with solitary individuals might be reduced for males in sexually dimorphic cercopithecoids, where males have a larger body size and defensive canine weaponry by comparison to smaller-bodied females. Traits of size and weaponry may simply be part of the co-evolution of life history variables with sexual selection which are mapped onto existing species-specific dispersal tactics.

Although there is a strong phylogenetic signal in measures of primate sexual dimorphism (e.g. Plavcan 2001), only a slight association between the extent of size dimorphism and dispersal strategy is found after statistically taking the effects of phylogeny into account (Lee and Kappeler 2003). Among the platyrrhines, male-dispersing species tend to have greater degrees of dimorphism than is seen in other dispersal modes, but this trend is by no means consistent across taxa (Fig. 9.2). The suggestion that dispersal and sexual dimorphism covary in relation to risks appears not to hold (see also Strier 1996).

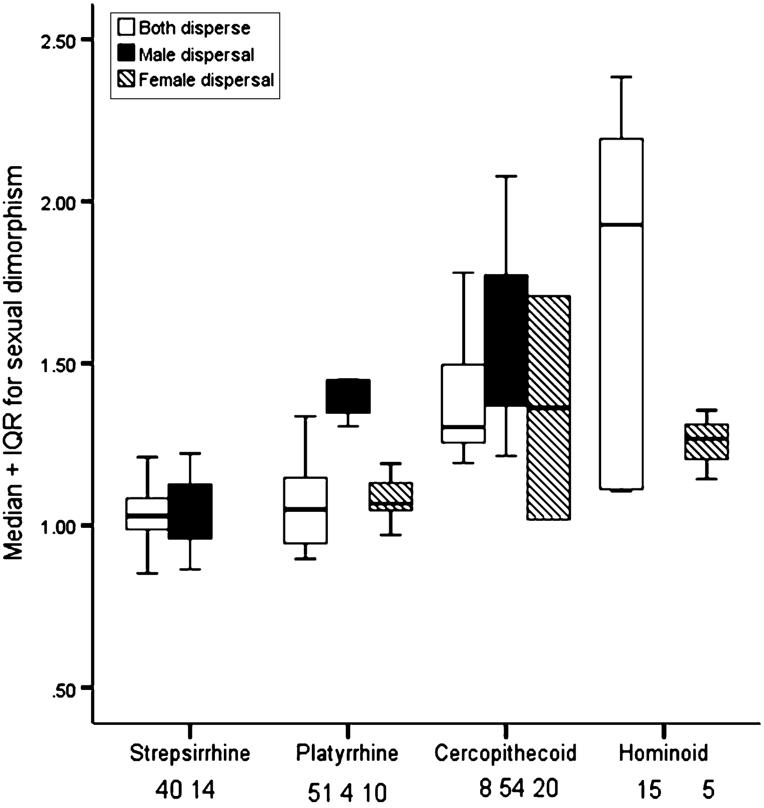


Fig. 9.2 Median and interquartile range of sexual size dimorphism (ratio of male to female body mass) by dispersal mode for major groups of primates. *N* of species for each dispersal mode are shown (Data from Lee and Kappeler 2003; Lee 2012)

The Constraints of Life History Evolution

Altering the pace of an evolved life history might produce heightened mortality risks or reduced reproductive rates as well as being costly in terms of the time required for an existing adaptation to shift, resulting in complex organismal and character constraints on evolution (Futuyma 2010). Correlated life history traits with female dispersal have long been noted (Yamagiwa, Chap. 11; Strier 2003, 2008); these are later maturation, slower rates of reproduction and greater care allocation to infants in terms of both energy and time.

Evolutionary causality in associations between dispersal and life history variation needs to be assessed for a large sample of primates, and we are only now starting to have an adequate dataset for such explorations. Using path analysis to examine the strength of associations among life history traits across a sample of primate taxa, it is clear that lifespan is a fundamental "driver" for rates of reproduction, while the overall costs of reproduction (energy for production and growth) are interrelated (Fig. 9.3). Separating causal structural equations by dispersal modes currently falls into the trap of phylogenetic bias (the over-representation of cercopithecids in measurements of life history traits) and a lack of accurate data more generally. For example, is lifespan generally longer for female-dispersing species with a concomitant slowing of rates of reproduction; or is the energy allocated to production and growth reduced as a function of behavioural strategies to sustain energy balance?

The complexity of covariation in selection for different traits in relation to dispersal can be illustrated by macaques. Willner and Martin (1985) suggested that the macaque life history strategy had shifted towards early female reproduction at a reduced body size by comparison to ancestral species. This provided modern macaques with the advantage of an increased reproductive output via a longer breeding lifespan and shortened the time for female reproductive maturation relative to male maturation. With rapid female maturation, males may have been required to disperse earlier during adolescence to avoid inbreeding. With this shift to a more rapid life history strategy to increase female reproductive rates, male reproductive tenure has shortened and paternity has become distributed among a larger number of different individuals (e.g. Soltis et al. 2001; Langos et al. 2013). Again, with female reproductive maturation at younger ages and at smaller body sizes, dispersal mortality risks might also fall differentially on these small females resulting in few females ever able to successfully disperse under selection for early first reproduction. This life history shift may have simply eliminated the capacity for female dispersal in macaques. We can still ask if selection is acting on primate life history evolution via differential age-specific survival or reproductive output – both of which vary between female- and male-dispersing species. This is a question that remains to be answered.

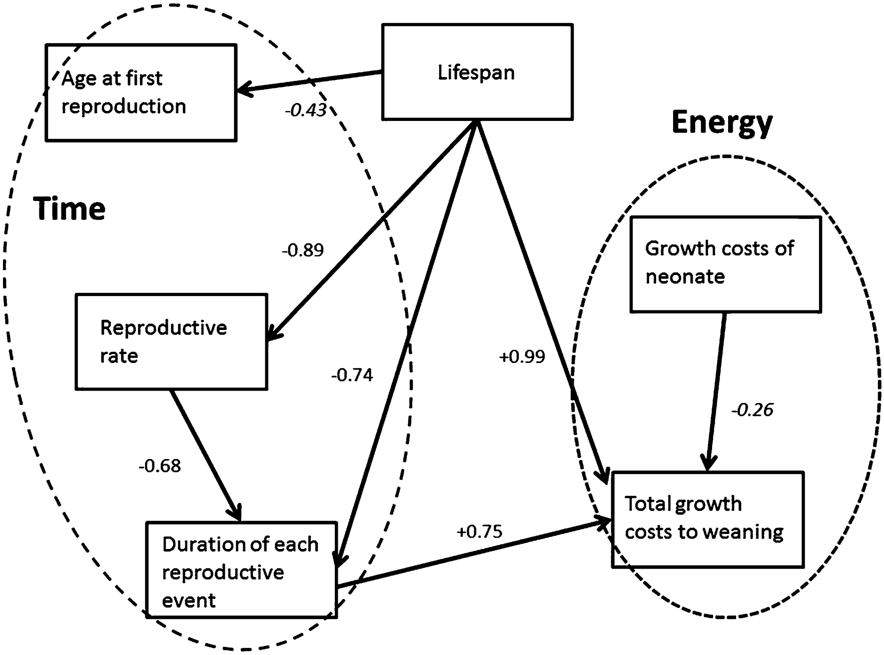


Fig. 9.3 Path analysis illustrating the strength of associations among life history traits in primates (N of species = 124, data from Lee and Kappeler 2003; Lee 2012). Best fit model using all traits ($\chi^2 = 13.63, p = 0.09$). Note that the sample size is small and unbalanced in terms of missing data, resulting in a generally poor model fit at this time. Associated trait error terms were <5 %, and most paths had r-values >0.60, suggesting reasonable causal and directional relationships. Energy traits and time traits are distinguished within the *two dotted circles*. Lifespan underlies most traits, and only the time trait of duration of reproductive events was linked with the energy trait of costs of growth to weaning

Conclusions

What we need in order to both formulate and test more sophisticated explanatory models for understanding how social strategies and social dynamics relate to dispersal in primates is a deeper perspective on the nature of individual social strategies within populations and how these interact with species traits of sociality such as relatedness and co-residence of sexes or group cohesiveness. Starting with the premise that necessity for outbreeding (e.g. Greenwood 1980; Lukas and Clutton-Brock 2011) drives the need to disperse, then the fundamental question is about which sex disperses and when over the course of a lifespan. This question has been extensively modelled for plants, birds and some mammals (Greenwood 1980; Johnson and Gaines 1990; Lawson and Perrin 2007). However individually based explanatory models are still lacking for most primates (but see Alberts and Altmann 1995; Borries 2000; Strier et al. Chap. 1).

Females and males both face mortality and reproductive risks in their natal groups as well as during dispersal – the nature and degree of these risks alone are inadequate as explanations for the sex-specific nature of dispersal. Female–female competition, like that between males, impacts on the availability of dispersal "space" or dispersal opportunities. Rather than there being generalised ecologically determined rules, we suggest that many opportunities for dispersal are local and demographic, and therefore, the nature of dispersal should be flexibly responsive. For example, are neighbourhoods saturated with individuals with similar survival and reproductive requirements, promoting distant or multiple dispersals rather than local settlements? In contexts requiring behavioural flexibility, rules such as those predicting which sex disperses and when may be violated.

However, sex-specific dispersal opportunities may also be constrained by the evolved pace of the species-typical life history. For example, when the costs of infant rearing are high and if these can be shared between group members, then specific reproductive strategies to maximise helping may arise which have at their basis residence (e.g. monogamy, related or unrelated helpers) and therefore dispersal modes.

Female reproductive energetics, associated with the trade-offs between energy and time in life history traits, are key determinants of female gregariousness in the context of intrinsic risks, social risks (infanticide, competition) and extrinsic risks (predation). Sex-specific dispersal tactics result in secondary benefits. For example, adding additional dispersing males to an existing female group provides protection from predation (Hill and Lee 1998; Hill and Dunbar 1998) as well as paternity confusion (e.g. Heistermann et al. 2001). While such differential advantages can result in social state switching between unimale and multi-male units (Opie et al. 2013), these advantages do not produce a change in dispersal mode. However, small-scale switching between dispersal modes in different groups of the same population as a function of local demographic variation such as group size or resource availability remains an option for managing reproduction, as noted by Moore and Ali (1984) and confirmed in recent studies (Miyamoto et al. 2013; Harris et al. 2009).

Possibly more critical to our understanding of dispersal and its consequences for primate social structure is the fundamental question of how aggregations of any sort relate to female reproductive energetics. The capacity to share the energy costs of reproduction and therefore to minimise both the extrinsic mortality risks and the time costs of infant rearing appears to be key to the existence of female grouping (see also Lukas and Clutton-Brock 2013). As discussed above, shared infant care is by no means restricted to kin, and it alone may be sufficient to promote female sociality. The capacity to use social dynamics to manage individual female energetics and produce reproductive advantages once groups have become established is associated with high degrees of fission–fusion dynamics (Aureli et al. 2008), and fission–fusion dynamics do indeed appear to be more common among the female-dispersing primates. A rule for "aggregate when necessary, fragment when not" which typifies fission–fusion social dynamics provides solutions to conflicts of reproductive and social interests as well as coincidences of interests.

Those conflicts of interest which cannot be resolved by fission–fusion dynamics represent major constraints on female dispersal in primate species with "fast" life histories. Teasing apart the linkages between evolved life history traits, reproductive energetics and dispersal modes, and how these more generally relate to sociality in primates, remains an intriguing task for primatologists.

Acknowledgements We thank the editors for inviting this contribution and stimulating new directions in our thinking and for their helpful and patient comments on the manuscript. We thank Anthony Ives for his input into the phylogenetic analysis and drawing Fig. 9.1.

References

Alberts SC, Altmann J (1995) Balancing costs and opportunities: dispersal in male baboons. Am Nat 145:279–306

Altmann J, Samuels A (1992) Costs of maternal care: infant-carrying in baboons. Behav Ecol Sociobiol 29:391–398

Andrews P (1981) Species diversity and diet in monkeys and apes during the Miocene. Symp Soc Study Hum Biol 21:25–61

Arnold C, Matthews LJ, Nunn CL (2010) The 10kTrees website: a new online resource for primate phylogeny. Evolut Anthropol 19:114–118

Aureli F, Schaffner CM, Boesch C, Bearder S, Call J, Chapman CA, Connor R, Di Fiore A, Dunbar RIM, Henzi PS, Holekamp K, Korstjens AH, Layton R, Lee P, Lehmann J, Manson JH, Ramos-Fernandez G, Strier K, van Schaik CP (2008) Fission-fusion dynamics: new research directions. Curr Anthropol 49:627–654

Bell AV, Hinde K, Newson L (2013) Who was helping? The scope for female cooperative breeding in early Homo. PLoS ONE 8:e83667

Borries C (2000) Male dispersal and mating season influxes in Hanuman langurs living in multi-male groups. In: Kappeler PM (ed) Primate males: causes and consequences of variation in group composition. Cambridge University Press, Cambridge, pp 146–158

Charpentier M, Peignot P, Hossaert-McKey M, Gimenez O, Setchell JM, Wickings EJ (2005) Constraints on control: factors influencing reproductive success in male mandrills (*Mandrillus sphinx*). Behav Ecol 16:614–623

Clarke A (1978) Sex ratio and local resource competition in a prosimian primate. Science 201:163–165

Clutton-Brock TH (1989) Female transfer and inbreeding avoidance in social mammals. Nature 337:70–72

Clutton-Brock TH (2009) Sexual selection in females. Anim Behav 77:3–11

Clutton-Brock TH, Janson C (2012) Primate socioecology at the crossroads: past, present, and future. Evolut Anthropol 21:136–150

Cords M (2000) The number of males in guenon groups. In: Kappeler PM (ed) Primate males: causes and consequences of variation in group composition. Cambridge University Press, Cambridge, pp 84–96

Crockett CM (1984) Emigration by female red howler monkeys and the case for female competition. In: Small MF (ed) Females on females: studies of primate female behavior. Alan R. Liss, New York, pp 159–173

Di Fiore A, Rendall D (1994) Evolution of social organization: a reappraisal for primates by using phylogenetic methods. Proc Natl Acad Sci 91:9941–9945

Emery Thompson M (2013) Comparative reproductive energetics of human and nonhuman primates. Annu Rev Anthropol 42:287–304

Foley RA, Lee PC (1989) Finite social space, evolutionary pathways, and reconstructing hominid behavior. Science 243:901–906

Futuyma DJ (2010) Evolutionary constraint and ecological consequences. Evolution 64:1865–1884

Goldizen AW (2003) Social monogamy and its variations in callitrichids: do these relate to the costs of infant care. In: Reichard U, Boesch C (eds) Monogamy: mating strategies and partnerships in birds, humans and other mammals. Cambridge University Press, Cambridge, pp 232–247

Goss-Custard JD, Dunbar RIM, Aldrich-Blake FPG (1972) Survival, mating and rearing strategies in the evolution of primate social structure. Folia Primatol 17:1–19

Greenwood PJ (1980) Mating systems, philopatry and dispersal in birds and mammals. Anim Behav 28:1140–1162

Harcourt AH, Stewart KS, Fossey D (1976) Male emigration and female transfer in wild mountain gorilla. Nature 263:226–227

Harris TR, Caillaud D, Chapman CA, Vigilant L (2009) Neither genetic nor observational data alone are sufficient for understanding sex-biased dispersal in a social-group-living species. Mol Ecol 18:1777–1790

Hawkes K, Coxworth JE (2013) Grandmothers and the evolution of human longevity: a review of findings and future directions. Evolut Anthropol 22:294–302

Hestermann M, Ziegler T, van Schaik CP, Launhardt K, Winkler P, Hodges JK (2001) Loss of oestrus, concealed ovulation and paternity confusion in free-ranging Hanuman langurs. Proc R Soc B 268:2445–2451

Hilário RR, Ferrari SF (2010) Four breeding females in a free-ranging group of buffy-headed marmosets (*Callithrix flaviceps*). Folia Primatol 81:31–40

Hill RA, Dunbar RIM (1998) An evaluation of the roles of predation rate and predation risk as selective pressures on primate grouping behaviour. Behaviour 135:411–430

Hill RA, Lee PC (1998) Predation risk as an influence on group size in cercopithecoid primates: implications for social structure. J Zool 245:447–456

Huchard E, Alvergne A, Féjan D, Knapp LA, Cowlishaw G, Raymond M (2010) More than friends? Behavioural and genetic aspects of heterosexual associations in wild chacma baboons. Behav Ecol Sociobiol 64:769–781

Huchard E, Canale CI, Le Gros C, Perret M, Henry PY, Kappeler PM (2012) Convenience polyandry or convenience polygyny? Costly sex under female control in a promiscuous primate. Proc R Soc B 279:1371–1379

Isbell LA (1991) Contest and scramble competition: patterns of female aggression and ranging behavior among primates. Behav Ecol 2:143–155

Isbell LA, Young TP (2002) Ecological models of female social relationships in primates: similarities, disparities, and some directions for future clarity. Behaviour 139:177–202

Isler K, van Schaik CP (2012) Allomaternal care, life history and brain size evolution in mammals. J Hum Evol 63:52–63

Jack K, Fedigan L (2004) Male dispersal patterns in white-faced capuchins, *Cebus capucinus*. 2: patterns and causes of secondary dispersal. Anim Behav 67:771–782

Johnson ML, Gaines MS (1990) Evolution of dispersal: theoretical models and empirical tests using birds and mammals. Annu Rev Ecol Syst 21:449–480

Kamilar JM, Cooper N (2013) Phylogenetic signal in primate behaviour, ecology and life history. Philos Trans R Soc B 368:20120341

Kappeler PM, Heymann EW (1996) Nonconvergence in the evolution of primate life history and socio-ecology. Biol J Linn Soc 59:297–326

Kappeler PM, Barrett L, Blumstein DT, Clutton-Brock TH (2013) Constraints and flexibility in mammalian social behaviour: introduction and synthesis. Philos Trans R Soc B 368:20120337

Key C, Aiello LC (2000) A prisoner's dilemma model of the evolution of paternal care. Folia Primatol 71:77–92

Langos D, Kulik L, Mundry R, Widdig A (2013) The impact of paternity on male–infant association in a primate with low paternity certainty. Mol Ecol 22:3638–3651

Lawson LJH, Perrin N (2007) Advances in our understanding of mammalian sex-biased dispersal. Mol Ecol 16:1559–1578

Lee PC (1994) Social structure and evolution. In: Slater P, Halliday T (eds) Behaviour and evolution. Cambridge University Press, Cambridge, pp 266–303

Lee PC (2012) Growth and investment in hominin life history evolution: patterns, processes and outcomes. Int J Primatol 33(6):1309–1331

Lee PC, Kappeler PM (2003) Socio-ecological correlates of phenotypic plasticity in primate life history. In: Kappeler PM, Pereira M (eds) Primate life histories. University of Chicago Press, Chicago, pp 41–65

Lukas D, Clutton-Brock TH (2011) Group structure, kinship, inbreeding risk and habitual female dispersal in plural-breeding mammals. J Evol Biol 24:2624–2630

Lukas D, Clutton-Brock TH (2013) The evolution of social monogamy in mammals. Science 341:526–530

Lukas D, Reynolds V, Boesch C, Vigilant L (2005) To what extent does living in a group mean living with kin? Mol Ecol 14:2181–2196

Lycett JE, Henzi SP, Barrett L (1998) Maternal investment in mountain baboons and the hypothesis of reduced care. Behav Ecol Sociobiol 42:49–56

Mace R, Alvergne A (2012) Female reproductive competition within families in rural Gambia. Proc R Soc Ser B Biol Sci 279:2219–2227

Macho GA (2013) An ecological and behavioural approach to hominin evolution during the Pliocene. Quat Sci Rev 96:23–31

Miyamoto MM, Allen JM, Gogarten JF, Chapman CA (2013) Microsatellite DNA suggests that group size affects sex-biased dispersal patterns in Red Colobus monkeys. Am J Primatol 75:478–490

Möller LM, Harcourt RG (2008) Shared reproductive state enhances female associations in dolphins. Int J Ecol 2008:1–5. doi:10.1155/2008/498390

Moore J (1984) Female transfer in primates. Int J Primatol 5:537–589

Moore J, Ali R (1984) Are dispersal and inbreeding avoidance related? Anim Behav 32:94–112

Nagy M, Günther L, Knörnschild M, Mayer F (2013) Female-biased dispersal in a bat with a female-defence mating strategy. Mol Ecol 22:1733–1745

Nishida T, Corp N, Hamai M, Hasegawa T, Hiraiwa-Hasegawa M, Hosaka K, Hunt K, Zamma K (2003) Demography, female life history, and reproductive profiles among the chimpanzees of Mahale. Am J Primatol 59:99–121

Opie C, Atkinson QD, Dunbar RI, Shultz S (2013) Male infanticide leads to social monogamy in primates. Proc Natl Acad Sci U S A 110:13328–13332

Packer C, Pusey AE (1979) Female aggression and male membership in troops of Japanese macaques and olive baboons. Folia Primatol 31:212–218

Packer C, Pusey AE (1983) Adaptations of female lions to infanticide by incoming males. Am Nat 121:716–728

Paradis E, Claude J, Strimmer K (2004) APE: analyses of phylogenetics and evolution in R language. Bioinformatics 20:289–290

Plavcan JM (2001) Sexual dimorphism in primate evolution. Am J Phys Anthropol 44:25–53

Pontzer H, Raichlen DA, Gordon AD, Schroepfer-Walker KK, Hare B, O'Neill MC, Muldoon KM, Ross SR (2014) Primate energy expenditure and life history. Proc Natl Acad Sci 111:1433–1437

Potts R (2004) Paleoenvironmental basis of cognitive evolution in great apes. Am J Primatol 62:209–228

Pusey AE (1980) Inbreeding avoidance in chimpanzees. Anim Behav 28:543–552

Qi XG, Li BG, Garber PA, Ji W, Watanabe K (2009) Social dynamics of the golden snub-nosed monkey (*Rhinopithecus roxellana*): female transfer and one-male unit succession. Am J Primatol 71:670–679

Reichard UH, Ganpanakngan M, Barelli C (2012) White-handed gibbons of Khao Yai: social flexibility, complex reproductive strategies, and a slow life history. In: Kappeler PM, Watts D (eds) Long-term field studies of primates. Springer, Berlin, pp 237–258

Rosetta L, Lee PC, Garcia C (2011) Energetics during reproduction: a doubly labeled water study of lactating baboons. Am J Phys Anthropol 144:661–668

Rubenstein DR (2012) Sexual and social competition: broadening perspectives by defining female roles. Philos Trans R Soc B 367:2248–2252

Setchell JM, Charpentier MJE, Abbott KM, Wickings EJ, Knapp LA (2010) Opposites attract: MHC-associated mate choice in a polygynous primate. J Evol Biol 23:136–148

Shultz S, Opie C, Atkinson QD (2011) Stepwise evolution of stable sociality in primates. Nature 479:219–222

Silk JB (1984) Local resource competition and the evolution of male-biased sex ratios. J Theor Biol 108:203–213

Silk JB (2009) Nepotistic cooperation in non-human primate groups. Philos Trans R Soc B 364:3243–3254

Silk JB, Beehner JC, Bergman TJ, Crockford C, Engh AL, Moscovice LR, Wittig RM, Seyfarth RM, Cheney DL (2009) The benefits of social capital: close social bonds among female baboons enhance offspring survival. Proc R Soc B 276:3099–3104

Soltis J, Thomsen R, Takenaka O (2001) The interaction of male and female reproductive strategies and paternity in wild Japanese macaques, *Macaca fuscata*. Anim Behav 62:485–494

Sommer V, Reichard U (2000) Rethinking monogamy: the gibbon case. In: Kappeler PM (ed) Primate males: causes and consequences of variation in group composition. Cambridge University Press, Cambridge, pp 159–168

Sterck EH, Watts DP, van Schaik CP (1997) The evolution of female social relationships in nonhuman primates. Behav Ecol Sociobiol 41:291–309

Sterck EH, Willems EP, Van Hooff JARAM, Wich SA (2005) Female dispersal, inbreeding avoidance and mate choice in Thomas langurs (*Presbytis thomasi*). Behaviour 142:845–868

Stokes EJ, Parnell RJ, Olejniczak C (2003) Female dispersal and reproductive success in wild western lowland gorillas (*Gorilla gorilla gorilla*). Behav Ecol Sociobiol 54:329–339

Strier KB (1994) Myth of the typical primate. Am J Phys Anthropol 37:233–271

Strier KB (1996) Male reproductive strategies in new world primates. Hum Nat 7:105–123

Strier KB (1999) Why is female kin bonding so rare? Comparative sociality of Neotropical primates. In: Lee PC (ed) Comparative primate socioecology. Cambridge University Press, Cambridge, pp 300–319

Strier KB (2003) Primate behavioral ecology: from ethnography to ethology and back. Am Anthropol 105:16–27

Strier KB (2008) The effects of kin on primate life histories. Annu Rev Anthropol 37:21–36

Strier KB, Chaves PB, Mendes SL, Fagundes V, Di Fiore A (2011) Low paternity skew and the influence of maternal kin in an egalitarian, patrilocal primate. Proc Natl Acad Sci 108:18915–18919

Strier KB, Lee PC, Ives AR (2014) Behavioral diversity and social states in primates. PLoS ONE 9(12):e114099

Takahata Y, Koyama N, Ichino SI, Miyamoto N, Soma T, Nakamichi M (2014) Female coexistence and competition in Ringtailed Lemurs: a review of a long-term study at Berenty, Madagascar. In: Yamagiwa J, Karczmarski L (eds) Primates and cetaceans: field research and conservation of complex mammalian societies. Springer, Heidelberg, pp 129–147

Tardif SD, Ross CN (2009) Integration of proximate and evolutionary explanation of reproductive strategy: the case of callitrichid primates and implications for human biology. Am J Hum Biol 21:731–738

Tennenhouse EM (2014) Inbreeding avoidance in male primates: a response to female mate choice? Ethology 120:111–119. doi:10.1111/eth.12187

Thierry B (2008) Primate socioecology, the lost dream of ecological determinism. Evolut Anthropol 17:93–96

Thierry B (2013) Identifying constraints in the evolution of primate societies. Philos Trans R Soc B 368(1618):1. doi:10.1098/rstb.2012.0342

van Noordwijk MA, van Schaik CP (2001) Career moves: transfer and rank challenge decisions by male long-tailed macaques. Behaviour 138:359–395 van Schaik CP (1999) The socioecology of fission-fusion sociality in orangutans. Primates 40:69–86

van Schaik CP, Janson CH (eds) (2000) Infanticide by males and its implications. Cambridge University Press, Cambridge

van Schaik CP, Kappeler PM (1996) The social systems of gregarious lemurs: lack of convergence with anthropoids due to evolutionary disequilibrium? Ethology 102:915–941

Watts DP (1990) Ecology of gorillas and its relation to female transfer in mountain gorillas. Int J Primatol 11:21–45

West SA, Pen I, Griffin AS (2002) Cooperation and competition between relatives. Science 296:72–75

Whitten PL (1983) Diet and dominance among female vervet monkeys (*Cercopithecus aethiops*). Am J Primatol 5:139–159

Williams JM, Pusey AE, Carlis JV, Farm BP, Goodall J (2002) Female competition and male territorial behaviour influence female chimpanzees' ranging patterns. Anim Behav 63:347–360

Williamson EA (2014) Mountain gorillas: a shifting demographic landscape. In: Yamagiwa J, Karczmarski L (eds) Primates and cetaceans: field research and conservation of complex mammalian societies. Springer, Tokyo, pp 273–287

Willner L, Martin RD (1985) Some basic principles of mammalian sexual dimorphism. In: Ghesquière J, Martin RD, Newcombe F (eds) Human sexual dimorphism. Taylor & Francis, London, pp 1–42

Chapter 10
Factors Influencing Grooming Social Networks: Insights from Comparisons of Colobines with Different Dispersal Patterns

Ikki Matsuda, Keiichi Fukaya, Cristian Pasquaretta, and Cédric Sueur

Introduction

Many species in Hominidae and Atelidae form a male-philopatric/female-dispersal social system (Di Fiore et al. 2011; Nakagawa 2013; Stumpf 2011). Although female dispersal is not the typical pattern for Cercopithecidae, reports of male-philopatric/female-dispersal or both-sex-dispersal social systems have increased in Colobinae (Table 10.1). Therefore, comparisons among colobine species with various dispersal patterns may provide insight on the influence of differences in dispersal patterns on their social relationships.

Animal social systems are the outcome of a network of interindividual relationships established by group members (Hinde 1976; Lott 1984). Among various types of interindividual social interactions, social grooming or allogrooming (hereafter grooming) is a common feature of many animal societies and is possibly the most commonly studied affiliative behaviour in primates (Schino 2001; Sueur et al. 2011a). Grooming is very common among Old World monkeys, particularly Cercopithecidae and Hominidae (Gouzoules and Gouzoules 1987). However, Colobinae, which includes at least 30 species that can be grouped into 4–9 genera distributed

---

I. Matsuda (✉)
Long-term Field Study Project, Primate Research Institute, Kyoto University, Inuyama, Aichi 484-8506, Japan
e-mail: matsuda.ikki.5a@kyoto-u.ac.jp; ikki.matsuda@gmail.com

K. Fukaya
The Institute of Statistical Mathematics, Tachikawa, Japan

C. Pasquaretta • C. Sueur
Département Ecologie, Physiologie et Ethologie, Centre National de la Recherche Scientifique, Paris, France

Institut Pluridisciplinaire Hubert Curien, Université de Strasbourg, Strasbourg, France

T. Furuichi et al. (eds.), *Dispersing Primate Females*,
Primatology Monographs, DOI 10.1007/978-4-431-55480-6_10

Table 10.1 Summary table on data (the proportion of time spent grooming, group size, dispersal pattern, type of minimum reproductive unit and social system) with the references used in this study; we referred to studies published by Dunbar (1991), Lehmann et al. (2007), Grüter (2009) and Grueter et al. (2013) as a starting point for our literature search and subsequently screened more recent literature

Species	Grooming (%)	Group size	Dispersal pattern	Type of unit	Social system	Source for grooming data
Presbytis comata	0.9	12	F	OM	Non-mod	Ruhiyat (1983)
Presbytis siamensis (aka *melalophos*)	0.0	18	M & F	OM	Mod	Bennett (1983)
Presbytis thomasi	1.3	5.8	M & F	OM	Non-mod	van Oijen (1992)
Presbytis potenziani	0.1	6	M & F	OM	Non-mod	Sangchantr (2004)
Presbytis rubicunda	0.0	7	M	OM	Non-mod	Davies (1984)
Trachypithecus leucocephalus	11.5	10.5	M & F	OM	Non-mod	Li and Rogers (2004a, b
Trachypithecus pileatus	0.4	13	M & F	OM	Mod	Stanford (1991)
Trachypithecus francoisi	2.0	12	F	MM	Non-mod	Zhou et al. (2007)
Semnopithecus entellus	6.0	20	M & F	OM	Non-mod	Newton (1992)
Semnopithecus schistaceus	4.4	34	F	MM	Non-mod	Sugiyama (1976)
Rhinopithecus bieti	6.1	11.5	M & F	OM	Mod	Kirkpatrick (1996)
Nasalis larvatus	2.8	20	M & F	OM	Mod	Boonratana (1993)
Colobus polykomos	0.7	9	F	MM	Non-mod	Refer to Dunbar (1991)
Colobus guereza	5.6	11	F	OM	Non-mod	Fashing (2001)
Colobus guereza	6.7	7	F	OM	Non-mod	Fashing (2001)
Colobus satanas	5.5	16	F	MM	Non-mod	McKey and Waterman (1982)
Colobus angolensis	5.0	300	F	MM	Non-mod	Fashing et al. (2007)

Colobus vellerosus	2.3	32	M & F	MM	Non-mod	Teichroeb et al. (2003)
Colobus vellerosus	0.4	7.5	M & F	OM	Non-mod	Teichroeb et al. (2003)
Colobus vellerosus	0.4	15.5	M & F	MM	Non-mod	Teichroeb et al. (2003)
Piliocolobus rufomitratus	2.1	19	M & F	MM	Non-mod	Marsh (1981)
Piliocolobus temminckii	5.4	27	M	MM	Non-mod	Starin (1991)
Piliocolobus kirkii	6.2	23	M & F	MM	Non-mod	Siex (2003)
Piliocolobus kirkii	5.1	36	M & F	MM	Non-mod	Siex (2003)
Piliocolobus kirkii	4.7	34	M & F	MM	Non-mod	Siex (2003)
Piliocolobus kirkii	7.4	20	M & F	MM	Non-mod	Siex (2003)
Piliocolobus kirkii	9.5	65	M & F	MM	Non-mod	Siex (2003)
Piliocolobus kirkii	8.6	38	M & F	MM	Non-mod	Siex (2003)
Piliocolobus kirkii	7.7	26	M & F	MM	Non-mod	Siex (2003)
Piliocolobus tephrosceles	5.8	82	M	MM	Non-mod	Clutton-Brock (1974)
Piliocolobus tephrosceles	4.5	19.9	M	MM	Non-mod	Struhsaker and Leland (1979)

We referred to Grüter (2009) for the definition of modular and non-modular social systems
Dispersal patterns: M, female philopatry/male dispersal; F, male philopatry/female dispersal; M & F, both-sex dispersal
Type of unit (minimum reproductive unit): *OM* one-male–multi-female unit, *MM* multi-male–multi-female unit
Social system: *Mod* modular social system, *Non-mod* non-modular social system

in Asia and Africa, show a wide range of ecological and societal traits (Oates and Davies 1994) but are known to spend less time on a daily basis on interindividual social interactions than other primate taxa in general. In addition, although many studies have described the proportion of time spent grooming as part of their activity budget investigation (Fashing 2011; Kirkpatrick 2011), studies beyond an investigation of the proportion of time spent grooming in colobines are sparse due to the lack of available information on the detailed grooming network within groups. Thus, investigations on the social functions of grooming in colobines on the basis of data on time spent grooming and grooming networks within their basic societal components, i.e. minimum reproductive units such as one-male–multi-female or multi-male–multi-female units, may provide preliminary comparative data useful for further understanding of colobine social systems.

In addition to the primary function of grooming for hygiene (Barton 1985; Furuya 1957; Tanaka and Takefushi 1993; Zamma 2011), grooming functions to increase social cohesion (Dunbar 1991; Lehmann et al. 2007; Sueur et al. 2011a). On the basis of a time-spent-grooming dataset of 44 free-living primates, Dunbar (1991) presented the first comprehensive review on the function of grooming in group cohesion. Dunbar (1991) concluded that grooming plays an essential role in group cohesion, because the proportion of time spent grooming is positively correlated with group size, both across and within species. This so-called Dunbar's group-cohesion hypothesis was further developed by Lehmann et al. (2007) with the consideration of additional factors affecting the proportion of time spent grooming, indicating that time spent grooming is not only determined by group size but also affected by dispersal patterns and sex ratio (number of females/males in a group) and indirectly affected by cognitive constraints and predation pressure. Further considerations of the grooming-need hypothesis that reflects the original hygiene function of grooming and the group-cohesion hypothesis were conducted by Grueter et al. (2013), although their results do not support the main prediction of Dunbar's group-cohesion hypothesis that the most important factor affecting time spent grooming is terrestriality, with group size having a weak or nonsignificant effect.

Although all previous studies have tried to generalise factors affecting time spent grooming in nonhuman primates across almost all taxa, it has not been a focus for colobines except for the Ph.D. dissertation by Grüter (2009), who preliminarily assessed factors influencing time spent grooming by Asian colobines. This author found a significant effect of terrestriality; noted that no other factors had been considered in the study by Lehmann et al. (2007), such as the individual dispersal pattern or the type of reproductive unit (one-male–multi-female or multi-male–multi-female). In addition, recent colobine socioecological studies have provided new findings on their social systems, including individual dispersal patterns and the rather complex spatiotemporal social dynamics, i.e. modular/multilevel society (Grüter 2009; Grueter et al. 2012a; Grueter and van Schaik 2009), which had previously not been included in the factors affecting time spent grooming.

Individual dispersal patterns are considered important factors not only affecting time spent grooming (Lehmann et al. 2007) but also possibly affecting organisation of the modular society, which is prevalent in three primate clades, including papionins, Asian colobines and hominins (Grueter et al. 2012a; Grueter et al. 2012b). For example, the strong interfemale alliances in grooming networks generally found in the female-philopatric/male-dispersed pattern, such as those observed in savanna baboons, may hinder the ability of males to segregate groups into separate smaller social organisation levels such as one-male–multi-female units, whereas male control of females, possibly delivered by the male-philopatric/female-dispersed pattern, such as that observed in hamadryas, limits expression of female bonds (Barton et al. 1996; Grueter et al. 2012a; Swedell 2002). Although colobines were previously thought to be female-philopatric/male-dispersed species (also labelled female-bonded species: Wrangham 1980), some species have been reconsidered as being both-sex-dispersed (e.g. Liu et al. 2007; Matsuda et al. 2012a; Ren et al. 2011). Thus, it is worth reconsidering the effects of newly revised individual dispersal patterns on time spent grooming by colobines together with group modularity.

Here, we examined the effects of social factors, i.e. the group size, dispersal pattern, type of group (minimum reproductive units) and group modularity, on the proportion of time spent grooming in 19 different colobine species. According to Dunbar's group-cohesion hypothesis (Dunbar 1991; Lehmann et al. 2007), we hypothesised that the group size and dispersal pattern are important factors affecting time spent grooming in colobines, as well as whether the species lives in a modular society, because species in modular societies may need to invest more time grooming among individuals within their minimum reproductive units to maintain higher society/band unit cohesion.

Equally important is a comparative study of the social relationships within colobine groups, because intragroup relationships are a cohesive force that binds groups together over space and time and are responsible for maintaining group integrity when smaller social units form larger groups. Thus, we examined the distribution of individual interactions such as grooming within groups to further understand the selective factors underlying colobine group cohesiveness.

Social network analysis (SNA) is a valuable tool that has been used recently to systematically investigate primate grooming networks (Kasper and Voelkl 2009; Sueur et al. 2011b). SNA is also useful to compare the patterning of relationships across different primate species (or groups) by comparing standardised data (Dufour et al. 2011; Matsuda et al. 2012b; Sueur et al. 2011c). Therefore, we examined and compared grooming interactions within minimum reproductive units across six colobine species using SNA. In particular, we focused on the centrality indices of individuals within units to identify the key individual(s) responsible for maintaining cohesion and stability within units. We predicted that males in the unit have the highest eigenvector centrality coefficients (cf. Sueur et al. 2011b) in species in which dispersal is skewed towards females (i.e. with male philopatry/female dispersal), which are generally unrelated to one another within units. In contrast, females in the unit have the highest eigenvector centrality coefficients in species in which dispersal is skewed towards males (i.e. with female philopatry/male dispersal).

As shown in previous studies, the species centrality coefficients characterised by bisexual dispersal were expected to be biased towards females because of the effect of the colobine-specific interfemale relationship, i.e. allomothering behaviour, which might facilitate female–female associations via infant handling (Matsuda et al. 2012b).

We also compared unit stability across species by assessing the clustering coefficient, a measure of the degree of social network cliquishness and the extent to which individuals connected to a focal animal are connected to each other. A higher clustering coefficient value represents a lower level of cliquishness. Specifically, if individuals connected to the focal subject of interest are fully connected to all other individuals, the clustering coefficient will be 1; if individuals connected to the focal subject are not connected to others, the clustering coefficient will be 0. In species with male philopatry/female dispersal, we expected to find a lower clustering coefficient for males than for females. This should not be the case in species with female philopatry/male dispersal because females should all be connected together and males should be connected to fully connected females and have higher clustering coefficients than females. Because adult females/males repeatedly migrate to other units, it may be difficult to establish firm grooming relationships for particular individuals within units in species with both-sex dispersal. Consequently, clustering coefficients in this species should be similar between males and females.

Finally, we used hierarchical cluster analysis to examine the number of subdivisions or cliques among adult females within units in each species. We expected to find more cliques in species with female philopatry/male dispersal than in those with male philopatry/female dispersal or both-sex dispersal because females in female-philopatric species may confine their grooming to kin (Furuichi 1984; Le Roux et al. 2011; Matsuda et al. 2012a). In contrast, in a species in which females are not philopatric, adult females regularly migrate to other groups. Thus, it may be more difficult for females to establish any strong and/or stable affiliative relationships with particular individuals within units (Furuichi 1989; Matsuda et al. 2012a); such a pattern would less likely lead to subdivision within units.

Methods

Proportion of Time Spent Grooming

All data on the (1) proportion of time spent grooming; (2) group size, i.e. size of the minimum reproductive unit; (3) dispersal pattern, i.e. male-philopatric/female-dispersed, female-philopatric/male-dispersed or both-sex-dispersed species; (4) type of minimum reproductive unit, i.e. one-male–multi-female or multi-male–multi-female unit and (5) social system, i.e. modular or non-modular society, related to colobine behaviour were taken from the literature (Table 10.1). We referred to a study by Grüter (2009) to define modular and other primate social systems. In addition, we used the size of the minimum reproductive unit as the size of the group in species in a modular society. This is because affiliative behaviour in modular societies is largely restricted to the nuclear one-male–multi-female unit, and grooming is uncommon in members of different units (Dunbar and Dunbar 1975; Grüter 2009; Grueter et al. 2012a; Kummer 1990; Zhang et al. 2012). Thus, using the band as the level of analysis may not be appropriate, because bands in some multilevel taxa may not constitute actual individualised societies as observed in the limited individual recognition in gelada bands (Bergman 2010). Because most colobine species are primarily arboreal, we did not consider terrestriality in our model, although it is one of the most important factors affecting time spent grooming in nonhuman primates (Grueter et al. 2013, but see Dunbar and Lehmann 2013). We referred to the studies published by Dunbar (1991), Lehmann et al. (2007), Grüter (2009) and Grueter et al. (2013) as a starting point for our literature search and subsequently screened more recent literature.

A study was included in our dataset in case all of the above-mentioned information, i.e. (1–5), was available. The linear mixed model was used to examine whether the proportion of time spent grooming by colobines was affected by several factors (2–5). The proportion of time spent grooming was logit transformed [log $(p/1-p)$] and treated as a normally distributed response variable. The other factors (2–5) were treated as explanatory variables. Group size was log transformed to reduce the influence of the extremely large values produced by several species such as *Colobus angolensis*. The square of the log of group size was also calculated to account for the possible quadratic relationship between the response variable and the log of group size. Other explanatory variables (3–5) were treated as categorical explanatory variables. In addition, a random intercept was determined for each species to account for the dependence of the response variable within a species. Because logit transformation is not applicable to zero values, we excluded two data points in which the proportion of time spent grooming was zero. Consequently, 29 samples were used for analysis. We examined a set of models with all possible combinations of the explanatory variables and ranked them by the corrected version of the Akaike information criterion (AIC) for small sample size, called the AICc (Burnham and Anderson 2002). These analyses were performed on R ver. 3.1.0 (R Development Core Team 2014) using the lmer function in the lme4 package, ver. 1.1-6 (Bates et al. 2014), and the dredge function in the MuMIn package, ver. 1.9.13 (Bartoń 2013).

Social Network Analysis

Data showing the detailed grooming network within units with individual identification were taken from the literature to measure the affiliative relationships in six colobine species: *Piliocolobus tephrosceles* with male philopatry/female dispersal (Struhsaker 1975); *Semnopithecus entellus* (Sugiyama 1965)[1] with female philopatry/male dispersal; and *Trachypithecus pileatus* (Stanford 1991), *Presbytis femoralis* (Megantara 1989),[2] *Nasalis larvatus* (Matsuda et al. 2012a) and *Rhinopithecus roxellana* (Yan 2012)[2] with both-sex dispersal. We unidirectionally rendered the matrices on the basis of the grooming data among individuals within the units to homogenise data across species. We calculated a grooming index (GI) for each species to standardise the dataset for methodological differences across species. Because the *N. larvatus* data were collected using focal animal sampling (see Matsuda et al. 2009 for details), GI from individual A to individual B was defined as follows: $GI_A(B) = [Gm_A(B)]/[F(A) + F(B)]$, where $Gm_A(B)$ was the time A spent grooming B and $F(A)$ and $F(B)$ were the observation times for A and B, respectively (Matsuda et al. 2012a). However, for the remaining datasets, GI was calculated by dividing each value by the total number of scans or observation times, because those data were collected using scan (*T. pileatus*) or ad libitum (*P. tephrosceles*, *S. entellus*, *P. femoralis* and *R. roxellana*) sampling.

We used SOCPROG 2.4 to analyse the social networks on the basis of GI (Sueur et al. 2011b; Whitehead 2009). We used two network variables to detect relevant features of social networks for each species: the eigenvector centrality coefficient and the clustering coefficient. The eigenvector centrality coefficient, which indicates the degree of connectivity of an individual to its group, was calculated using the number and strength of connections of an individual whilst considering the number and strength of connections of each partner (Hanneman and Riddle 2005). The clustering coefficient is a measure of how well the associates of an individual are associated with each other. It describes the cliquishness of the network and measures the extent to which the associates of an individual are clustered in space. The eigenvector centrality and clustering coefficients are values ranging from 0 to 1, regardless of the methods used to collect data and other socio-demographic parameters. This is why we used these coefficients to compare species as well as the effects of sex or dispersal between species. Even if there are small differences between individuals due to methods or social parameters, the manner in which individuals are ranked according to their centralities will not change, allowing us to compare groups and study the effects of socio-demographic factors.

We applied a Markov chain Monte Carlo approach to examine the effects of the dispersal pattern, type of minimum reproductive unit and social system on species eigenvector centrality and clustering coefficients, because we could estimate the posterior density distribution of the parameters if the sum of the contrasts for a factor was zero. The eigenvector centrality and clustering coefficients were treated

---

[1] *S. entellus* was reported as a both-sex-dispersal species (Newton 1992) in Table 10.1, although we did not use the source for social network analysis because the detailed grooming network within units with individual identification was not available. Note that such information is available in Sugiyama (1965) but described as female-philopatric/male-dispersed species.

[2] *P. femoralis* and *R. roxellana* are not in Table 10.1, because several factors were not available for the analysis.

Table 10.2 Unbalanced dataset preventing the use of a frequentist generalised mixed model approach

Dispersal pattern	Type of unit	
	Multi-male–multi-female	One-male–multi-female
Both-sex-dispersed	0	23
Male-philopatric/female-dispersed	7	0
Female-philopatric/male-dispersed	13	0

as response variables in two different univariate mixed-effect models using the species ID as random factor. We evaluated the percentage of variance explained by differences among species in each model (package MCMCglmm, Markov chain Monte Carlo generalised linear mixed models in R; Hadeld 2010). In this context, we applied a Bayesian approach, which allows for the use of nested categorical predictors, with zero output for some cases but not for others, in particular, the species dispersal patterns and their reproductive units (Table 10.2).

We performed the hierarchical cluster analysis using Ward's linkage method to assess the number of subdivisions or cliques among adult females in each species. We used the modularity 1 option [following the definition of Newman (2004); for details see Whitehead (2009)] to automatically detect subgroups of individuals with stronger grooming relationships using a modularity coefficient >0.3 (Newman 2004; Whitehead 2009).

Limitations of the Analysis

We applied data published on the proportion of time spent grooming to analyse factors influencing this proportion, although we realised that applying meta-regression analysis data may be a more reliable approach because differences in the degree of estimation error among studies are considered (Cooper et al. 2009). The reason why we used the proportion without considering the degree of estimation error was because of a limitation in data collection from the published data; such information (the degree of estimation error) was not provided in some journal articles or theses. Similar to other analyses investigating the effects of the proportion of time spent grooming (Grüter 2009; Grueter et al. 2013; Lehmann et al. 2007), we comprehensively analysed the published data for this proportion without considering their precision (but see Majolo et al. 2008). We encourage archiving the standard error of the proportion of time spent grooming as well as its estimate in future studies for more reliable inferences.

In addition to analyses of the proportion of time spent grooming, the results applied to SNA should be interpreted with caution because of differences in the methods used to generate the data. Although comparisons across behavioural categories and differently derived datasets are not ideal, all sampling was a valid representation of the overall patterns of affiliative interaction. The most important aspect is a dataset that is large enough to decrease the expected error of the association index (Whitehead 2008). Despite the disparities in datasets, our results are valuable as preliminary comparative data that may be useful in designing future analyses.

Results

Colobine Grooming and Social System

Time spent grooming by 19 colobine species (Table 10.1) ranged from 0.1 to 11.5 % (mean, 4.5; standard deviation, 3.0). The most prevalent dispersal pattern was both-sex dispersal; of the 19 colobine species, seven had a female-philopatric/male-dispersed pattern (36.8 %), two had a male-philopatric/female-dispersed pattern (10.5 %) and 10 had a both-sex-dispersed pattern (52.6 %). The most common type of minimum reproductive unit was one-male–multi-female unit/group in Asian colobines (80.0 %, 8/10 of the species) and multi-male–multi-female unit/group in African colobines (88.8 %, 8/9 of the species; note that *C. vellerosus* exhibited both unit types). Of the 19 species, only four, i.e. *N. larvatus*, *P. siamensis* (aka *melalophos*), *R. bieti* and *T. pileatus*, had a modular social system (Grüter 2009).

Factors Affecting Time Spent Grooming

A summary of the model selection is shown in Table 10.3. The best-fit model, which was evaluated using the AICc criterion, included only the log of group size, which had a positive effect on the proportion of time spent grooming (Fig. 10.1, $y = -5.48 + 0.576x$). However, the Δ-AICc value of some models was considerably small (e.g. <2.0), suggesting a high uncertainty in the model selection procedure. In such a case, an inference based on the best AIC(c) model may be misleading because the data do not clearly support the best model, and an inference based on all models rather than that based on the best selected model may be a more robust approach (multimodel inference: Burnham and Anderson 2002). The measure of relative variable importance, one of the multimodel inference outcomes (Burnham and Anderson 2002), indicates strong evidence for the importance of the log of group size to explain the variation in the time spent grooming by colobines: 0.81 for the log of group size, 0.56 for square of the log of group size, 0.05 for the dispersal pattern, 0.22 for the type of minimum reproductive unit and 0.28 for the social system (Table 10.3).

Table 10.3 Summary of model selection

Log (group size)	Log (group size)^2	Dispersal	Type of minimum reproductive units	Social system	df	Log-likelihood	AICc	Δ-AICc	AICc weight
+					4	−36.557	82.781	0.000	0.220
+	+				5	−35.099	82.807	0.026	0.217
+				+	5	−35.959	84.527	1.746	0.092
+	+			+	6	−34.428	84.674	1.894	0.085
	+				4	−37.516	84.698	1.917	0.084
+			+		5	−36.343	85.296	2.515	0.062
+	+		+		6	−35.061	85.940	3.160	0.045
	+		+		5	−37.003	86.616	3.835	0.032
	+			+	5	−37.021	86.651	3.870	0.032
+	+		+	+	7	−33.779	86.892	4.111	0.028
+			+	+	6	−35.945	87.707	4.927	0.019
+		+			6	−36.157	88.133	5.352	0.015
			+		4	−39.584	88.834	6.054	0.011
+	+	+			7	−34.765	88.863	6.083	0.010
					3	−40.963	88.886	6.105	0.010
	+		+	+	6	−36.805	89.428	6.647	0.008
	+	+			6	−37.045	89.908	7.127	0.006
+		+		+	7	−35.788	90.908	8.128	0.004
				+	4	−40.868	91.402	8.621	0.003
+		+	+		7	−36.093	91.519	8.738	0.003
			+	+	5	−39.575	91.759	8.979	0.002
+	+	+		+	8	−34.357	91.914	9.134	0.002
+	+	+	+		8	−34.509	92.219	9.438	0.002
	+	+		+	7	−36.760	92.854	10.073	0.001

(continued)

Table 10.3 (continued)

Log (group size)	Log (group size)ˆ2	Dispersal	Type of minimum reproductive units	Social system	df	Log-likelihood	AICc	Δ-AICc	AICc weight
	+	+	+		7	−36.781	92.894	10.114	0.001
		+			5	−40.282	93.173	10.392	0.001
+	+	+	+	+	9	−33.497	94.467	11.687	0.001
		+	+		6	−39.392	94.603	11.822	0.001
+		+	+	+	8	−35.786	94.773	11.992	0.001
		+		+	6	−40.279	96.375	13.595	0.000
	+	+	+	+	8	−36.629	96.458	13.678	0.000
		+	+	+	7	−39.366	98.066	15.285	0.000
Summed AICc weight for predictor variables (the measure of relative variable importance)									
0.806	0.556	0.049	0.216	0.278					

‘+’ indicates inclusion of the variable in the model. The bottom row shows the measure of relative variable importance (Burnham and Anderson 2002), which is calculated as the total sum of the AICc weight of all models in which the given predictor variable occurs

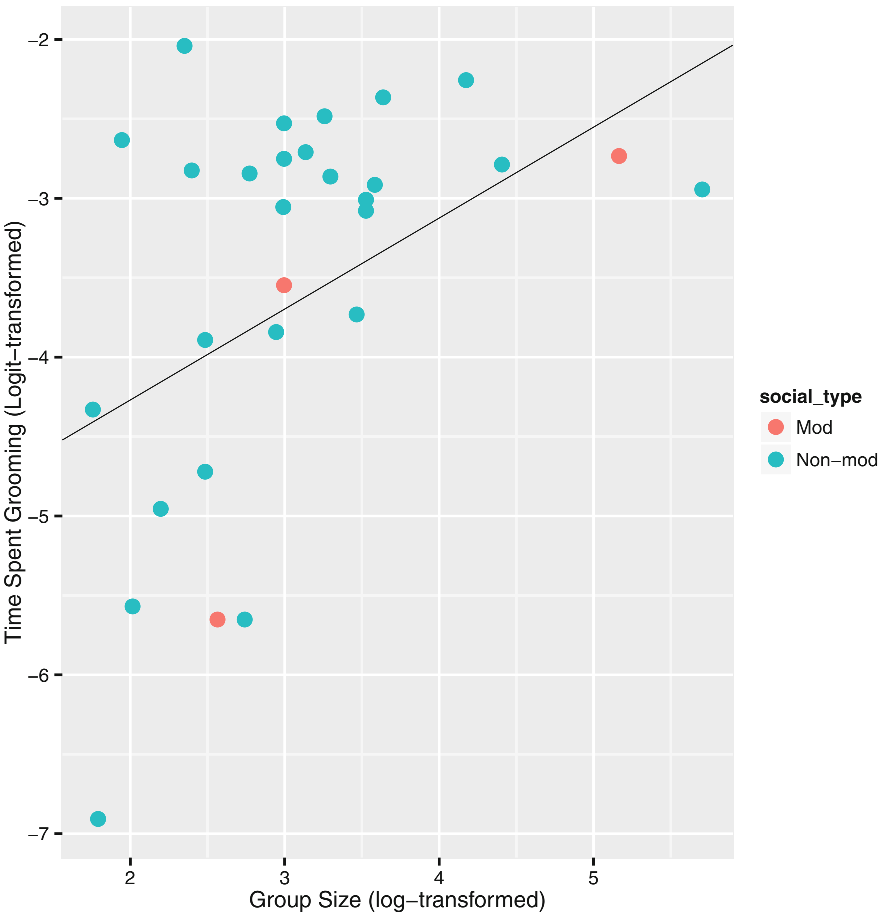


Fig. 10.1 Relationship between group size (log transformed) and the proportion of time spent grooming (logit transformed). The *solid line* represents the regression line for the best model, i.e. the model with the lowest AICc value (Table 10.3)

Grooming Network in Six Colobines

Sex Differences in the Eigenvector Centrality Coefficient

The five colobine species with female philopatry/male dispersal and both-sex dispersal showed higher mean eigenvector centrality coefficients for females within the units than for males; the males were peripheral to the social networks (Fig. 10.2a). However, one species (*P. tephrosceles*) with male philopatry/female dispersal showed the opposite, i.e. males were central to the social network and females were peripheral.

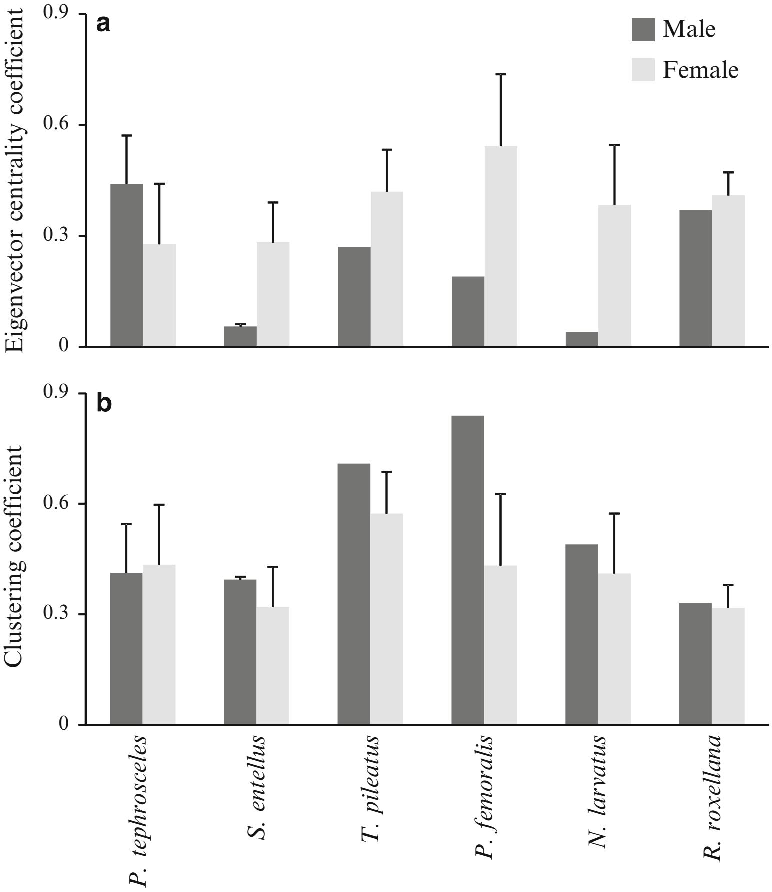


Fig. 10.2 Mean ± standard deviation (**a**) eigenvector centrality coefficients and (**b**) clustering coefficients of adult males and females in six primate species, i.e. *P. tephrosceles* (male philopatry/female dispersal), *S. entellus* (female philopatry/male dispersal), *T. pileatus* (both-sex dispersal), *P. femoralis* (both-sex dispersal), *N. larvatus* (both-sex dispersal) and *R. roxellana* (both-sex dispersal)

The eigenvector centrality model also supported the above-mentioned trends (Table 10.4), i.e. males were generally less central than females. In addition, the significant effect ($p = 0.003$; see Table 10.5) of the interaction between the sex and dispersal of individuals was supported, i.e. males had a higher centrality than females in male-philopatric/female-dispersed species. In contrast, males had a lower centrality than females in female-philopatric/male-dispersed and both-sex-dispersed species (Fig. 10.3). Differences among species explained less than 0.001 % of the variance in the eigenvector centrality measure, indicating that the species presented similar eigenvector centrality values.

Table 10.4 Fixed effects for the eigenvector centrality model

	Post. mean	L – 95 % CI	U – 95 % CI	pMCMC
Intercept	−7.070e + 02	−9.934e + 04	9.346e + 04	0.98844
Sex (male)	−2.161e-01	−3.690e-01	−8.197e-02	**0.00378**
Dispersal pattern (female-philopatric/male-dispersed)	7.072e + 02	−9.346e + 04	9.934e + 04	0.98844
Dispersal pattern (male-philopatric/female-dispersed)	7.072e + 02	−9.346e + 04	9.934e + 04	0.98844
Social system (modular society)	−9.922e-02	−2.514e-01	5.026e-02	0.18111
Unit type (one-male–multi-female unit)	7.075e + 02	−9.346e + 04	9.934e + 04	0.98844
Sex (male): dispersal pattern (female-dispersed)	3.777e-01	1.361e-01	6.253e-01	**0.00311**
Sex (male): dispersal pattern (male-dispersed)	−1.044e-02	−2.578e-01	2.378e-01	0.92844

Posterior mean and their upper [U – 95 % confidence interval (CI)] and lower (L – 95 % CI) CIs are provided. Significant *P*-values (pMCMC) are indicated in *bold*. The factor condition used as contrast for the coefficient estimate is indicated in parentheses. Males generally had a lower estimated eigenvector centrality than females (i.e. the difference in the estimated mean was -2.161×10^{-1}). Moreover, males had a higher eigenvector centrality than females when comparing the two sexes in the female-dispersal pattern (the difference in the estimated slope with the male/female pattern condition was 3.777×10^{-1})

Table 10.5 Fixed effects for the clustering coefficient model

	Post. mean	L – 95 % CI	U – 95 % CI	pMCMC
Intercept	8.706e + 02	−1.008e + 05	9.390e + 04	0.9829
Sex (male)	1.529e-01	1.795e-03	3.051e-01	0.0527
Dispersal pattern (female-philopatric/male-dispersed)	−8.701e + 02	−9.390e + 04	1.008e + 05	0.9829
Dispersal pattern (male-philopatric/female-dispersed)	−8.702e + 02	−9.390e + 04	1.008e + 05	0.9829
Social system (modular society)	−7.186e-02	−5.545e-01	4.404e-01	0.5889
Unit type (one-male–multi-female unit)	−8.701e + 02	−9.390e + 04	1.008e + 05	0.9829
Sex (male): dispersal pattern (female-dispersed)	−1.741e-01	−4.377e-01	8.950e-02	0.1864
Sex (male): dispersal pattern (male-dispersed)	−7.922e-02	−3.375e-01	1.934e-01	0.5436

Posterior mean and their upper [U – 95 % confidence interval (CI)] and lower (L – 95 % CI) CIs are provided

Sex Differences in the Clustering Coefficient

The mean clustering coefficient tended to be higher in males than in females in the five species with female philopatry/male dispersal and both-sex dispersal (Fig. 10.2b), suggesting that males are connected to individuals who are themselves

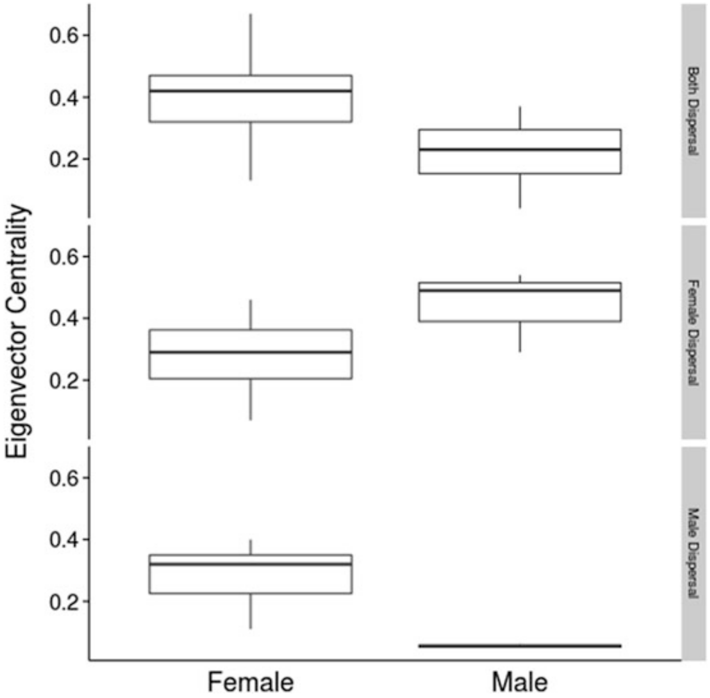


Fig. 10.3 Influence of the interaction between the type of individual dispersal and their sex on individual eigenvector centrality. The graphs describe each of the three possible dispersal types. The box-and-whisker plots represent eigenvector centrality distributions for each dispersal type divided by the sex. The upper and lower limits of the box represent the upper and lower quartiles (0.75 and 0.25, respectively) of the observed distributions. The upper and lower whiskers indicate the maximum and minimum values observed excluding possible outliers of the distributions. The *horizontal solid line* represents the median of the distribution

linked together. However, the mean clustering coefficient of females was slightly higher than that of males in *P. tephrosceles* with male philopatry/female dispersal (Fig. 10.2b) because the males developed stable relationships.

The clustering coefficient was not significantly influenced by any of the variables in the model (Table 10.5). Differences among species explained 49 % of the variance of the clustering coefficient measure. This result may be the reason for not observing any significant effect of the predictors in the model with the clustering coefficient as the response variable.

Female Relationships

The hierarchical cluster analysis revealed various levels of cliquishness among adult females in each species unit. The number of cliques, corrected by the number of adult females within units, was 0.75 in *P. tephrosceles*, 0.55 in *S. entellus*, 0.40 in *R. roxellana*, 0.33 in *N. larvatus*, 0.33 in *P. femoralis* and 0.20 in *T. pileatus.* More clustering (male philopatry/female dispersal > female philopatry/male dispersal > both-sex dispersal) indicates that the relationships among females were more differentiated.

Discussion

This study is the first attempt to investigate in detail the grooming behaviour in colobines exhibiting flexible/complex social organisation compared with that in other primate taxa, i.e. three different types of individual dispersal patterns, two different minimum reproductive units and two different social systems, on the basis of comprehensive analyses. Although colobines showed various types of social organisation, the variation in the proportion of time spent grooming across the 19 species was mostly explained by the classical model (group cohesion) of Dunbar (1991), i.e. group size is the most important factor with a positive effect. This result suggests that colobines must spend a large proportion of their time grooming to maintain cohesion within their social group, i.e. minimal reproductive unit. However, it was impossible to determine the detailed mechanism on the basis of our analysis, i.e. whether they groom a larger number of individuals in larger groups or whether they allocate increased grooming effort to a few key grooming partners. Nonetheless, the latter reason may well explain the mechanism for our further investigations focusing on colobine grooming networks, because they appeared to be influenced by their individual dispersal patterns; they may have some key grooming partners within their minimum reproductive unit depending on their individual dispersal patterns. The result of the present study that grooming played an essential role in group cohesion among colobines agrees with that of comprehensive studies on grooming behaviours in nonhuman primates (Dunbar 1991; Lehmann et al. 2007), although colobines spent less time on a daily basis grooming than other primates.

The specificity of the social system reported for several colobines, i.e. the modular social system, was a surprisingly less important factor affecting their time spent grooming, although it was assumed that colobines with modular societies need to invest more time grooming to maintain unit cohesion at a higher level of society/band. This may be because the sample size for the species in a modular society was small ($n = 3$). In addition to sample size, this result may be explained by the allomothering behaviour in colobines; many female–female interactions in colobines are related to the exchange of infants among adult females, which is not as common in cercopithecines compared to colobines, possibly because it is less permitted by mothers and more risky to infants (Maestripieri 1994). Indeed, allomothering behaviour such as grooming exchanges is important for establishing social relationships among colobine females, including those in a modular society (Matsuda et al. 2012b; Zhang et al. 2012). Colobines in a modular society may more frequently exhibit allomothering behaviour than those in a non-modular society, to maintain unit cohesion in a crowded society. Further research focusing on allomothering behaviour in colobines and comparisons of its frequency between those in modular and non-modular societies is warranted to test this possibility and better understand the factors affecting time spent allogrooming in colobines.

Lehmann et al. (2007) showed that the female-dispersal pattern influences the proportion of time spent grooming in nonhuman primates. The proportion of time spent grooming is generally higher in species with female philopatry Lehmann et al. (2007). However, we could not detect this pattern, because our analysis only focused on colobines. One explanation for more time spent grooming in female-philopatric species is that they generally show a tendency for stronger social bonding with females to maintain group integrity and coherence through time (Lehmann et al. 2007). However, because colobine females with female philopatry/male dispersal and both-sex dispersal typically show less differentiated relationships within units compared to other primate taxa, such as macaques with female philopatry/male dispersal (e.g. Matsuda et al. 2012a; Matsuda et al. 2012b; Takahashi and Furuichi 1998; see also Fig. 10.4), in this study, female-dispersal patterns may not have been detected as a significant factor affecting time spent grooming.

Although individual colobine dispersal patterns were not a significant factor affecting the proportion of time spent grooming, the SNA results indicated that differences in interindividual relationships and mechanisms underlying unit cohesion across species were affected by the dispersal pattern. Our analyses based on the eigenvector centrality coefficient revealed that the key individuals maintaining the social networks differed according to the dispersal pattern. Colobines characterised by female philopatry/male dispersal and both-sex dispersal followed typical patterns reported for colobine species, i.e. patterns of affiliative behaviours primarily being a female affair and of males generally being peripheral to social interactions (Kirkpatrick 2011; Matsuda et al. 2012b). Because females in species with female philopatry/male dispersal (*S. entellus*) are more related to each other within the unit than to males, centrality is biased towards females. Species centrality in the both-sex-dispersal system is also biased towards females, although it was expected that there were no key individual(s) within units. One explanation for the higher centrality of females in these species may be the frequency of exhibiting allomothering behaviour in colobines (Matsuda et al. 2012b). Females within units frequently associate with each other via infant handling; thus, their centrality may be higher than that of males. This allomothering hypothesis also supports the result of centrality that is biased towards males in species with male philopatry/female dispersal, where allomothering is rare, such as in *P. tephrosceles* (Struhsaker 2010). The higher relatedness among philopatric males within the unit compared to females would also be a reasonable explanation for the higher centrality of males in this species.

In this study, males did not show higher clustering coefficients than females in species with different dispersal patterns. The lack of significant sex-related differences in clustering coefficients in colobines compared to other primate taxa indicates that there is a sex-related difference in the manner in which individuals in

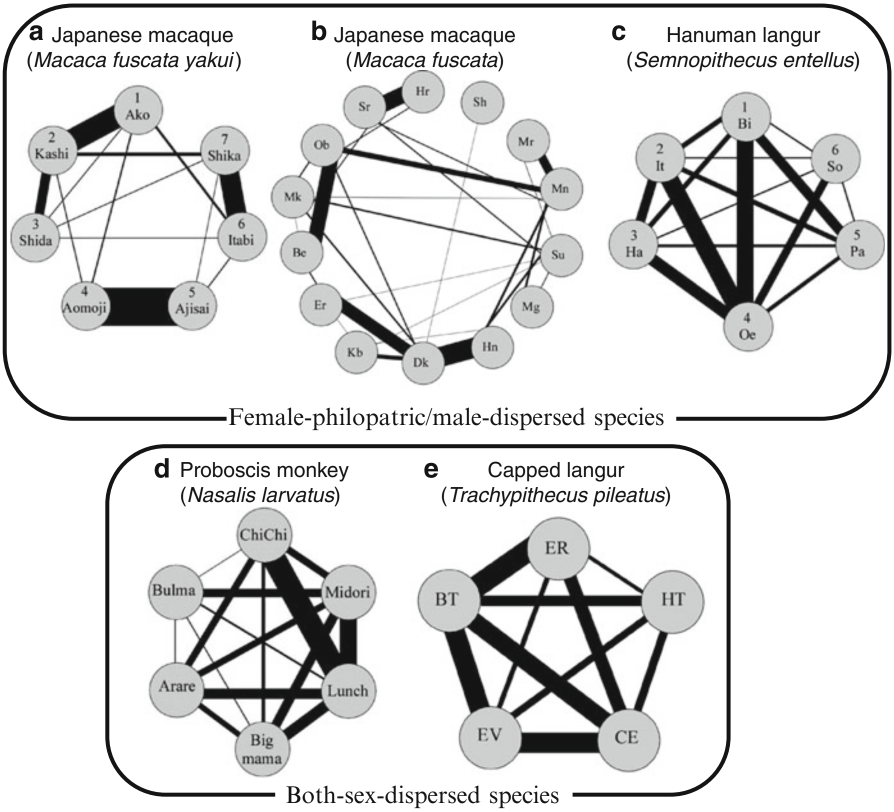


Fig. 10.4 Grooming network among adult females in species with female philopatry/male dispersal (**a**–**c**) and both-sex dispersal (**d**, **e**). Dataset from Matsuda et al. (2012a). Numbers within *circles* indicate the hierarchical order within the groups, and individuals are connected by lines whose width represents values standardised by total grooming index for each species in the grooming matrix (see more detailed methodology in Matsuda et al. 2012a). The grooming network pattern of a colobine species with female philopatry/male dispersal, i.e. the hanuman langur, is clearly different from macaques with the same dispersal pattern; note that the patterns appear to be more similar among colobines even with different dispersal patterns

each species are clustered. This result may also be explained by the finding that colobine species have a less hierarchical and differentiated society compared to that in other primate taxa (Matsuda et al. 2012a). Indeed, a significant difference in clustering coefficients between the sexes has been reported in species with female philopatry/male dispersal, such as gelada and macaques, in which clustering coefficients are characterised by a matrilineal structure; strong female–female bonds; and stable, linear dominance hierarchies with matrilineal rank inheritance (e.g. Matsuda et al. 2012b; Sueur et al. 2011c).

The hierarchical cluster analysis results showed that there may be a certain effect of the dispersal pattern on colobine female–female relationships within units.

We found a higher level of cliquishness in *S. entellus* characterised by female philopatry/male dispersal than in species with both-sex dispersal. This is because female-philopatric colobine species may confine their grooming to female kin with whom they develop stable relationships, although such relationships may be rather lose compared to female–female relationships in other primate taxa with female philopatry, such as Japanese macaques (Fig. 10.4). Because adult females repeatedly migrate to units in species with both-sex dispersal, it may be more difficult to establish a strong and stable grooming relationship. Surprisingly, the highest level of cliquishness was found in *P. tephrosceles*, a species with male philopatry/female dispersal in this study. This may be because females formed rigid relationships with specific cliqued males within the multi-male–multi-female units, i.e. the male–female relationship was strong. In other words, rather differentiated male relationships within the unit of male-philopatric/female-dispersed species produced differentiated female relationships.

In summary, we report the results of the first quantitative comparison of the proportion of time spent grooming by colobines and of the interindividual relationships within units among colobines based on grooming networks. We found that variations in the proportion of time spent grooming across the 19 different colobine species were mostly explained by the classical group-cohesion model originally proposed by Dunbar (1991), i.e. group size is the most important factor with a positive effect. This result indicates that colobines must spend a higher proportion of their time grooming to maintain cohesion of their larger social group, i.e. minimal reproductive unit. Although individual colobine dispersal patterns had no significant effect on the proportion of time spent grooming, the SNA indicated that differences across six species in interindividual relationships and the mechanisms underlying unit cohesion were affected by their dispersal patterns. Our findings provide insights into the colobine society, such as the effect of group size and individual dispersal pattern on grooming, although grooming behaviour was previously not a central subject of colobine studies because they spend less time on a daily basis on interindividual social interactions than other primates. Researchers should continue to examine the social interactions in colobine species in detail.

Acknowledgements Some parts of this paper were originally prepared for the symposium on ‘Flexibility in social relationships in female-dispersal primate species’ which was held in the 24th Congress of International Primatological Society at Cancun, Mexico, 2012. We thank T. Furuichi, J. Yamagiwa and F. Aureli for inviting us to contribute to this book. Our deepest appreciation goes to C. C. Grüter because, without his kind instruction from the time of searching the grooming dataset was started until its bound form, this chapter would not have been possible. CS gratefully acknowledges the support of the University of Strasbourg Institute for Advanced Study (USIAS) and of the Fyssen Foundation. This study was partly financed by HOPE and Human Evolution Project of KUPRI and JSPS Grant-in-Aid for Challenging Exploratory Research (24657170 to IM), for Young Scientist (26711027 to IM), for Scientific Research (20252413 to H. Ihobe; 25291100 to G. Hanya) and for Strategic Young Researcher Overseas Visits Program for Accelerating Brain Circulation, to KUPRI. Lastly, we would like to thank Enago (www.enago.jp) for the English language review.

References

Barton R (1985) Grooming site preferences in primates and their functional implications. Int J Primatol 6:519–532

Bartoń K (2013) MuMIn: multi-model inference, R package version 1.9, 13 edn. http://CRAN.R-project.org/package=lme4

Barton RA, Byrne RW, Whiten A (1996) Ecology, feeding competition and social structure in baboons. Behav Ecol Sociobiol 38:321–329

Bates D, Maechler M, Bolker B (2014) lme4: linear mixed-effects models using Eigen and S4, R package version 1.1-6 edn. http://CRAN.R-project.org/package=lme4

Bennett EL (1983) The banded langur: ecology of a colobine in west Malaysian rain-forest. Sidney Sussex College, Cambridge

Bergman TJ (2010) Experimental evidence for limited vocal recognition in a wild primate: implications for the social complexity hypothesis. Proc R Soc B Biol Sci 277:3045–3053

Boonratana R (1993) The ecology and behaviour of the proboscis monkey (*Nasalis larvatus*) in the lower Kinabatangan. Mahidol University, Bangkok

Burnham KP, Anderson DR (2002) Model selection and multimodel inference: a practical information-theoretic approach, 2nd edn. Springer, New York

Clutton-Brock TH (1974) Activity patterns of red colobus (*Colobus badius tephrosceles*). Folia Primatol 21:161–187

Cooper H, Hedges LV, Valentine JC (2009) Handbook of research synthesis and meta-analysis, 2nd edn. Russel Sage Foundation, New York

Davies AG (1984) An ecological study of the red leaf monkey (*Presbytis rubicunda*) in the Dipterocarp Forest of Northern Borneo. University of Cambridge, Cambridge

Di Fiore A, Link A, Campbell CJ (2011) The atelines: behavioral and socioecological diversity in a New World monkey radiation. In: Campbell CJ, Fuentes A, MacKinnon KC, Bearder SK, Stumpf RM (eds) Primate in perspective, 2nd edn. Oxford University Press, Oxford, pp 155–188

Dufour V, Sueur C, Whiten A, Buchanan-Smith HM (2011) The impact of moving to a novel environment on social networks, activity and wellbeing in two new world primates. Am J Primatol 73:802–811

Dunbar RIM (1991) Functional significance of social grooming in primates. Folia Primatol 57:121–131

Dunbar R, Dunbar E (1975) Social dynamics of gelada baboons. Karger, Basel

Dunbar RIM, Lehmann J (2013) Grooming and social cohesion in primates: a comment on Grueter et al. Evolut Hum Behav 34:453–455

Fashing PJ (2001) Activity and ranging patterns of guerezas in the Kakamega Forest: intergroup variation and implications for intragroup feeding competition. Int J Primatol 22:549–577

Fashing PJ (2011) African colobine monkeys: their behavior, ecology, and conservation. In: Campbell CJ, Fuentes A, MacKinnon KC, Bearder SK, R.M. S (eds) Primates in perspective, 2nd edn. Oxford University Press, Oxford, pp 203–229

Fashing PJ et al (2007) Activity and ranging patterns of *Colobus angolensis ruwenzorii* in Nyungwe Forest, Rwanda: possible costs of large group size. Int J Primatol 28:529–550

Furuichi T (1984) Symmetrical patterns in non-agonistic social interactions found in unprovisioned Japanese macaques. J Ethol 2:109–119

Furuichi T (1989) Social interactions and the life history of female *Pan paniscus* in Wamba, Zaire. Int J Primatol 10:173–197

Furuya Y (1957) Grooming behavior in the wild Japanese monkeys. Primates 1:47–72

Gouzoules S, Gouzoules H (1987) Kinship. In: Smuts BB, Cheney DL, Seyfarth RM, Wrangham RW, Struhsaker TT (eds) Primate societies. University of Chicago Press, Chicago, pp 299–305

Grueter CC, van Schaik CP (2009) Evolutionary determinants of modular societies in colobines. Behav Ecol 21:63–71

Grueter CC, Chapais B, Zinner D (2012a) Evolution of multilevel social systems in nonhuman primates and humans. Int J Primatol 33:1002–1037

Grueter CC, Matsuda I, Zhang P, Zinner D (2012b) Multilevel societies in primates and other mammals: introduction to the special issue. Int J Primatol 33:993–1001

Grueter CC, Bissonnette A, Isler K, van Schaik CP (2013) Grooming and group cohesion in primates: implications for the evolution of language. Evol Hum Behav 34:61–68

Grüter CC (2009) Determinants of modular societies in snub-nosed monkeys (*Rhinopithecus bieti*) and other Asian colobines, vol. Ph.D. Universität Zürich, Zürich

Hadeld JD (2010) MCMC Methods for multi-response generalized linear mixed models: the MCMCglmm R Package. J Stat Softw 33:1–22

Hanneman RA, Riddle M (2005) Introduction to social network methods. University of California, Riverside

Hinde R (1976) Interactions, relationships and social structure. Man 11:1–17

Kasper C, Voelkl B (2009) A social network analysis of primate groups. Primates 50:343–356

Kirkpatrick RC (1996) Ecology and behavior of the Yunnan snub-nosed langur (*Rhinopithecus bieti*, Colobinae). University of California, Davis

Kirkpatrick RCIE (2011) The Asian colobines: diversity among leaf-eating monkeys. In: Campbell CJ, Fuentes A, MacKinnon KC, Bearder SK, Stumpf RM (eds) Primates in perspective, 2nd edn. Oxford University Press, Oxford, pp 189–202

Kummer H (1990) The social system of hamadryas baboons and its presumable evolution. In: de Mello MT, Whiten A, Byrne RW (eds) Baboons: behaviour and ecology, use and care. Selected proceedings of the XIIth congress of the International Primatological Society, Brasilia, Brazil, pp 43–60

Le Roux A, Beehner JC, Bergman TJ (2011) Female philopatry and dominance patterns in wild geladas. Am J Primatol 73:422–430

Lehmann J, Korstjens AH, Dunbar RIM (2007) Group size, grooming and social cohesion in primates. Anim Behav 74:1617–1629

Li Z, Rogers E (2004a) Habitat quality and activity budgets of white-headed langurs in Fusui, China. Int J Primatol 25:41–54

Li Z, Rogers E (2004b) Social organization of white-headed langurs *Trachypithecus leucocephalus* in Fusui, China. Folia Primatol (Basel) 75:97–100

Liu Z, Ding W, Grueter CC (2007) Preliminary date on the social organization of black-and-white snub-nosed monkeys *Rhinopithecus bieti* at Tacheng, China. Acta Theriol Sin 27:120–122

Lott DF (1984) Intraspecific variation in the social-systems of wild vertebrates. Behaviour 88:266–325

Maestripieri D (1994) Social structure, infant handling, and mothering styles in group-living old world monkeys. Int J Primatol 15:531–553

Majolo B, de Bortoli VA, Schino G (2008) Costs and benefits of group living in primates: group size effects on behaviour and demography. Anim Behav 76:1235–1247

Marsh CW (1981) Time budget of Tana river red colobus. Folia Primatol 35:30–50

Matsuda I, Tuuga A, Higashi S (2009) The feeding ecology and activity budget of proboscis monkeys. Am J Primatol 71:478–492

Matsuda I, Tuuga A, Bernard H, Furuichi T (2012a) Inter-individual relationships in proboscis monkeys: a preliminary comparison with other non-human primates. Primates 53:13–23

Matsuda I et al (2012b) Comparisons of intraunit relationships in nonhuman primates living in multilevel social systems. Int J Primatol 33:1038–1053

McKey D, Waterman PG (1982) Ranging behaviour of a group of black colobus (*Colobus satanas*) in the Douala-Edea Reserve, Cameroon. Folia Primatol 39:264–304

Megantara EN (1989) Ecology, behavior and sociality of Presbytis femoralis in Eastcentral Sumatra. In: Ehara A, Kawamura S (eds) Comparative primatology monographs, no. 2, Primate Research Institute, Kyoto University, Inuyama, pp 171–301

Nakagawa N (2013) The function and evolutionary history of primate groups: focusing on sex differences in locational dispersal. In: Kwai Y (ed) Groups: the evolution of human sociality. Kyoto University Press, Kyoto, pp 79–110

Newman ME (2004) Analysis of weighted networks. Phys Rev E 70(5):056131

Newton P (1992) Feeding and ranging patterns of forest hanuman langurs (*Presbytis entellus*). Int J Primatol 13:245–285

Oates JF, Davies AG (1994) What are the colobines? In: Davies AG, Oates JF (eds) Colobine monkeys: their ecology, behaviour and evolution. Cambridge University Press, Cambridge, pp 1–9

R Development Core Team (2014) R: a language and environment for statistical computing. Foundation for Statistical Computing, Vienna

Ren B, Li D, He X, Qiu J, Li M (2011) Female resistance to invading males increases infanticide in langurs. PLoS One 6:e18971

Ruhiyat Y (1983) Socio-ecological study of *Presbytis aygula* in West Java. Primates 24:344–359

Sangchantr S (2004) Social organization and ecology of Mentawai leaf monkeys (*Presbytis potenziani*). Columbia University, New York

Schino G (2001) Grooming, competition and social rank among female primates: a meta-analysis. Anim Behav 62:265–271

Siex KS (2003) Effects of population compression on the demography, ecology, and behavior of the Zanzibar red colobus monkey (*Procolobus kirkii*). Duke University, Durham

Stanford CB (1991) The capped langur in Bangladesh: behavioral ecology and reproductive tactics. S Karger Pub, New York

Starin ED (1991) Socioecology of the red colobus monkey in the Gambia with particular reference to female–male differences and transfer patterns. City University of New York, New York

Struhsaker TT (1975) Red colobus monkey, George B. Schaller edn. University of Chicago Press, Chicago

Struhsaker TT (2010) The red colobus monkeys: variation in demography, behavior, and ecology of endangered species. Oxford University Press, New York

Struhsaker TT, Leland L (1979) Socioecology of five sympatric monkey species in the Kibale Forest, Uganda. Adv Stud Behav 9:159–228

Stumpf RM (2011) Chimpanzees and bonobos. In: Campbell CJ, Fuentes A, MacKinnon KC, Bearder SK, Stumpf RM (eds) Primates in perspective. Oxford University Press, Oxford, pp 340–356

Sueur C, Deneubourg JL, Petit O, Couzin ID (2011a) Group size, grooming and fission in primates: a modeling approach based on group structure. J Theor Biol 273:156–166

Sueur C, Jacobs A, Amblard F, Petit O, King AJ (2011b) How can social network analysis improve the study of primate behavior? Am J Primatol 73:703–719

Sueur C, Petit O, De Marco A, Jacobs AT, Watanabe K, Thierry B (2011c) A comparative network analysis of social style in macaques. Anim Behav 82:845–852

Sugiyama Y (1965) Behavioral development and social structure in two troops of hanuman langurs (*Presbytis entellus*). Primates 6:213–247

Sugiyama Y (1976) Characteristics of the ecology of the Himalayan langurs. J Hum Evol 5:249–277

Swedell L (2002) Affiliation among females in wild hamadryas baboons (*Papio hamadryas hamadryas*). Int J Primatol 23:1205–1226

Takahashi H, Furuichi T (1998) Comparative study of grooming relationships among wild Japanese macaques in Kinkazan A troop and Yakushima M troop. Primates 39:365–374

Tanaka I, Takefushi H (1993) Elimination of external parasites (lice) is the primary function of grooming in free-ranging Japanese macaques. Anthropol Sci 101:187–193

Teichroeb JA, Saj TL, Paterson JD, Sicotte P (2003) Effect of group size on activity budgets of *Colobus vellerosus* in Ghana. Int J Primatol 24:743–758

van Oijen JAMC (1992) Sex differences in feeding behaviour of adult Thomas langurs. Utrecht University, Utrecht

Whitehead H (2008) Precision and power in the analysis of social structure using associations. Anim Behav 75:1093–1099

Whitehead H (2009) SOCPROG programs: analysing animal social structures. Behav Ecol Sociobiol 63:765–778

Wrangham RW (1980) An ecological model of female-bonded primate groups. Behaviour 75:262–300

Yan C (2012) Social interaction and dispersal patterns of golden snub-nosed monkeys (*Rhinopithecus roxellana*) living in multi-level societies, vol. Ph.D. University of Illinois at Urbana-Champaign, Champaign

Zamma K (2011) Frequency of removal movements during social versus self-grooming among wild chimpanzees. Primates 52:323–328

Zhang P, B-g L, X-g Q, MacIntosh AJJ, Watanabe K (2012) A proximity-based social network of a group of Sichuan snub-nosed monkeys (*Rhinopithecus roxellana*). Int J Primatol 33:1081–1095

Zhou Q, Wei F, Huang C, Li M, Ren B, Luo B (2007) Seasonal variation in the activity patterns and time budgets of *Trachypithecus francoisi* in the Nonggang Nature Reserve, China. Int J Primatol 28:657–671

Chapter 11
Evolution of Hominid Life History Strategy and Origin of Human Family

Juichi Yamagiwa

Female Dispersal and Life History Traits in Primates

Group-living primates are classified into female-bonded species and female-dispersal species, based on the patterns of female dispersal after maturity (Wrangham 1980). Most of cercopithecines, including *Macaca*, *Papio*, *Theropithecus*, *Erythrocebus*, and *Cercopithecus*, form a group in which females remain during their entire life (Strier 1994). Kin-related females usually associate and form coalitions with them in agonistic contexts (Watanabe 1979; Silk 1982; Dunbar 1988; Harcourt 1992; Henzi and Barrett 1999). Cooperation and support of kin-related females increase female reproductive success. The linear dominance rank is stable among females and between kin-groups of females. Females of the kin-groups with higher rank have higher reproductive success than females of kin-groups with lower rank (Drickamer 1974; Silk 1987; Itoigawa et al. 1992; Paul and Kuester 1996). On the other hand, females of Hominidae (orangutans, gorillas, chimpanzees, and bonobos) and Atelinae (howler monkeys, wooly monkey, spider monkeys, and muriquis) usually leave their natal groups and spend their reproductive life without related females (Wrangham 1987; Yamagiwa 1999; Strier 1999a). Social relationships with males or unrelated females that they join are important for their reproductive success. The elder females or females joining earlier are dominant to younger females or those joining later (Goodall 1986; Watts 1991a; Idani 1991; Crockett and Pope 1993; Printes and Strier 1999; Nishimura 2003). However, intervention by males in conflicts (Watts 1997), sociosexual behavior among females (Kano 1992), and the fission–fusion dynamics of grouping (Wrangham and Smuts 1980; Goodall 1986; Strier 1992) reduce dominance effects and prevent

---

J. Yamagiwa (✉)
Kyoto University, Sakyo, Kyoto, 606-8502 Japan
e-mail: yamagiwa.juichi.4m@kyoto-u.ac.jp

T. Furuichi et al. (eds.), *Dispersing Primate Females*,
Primatology Monographs, DOI 10.1007/978-4-431-55480-6_11

females from having prolonged antagonistic interactions. Because of the lack of support from kin-related females, male reproductive strategies including infanticide may affect life history parameters in female-dispersal species (Strier 1999a, b; Harcourt and Stewart 2007).

Female-dispersal species tend to have a slower life history (gestation length, weaning age, age at first reproduction, and inter-birth interval) than the female-philopatric species, except for neonatal weight and weaning weight, which may be determined in relationship to female body weight (Strier 1999a; Kappeler et al. 2003; Harcourt and Stewart 2007; Yamagiwa et al. 2014). Adding to ecological factors such as food availability and predation pressure, male reproductive tactics may affect the cost of female transfer and shape the fast–slow continuum (the degree of speed in reproduction and growth) in the life history traits of female-dispersal species. Female-dispersal species form various social structures, such as solitary, monogamous, polygynous, or multi-male/multi-female groups. Among female-dispersal species, Hominidae have the most diverse social structure and large variation in life history features.

Female orangutans, who usually live a solitary life, show the slowest life history in the wild (15.4 years old as the mean age at first reproduction and 9.3 years as the mean inter-birth interval for Sumatran orangutans, Wich et al. 2009). Maturing female orangutans need a longer time to establish their own home range and relationships with reproductive mates than female gorillas, chimpanzees, and bonobos, who transfer into other groups immediately after emigration. Female mountain gorillas show the lowest age (10.1 years old) at first reproduction and the shortest inter-birth interval (3.9 years) (Watts 1991a, b). Intensive caretaking of immature by male gorillas may facilitate early weaning, and infanticide by males may promote a prolonged bonding between a protector male and females to shorten the inter-birth interval (Harcourt and Stewart 2007; Robbins et al. 2009; Yamagiwa et al. 2014).

Recent advances in DNA and isotope analyses have revealed a tendency of female dispersal and male philopatry in Pliocene–Pleistocene hominins, such as *Australopithecus africanus*, *Paranthropus robustus*, and *Homo neanderthalensis* (Copeland et al. 2011; Lalueza-Fox et al. 2011). Modern societies of hunter-gatherers are also characterized by female dispersal, although both sexes tend to disperse in most of them (Marlowe 2004; Alvarez 2004; Hill et al. 2011). However, human social structure has different features (multileveled based on family units, extended kinship, and daily fission–fusion dynamics) from those of great apes (Chapais 2011; Foley and Gamble 2009. Life history traits of modern humans are also different from those of great apes (later age at first reproduction, while shorter inter-birth interval). When and how did these traits emerge in human clade? The relationship between social and life history features unique to humans should be considered by reconstruction of human evolutionary history. In this chapter, I analyze the order of these features' emergence and the factors shaping them by considering those of great apes, fossil evidence, and the subsistence of foragers.

Uniqueness of Human Life History

Among mammals, primates show the slowest life history, such as long gestation, small litter size, long lactation, long juvenile period, long inter-birth interval, and long life span (Harvey et al. 1987; Read and Harvey 1989; Ross 1998). Modern humans have features similar to those of other primates but also have earlier age at weaning, shorter inter-birth interval, later age at sexual maturity, and longer life span compared to the great apes (Kaplan et al. 2000; Robson et al. 2006). Menopause (reproductive senescence) and an extended post-reproductive period are only found in human females (Thompson et al. 2007). These features unique to humans have possibly emerged with human-specific social features, such as communal breeding, strong parental investment, extended kinship, division of labor, and multilevel social structure (Foley and Gamble 2009; Chapais 2011). There have been many arguments over when and how these life history features unique to modern humans emerge in the evolutionary history of hominids.

Fossil evidence shows bipedal locomotion as the first morphological feature in the human clade after differentiation from *Homo–Pan* latest common ancestor (LCA) (Brunet et al. 2002). It may have decreased the energetic costs of terrestrial locomotion to expand daily range (Leonard and Robertson 1997). A dietary shift is expected in this period from vegetative foods to widely dispersed and nutrient-dense resources, such as nuts and underground tubers (Foley and Lee 1989; Laden and Wrangham 2005). Bipedalism also led to low-cost transport and complex tool use in the early stage of human clade (Kaplan et al. 2000). Sequential use of different woody tools by chimpanzees for collecting honey or termites has been observed in the wild (Boesch et al. 2009; Sanz and Morgan 2010; Wilfried and Yamagiwa 2014). Similar or more complex tool use is expected for bipedal hominins in later Miocene. Reduction of canine size in the early stage of human evolution suggests a reduction in aggressive interactions and a preference for cooperative intra- and intersexual relationships (Plavcan and van Schaik 1997; Plavcan 2000; Lovejoy 2009). The first sign of an increase in brain size (*Homo habilis* at 2 Ma) followed the emergence of stone tools for cutting meat from carcass (possible increase in meat consumption) at 2.3–2.6 Ma (Foley and Gamble 2009; Prat et al. 2005). The appearance of delayed maturation, which coincided with the increase in brain size, has been estimated from patterns of dental development (Smith 1994).

Delayed maturation is a common feature of great apes and humans, compared to other primates, but it is also the most conspicuous human feature. As a possible cause, the size of the birth canal may have imposed a constraint on brain growth in the course of human evolution. Bipedalism transformed the human pelvis so that it could support upper body weight with a narrow canal, through which a large brain could not pass (Rosenberg and Trevathan 1995; Lovejoy 2005). A human mother could not have a baby with a large enough brain to develop into adult size at the same speed as the brain of great apes. This obstetrical dilemma was solved by delivery of the fetus at a much earlier stage of development (Rosenberg and Trevathan 1995). The human brain functions at a high energy cost (Aiello and Wheeler 1995). In particular, the brain of a human child in the growing stage imposes the highest costs, and a large volume of fat supports the rapid brain development of a human baby (Cunnane and Crawford 2003). Providing much energy for brain development may have resulted in delayed maturation within human life history.

The earlier age at weaning and the short inter-birth interval may have interacted with each other and evolved in the early stage of human evolution (Lovejoy 1981). In order to increase fecundity, female mammals can adopt two reproductive strategies: (1) giving birth to multiplets and (2) increasing the number of births during the limited reproductive span. Among primates, some prosimians and new world monkeys tend to have twins or triplets. But old-world monkeys and great apes usually have a single baby at birth, and human ancestors may have adopted this second strategy. Early weaning leads to cessation of suckling and to resumption of cycling. Therefore, it may have shortened the inter-birth interval and increased the number of births and offspring.

Why did human ancestors increase fecundity? This is because since the late Miocene they have expanded their habitat into arid areas including fragmented forests, woodlands, and savanna (Reed 1997; Elton 2008), where they faced higher predation pressure than in the forest (Fig. 11.1). Terrestrial predators, such as lions and hyenas (more species with larger body size than the modern species in Africa in the late Miocene; see Hart and Sussman 2005), may have increased mortality of human ancestors, especially the mortality of immatures. They needed to compensate for this high mortality risk by increasing fecundity (Lovejoy 1981). Higher predation pressure leads primates to rapid life history traits (Janson and van Schaik 1993). Primates living in savanna and secondary forests (more unpredictable habitats) have higher birth rates and earlier age at first reproduction than in tropical rain forests (Ross 1988). Macaque species living in a variety of habitats, including open areas, have a shorter inter-birth interval and an earlier age at first reproduction than macaques living in the forest (Ross 1992). As with these nonhuman primates, high predation pressure led to rapid life history of human ancestors in the arid areas.

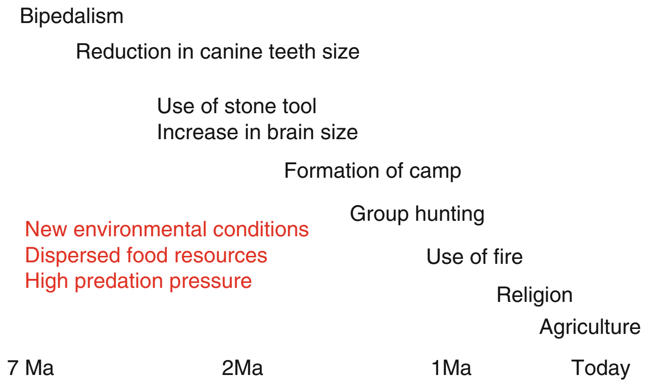


Fig. 11.1 Emergence of human-specific features

The uniqueness of human life history is its mix of slow (delayed maturation, later age at parturition, and long life span) and rapid traits (early age at weaning, short inter-birth interval). Such a complex combination of life history traits coincided with bipedalism and encephalization to solve various socio-ecological problems that human ancestors faced outside of tropical forests. Consequently, they acquired the ability to raise many independent children who grow up slowly. The formation of the human family might have been one of the strategies they took to survive such risky environments. Social features characterizing human family, such as monogamy, multilevel community structure, daily fission–fusion dynamics, exogamy, incest taboo, extended kinship, and division of labor (Imanishi 1961; Murdock 1965; Lovejoy 1981; Furuichi 2006; Aureli et al. 2008; Foley and Gamble 2009; Chapais 2011), might have coevolved with the unique life history traits of humans. However, direct comparisons between humans and great apes have been difficult until recently due to the lack of long-term data on great apes (Nishida et al. 2003; Wich et al. 2009; Yamagiwa et al. 2014). It is still unknown how the human family was created from common social and life history features among humans and great apes, although some authors tried to explain the relationships between life history traits and social features in the evolutionary history of hominids (Foley and Gamble 2009; Hill et al. 2009; Grueter et al. 2012; Chapais 2013).

In this chapter, I attempt to find strong links between particular social features and life history traits of humans as their survival strategies under fluctuating environments through comparisons with social and life history traits of great apes (orangutans, gorillas, chimpanzees, and bonobos). Unlike human ancestors, great apes have evolved within the tropical forests and have never extended their range far into the savanna. They all have relatively slow life history traits and common social and cognitive features, such as female dispersal and self-recognition (Goodall 1986; Kano 1992; Russon et al. 1998; Harcourt and Stewart 2007; Wich et al. 2009). These findings suggest that females reproduce independently from their relatives and that they have ability of intentional decision making. However, they also differ from each other in social features: solitary life of orangutans, polygynous and cohesive group of gorillas, and multi-male and multi-female groups with a high degree of fission–fusion dynamics of *Pan* species. The life history traits of hominids may have evolved with such variable social features of hominoids. Thus, I first compare life history traits among great apes and humans in order to find variability of traits within and between species in their evolution.

Comparison of Life History Traits Among Great Apes

The ancestral type of great apes first appeared in the early Miocene in Africa, differentiated into many species, and dispersed into Asia and Europe (Fleagle 1999). However, during these 20 Ma, the diversity of Cercopithecine monkeys increased, while the diversity of hominoids decreased (Andrews 1981). The reasons for this shift may be attributed to differences in feeding and life history strategies between cercopithecoids and hominoids, under the large climatic changes in the late Miocene and Pleistocene periods. Like modern great apes, fossil hominoids have larger body size than fossil cercopithecoids, possibly due to their weaker digestive abilities.

Great apes are less able to digest unripe fruit and mature leaves than are Cercopithecine monkeys, who have evolved specialized gut systems in which microbial fermentation precedes digestion and absorption (Parra 1978; Chivers and Hladik 1980; Lambert 1998, 2002). These dietary constraints may have forced great apes to broaden their diet and to increase their social flexibility. All great apes have a strong preference for ripe fruit and show various fallback food strategies during periods of fruit scarcity (Yamagiwa 2004). Vegetative foods, such as leaves, bark, and terrestrial herbs, constitute their fallback foods (Galdikas 1988; Knott 1999; Doran et al. 2002; Marshall and Wrangham 2007; Yamagiwa and Basabose 2009). Some fruits with a prolonged availability, such as figs, are used as filler fallback fruits by orangutans and chimpanzees (van Schaik 1999; Wrangham et al. 1993). Animal foods and tool-using behavior may also supplement the scarcity of fruit for chimpanzees (Yamakoshi 1998; Yamagiwa and Basabose 2009). Their grouping patterns basically reflect their tactics to mitigate ecological constraints (food shortage and predation) in the natural habitats. Large annual fluctuation in fruit availability may prevent arboreal and frugivorous orangutans from a prolonged group life (Galdikas 1988; van Schaik 1999). A folivorous and herbivorous diet enables terrestrial gorillas to form a cohesive group without territoriality between neighboring groups (Watts 1996; Yamagiwa et al. 2003; Doran-Sheehy et al. 2004). Fluid grouping of chimpanzees and frequent sexual interactions of bonobos mitigate the social tension caused by feeding competition (Wrangham 1986; Newton-Fisher et al. 2000; Boesch and Boesch-Achermann 2000; Basabose 2004; Kuroda 1984; Furuichi 1987). These differences in their socio-ecological features are linked to life history traits (Fig. 11.2).

As with other mammalian taxa, larger primates tend to show slower life history than smaller primates (Charnov 1991, 1993; Purvis and Harvey 1995). Besides, among primates, female-dispersal species show slower life history traits than female-philopatric species with the same body weight (Yamagiwa et al. 2014). The cost of female transfer may affect the fast–slow continuum in the life history traits of female-dispersal species. All female great apes tend to avoid reproduction in their natal groups. They need to choose a suitable range where they can get enough food and suitable mates for reproduction at their own discretion. Unlike some Cercopithecine monkeys that usually associate and form coalition with kin-related females, female great apes need to reproduce alone or among unrelated conspecifics. Such reproduction independent from their kin may delay the start of reproduction. As with the present great apes, the fossil hominoids may have social features of female dispersal and slow life history. Later age at first reproduction and longer inter-birth interval prevent great apes from having a swift increase in population size and, in particular, a rapid recovery from population crush. These differences in the speed of life history may have caused the shift from domination by hominoids to domination by cercopithecoids during the large climatic changes in the Miocene and Pleistocene.

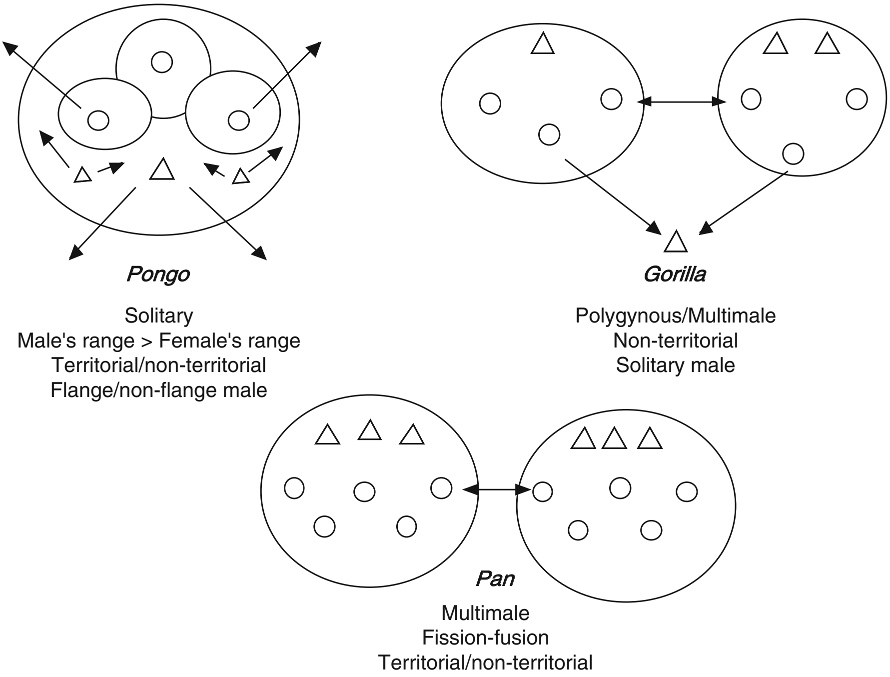


Fig. 11.2 Social structure of great apes

The differences in life history traits among great apes are inconsistent with female body weight (Table 11.1). The largest female gorillas have the lowest age at first reproduction and the shortest inter-birth interval. Although ecological factors, such as frugivorous diet and arboreal lifestyle, may promote a slow life history among extant apes (Doran et al. 2002; van Schaik and Deaner 2002; Wich et al. 2004), social factors may also influence the life history parameters of female apes (Furuichi 1997; Williams et al. 2002; Nishida et al. 2003; Harcourt and Stewart 2007; Wich et al. 2009; Yamagiwa et al. 2014). Female independent travel may have great influences on the fast–slow continuum in the life histories of female apes (Fig. 11.3). Female orangutans usually spend a solitary life and have the slowest life history. Solitary travel for weeks or months has rarely been seen for female chimpanzees, bonobos, or gorillas, who may easily find mates for reproduction in the group they join, and association with males may promote faster reproduction than orangutans (Goodall 1986; Boesch and Boesch-Achermann 2000; Watts 2003; Stokes et al. 2003).

Stable association between males and females and the male's care of infants may promote faster life history. The high dependence of female gorillas on a particular male with high protective abilities may hasten female reproduction, and the male gorilla's intensive care of infants, such as protection against predators or infanticidal males, tolerance for immature to feed close to him, playmate, and

Table 11.1 Life history traits of great apes and modern humans

Species	Adult female body mass	Neonatal mass	Endocranial volume	Gestation length	Age at weaning	Age at menarche	Age at first molar emergence	Age at first reproduction	Inter-birth interval	Maximum life span
	kg	kg	cm^3	Day	Year	Year	Year	Year	Year	Year
Orangutan	37.8	2	346	260	7	12	3.5–4.6	15.6	8.5	58.7
Gorilla	95.2	2.1	433	255	4.1	9	3.2	10	4.4	54
Chimpanzee	35.4	1.8	356	225	4.5	12	3.1–4.1	13.3	5.5	53.4
Bonobo	33.4	1.4	326	240	4.5	8.5		14.2	4.8	50
Modern human	45.5	3.3	1,212	270	2.8	16	4.7–7.1	19.5	3.7	85

Source: Robson and Wood (2008), Humphrey (2010), Marlowe (2012), van Schaik and Isler (2012), and Yamagiwa et al. (2014)

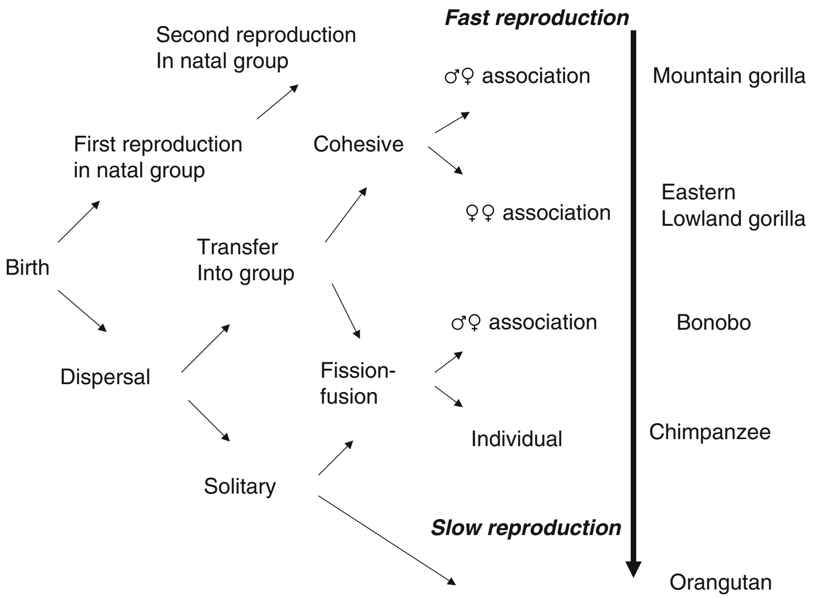


Fig. 11.3 Costs of female transfer and fast–slow continuum of life history

intervention of conflicts between immature, may facilitate weaning at an earlier age (Watts 2000; Harcourt and Stewart 2007). Although *Pan* species usually form a large group including females and males, they have longer life history traits than gorillas, probably due to the lack of the male's care of infants. Bonobos show lower degree of fission–fusion dynamics than chimpanzees (Goodall 1986; Kano 1992). High gregariousness and promiscuous mating in bonobos may facilitate their search for mating partners and lead to a shorter inter-birth interval than chimpanzees (Kano 1992; Furuichi and Hashimoto 2002; Yamagiwa et al. 2014). There are two types of sexually mature male orangutans (Galdikas 1985; Rodman and Mitani 1987; van Schaik and van Hooff 1996). A flanged male, with fully developed secondary sexual features, has his own territorial range and maintains antagonistic relationships with other males. A non-flanged male, mature but without these sexual features, roams between ranges of flanged males and occasionally forces females to mate with him. Female orangutans with dependent infants rarely associate with either type of male. The lack of the male's care of infants and protection may promote the female's solitary travel and preclude early weaning and reproduction (Delgado and van Schaik 2000; Wich et al. 2009).

Sexual coercion of males may have a strong influence on life history traits. Killing of infants by the male is regarded as his reproductive strategy to resume the mother's cycling, to increase mating opportunity, and thus to increase his reproductive success (van Schaik 2000; Kappeler et al. 2003). Infanticide by males has occurred in chimpanzees and gorillas (see below), while it has rarely been reported in gibbons, orangutans, and bonobos (van Schaik 2000). The high probability of paternity with pair bonding (gibbons), lack of estrous sign and less probability of prolonged consort with females in solitary life (orangutans), and confused paternity with highly promiscuous mating (bonobos) may have prevented males from developing infanticide as reproductive tactics. The male's tendency to increase the probability of paternity and the female's choice of multiple mating partners in chimpanzees and gorillas may constitute causal factors of infanticide. This has occurred frequently in mountain gorillas in the Virungas, while it has rarely been reported in other populations (Fossey 1984; Watts 1989; Yamagiwa et al. 2009). Mountain gorillas in the Virunga population are characterized by large group size and multi-male group composition. The risk of infanticide is highest in the absence of a mature male within a group (Watts 1989). In order to avoid infanticide, females tend to join a group with multiple males to seek more reliable protection, and this female choice may enable males to remain in their natal groups after maturity (Watts 1996; Robbins 1999). A comparison between Virunga (infanticide) and Kahuzi (no infanticide) populations shows higher infant mortality (34 % vs. 26 %), shorter interval between consecutive viable births (3.9 vs. 4.6 years), and shorter interval between the death of an infant and the next birth (1.0 vs. 2.2 years) in Virunga than in Kahuzi (Yamagiwa et al. 2003, 2014). Infanticide by males has occurred in eastern chimpanzees but not in western chimpanzees (Takahata 1985; Newton-Fisher 1999; Watts and Mitani 2000; Murray et al. 2007). However, this may not affect the inter-birth interval. A comparison among four long-term study sites (eastern chimpanzees, Gombe and Mahale; western chimpanzees, Taï and Bossou) shows a similarity in inter-birth interval (5.2–5.8 years on average). On the other hand, the age at first reproduction in Bossou (10.9 years on average), where no infanticide has been reported, is earlier than those of other populations (13.2–14.3 years). Highly nutritional foods and isolated conditions may influence the age of first reproduction in Bossou (Sugiyama 1997, 2004). The study group of Bossou has been isolated from neighboring groups for 26 years. Most of the females had first reproduction in their natal group, and a single mature male monopolized copulation with females for more than 10 years (Sugiyama 1999, 2004). These observations suggest that a male's monopolized copulation promote rapid reproduction, while conflicts among males that cause coercive copulation and infanticide may lead to slow reproduction.

Based on comparisons of these variations in social and life history features among great apes, we can imagine possible features for human ancestors, when they started a new life outside tropical forests. First, our human ancestors may have had female-dispersal features, since all female great apes tend to disperse from their mothers. Second, they might have had from the beginning a slow life history (later age at weaning, later age at first reproduction, and longer inter-birth interval) as observed in all great apes. Third, the possible ecological factors promoting rapid life history traits of human ancestors include high predation pressure, which increased infant mortality, and provisioning, which improved the nutritional conditions of females and immatures. Fourth, the possible social factors promoting rapid life history traits of human ancestors include stable associations among females and prolonged associations of females with the particular males that protected them against predation and infanticide. The male's abilities of protection and infant care would have been important for human ancestors to survive in open land with high predation pressure and sparse distribution of high-quality foods.

Suggestions from Fossil Evidences of Human Ancestors

The arguments for the social structure of human ancestors have been based on sexual dimorphism in body weight and canine teeth, due to the high correlation between them (Lovejoy 1981; Plavcan 1993). Among modern primate species, large sexual dimorphism in body weight is linked to a polygynous social structure, and the height of canine teeth indicates the intensity of the male's aggression (Clutton-Brock et al. 1977; Plavcan 1993; Fleagle 1999). However, the relation of the two indexes in human evolutionary history is still unclear; sexual dimorphism in body weight decreased gradually, while the height of canine teeth was already low in the early stage of human evolution such as *Ardipithecus ramidus* (Plavcan and van Schaik 1997; Suwa et al. 2009). The body weight of male *Australopithecus afarensis* (3–3.5 Ma) was estimated to be more than 1.5 times that of the female by comparison, although much smaller dimorphism was estimated (Fleagle 1999); this ratio is 1.1–1.2 for modern humans, 1.2–1.3 for modern chimpanzees, and 1.5–1.7 for modern gorillas (McHenry and Coffing 2000). On the other hand, the height of canine teeth in *A. afarensis* was very small, as also observed in modern humans. Recent findings of *Ardipithecus ramidus* (6 Ma) show low height of canine teeth in both sexes, similar to the canine size of female chimpanzees (Suwa et al. 2009). Plavcan (2000) explained such inconsistencies by citing different selections for body weight and canine teeth: Predation pressure favored large sexual dimorphism in both traits, but frequent use of tools such as weapons for fighting may reduce the function of the male's canine teeth.

Recent studies on *A. afarensis* using random sampling methods show smaller sexual dimorphism in body mass similar to modern humans (Reno et al. 2003, 2010). Moreover, the body mass of *A. ramidus* is considered as nearly monomorphic (Lovejoy et al. 2009; White et al. 2009). These reports support the prediction that human ancestors such as *A. ramidus* in the early stage of evolution had already acquired bipedalism, reduced sexual dimorphism, and monogamous social structure with provisioning by males (Lovejoy 1981). Although there are still many arguments over sexual dimorphism in *A. afarensis*, we can hypothesize that the *Homo–Pan* LCA had a social structure with female dispersal similar to chimpanzees, but with more monomorphic characteristics than chimpanzees. White et al. (2009) predicted that the large canine teeth of male chimpanzees had appeared after differentiation from the human lineage and that terrestrial locomotion and high predation pressure in open land had increased sexual dimorphism in the body mass of *A. afarensis*.

One of the distinct features in the life history of humans is early weaning (Table 11.1). Modern humans living in traditional and natural-fertility societies without birth control wean at 2–3 years, which is younger than great apes based on the estimation from inter-birth intervals (gorillas: 3–4 years, chimpanzees: 5–6 years, orangutans: 7–9 years). Early weaning has the function of stopping the lactational suppression of ovulation and thus reducing inter-birth interval, but it increases risks such as infant mortality and morbidity from infectious and parasitic diseases that potentially restrict growth and development (Taylor et al. 1999; Kennedy 2005). In nonhuman primates, weaning tends to occur when the infant reaches about 33 % of adult body weight (Charnov and Berrigan 1993) or when the first molar (M1) erupts (Smith 1992). Based on these assumptions, the weaning age of modern humans is 5–7 years, far older than the actual weaning age. Apparently our ancestors selected rapid population growth by early weaning, despite its high risks (Martines et al. 1994). This feature has probably evolved in open land with high predation pressure, as observed in nonhuman primates (Ross 1992; Janson and van Schaik 1993). The feature of early weaning had already started in *Homo neanderthalensis*, from analysis of barium distributions in teeth on cessation of breast-feeding at 1.2 years (Austin et al. 2013). It has also coevolved with encephalization. Kennedy (2005) argued that selection in humans had favored not merely the survival but also the intellectual potential of the child and, moreover, suggested that the early shift to adult foods had been necessary at a critical period of neurological development. However, if early weaning was the tactic used to increase fecundity as compensation for increased mortality in open lands, it had possibly started in the early stage of human evolution, when human ancestors extended their range into the savanna (Fig. 11.4). In the savanna environment, population growth

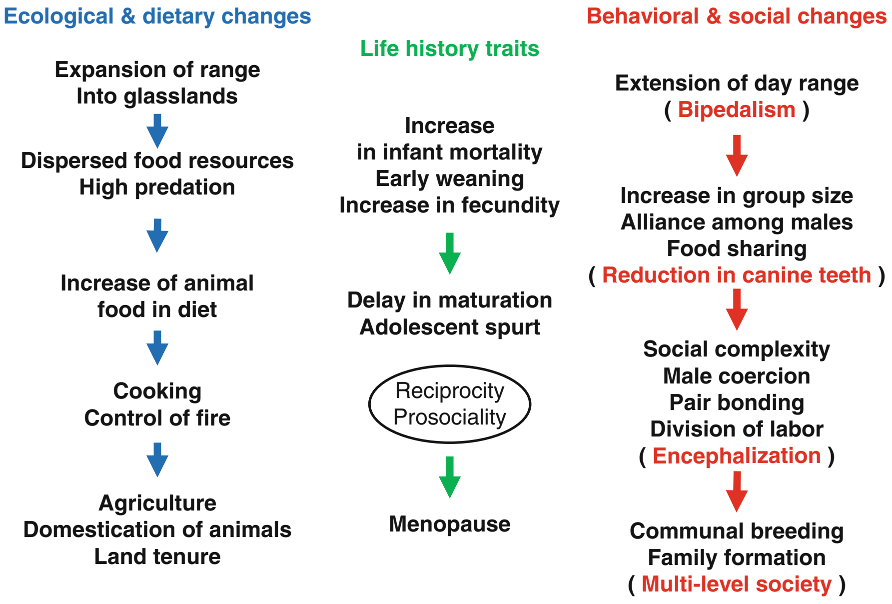


Fig. 11.4 Evolutionary history of hominids

is not expected to have occurred with the late weaning and long inter-birth interval that are characteristics of the modern great apes living in tropical forests with more stable food availability and security (Galdikas and Wood 1990; Nishida 1990; Watts 1991b). Early weaning, therefore, would have been accompanied by innovations in foods and improvement of security in the savanna.

Some important behavioral shifts possibly occurred in the evolutionary history of humans. First, the division of labor for gathering foods appeared as an extension of food sharing before encephalization (Lovejoy 1981). Food sharing or transfer is observed in nonhuman primates, especially in great apes and callitrichids (Feistner and McGrew 1989; Price and Feistner 1993; Huck et al. 2004). In chimpanzees, meat and plant foods are frequently shared among the same community's members, and food transfer has been suggested as a means of trade for social commodities such as grooming, coalition, and sexual access (McGrew 1975; Nishida et al. 1992; Boesch and Boesch-Achermann 2000). The high level of food transfer in callitrichids may be related to their cooperative breeding system. From phylogenetic analyses of food transfer in primates, Jaeggi and van Schaik (2011) predicted that food sharing among adults only evolved in species already sharing with offspring, regardless of diet. However, nonhuman primates rarely transport foods to share with their conspecifics. Great apes and humans have no cheek pouch to temporarily stock foods being processed as do some Cercopithecine monkeys, and their feeding is limited to food patches. In the savanna, where human ancestors extended their range, dispersed foods and high predation pressure may have forced them to select safe feeding places for immatures. Adult individuals changed association patterns with daily fission–fusion dynamics for gathering, transporting, and sharing foods with their offspring and exchanged information in the limited safe site, which led to information center, central place for foraging, and home base (Isaac 1978; Potts 1984; Marlowe 2006; Aureli et al. 2008). Bipedalism may have promoted such tasks as using hands for transporting foods (Lovejoy 1981). Early weaning implies the presence of effective parental provisioning (Galdikas and Wood 1990). Frequent food sharing may have improved nutritional conditions to increase fecundity, which in turn promoted cooperative breeding and food sharing. High-quality foods such as nuts and underground tubers were also exploited using tools for provisioning and sharing (Wrangham and Conklin-Brittain 2003; Wood and Strait 2004).

A second type of behavioral shift probably occurred prior to encephalization. A larger brain needs more energy intake from high-quality foods, and this requirement possibly increased animal foods in the diet of human ancestors (Aiello and Wheeler 1995). The first increase in brain size appeared in *Homo habilis* at approximately 2 Ma. Evidence of the first stone tools was found in Ethiopia and dated at 2.3–2.6 Ma, and these are assumed to have been used as knifelike wedges (Kimbel et al. 1996; Semaw et al. 2003). Bones bearing cut marks found nearby indicate that these stone tools were used for butchery and carcass manipulation. These findings suggest that the shift to tool-assisted butchery and scavenging appeared prior to the distinct increase in brain size (Asfaw et al. 1999; Semaw et al. 2003).

The third behavioral shift may have preceded the final increase in brain size to the level of modern humans at 0.6 Ma. The large brain of modern humans (three times larger than that of gorillas) needs more than 20 % of basal metabolic rate compared to 13 % on average for nonhuman primates, while there is no evidence of an increase in basal metabolism due to an enlarged brain (Aiello and Wheeler 1995). Aiello and Wheeler (1995) compared organ mass and shape of the rib cage among humans, nonhuman primates, and *Australopithecus afarensis*, and they hypothesized that a possible solution to this dilemma was the compensation of energy by a reduction in gut size. Since gut size is associated with diet and digestibility of food (Milton 1986; Martin 1990), the increase in meat consumption and cooking by using fire may have contributed to the supply of more energy to the brain by improving food quality and digestibility (Aiello and Wheeler 1995; Wrangham 2006, 2009). The evidence of fossils and their remains shows the gradual increase in the use of tools and fire for processing animal tissue by *Homo erectus* (Shipman and Walker 1989; Goren-Inbur et al. 2004; Berna et al. 2012).

The last behavioral shift was agriculture and domestication of animals to produce nutritious and digestible foods around the beginning of the Holocene. These remarkable innovations in human-specific foods promoted settlement and formation of communities, which led to systematic activities to improve life history strategies of *Homo sapiens*. However, life history traits unique to humans, such as early weaning, late eruption of molar teeth, delayed somatic development, short interbirth interval, and long post-reproductive period, had already appeared before the emergence of agriculture. The important questions, therefore, are when these traits appeared and which social features were created to support them.

Encephalization undoubtedly led to delayed somatic development, since the rapid growth of the human brain requires allocation of energy to brain growth. Using the volume of the braincase as a proxy for brain size, Zollikofer and Ponce de Léon (2010) concluded that large neonate brains and high sustained growth rates after birth were already present in the LCA of *H. sapiens* and *H. neanderthalensis* at least 0.5 Ma. Recent reports indicate that *H. erectus* had a somatic growth trajectory more similar to chimpanzees than to modern humans, although they attained body sizes in the range of modern humans, as observed in the Nariokotome boy (Anton 2003; Gurven and Walker 2006; Dean 2007). Rapid brain growth and delayed somatic growth brought *H. erectus* and *H. neanderthalensis* immobile infants and an adolescent growth spurt (Leigh and Shea 1996; Leigh 2001; Gurven and Walker 2006).

The adolescent growth spurt also occurs in great apes, but at earlier ages than in modern humans (Leigh and Shea 1996). It occurs in the somatic growth trajectory of both female and male humans, while it is only distinct in male apes (Bogin 1999a, b, 2001; but see Hamada and Udono 2002). Analyses of growth trajectories in skeletons of *H. neanderthalensis* show the presence of an adolescent growth spurt in both sexes (Ruff et al. 1997; Churchill 1998; Zollikofer and Ponce de Léon 2010). Adolescence includes the long period (10–18 years for girls, 12–21 years for boys) of postpubertal growth in modern humans, and teenage girls and boys remain immature in terms of sociocultural knowledge and experience (Schlegel and Barry 1991; Kaplan et al. 2000; Bogin 2009). The adolescent growth spurt may cause many problems for human children, who start to have various social interactions outside their families in complex societies.

The problems after the early weaning and during the adolescent growth spurt required alloparental care and facilitated cooperation within and between groups, which probably led to a new organization of human society. If early weaning evolved to increase the fecundity of hominids, frequent food transfer and communal breeding may have developed to support it, as observed in tamarins and marmosets (Ruiz-Miranda et al. 1999; Huck et al. 2004; Rapaport 2006). Hawkes et al. (1998) hypothesized that selection for lower adult mortality and greater longevity (extension of postmenopausal period) allowed for evolution of prolonged growth in hominids (the "grandmother hypothesis"). However, while data on modern hunter-gatherers indicate the great contributions of post-reproductive women to child care, tool making, and food processing, there is no evidence of reproductive success in post-reproductive women (Kaplan et al. 2000). Fossil and archaeological data suggest no evidence that a sufficient number of older individuals survived to provide significant aid in child care (Kennedy 2003). A comparison of the ratio of older to younger adults in Paleolithic and Neanderthal fossil sites suggests that a distinct survivorship of older individuals appeared in the Upper Paleolithic and that it is not a biological attribute but reflects cultural adaptations (Gaspari and Lee 2006). Bogin (2009) proposed an alternative hypothesis that the development of increased biocultural resilience during the years of human growth and development promotes greater survival to adulthood, adult survival, longevity, and reproductive success (reserve-capacity hypothesis). Based on these arguments, we can conclude that first the early weaning occurred to increase fecundity in the evolutionary history of hominids, then the adolescent growth spurt followed the increase in brain size, and finally the extension of longevity after menopause appeared in recent times.

Social Evolution and Emergence of Human Family

As described previously, common social features among great apes suggest that our *Homo–Pan* LCA may have had a society characterized by female dispersal (Table 11.2). Due to its high costs, female dispersal occurs in primate species living in and around tropical forests, in which high-quality foods such as fruit are available during the whole year and arboreal life protects them against terrestrial predators (Yamagiwa et al. 2014). An exceptional example is *Hamadryas* baboons living in grasslands within a multilevel society, in which small polygynous groups aggregate to form a large band or troop and females transfer within bands (Kummer 1968). The lack of competitive food resources in grasslands may prevent females from forming kin-based coalitions, and the high predation pressure may lead to frequent association and alliance formation among males of different polygynous groups (Barton et al. 1996). Adding to these ecological factors, sexual coercion, including infanticide, may have promoted cooperation among kin-related leader males of different groups and facilitated modular society (Grueter et al. 2012). When early hominids extended their range into open land, they may have faced the same problems as papionins in promoting a multilevel social system.

Table 11.2 Social features and mating strategies of great apes and modern humans

Species	Social structure	Dispersal/philopatry	Sexual dimorphism in body mass	Mating system	Sign of estrus	Paternal care	Infanticide
Orangutan	Solitary	♂ ♀ dispersal	2.2	Temporal consort	None	None	None
Gorilla	Unimale or multi-male polygyny	♀ dispersal, ♂ dispersal/philopatry	1.6	Prolonged consort	Slight swelling	Frequent	Occasional
Modern human	Multileveled with families	♂ ♀ dispersal/philopatry	1.2	Prolonged consort	None	Frequent	Occasional
Chimpanzee	Multi-male and multi-female	♀ dispersal, ♂ philopatry	1.2	Promiscuous	Exaggerated swelling	Rare	Occasional
Bonobo	Multi-male and multi-female	♀ dispersal, ♂ philopatry	1.3	Promiscuous	Exaggerated swelling	Rare	None

Source: Mitani et al. (1996), Furuichi and Hashimoto (2002), Lindenfors (2002), Harcourt and Stewart (2007), Utami et al. (2009), and Marlowe (2012)

The distinct difference in social organization among great apes is male dispersal (orangutans and gorillas) or philopatry (chimpanzees and bonobos), although local variation in the degree of male dispersal is found in gorillas. Male orangutans tend to disperse in a wider range than female orangutans (Singleton and van Schaik 2002; Knott et al. 2008; Morrogh-Bernard et al. 2011), while male gorillas tend to remain near the range of their natal groups or to breed in their natal groups (Robbins et al. 2004; Bradley et al. 2004; Stoinski et al. 2009; but see Inoue et al. 2013). Although the recent isotopic and genetic analyses of fossil hominids predict the tendency of female dispersal and male philopatry (Copeland et al. 2011; Lalueza-Fox et al. 2011; Vigilant and Langergraber 2011), it is not a strong tendency and the dispersal patterns of both sexes is dominant in the present hunter-gatherers (Marlowe 2004; Alvarez 2004; Hill et al. 2011). These may suggest that the strict male philopatry of *Pan* species is derived after the differentiation of the chimpanzee and human clades and that patrilocality in humans became more prevalent with food production by agriculture and livestock raising (Destro-Bisol et al. 2004; Koenig and Borries 2012).

Which factors have promoted multilevel social structure with kin-based male coalition and a particular male–female pair bonding unique to humans? High predation pressure possibly strengthened coalition among males against predators, and increased fecundity led to food sharing and communal breeding in early hominids (Fig. 11.5). Group size along with the number of mates for copulation should have increased. In such a situation, papionins increased sexual dimorphism to reinforce the male's ability of mate guarding (Grueter et al. 2012). Another choice was to increase promiscuity as observed in chimpanzees and bonobos with overt

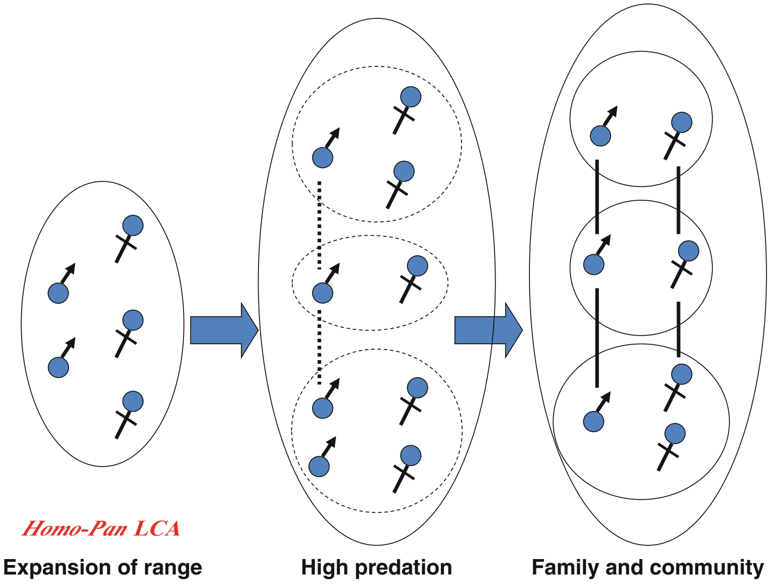


Fig. 11.5 Human ancestral society

sexual swelling (Nishida and Hosaka 1996; Kano 1992). However, human ancestors may not have adopted either option. Fossil evidence indicates that the height of the canine teeth was low in the early stage of human evolution (Plavcan 2000; Suwa et al. 2009), and the social structure of the present hunter-gatherers (Turnbull 1961; Marlowe 2003; Kaplan et al. 2009; Layton et al. 2012) suggests that a monogamous mating system has been common in human societies since before the emergence of agriculture and land tenure. Grueter et al. (2012) hypothesized two steps for emergence of multilevel human society. The first step was from the multi-female and multi-male group with promiscuous mating to the multiharem group with polygyny as observed in all multilevel societies of nonhuman primates, and the second step was from polygyny to monogamy in response to an increase in the dependency of children and in paternal investment. However, promiscuity was not the common feature of great apes and humans, and *Homo–Pan* LCA may not have showed overt sign of estrus. Sillén-Tullberg and Moller (1993) analyzed the relationship between monogamous mating systems and visual signs of ovulation in nonhuman primates phylogenetically, and they concluded that the lack of ovulatory signs is more likely to promote monogamy than vice versa. These findings suggest that large canine teeth and the overt swelling of sexual skins observed in *Pan* species are features derived after differentiation from the human clade. The *Homo–Pan* LCA may have had a society in which sexual dimorphism was low and females did not show visual signs of ovulation.

An increase in brain size and the subsequent delay in somatic growth may have increased parental investment in offspring to a longer period. The brain size (1,400 g) of modern humans is 3.5 times larger than that of chimpanzees. It is approximately 2.3 % of the body weight and uses approximately 23 % of the body's daily energy requirement (Aiello and Wheeler 1995). The brain of a newborn infant needs 74 % of the body energy intake, and juveniles at the age of 10–11 years still need 34 % (Holliday 1971). Human babies are born with large body fat deposits as insurance for the developing brain (Cunnane and Crawford 2003). Just before birth, fat deposition on the human fetus accounts for 90 % of its weight gain (Battaglia and Meschina 1973). Therefore, human brain evolution depended on an abundant, reliable, and nutritious food supply for a long period during pregnancy and after birth. When the brain size of *Homo habilis* increased at 2 Ma, they did not hunt live game but collected high-quality foods such as carrion, marrow, and tubers. Use of fire and cooking may have gradually reduced gut size to provide more energy for brain development (Aiello and Wheeler 1995; Wrangham 2009). Provisioning would have been prevalent among adults, and the division of labor was promoted under the risky environments of large terrestrial predators. The complexities of diet and social life followed the increase in brain size (Jerison 1973; Clutton-Brock and Harvey 1980; Milton 1981; Dunbar 1996). Ripe fruits, extractive foods, tool use, and increasing group size with complex social interactions improved the memories and intellectual behavior of *H. erectus*, *H. neanderthalensis*, and *H. sapiens*. In the forager societies, human juveniles have a long dependency on adults, and men provide most of the energy surplus that is used to subsidize juveniles and reproductive-aged women (Kaplan et al. 2000).

These requirements from life history strategies unique to the *Homo* clade probably promoted the division of labor between sexes and reinforced the formation of family, the basic reproductive unit of humans, which had already been created in the early stage of human evolution. Division of labor in protection, gathering food, cooking, provisioning, and cooperative rearing of infants may have strengthened bonding between monogamous pairs and among related females (Wrangham 2009; Hrdy 2009).

Human sociality is strongly based on the abilities of empathy and other-regarding sentiments (Batson and Powell 1998; Fehr and Fischbacher 2005. Cooperation and reciprocating interactions observed in nonhuman primates imply deep roots of empathy in primate evolution (de Waal 1996; Silk 2007). In particular, chimpanzees show a wide range of cooperation in forming coalitions, hunting, sharing food, and patrolling their range borders (Nishida and Hosaka 1996; Mitani et al. 2000; Boesch and Boesch-Achermann 2000). They also show compassion and empathy for others in distress or injury (Boesch 1992; O'Connell 1995; Flack and de Waal 2000). However, most cooperative activities in nonhuman primates are limited among kin relatives or within a group, and the other-regarding behavior of chimpanzees is mostly based on selfish motivation (Jansen et al. 2006; Vonk et al. 2008; Yamamoto and Tanaka 2010; Silk and House 2011). By contrast, humans participate in a wide range of activities that benefit others including non-kin individuals and non-group members, and they show regard for the welfare of other people who are poor, sick, or aged (Fig. 11.6). The emergence of these prosocial behaviors would have been after the differentiation of the *Pan* and human clades.

Recent studies on callitrichids suggest that other-regarding preferences may have developed in cooperative breeding. Burkart and van Schaik (2011) compared social tolerance and service to other group members among Japanese macaques (independent breeding system), common marmosets (cooperative breeding system),

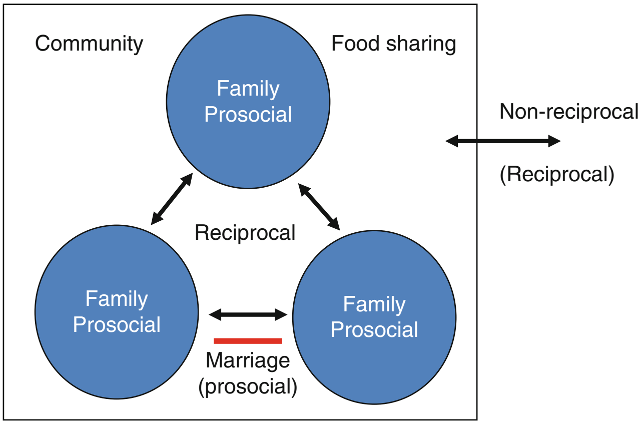


Fig. 11.6 A community structure of modern humans

and capuchin monkeys (an intermediate breeding system), and they concluded that social tolerance was slightly higher in marmosets than in capuchins and much higher in both compared to macaques, but only marmosets provided service to other group members. In common marmosets, the extent of expressed prosociality was positively correlated with the duration of the pair bond as well as with the number of offspring produced together (Burkart et al. 2007). The limited other-regarding behavior in great apes implies that the evolution of prosociality may not require advanced cognitive ability but rather evolved along with cooperative breeding. Early weaning and delayed maturation resulted in similar conditions to those of callitrichids in early hominids, as shown by caring for many independent infants in cooperation with other group members. Provisioning was indispensable for weaned infants with large, rapidly growing brains. The high risk of predation promoted an association of several family groups and division of labor between females and males and probably promoted male's collection and transportation of digestible and high-nutritional foods for females and infants at the safe place. These conditions facilitated the prevalence of food sharing among adults (Jaeggi and van Schaik 2011). Thus empathy, sympathy, and prosociality derived from communal breeding, and provisioning in risky habitats may have led to the formation of large groups including several families in human ancestral societies.

The first possible human family in human clade is assumed to be monogamous and polygynous groups that were associated loosely in a community. Females lacked any sign of estrus and transferred between family groups within or between communities, and males dispersed from their natal family groups to search for mating partners, but remained in a community to cooperate with kin-related males. A community with substructures of various compositions of families had a tendency of fission–fusion dynamics for different daily tasks (Aureli et al. 2008). Increased animal foods in the diet of *Homo* clade facilitated encephalization, and early weaning and subsequent delayed maturation further reinforced cooperative breeding and division of labor for provisioning their offspring, which had been created in the early stage of human evolution. Increased requirements of provisioning also promoted preparation of high-quality foods by using tools and fire in *Homo* clade. These changes in life history and feeding technology led to a multilevel community structure in which several families cooperated with each other in diverse tasks of subsistence. This formation might have been resilient against severe conditions in arid areas and enabled *Homo erectus* to expand their distribution out of Africa. The most important innovation in diet at this stage was cooking and control of fire. Cooking increased the digestibility of plants and meat and conserved energy and time for brain growth and social interactions (Wrangham et al. 1999; Wrangham and Conklin-Brittain 2003; Boback et al. 2007). It also facilitated bonding between individual females and males to facilitate a family formation within the larger community structure (Foley and Gamble 2009). These nested social structures in which family units were embedded within larger kin-based communities characterize human society at present (Chapais 2011). Brain size became equivalent to that of modern humans between 600 and 300 Ka (*Homo heidelbergensis* and *H. neanderthalensis*). Fossil evidence shows that both childhood and adolescent stages (early weaning and delayed maturation with a distinct spurt in somatic growth) emerged by 780 Ka (Thompson et al. 2003). Before reaching the brain size of modern humans, hominids would have established cooperative provisioning and care of offspring during a long dependency. Most of the life history traits unique to humans are found in both *H. neanderthalensis* and *H. sapiens* before the emergence of agriculture and the domestication of animals (Foley and Gamble 2009; Chapais 2013). The cognitive ability of modern humans grows rapidly to a peak of 26 years and then gradually decreases while maintaining a high level until 60–80 years of age (McArdle et al. 2002). This suggests the great contribution of aged individuals to the development of human children (Bogin 2009). However, a prolonged post-reproductive period is found only in the Upper Paleolithic (Gaspari and Lee 2006). Menopause is not found in great apes, and there is little evidence on the survival of aged or handicapped individual until the emergence of modern humans (Thompson et al. 2007; Bogin 2009). This implies that extension of the post-reproductive span necessitated additional social skills, such as language. Communication using language enabled aged people to transmit their past experiences and knowledge to younger generations and facilitated nursing behavior for aged people with strong other-regarding sentiments. Biocultural development would have enabled modern humans to acquire such features.

Conclusions

Modern humans have unique life history traits compared to great apes, such as earlier age at weaning, later age at sexual maturity, shorter inter-birth interval, and longer life span. These features did not emerge together in the evolutionary history of hominids but interacted with each other to promote human adaptive abilities to new environments out of tropical forests and out of Africa. I analyzed the order of these traits' emergence and the factors shaping each trait by considering the life history traits of great apes, fossil evidence, and the subsistence of foragers.

A comparison with great apes predicts that changes in diet and social features may have preceded or coincided with the development of human's life history traits. Based on a comparison of social features among great apes, the *Homo–Pan* LCA may have lived in a medium-sized group with a multi-male and multi-female social structure characterized by a strong tendency of female transfer between groups and a weak tendency of male philopatry. They also had small sexual dimorphism in body mass, with females showing no overt sign of estrus. Large climatic changes in the late Miocene forced the human ancestors to expand their distribution from tropical forests to open lands. The dispersed food resources and high predation pressure they faced in the new environments constituted the driving force behind provisioning and early weaning, which shortened the inter-birth interval and increased the fecundity of early hominids. The dietary innovation of collecting high-quality foods including meat preceded encephalization and promoted a division of labor between sexes in foraging. Increased brain size led to the allocation of energy to rapid brain growth and caused a delay in somatic growth. Such changes in life history traits resulted in the emergence of childhood and adolescence unique to humans. The long dependency inherent to these periods required cooperative breeding and pair bonding, while risky environments strengthened kin-based alliance among males. Cooking and control of fire increased digestive ability and expanded the dietary range of hominids. Reductions in the time energy spent on processing and consuming foods allowed them to expand their social interactions. The prevalence of provisioning and food sharing in adulthood solicited development of reciprocity and prosociality, which possibly led to the creation of a multilevel community structure consisting of families, as observed in modern foragers' societies. This social structure might have increased the resilience of the *Homo* clade to severe conditions in the new environments and led them in their first steps out of Africa. Menopause and extension of the post-reproductive period may have emerged recently, contributing to the increased survival of immatures and overall population growth. The development of speech using language and other cultural innovations played important roles in shaping this remarkable life history trait unique to modern humans.

Acknowledgements This study was financed in part by the Grants-in-Aid for Scientific Research by the Ministry of Education, Culture, Sports, Science and Technology, Japan (No. 162550080, No. 19107007, and No. 24255010 to J. Yamagiwa); the Global Environmental Research Fund of the Japanese Ministry of the Environment (F-061 to T. Nishida, Japan Monkey Centre); the Kyoto University Global COE Program "Formation of a Strategic Base for Biodiversity and Evolutionary research"; and SATREPS of JST/JICA.

References

Aiello LC, Wheeler P (1995) The extensive-tissue hypothesis: the brain and the digestive system in human and primate evolution. Curr Anthropol 36:199–221

Alvarez HP (2004) Residence groups among hunter-gatherers: a view of the claims and evidence for patrilocal bands. In: Chapais B, Berman CM (eds) Kinship and behavior in primates. Oxford University Press, Oxford, pp 420–442

Andrews P (1981) Species diversity and diet in monkeys and apes during the Miocene. In: Stringer CB (ed) Aspects of human evolution. Taylor & Francis Ltd., London, pp 25–61

Anton SC (2003) Natural history of *Homo erectus*. Yearb Phys Anthropol 46:126–169

Asfaw B, White T, Lovejoy O, Latimer B, Simpson S, Suwa G (1999) *Australopithecus garhi*: a new species of early hominid from Ethiopia. Science 284:629–635

Aureli F, Schaffner CM, Boesch C, Bearder SK, Call J, Chapman CA, Connor R, Di Fiore A, Dunbar RIM, Henzi SP, Holekamp K, Korstjens AH, Layton R, Lee P, Lehmann J, Manson JH, Ramos-Fernandez G, Strier KB, van Schaik CP (2008) Fission-fusion dynamics: new research frameworks. Curr Anthropol 49:627–654

Austin C, Smith TM, Bradman A, Hinde K, Joannes-Boyau R, Bishop D, Hare DJ, Foble P, Eskenazi B, Arora M (2013) Barium distributions in teeth reveal early life dietary transitions in primates. Nature 498:12169–12173

Barton RA, Byrne RW, Whiten A (1996) Ecology, feeding competition, and social structure in baboons. Bahav Ecol Sociobiol 38:321–329

Basabose AK (2004) Fruit availability and chimpanzee party size at Kahuzi montane forest, Democratic Republic of Congo. Primates 45:211–219

Batson CD, Powell AA (1998) Altruism and prosocial behavior. In: Milton T, Lerner MJ (eds) Handbook of psychology: personality and social psychology, vol 5. Wiley, Hoboken, pp 463–484

Battaglia FC, Meschina G (1973) Foetal metabolism and substrate utilization. Foetal and neonatal physiology. In: Proceedings of Sir Joseph Barcroft Centenary symposium. Cambridge University Press, Cambridge, pp 382–395

Berma F, Goldberg P, Horwitz LK, Brink J, Holt S, Bamford M, Chazan M (2012) Microstratigraphic evidence of in situ fire in the Acheulean strata of Wonderwerk Cave, Northern Cape province, South Africa. Proc Natl Acad Sci 109:7593–7594

Boback SM, Cox CL, Ott BD, Carmody R, Wrangham RW, Secor SM (2007) Cooking and grin ding reduce the cost of meat digestion. Comp Biochem Physiol A Mol Integr Physiol 148:651–656

Boesch C (1992) New elements of a theory of mind in wild chimpanzees. Behav Brain Sci 15:149–150

Boesch C, Boesch-Achermann H (2000) The Chimpanzees of the Taï Forest: behavioural ecology and evolution. Oxford University Press, Oxford

Boesch C, Head J, Robbins MM (2009) Complex tool sets for honey extraction among chimpanzees in Loango National Park, Gabon. J Hum Evol 56:560–569

Bogin B (1999a) Evolutionary perspective on human growth. Annu Rev Anthropol 28:109–153

Bogin B (1999b) Patterns of human growth, 2nd edn. Cambridge University Press, Cambridge

Bogin B (2001) The growth of humanity. Wiley-Liss, New York

Bogin B (2009) Childhood, adolescence, and longevity: a multilevel model of the evolution of reserve capacity in human life history. Am J Hum Biol 21:567–577

Bradley BJ, Doran-Sheehy DM, Lukas D, Boesch C, Vigilant L (2004) Dispersal male networks in western gorillas. Curr Biol 14:510–513

Brunet M, Guy F, Pilbeam D, Mackaye HT, Likius A, Ahounta D, Beauvilain A, Blondel C, Bocherens H, Boisserie JR, De Bonis L, Coppens Y, Dejax J, Denys C, Duringer P, Eisenmann V, Fanone G, Fronty P, Geraads D (2002) A new hominid from the Upper Miocene of Chad, Central Africa. Nature 418:145–151

Burkart JM, van Schaik CP (2011) Group Service in macaques (*Macaca fuscata*), capuchins (*Cebus apella*) and marmosets (*Callithrix jacchus*): a comparative approach to identifying proactive prosocial motivations. J Comp Psychol 127:212–225

Burkart JM, Fehr E, Efferson C, van Schaik CP (2007) Other regarding preferences in a non-human primate, the common marmoset (*Callithrix jacchus*). Proc Natl Acad Sci U S A 104:19762–19766

Chapais B (2011) The deep social structure of humankind. Science 331:1276–1277

Chapais B (2013) Monogamy, strongly bonded groups, and the evolution of human social structure. Evol Anthropol 22:52–65

Charnov EL (1991) Evolution of life history variation among female mammals. Proc Natl Acad Sci USA 88:1134–1137

Charnov EL (1993) Life history invariants: some explorations of symmetry in evolutionary ecology. Oxford University Press, Oxford

Charnov E, Berrigan D (1993) Why do female primates have such long lifespans and so few babies? Or life in the slow lane. Evol Anthropol 1:191–194

Chivers DJ, Hladik CM (1980) Morphology of the gastrointestinal tract in primates: comparisons with other mammals in relation to diet. J Morphol 116:337–386

Churchill SE (1998) Cold adaptation, heterochrony, and Neanderthals. Evol Anthropol 7:46–61

Clutton-Brock TH, Harvey PH (1980) Primates, brain and ecology. J Zool Lond 109:309–323

Clutton-Brock TH, Harvey PH, Rudder B (1977) Sexual dimorphism, socionomic sex ratio and body weight in primates. Nature 269:797–800

Copeland SR, Sponheimer M, de Ruiter DJ, Lee-Thorp JA, Codron D, le Roux PJ, Grimes V, Richards MP (2011) Strontium isotope evidence for landscape use by early hominins. Nature 474:76–78

Crockett CM, Pope TR (1993) Consequences of sex differences in dispersal for juvenile red howler monkeys. In: Pereira ME, Fairbanks LA (eds) Juvenile primates: life history, development, and behavior. Oxford University Press, Oxford, pp 104–118

Cunnane SC, Crawford MA (2003) Survival of the fattest: fat babies were the key to evolution of the large human brain. Comp Biochem Physiol Part A 136:17–26

De Waal FBM (1996) Good natured: the origin of right and wrong in human and other animals. Harvard University Press, Cambridge

Dean C (2007) Growing up slowly 160,000 years ago. Proc Natl Acad Sci USA 104:6093–6094

Delgado R, van Schaik CP (2000) The behavioral ecology and conservation of the orangutan (*Pongo pygmaeus*): a tale of two islands. Evol Anthropol 9:201–218

Destro-Bisol G, Donati F, Coia V, Boschi I, Verginelli F, Caglià A, Tofanelli S, Spedini G, Capelli C (2004) Variation of female and male lineages in sub-Saharan populations: the importance of socio-cultural factors. Mol Biol Evol 21:1673–1682

Doran DM, McNeilage A, Greer D, Bocian C, Mehlman P, Shah N (2002) Western lowland gorilla diet and resource availability: new evidence, cross-site comparisons, and reflections on indirect sampling methods. Am J Primatol 58:91–116

Doran-Sheehy DM, Greer D, Mongo P, Schwindt D (2004) Impact of ecological and social factors on ranging in western gorillas. Am J Primatol 64:207–222

Drickamer LC (1974) A ten-year summary of reproductive data for free ranging *Macaca mulatta*. Folia Primatol 21:61–80

Dunbar RIM (1988) Primate social system. Helm, London

Dunbar RIM (1996) The social brain hypothesis. Evol Anthropol 6:178–190

Elton S (2008) The environmental context of human evolutionary history in Eurasia and Africa. J Anat 212:377–393

Fehr E, Fischbacher U (2005) The economics of strong reciprocity. In: Gintis H, Bowles S, Boyd R, Fehr E (eds) Moral sentiments and material interests: on the foundations of cooperation in economic life. MIT Press, Cambridge, pp 151–191

Feistner ATC, McGrew WC (1989) Food sharing in primates: a critical review. In: Seth PK, Seth S (eds) Perspectives in primate biology, vol 3. Today and Tomorrow Printers and Publishers, New Delhi, pp 21–36

Flack JC, de Waal FBM (2000) 'Any animal whatever': Darwinian building blocks of morality in monkeys and apes. J Conscious Stud 7:1–29

Fleagle JG (1999) Primate adaptation and evolution. Academic, San Diego

Foley R, Gamble C (2009) The ecology of social transitions in human evolution. Philos Trans R Soc 364:3267–3279

Foley RA, Lee PC (1989) Finite social space, evolutionary pathways, and reconstructing hominid behavior. Science 243:901–906

Fossey D (1984) Infanticide in mountain gorillas (*Gorilla gorilla beringei*) with comparative notes on chimpanzees. In: Hausfater G, Hrdy SB (eds) Infanticide: comparative and evolutionary perspectives. Aldine, Hawthorne, New York, pp 217–236

Furuichi T (1987) Sexual swelling, receptivity and grouping of wild pygmy chimpanzee females at Wamba, Zaire. Primates 28:309–318

Furuichi T (1997) Agonistic interactions and matrifocal dominance rank of wild bonobos (*Pan paniscus*) at Wamba. Int J Primatol 18:855–875

Furuichi T (2006) Evolution of the social structure of hominoids. In: Ishida H, Tuttle R, Pickford M, Nakatsukasa M, Ogihara N (eds) Human origins and environmental backgrounds. Springer, New York, pp 235–248

Furuichi T, Hashimoto C (2002) Why female bonobos have a lower copulation rate during estrus than chimpanzees? In: Boesch C, Hohmann G, Marchant LF (eds) Behavioral diversity in chimpanzees and bonobos. Cambridge University Press, New York, pp 156–167

Galdikas BMF (1985) Orangutan sociality at Tanjung Puting, Central Borneo. Int J Primatol 9:1–35

Galdikas BMF (1988) Orangutan diet, ranging and activity at Tanjung Puting, central Borneo. Int J Primatol 9:1–35

Galdikas B, Wood J (1990) Birth spacing patterns in humans and apes. Am J Phys Anthropol 83:185–191

Gaspari R, Lee S-H (2006) Is human longevity a consequence of cultural change or modern biology? Am J Phys Anthropol 129:512–517

Goodall J (1986) The chimpanzees of Gombe. Belknap, Cambridge

Goren-Inbur N, Alperson N, Kislev M, Simchoni O, Melamed Y, Ben-Nun A, Werker E (2004) Evidence of Hominid Control of fire at Gesher benot Ya'aqov, Israel. Science 304:725–727

Grueter CC, Chapais B, Zinner D (2012) Evolution of multilevel social systems in nonhuman primates and humans. Int J Primatol 33:1002–1037

Gurven M, Walker R (2006) Energetic demand of multiple dependents and the evolution of slow human growth. Proc R Soc B 273:835–841

Hamada Y, Udono T (2002) Longitudinal analysis of length growth in chimpanzee (*Pan troglodytes*). Am J Phys Anthropol 118:268–284

Harcourt AH (1992) Coalitions and alliances: are primates more complex than non-primates? In: Harcourt AH, de Waal FBM (eds) Coalitions and alliances in human and other animals. Oxford University Press, Oxford, pp 445–472

Harcourt AH, Stewart KJ (2007) Gorilla society: conflict, compromise and cooperation between the sexes. The University of Chicago Press, Chicago

Hart D, Sussman RW (2005) Man the hunted: primates, predators, and human evolution. Westview Press, New York

Harvey PH, Martin RD, Clutton-Brock TH (1987) Life histories in comparative perspective. In: Smuts BB, Cheney DL, Seyfarth RM, Wrangham RW, Struhsaker TT (eds) Primate societies. University of Chicago Press, Chicago, pp 181–196

Hawkes K, O'Connell JF, Blurton Jones NG, Alvarez H, Charnov EL (1998) Grandmothering, menopause, and the evolution of human life histories. Proc Natl Acad Sci 95:1336–1339

Henzi P, Barrett L (1999) The value of grooming to female primates. Primates 40:47–59

Hill K, Barton M, Hurtado AM (2009) The emergence of human uniqueness: characters underlying behavioral modernity. Evol Anthropol 18:187–200

Hill KR, Walker RS, Božičević M, Eder J, Headland T, Hewlett B, Hurtado AM, Marlowe F, Wiessner P, Wood B (2011) Co-residence patterns in hunter-gatherer societies show unique human social structure. Science 331:1286–1289

Holliday M (1971) Metabolic rate and organ size during growth from infancy to maturity and during late gestation and early infancy. Pediatrics 47:169–172

Hrdy SB (2009) Mothers and others: the evolutionary origins of mutual understanding. Belknap, Cambridge, MA

Huck M, Löttker P, Heymann EW (2004) The many faces of helping: possible costs and benefits of infant carrying and food transfer in wild moustached tamarins (*Saguinus mystax*). Behaviour 141:915–934

Humphrey LT (2010) Weaning behavior in human evolution. Semin Cell Dev Biol 21:453–461

Idani G (1991) Social relationships between immigrant and resident bonobo (*Pan paniscus*) females at Wamba. Folia Primatol (Basel) 57:83–95

Imanishi K (1961) The origin of the human family: a primatological approach. Jpn J Ethnol 25:119–138

Inoue E, Akomo-Okoue EF, Ando C, Iwata Y, Judai M, Fujita S, Hongo S, Nze-Nkogue C, Inoue-Murayama M, Yamagiwa J (2013) Male genetic structure and paternity in western lowland gorillas (*Gorilla gorilla gorilla*). Am J Phys Anthropol 151:583–588

Isaac G (1978) The food-sharing behavior of protohuman hominids. Sci Am 238:90–108

Itoigawa N, Tanaka T, Ukai N, Fujii H, Kurokawa T, Koyama T, Ando A, Watanabe Y, Imakawa S (1992) Demography and reproductive parameters of a free-ranging group of Japanese macaques (*Macaca fuscata*) in Katsuyama. Primates 33:49–68

Jaeggi AV, van Schaik CP (2011) The evolution of food sharing in primates. Behav Ecol Sociobiol 65:2125–2140

Jansen K, Hare B, Call J, Tomasello M (2006) What's in it for me? Self-regard precludes altruism and spite in chimpanzees. Proc R Soc Lond Ser B 273:1013–1021

Janson CH, van Schaik CP (1993) Ecological risk aversion in juvenile primates: slow and steady wins the race. In: Pereira ME, Fairbanks LA (eds) Juvenile primates, development and behavior. Oxford University Press, Oxford, pp 57–74

Jerison HJ (1973) Evolution of the brain and intelligence. Academic, New York

Kano T (1992) The last ape: pygmy chimpanzee behavior and ecology. Stanford University Press, Stanford

Kaplan H, Hill K, Lancaster J, Hurtado AM (2000) A theory of human life history evolution: diet, intelligence, and longevity. Evol Anthropol 9:156–185

Kaplan HS, Hooper PL, Gurven M (2009) The evolutionary and ecological roots of human social organization. Philos Trans R Soc Lond B Biol Sci 364:3289–3299

Kappeler PM, Pereira ME, van Schaik CP (2003) Primate life histories and socioecology. In: Kappeler PM, Pereira ME (eds) Primate life histories and socioecology. Chicago University Press, Chicago, pp 1–23

Kennedy GE (2003) Paleolithic grandmothers? Life history theory and early homo. J R Anthropol Inst 9:549–572

Kennedy GE (2005) From the ape's dilemma to the weanling's dilemma: early weaning and its evolutionary context. J Hum Evol 48:123–145

Kimbel WH, Walter RC, Johanson DC, Reed KE, Aronson JL, Assefa Z, Marean CW, Eck GG, Bobe R, Hovers E, Rak Y, Vondra C, Yemane T, York D, Chen Y, Evensen NM, Smith PE (1996) Late Pliocene *Homo* and Oldwan tools from the Hadar Formation (Kada Hadar Member), Ethiopia. J Hum Evol 31:549–561

Knott CD (1999) Orangutan behavior and ecology. In: Dolhinow P, Fuentes A (eds) The nonhuman primates. Mayfield Publishing Co., Mountain View, pp 50–57

Knott CD, Beaudrot L, Snaith T, White S, Tschauner H, Planansky G (2008) Female-female competition in Bornean orangutans. Int J Primatol 29:975–997

Koenig A, Borries C (2012) Hominid dispersal and human evolution. Evol Anthropol 21:108–112

Kummer H (1968) Social organization of hamadryas baboons. A field study. University Chicago Press, Chicago

Kuroda S (1984) Interaction over food among pygmy chimpanzees. In: Susman RL (ed) The pygmy chimpanzee: evolutionary biology and behavior. Plenum Press, New York, pp 301–324

Laden G, Wrangham RW (2005) The rise of the hominids as an adaptive shift in fallback foods: plant underground storage organs (USOs) and australopith origins. J Hum Evol 49:482–498

Lalueza-Fox C, Rosas A, Estalrrich A, Giglia E, Camposc PF, García-Tabernerob A, García-Vargasb S, Sánchez-Quintoa F, Ramíreza O, Civitd S, Bastirb M, Huguete R, Santamaríaf D, Gilbertc MTP, Willerslevc E, de la Rasillaf M (2011) Genetic evidence for patrilocal mating behavior among Neandertal groups. Proc Natl Acad Sci USA 108:250–253

Lambert JE (1998) Primate digestion: interactions among anatomy, physiology, and feeding ecology. Evol Anthropol 7:8–20

Lambert JE (2002) Digestive retention times in forest guenons (*Cercopithecus* spp.) with reference to chimpanzees (*Pan troglodytes*). Int J Primatol 23:1169–1185

Layton R, O'Hara S, Bilsborough A (2012) Antiquity and social functions of multilevel social organization among human hunter-gatherers. Int J Primatol 33:1215–1245

Leigh SR (2001) Evolution of human growth. Evol Anthropol 10:223–236

Leigh SR, Shea BT (1996) Ontogeny of body size variation in African apes. Am J Phys Anthropol 99:43–65

Leonard WR, Robertson ML (1997) Comparative primate energetics and hominid evolution. Am J Phys Anthropol 102:265–281

Lindenfors P (2002) Sexually antagonistic selection on primate size. J Evol Biol 15:595–607

Lovejoy CO (1981) The origin of man. Science 211:475–488

Lovejoy CO (2005) The natural history of human gait and posture, Part 1. Spine and pelvis. Gait Posture 21:95–112

Lovejoy CO (2009) Reexamining human origins in light of *Ardipithecus ramidus*. Science 326:74e1–74e8

Lovejoy CO, Simpson SW, White TD, Asfaw B, Suwa G (2009) Careful climbing in the Miocene: the forelimbs of *Ardipithecus ramidus* and humans are primitive. Science 326:70e1–70e8

Marlowe FR (2003) Paternal investment and the human mating system. Behav Process 51:45–61

Marlowe FW (2004) Marital residence among foragers. Curr Anthropol 45:277–284

Marlowe FW (2006) Central place provisioning: the Hadza as an example. In: Hohmann G, Robbins MM, Boesch C (eds) Feeding ecology in apes and other primates. Cambridge University Press, Cambridge, pp 359–377

Marlowe FW (2012) The socioecology of human reproduction. In: Mitani JC, Call J, Kappeler PM, Palombit RA, Silk JB (eds) Evolution of primate society. The University of Chicago Press, Chicago, pp 467–486

Marshall AJ, Wrangham R (2007) Evolutionary consequences of fallback foods. Int J Primatol 28:1219–1235

Martin RD (1990) Primate origins and evolution. Chapman and Hall, London

Martines J, Habicht J, Ashworth A, Kirkwood B (1994) Weaning in southern Brazil: is there a "weaning's dilemma"? J Nutr 124:1189–1198

McArdle JJ, Ferrer-Caja E, Hamagami F, Woodcock KW (2002) Comparative longitudinal structural analysis of the growth and decline of multiple intellectual abilities over the life span. Dev Psychol 38:115–142

McGrew WC (1975) Patterns of plant food sharing by wild chimpanzees. In: Kondo S, Kawai M, Ehara A (eds) Contemporary primatology: proceedings of the 5th international congress of primatology, Nagoya. Karger, Basel, pp 304–309

McHenry HM, Coffing H (2000) *Australopithecus* to *Homo*: transformations in body and mind. Annu Rev Anthropol 29:125–146

Milton K (1981) Distribution patterns of tropical plant foods as an evolutionary stimulus to primate mental development. Am Anthropol 83:534–548

Milton K (1986) Features of digestive physiology in primates. News Physiol Sci 1:76–79

Mitani JC, Gros-Louis J, Richard AF (1996) Sexual dimorphism, the operational sex-ratio, and the intensity of male competition in polygynous primates. Am Nat 147:966–980

Mitani JC, Merriwether DA, Zhang C (2000) Male affiliation, cooperation, and kinship in wild chimpanzees. Anim Behav 54:885–893

Morrogh-Bernard H, Morf N, Chivers D, Krützen M (2011) Dispersal patterns of orangutans (*Pongo* spp.) in a Bornean peat-swamp forest. Int J Primatol 32:362–376

Murdock GP (1965) Social structure. Free Press, New York

Murray CM, Wrobleski E, Pusey AE (2007) New case of intragroup infanticide in the chimpanzees of Gombe National Park. Int J Primatol 28:23–37

Newton-Fisher NE (1999) Infant killers of Budongo. Folia Primatol 70:167–169

Newton-Fisher NE, Reynolds V, Plumptre AJ (2000) Food supply and chimpanzee (*Pan troglodytes schweinfurthii*) party size in the Budongo forest reserve, Uganda. Int J Primatol 21:613–628

Nishida T (1990) The chimpanzees of the Mahale Mountains: sexual and life history strategies. Tokyo University Press, Tokyo

Nishida T, Hosaka K (1996) Coalition strategies among adult male chimpanzees of the Mahale Mountains. In: McGrew WC, Marchant LF, Nishida T (eds) Great ape societies. Cambridge University Press, Cambridge, pp 114–134

Nishida T, Hasegawa T, Hayaki H, Takahata Y, Uehara S (1992) Meat-sharing as a coalition strategy by an alpha male chimpanzee? In: Nishida T, McGrew WC, Marler P, Pickford M, de Waal FBM (eds) Topics in primatology, vol 1, Human origins. University of Tokyo Press, Tokyo, pp 159–174

Nishida T, Corp N, Hamai M, Hasegawa T, Hiraiwa-Hasegawa M, Hosaka K, Hunt KD, Itoh N, Kawanaka K, Matsumoto-Oda A, Mitani JC, Nakamura M, Norikoshi K, Sakamaki T, Turner L, Uehara S, Zamma K (2003) Demography, female life history, and reproductive profiles among the chimpanzees of Mahale. Am J Primatol 59:99–121

Nishimura A (2003) Reproductive parameters of wild female *Lagothrix lagotricha*. Int J Primatol 24:707–722

O'Connell SM (1995) Empathy in chimpanzees: evidence for theory of mind? Primates 36:397–410

Parra R (1978) Comparison of foregut and hindgut fermentation in herbivores. In: Montgomery GG (ed) The ecology of arboreal folivores. Smithsonian Institution Press, Washington, DC, pp 205–230

Paul A, Kuester J (1996) Differential reproduction in male and female Barbary macaques. In: Fa JE, Lindburg DG (eds) Evolution and ecology of macaque societies. Cambridge University Press, Cambridge, pp 293–317

Plavcan JM (1993) Canine size and shape in male anthropoid primates. Am J Phys Anthropol 92:201–216

Plavcan JM (2000) Inferring social behavior from sexual dimorphism in the fossil record. J Hum Evol 39:327–344

Plavcan JM, van Schaik CP (1997) Interpreting hominid behavior on the basis of sexual dimorphism. J Hum Evol 32:345–374

Potts R (1984) Home bases and early hominids. Am Sci 72:338–347

Prat S, Brugal JP, Tiercelin JJ, Barrat JA, Bohn M, Delagnes A, Harmande S, Kimeuf K, Kibunjiaf M, Texierg P-J, Roche H (2005) First occurrence of early *Homo* in the Nachukui formation (West Turkana, Kenya) at 2.3–2.4 Myr. J Hum Evol 49:1008–1012

Price EC, Feistner ATC (1993) Food sharing in Lion Tamarins: tests of three hypotheses. Am J Primatol 31:211–221

Printes RC, Strier KB (1999) Behavioral correlates of dispersal in female muriquis (*Brachyteles arachnoides*). Int J Primatol 20:941–960

Purvis A, Harvey PH (1995) Mammalian life history evolution: a comparative test for Charnov's model. J Zool 237:259–283

Rapaport LG (2006) Provisioning in wild golden lion tamarins (*Leontopithecus rosalia*): benefits to omnivorous young. Behav Ecol 17:212–221

Read AF, Harvey PH (1989) Life history differences among the eutherian radiations. J Zool 219:329–353

Reed K (1997) Early hominid evolution and ecological change through the African Plio-Pleistocene. J Hum Evol 32:289–322

Reno PL, Meindl RS, McCollum MA, Lovejoy CO (2003) Sexual dimorphism in *Australopithecus afarensis* was similar to that of modern humans. Proc Natl Acad Sci 100:9404–9409

Reno PL, McCollum MA, Meindl RS, Lovejoy CO (2010) An enlarged postcranial sample confirms *Australopithecus afarensis* dimorphism was similar to modern humans. Philos Trans R Soc Lond B365:3355–3363

Robbins MM (1999) Male mating patterns in wild multimale mountain gorilla groups. Anim Behav 57:1013–1020

Robbins MM, Bermejo M, Cipolletta C, Magliocca F, Parnell RJ, Stokes E (2004) Social structure and life history patterns in western gorillas (*Gorilla gorilla gorilla*). Am J Primatol 64:145–159

Robbins AM, Stoinski TS, Fawsett KA, Robbins MM (2009) Socioecological influences on the dispersal of female mountain gorillas: evidence of a second folivore paradox. Behav Ecol Sociobiol 63:477–489

Robson SL, Wood B (2008) Hominin life history: reconstruction and evolution. J Anat 212:394–425

Robson SL, van Schaik C, Hawkes K (2006) The derived features of human life history. In: Paine RL, Hawkes K (eds) The evolution of human life history. School of American Research Press, Santa Fe, pp 17–44

Rodman PS, Mitani JC (1987) Orangutans: sexual dimorphism in a solitary species. In: Smuts BB, Cheney DL, Seyfarth RM, Wrangham RW, Struhsaker TT (eds) Primate societies. University of Chicago Press, Chicago, pp 146–154

Rosenberg K, Trevathan W (1995) Bipedalism and human birth: the obstetrical dilemma revisited. Evol Anthropol 4:161–168

Ross C (1988) The intrinsic rate of natural increase and reproductive effort in primates. J Zool (Lond) 214:199–219

Ross C (1992) Life history patterns and ecology of macaque species. Primates 33:207–215

Ross C (1998) Primate life histories. Evol Anthropol 6:54–63

Ruff CB, Trinkaus E, Holliday TW (1997) Body mass and encephalization in Pleistocene *Homo*. Nature 387:173–176

Ruiz-Miranda CR, Kleiman DG, Dietz JM, Moraes E, Grativol AD, Baker AJ, Beck BB (1999) Food transfers in wild and reintroduced golden lion tamarins, *Leontopithecus rosalia*. Am J Primatol 48:305–320

Russon AE, Bard KA, Parker ST (1998) Reaching into thought: the mind of the great apes. Cambridge University Press, Cambridge

Sanz C, Morgan D (2010) Complexity of chimpanzee tool using behaviors. In: Lonsdorf EV, Ross SR, Matsuzawa T (eds) The mind of the chimpanzee: ecological and experimental perspectives. University of Chicago Press, Chicago, pp 127–140

Schlegel A, Barry H III (1991) Adolescence: an anthropological inquiry. Free Press, New York

Semaw S, Rogers M, Quade J, Renne P, Bulter R, Dominguez-Rodrigo M, Stout D, Hart W, Pickering T, Simpson S (2003) 2.6-million-year-old stone tools and associated bones from OGS-6 and OGS-7, Gona, Afar, Ethiopia. J Hum Evol 45:169–177

Shipman P, Walker A (1989) The costs of becoming a predator. J Hum Evol 18:373–392

Silk J (1982) Altruism among female *Macaca radiata*: explanations and analysis of patterns of grooming and coalition formation. Behaviour 79:162–168

Silk J (1987) Social behavior in evolutionary perspective. In: Smuts BB, Cheney DL, Seyfarth RM, Wrangham RW, Struhsaker TT (eds) Primate societies. University of Chicago Press, Chicago, pp 318–329

Silk JB (2007) Empathy, sympathy, and prosocial preferences in primates. In: Dunbar RIM, Barrett L (eds) Oxford handbook of evolutionary psychology. Oxford University Press, New York, pp 115–126

Silk JB, House JB (2011) Evolutionary foundations of human prosocial sentiments. Proc Natl Acad Sci 108:10910–10917

Sillén-Tullberg B, Moller AP (1993) The relationship between concealed ovulation and mating systems in anthropoid primates: a phylogenetic analysis. Am Nat 141:1–25

Singleton I, van Schaik CP (2002) The social organization of a population of Sumatran orangutans. Folia Primatol 73:1–20

Smith BH (1992) Life history and the evolution of human maturation. Evol Anthropol 1:134–142

Smith BH (1994) Patterns of dental development in *Homo*, *Australopithecus*, *Pan*, and *Gorilla*. Am J Phys Anthropol 94:307–325

Stoinski TS, Vecellio V, Nagaboyamahina T, Ndagijimana F, Rosenbaum S, Fawcett KA (2009) Proximate factors influencing dispersal decisions in male mountain gorillas, *Gorilla beringei beringei*. Anim Behav 77:1155–1164

Stokes EJ, Parnell RJ, Olejniczak C (2003) Female dispersal and reproductive success in wild western lowland gorillas (*Gorilla gorilla gorilla*). Behav Ecol Sociobiol 54:329–339

Strier KB (1992) Atelinae adaptations: behavioral strategies and ecological constraints. Am J Phys Anthropol 88:515–524

Strier KB (1994) Myth of the typical primate. Yearb Phys Anthropol 37:233–271

Strier KB (1999a) The atelines. In: Dolhinow P, Fuentes A (eds) The nonhuman primates. Mayfield, Mountain View, pp 109–122

Strier KB (1999b) Why is female kin bonding so rare? Comparative sociality of neotropical primates. In: Lee PC (ed) Comparative primate socioecology. Cambridge University Press, Cambridge, pp 300–319

Sugiyama Y (1997) Social tradition and the use of tool-composites by wild chimpanzees. Evol Anthropol 6:23–27

Sugiyama Y (1999) Socioecological factors of male chimpanzee migration at Bossou, Guinea. Primates 40:61–68

Sugiyama Y (2004) Demographic parameters and life history of chimpanzees at Bossou, Guinea. Am J Primatol 124:154–165

Suwa G, Kono RT, Simpson SW, Asfaw B, Lovejoy CO, White TD (2009) Paleobiological implications of the Ardipithecus ramidus dentition. Science 326:94–99

Takahata Y (1985) Adult male chimpanzees kill and eat newborn infant: newly observed intragroup infanticide and cannibalism in Mahale National Park, Tanzania. Folia Primatol 44:161–170

Taylor H, Vazquez-Geffroy M, Samuels S, Taylor D (1999) Continuously recorded suckling behavior and its effect on lactational amenorrhoea. J Biosoc Sci 31:289–310

Thompson JL, Nelson AJ, Krovitz GE (2003) Hominid growth and development: the modern context. In: Thompson JL, Krovitz GE, Nelson AJ (eds) Patterns of growth and development in the genus Homo. Cambridge University Press, New York, pp 170–187

Thompson ME, Jones JH, Pusey AE, Brewer-Marsden S, Goodall J, Marsden D, Matsuzawa T, Nishida T, Reynolds V, Sugiyama Y, Wrangham RW (2007) Aging and fertility patterns in wild chimpanzees provide insights into evolution of menopause. Curr Biol 17:2150–2156

Turnbull CM (1961) The forest people. Simon & Schuster, New York

Utami AS, Mitra ST, Goossens B, James SJ, Knott CD, Morrogh BHC, van Schaik CP, van Noordwijk MA (2009) Orangutan mating behavior and strategies. In: Wich SA, Utami AS, Setia TM, van Schaik CP (eds) Orangutans: geographic variation in behavioral ecology and conservation. Oxford University Press, New York, pp 235–244

Van Schaik CP (1999) The socioecology of fission-fusion sociality in orangutans. Primates 40:60–86

Van Schaik CP (2000) Infanticide by male primates: the sexual selection hypothesis revisited. In: Van Schaik CP, Janson CH (eds) Infanticide by males and its implications. Cambridge University Press, Cambridge, pp 27–60

Van Schaik CP, Deaner RO (2002) Life history and cognitive evolution in primates. In: de Waal FBM, Tyack PL (eds) Animal social complexity. Harvard University Press, Cambridge, MA

Van Schaik CP, Isler K (2012) Life-history evolution. In: Mitani JC, Call J, Kappeler PM, Palombit RA, Silk JB (eds) Evolution of primate society. The University of Chicago Press, Chicago, pp 220–244

Van Schaik CP, van Hooff JARAM (1996) Toward an understanding of the orangutan's social system. In: McGrew WC, Marchant LF, Nishida T (eds) Great ape societies. Cambridge University Press, Cambridge, pp 3–15

Vigilant L, Langergraber KE (2011) Inconclusive evidence for patrilocality in Neandertals. Proc Natl Acad Sci USA 108:E87

Vonk J, Brosnan SF, Silk JB, Henrich J, Richardson AS, Lambeth SP, Schapiro SJ, Povinelli DJ (2008) Chimpanzees do not take advantage of very low cost opportunities to deliver food to unrelated group members. Anim Behav 75:1757–1770

Watanabe K (1979) Alliance formation in a free-ranging troop of Japanese macaques. Primates 20:459–474

Watts DP (1989) Infanticide in mountain gorillas: new cases and a reconsideration of the evidence. Ethology 81:1–18

Watts DP (1991a) Harassment of immigrant female mountain gorillas by resident females. Ethology 89:135–153

Watts DP (1991b) Mountain gorilla reproduction and sexual behavior. Am J Primatol 24:211–225

Watts DP (1996) Comparative socio-ecology of gorillas. In: McGrew WC, Marchant LF, Nishida T (eds) Great ape societies. Cambridge University Press, Cambridge, pp 16–28

Watts DP (1997) Agonistic interventions in wild mountain gorilla groups. Behaviour 134:23–57

Watts DP (2000) Causes and consequences of variation in male mountain gorilla life histories and group membership. In: Kappeler P (ed) Primate males. Cambridge University Press, Cambridge, pp 169–179

Watts DP (2003) Gorilla social relationships: a comparative overview. In: Taylor AB, Goldsmith ML (eds) Gorilla biology: a multidisciplinary perspective. Cambridge University Press, Cambridge, pp 302–327

Watts DP, Mitani JC (2000) Infanticide and cannibalism by male chimpanzees at Ngogo, Kibale National Park, Uganda. Primates 41:357–365

White TD, Asfaw B, Beyene Y, Haile-Selassie Y, Lovejoy CO, Suwa G, WoldeGabriel G (2009) *Ardipithecus ramidus* and the paleobiology of early hominids. Science 326:75–86

Wich SA, Utami-Atmoko SS, Mitra Setia T, Rijksen HD, Schurmann C, van Hooff JARAM, van Schaik CP (2004) Life history of wild Sumatran orangutans (*Pongo abelii*). J Hum Evol 47:385–398

Wich SA, de Vries H, Ancrenaz M, Perkins L, Shumaker RW, Suzuki A, van Schaik CP (2009) Orangutan life history variation. In: Wich SA, Utami SS, Mitra Setia T, van Schaik CP (eds) Orangutans: geographical variation in behavioral ecology and conservation. Oxford University Press, Oxford, pp 65–75

Wilfried GE, Yamagiwa J (2014) Use of tool sets by chimpanzees for multiple purposes in Moukalaba-Doudou National Park, Gabon. Primates 55(4):467–472. doi:10.1007/s10329-014-0431-5

Williams J, Pusey AE, Carlis JV, Farm BP, Goodall J (2002) Female competition and male territorial behaviour influence female chimpanzees' ranging patterns. Anim Behav 63:347–360

Wood B, Strait D (2004) Patterns of resource use in early Homo and paranthropus. J Hum Evol 46:119–162

Wrangham RW (1980) An ecological model of female-bonded primate groups. Behaviour 75:262–300

Wrangham RW (1986) Ecology and social relationships in two species of chimpanzees. In: Rubenstein DI, Wrangham RW (eds) Ecological aspects of social evolution: birds and mammals. Princeton University Press, Princeton, pp 352–378

Wrangham RW (1987) Evolution of social structure. In: Smuts BB, Wrangham RW, Cheney DL, Struhsaker TT, Seyfarth RM (eds) Primate societies. University of Chicago Press, Chicago, pp 282–296

Wrangham RW (2006) The cooking enigma. In: Ungar P (ed) Early hominid diet: the known, the unknown, and the unknowable. Oxford University Press, New York, pp 308–323

Wrangham RW (2009) Catching fire: how cooking made us human. Basic Books, New York

Wrangham RW, Conklin-Brittain NL (2003) The biological significance of cooking in human evolution. Comp Biochem Physiol Part A 136:35–46

Wrangham RW, Smuts B (1980) Sex differences in the behavioral ecology of chimpanzees in the Gombe National Park, Tanzania. J Reprod Fertil Suppl 28:13–31

Wrangham RW, Conklin NL, Etot G, Obua J, Hunt KD, Hauser MD, Clark AP (1993) The value of figs to chimpanzees. Int J Primatol 14:243–256

Wrangham RW, Jones JH, Laden G, Pilbeam D, Conklin-Brittain N (1999) The raw and the stolen-cooking and the ecology of human origins. Curr Anthropol 40:567–594

Yamagiwa J (1999) Socioecological factors influencing population structure of gorillas and chimpanzees. Primates 40:87–104

Yamagiwa J (2004) Diet and foraging of the great apes: ecological constraints on their social organizations and implications for their divergence. In: Russon AE, Begun DR (eds) The evolution of thought: evolutionary origins of great ape intelligence. Cambridge University Press, Cambridge, pp 210–233

Yamagiwa J, Basabose AK (2009) Fallback foods and dietary partitioning among *Pan and Gorilla*. Am J Phys Anthropol 140:739–750

Yamagiwa J, Kahekwa J, Basabose AK (2003) Intra-specific variation in social organization of gorillas: implications for their social evolution. Primates 44:359–369

Yamagiwa J, Kahekwa J, Basabose AK (2009) Infanticide and social flexibility in the genus *Gorilla*. Primates 50:293–303

Yamagiwa J, Shimooka Y, Sprague DS (2014) Life history tactics in monkey and apes: focus on female-dispersal species. In: Yamagiwa J, Karczmarski L (eds) Primate and cetacean: field research and conservation of complex mammalian societies. Springer, Tokyo, pp 173–206

Yamakoshi G (1998) Dietary responses to fruit scarcity of wild chimpanzees at Bossou, Guinea: possible implications for ecological importance of tool use. Am J Phys Anthropol 106:283–295

Yamamoto S, Tanaka M (2010) The influence of kin relationship and reciprocal context on chimpanzees' other-regarding preferences. Anim Behav 79:595–602

Zollikofer CPE, Ponce de Léon MS (2010) The evolution of hominid ontogenies. Semin Cell Dev Biol 21:441–452

Conclusion: Emerging Patterns and Challenges for Dispersing Female Primates

Filippo Aureli

As stated in the Preface, our volume is about the "difficult" sex in female-dispersal species. In part because it is arduous to track females when they disperse from the natal group, there is limited knowledge about them. Therefore, there are many unanswered questions. How do females behave after leaving their natal group? For how many months or years do they live solitarily before immigrating into new groups? In which groups do females choose to immigrate? And how do they do so? How many groups do they visit or in how many do they stay in throughout their lifetime? The chapters of this book have answered these questions by reviewing the evidence available so far in the more clear-cut cases of primate female-dispersal species with male philopatry. These chapters also reviewed the life histories and social relationships of these females. We learned that we need to be careful in making generalizations based on a handful of studies because a high degree of intraspecific variation emerges when comparing findings on the same species at different sites (e.g., Hashimoto and Furuichi, Chap. 5). We also learned about the incompleteness of our knowledge and the many challenges ahead. Still, this book represents a step forward in unveiling the secrets of females in female-dispersal species. In reviewing where we stand today, several areas can be identified where additional data and theoretical development are needed. Below each area is highlighted with the awareness that addressing them will not be easy, as expected for the "difficult" sex.

F. Aureli (✉)
Instituto de Neuroetología, Universidad Veracruzana, Av. Dr. Castelazo Ayala S/N, Col. Industrial Animas, Ap 566, Cp 91190 Xalapa, Veracruz, Mexico

T. Furuichi et al. (eds.), *Dispersing Primate Females*,
Primatology Monographs, DOI 10.1007/978-4-431-55480-6

Why Dispersing?

Socioecological models focusing on females labeled the “difficult” sex as nonbonded (Wrangham 1980), nonresident (van Schaik 1989), or dispersal egalitarian (Sterck et al. 1997). Although these models have been powerful heuristic tools for explaining female behavior, various forms of criticism have recently been raised about the mismatch between the model predictions and the observed variation in primate behavior (Snaith and Chapman 2007; Thierry 2008; Clutton-Brock and Janson 2012; Koenig et al. 2013). Alternative perspectives are needed, especially those that take phylogeny and intraspecific flexibility into account. A perspective focusing on the costs of reproduction is particularly inspiring (Lee and Strier, Chap. 9). For example, as these authors pointed out, trade-offs between time spent for infant care and time spent for reproduction within a lifespan may constrain female social strategies more than competitive trade-offs about energy intake.

It is likely that multiple factors, such as inbreeding avoidance, reduced competition, predation and infanticide protection, and need of kin for support, play a role in determining dispersal patterns as there is flexibility within the same species. Whether females or males or both sexes disperse from the natal group may be a response to local conditions, such as local energy availability affecting female maturation age, length of male tenure influencing female breeding opportunities, and the degree of habitat fragmentation possibly limiting dispersal opportunities (Lee and Strier, Chap. 9). Thus, local variation appears to exist within the species-typical dispersal patterns, i.e., when behavioral flexibility is beneficial, the species-typical dispersal pattern may be violated (Lee and Strier, Chap. 9). For example, Matsuura (Chap. 7) showed that there is high degree of flexibility in dispersal patterns even within a single Pygmy village. In addition, the first violation of male philopatry species-typical dispersal patterns of spider monkeys was recently documented when opportunities arise (Aureli et al. 2013). Although variation in dispersal patterns is reported in various chapters of Part I and II, more research effort on “difficult” females is needed. Long-term studies are especially important to reveal more variation in species-typical dispersal patterns, which in turn will help us to understand the factors and conditions affecting female dispersal. Further research is also needed to answer the interesting question raised in the book Preface about whether dispersal patterns are more variable in female-dispersal species than in male-dispersal species.

Implications for Life History Traits

Life history traits, such as later maturation, slower rates of reproduction, and greater energy and time allocation to infants, are overall correlated with female dispersal (Lee and Strier, Chap. 9; Yamagiwa, Chap. 11). These findings may have important implications for the costs and benefits of female dispersal, but more details are needed for thorough analyses.

Several Part I and II chapters have provided updated information on the life history of females in the most typical female-dispersal species where males are philopatric. The compilation of this information in one volume makes us realize both the accomplishments and the limitations. For example, although the many decades of research on mountain gorillas and chimpanzees have provided invaluable data, we still rely on a handful of populations and there are still many critical details for which data are missing (Robbins and Robbins, Chap. 4; Hashimoto and Furuichi, Chap. 5). In spider monkeys, data from multiple species are often pulled together to give an overall picture because no sufficient data are available for each species (Vick 2008; Shimooka, Chap. 2). Information is even lacking from human populations (Imamura, Chap. 8; Yamagiwa, Chap. 11). These shortcomings make us lose potentially meaningful variation related to local conditions.

Females seem to be more of a “difficult” sex regarding life history traits than males. For example, as reported by Lee and Strier (Chap. 9), lifespan seems to play an important role in determining reproductive rates, but the role of dispersal patterns cannot be assessed yet. This is because Cercopithecidae species are overrepresented in the available data for life history traits. All species covered in this volume belong to the set of underrepresented species. Thus, the update of life history information provided by the chapters of this volume is an important contribution toward achieving a database that will allow powerful comparative analyses for a full understanding of the implications of female dispersal for life history traits.

Social Relationships Are More than Associations

It is challenging to characterize social relationships between females in female-dispersal species in the same detail as has been done in female-philopatric species. Indeed, this is one reason why they are the “difficult” sex. The challenge may be due to the difficulty in collecting detailed data on social interactions of these females, the actual rarity of their social interactions, or both. Hinde’s (1979) powerful framework can be of help here. The framework links social relationships to the observable social interactions among group members and the inferred group social structure. This is because the occurrence and outcome of any one interaction between two individuals affects the occurrence and outcome of their subsequent interactions, so that the unique history of interactions between two individuals constitutes their social relationship. Thus, social relationships are emergent properties derived from the patterning of interactions between individuals over time (Aureli et al. 2012a; Seyfarth and Cheney 2012).

Individuals change their behavior depending on the context and the quality of their relationships with potential partners. Thus, they need to assess the quality of their relationships with others. These assessments are done based on the information contained in the various interactions previously exchanged with each of their partners (Aureli and Schaffner 2002). Individuals must therefore integrate information about the frequency, duration, quality, and consequences of different types of interactions with each of their partners, convert this into some kind of common currency, and update this information across time. This kind of bookkeeping appears cognitively demanding, but it does not need to be as this can be achieved through emotional mediation (Aureli and Schaffner 2002; Aureli and Whiten 2003; Schino and Aureli 2009). Emotional mediation allows individuals to predict the actions and responses of their partners with reasonable accuracy based on their past interactions, i.e., on the quality of their social relationships, facilitating social intercourse. Such a process also allows individuals to reap the benefits from differentiated social relationships, including selective tolerance around resources, cooperative hunting, food sharing, mating privileges, agonistic support, and protection against external threats (Cords 1997; van Schaik and Aureli 2000), which in turn provide fitness payoffs (Silk 2012).

Examples of the challenge in characterizing social relationships between females in female-dispersal species can be found in several chapters of this volume. Proximity data were used to characterize social relationships in muriquis and woolly monkeys (Strier et al., Chap. 1; Stevenson et al., Chap. 3), and data on being in the same subgroup (or party) were used for spider monkeys, bonobos, and chimpanzees (Shimooka, Chap. 2; Hashimoto and Furuichi, Chap. 5). For the comparative analysis of colobine species, time spent grooming was used (Matsuda et al., Chap. 10), whereas several social interactions, but only for two individuals, were used to characterize the development of the social relationships of immigrant female bonobos (Sakamaki et al., Chap. 6).

Relationship quality is unlikely to consist of a single dimension, but it is likely to comprise several aspects (Aureli et al. 2012a). Focusing on one type of interaction as an indicator of relationship quality or a few interactions combined in an arbitrary index may therefore be reductive and run the risk reflecting the researcher's assumptions more than the animals' perspectives. An alternative approach is to use data from a variety of interactions to statistically extract components that represent different dimensions of social relationships (Fraser et al. 2008). Such extracted components offer comprehensive, conceptually coherent measures and provide an objective assessment of the quality of relationships within a particular group. Thus, although it is challenging, it is important to characterize social relationships using multiple types of interactions dispersing females exchange.

Fission-Fusion Dynamics and Dispersal Patterns

The degree of fission-fusion dynamics is a characteristic of a social system (Kappeler and van Schaik 2002; Aureli et al. 2008). It depends on the temporal variation in spatial cohesion among group members, the temporal variation in subgroup (or party) size, and the temporal variation in subgroup composition (Aureli et al. 2008). A high degree of fission-fusion dynamics is usually found when individuals belonging to the same group are rarely all together, but they split and merge in subgroups of variable size and membership. Several of the species covered in this volume fit this pattern, at least certain populations in some periods. Overall, a high degree of fission-fusion dynamics is disproportionately present in species with female dispersal and male philopatry compared to other primate species.

The likely reason for this bias is that a high degree of fission-fusion dynamics is a way to reduce food competition by adjusting subgroup size to local resource availability (Kummer 1971). Under these conditions, females do not need cooperation with kin to be successful in within- and between-group competition (van Schaik 1989). This leads to low constraints for female dispersal from the natal group and low selective pressure for the development of highly differentiated relationships among females, explaining some of the patterns reviewed above.

Fission-fusion dynamics may create unique challenges and opportunities for social interaction, with possibly distinctive selective pressures on underlying communicative and cognitive abilities (Aureli et al. 2008). Given the bias in species with a high degree of fission-fusion dynamics toward those with female dispersal and male philopatry, it would be important to examine whether such challenges, opportunities, and selective pressures are present more in these species than in others with different dispersal patterns. Comparative analyses can accomplish this testing, but measures that capture the various dimensions of fission-fusion dynamics need to be developed (see Aureli et al. 2012b for a step in this direction).

Nonprimates and Conservation

Some of the primate species with female dispersal and male philopatry are possibly among the best examples of ecological convergence. For example, there is a resemblance in many aspects of the social system of two not closely related species, such as chimpanzees and spider monkeys (Symington 1990; Chapman et al. 1995; Di Fiore et al. 2011). Although most of these aspects regard males, convergence regarding females is possible as well (Shimooka, Chap. 2; Hashimoto and Furuichi, Chap. 5). It is also likely that new research and powerful comparative analyses will reveal similar ecological convergence between primate and nonprimate species.

Gathering the data for these analyses is however challenging because of the length of time required to accumulate individual-based data on long-lived females that mature and reproduce slowly such as the dispersing females reviewed in this volume. This challenge calls for funding agencies to be particularly sensitive in supporting long-term field studies (Kappeler and Watts 2012). Another challenge is based on the realization that in some cases data for one species come mainly from one or a few populations. This is often because only a few populations of these species are left, which is obviously the case for muriquis (Strier et al., Chap. 1) and mountain gorillas (Robbins and Robbins, Chap. 4). Thus, the need for more data on the “difficult” sex is also a call for the conservation of female-dispersal species.

References

Aureli F, Schaffner CM (2002) Relationship assessment through emotional mediation. Behaviour 139:393–420

Aureli F, Whiten A (2003) Emotions and behavioral flexibility. In: Maestripieri D (ed) Primate psychology – the mind and behavior of human and nonhuman primates. Harvard University Press, Cambridge, MA, pp 289–323

Aureli F, Schaffner CM, Boesch C, Bearder S, Call J, Chapman CA, Connor R, Di Fiore A, Dunbar RIM, Henzi PS, Holekamp K, Korstjens AH, Layton R, Lee P, Lehmann J, Manson JH, Ramos-Fernandez G, Strier K, van Schaik CP (2008) Fission-fusion dynamics: new research directions. Curr Anthropol 49:627–654

Aureli F, Fraser ON, Schaffner CM, Schino G (2012a) The regulation of social relationships. In: Mitani J, Call J, Kappeler P, Palombit R, Silk J (eds) The evolution of primate societies. University of Chicago Press, Chicago, pp 531–551

Aureli F, Schaffner C, Asensio N, Lusseau D (2012b) What is a subgroup? How socioecological factors influence inter-individual distance. Behav Ecol 23:1308–1315

Aureli F, Di Fiore A, Murillo-Chacon E, Kawamura S, Schaffner CM (2013) Male philopatry in spider monkeys revisited. Am J Phys Anthropol 152:86–95

Chapman CA, Wrangham RW, Chapman LJ (1995) Ecological constraints on group size: an analysis of spider monkey and chimpanzee subgroups. Behav Ecol Sociobiol 36:59–70

Clutton-Brock TH, Janson C (2012) Primate socioecology at the crossroads: past, present, and future. Evolut Anthropol 21:136–150

Cords M (1997) Friendships, alliances, reciprocity and repair. In: Whiten A, Byrne RW (eds) Machiavellian intelligence II. Cambridge University Press, Cambridge, pp 24–49

Di Fiore A, Link A, Campbell CJ (2011) The atelines: behavior and socioecological diversity in a New World monkey radiation. In: Campbell CJ, Fuentes AF, MacKinnon KC, Bearder S, Stumpf R (eds) Primates in perspective. Oxford University Press, Oxford, pp 155–188

Fraser ON, Stahl D, Aureli F (2008) Stress reduction through consolation in chimpanzees. Proc Natl Acad Sci U S A 105:8557–8562

Hinde RA (1979) Towards understanding relationships. Academic, London

Kappeler PM, van Schaik CP (2002) Evolution of primate social systems. Int J Primatol 23:707–740

Kappeler PM, Watts DP (2012) Long-term field studies of primates. Springer, Berlin

Koenig A, Scarry CJ, Wheeler BC, Borries C (2013) Variation in grouping patterns, mating systems and social structure: what socioecological models attempt to explain. Philos Trans R Soc B 368:20120348

Kummer H (1971) Primate societies: group techniques of ecological adaptation. Aldine, Chicago

Schino G, Aureli F (2009) Reciprocal altruism in primates: partner choice, cognition and emotions. Adv Stud Behav 39:45–69

Seyfarth RM, Cheney DL (2012) The evolutionary origin of friendship. Annu Rev Psychol 63:153–177

Silk JB (2012) The adaptive value of sociality. In: Mitani J, Call J, Kappeler P, Palombit R, Silk J (eds) The evolution of primate societies. University of Chicago Press, Chicago

Snaith TV, Chapman CA (2007) Primate group size and socioecological models: do folivores really play by different rules? Evolut Anthropol 16:94–106

Sterck EH, Watts DP, van Schaik CP (1997) The evolution of female social relationships in nonhuman primates. Behav Ecol Sociobiol 41:291–309

Symington MM (1990) Fission-fusion social organization in *Ateles* and *Pan*. Int J Primatol 11:47–61

Thierry B (2008) Primate socioecology, the lost dream of ecological determinism. Evolut Anthropol 17:93–96 van Schaik CP (1989) The ecology of social relationships amongst primate females. In: Standen V, Foley RA (eds) Comparative socioecology: the behavioural ecology of humans and other mammals. Blackwell Scientific, Oxford, pp 195–218

van Schaik CP, Aureli F (2000) The natural history of valuable relationships in primates. In: Aureli F, de Waal FBM (eds) Natural conflict resolution. University of California Press, Berkeley, pp 307–333

Vick LG (2008) Immaturity in spider monkeys: a risky business. In: Campbell C (ed) Spider monkeys: behavior ecology and evolution of the genus Ateles. Cambridge University Press, Cambridge, pp 288–328

Wrangham RW (1980) An ecological model of female-bonded primate groups. Behaviour 75:262–299

Index

A
Abstinence, 198, 199
Activity budget, 51, 86, 87, 91, 234
Adolescent growth spurt, 268, 269
Age at dispersal, 7, 17, 19
Ages at first reproduction (AFR), 4, 15–19, 216, 256, 258, 260–262, 264
Agonistic interaction, 38–39, 54, 67, 80, 109, 130–131, 149, 152, 153, 156, 160, 256
Alliance, 65, 94, 166, 195, 221, 235, 269
Allomothering, 221, 236, 247–248
Ardipithecus ramidus (A. ramidus), 265
Arrangement of marriages, 195
Association indices, 15, 24, 27, 28, 30, 33, 38, 46, 59, 63, 114, 116, 117, 240
Association pattern, 14, 24, 32, 34, 38–40, 64, 65, 105–121, 267
Ateles belzebuth (A. belzebuth), 23, 24, 26, 35, 36, 38, 39
Ateles geoffroyi (A. geoffroyi), 23, 24, 26, 27, 32, 35–39
Ateles hybridus (A. hybridus), 23
Ateles paniscus (A. paniscus), 23, 24, 35
Australopithecus afarensis (A. afarensis), 265, 268
Australopithecus africanus (A. africanus), 256

B
Bilocality, 186, 208
Bipedalism, 257, 259, 265, 267
Bipedal locomotion, 257
Birth interval, 187, 198, 199
Bisexually bonded community model, 109–113, 121
Bonobo, 23, 38, 39, 83, 105–121, 127–161, 255, 256, 259–264, 271, 290
Both-sex-dispersed, 231, 233, 235, 236, 238–240, 243–250
Brachyteles hypoxanthus (B. hypoxanthus), 5, 19
Brain size, 257, 267–269, 272, 274, 275
Brazilian Atlantic forest, 5
Breast feeding, 191, 198, 266

C
Central Kalahari San, 186–188, 208
Cercopithecidae, 3, 219, 223, 231, 247, 255, 289
Cercopithecine, 3, 219, 247, 255
Chest rubbing, 61, 63, 65
Childbirth, 173, 177, 178, 187, 195, 197–199
Chimpanzee(s), 4, 15, 23, 24, 38, 39, 47, 64, 83, 95, 105–121, 127, 128, 143, 146, 156–161, 217, 255–257, 259–273, 289–291
Clique, 113, 118, 119, 236, 239, 246, 250
Clustering coefficient, 236, 238, 244–246, 248, 249
Coalition, 39, 40, 46, 94, 127, 195, 255, 260, 267, 269, 271, 273
Colobinae, 90, 231–250, 290
Colonization, 5, 16–18
Colonizer, 9
Complex network, 40, 204, 247, 268, 272
Conservation, 3–20, 179, 274, 291

T. Furuichi et al. (eds.), *Dispersing Primate Females*,
Primatology Monographs, DOI 10.1007/978-4-431-55480-6

Contest hooting, 131, 153
Cooperation, 39, 46, 47, 64, 83, 105, 113, 128, 159–161, 165, 167, 185, 216, 255, 257, 267, 269, 273–276, 290, 291
Copulation, 16, 26, 27, 35, 40, 77, 82, 83, 93, 119, 120, 131, 140, 146, 154–156, 159, 264, 271
Co-residence pattern, 167, 185
Corridor, 18
Costs of dispersal, 4, 11, 79–81, 86, 94–97
Co-wife, 200–202
Cross-cousin, 194, 195
Cycling female, 27, 30, 34, 35, 38–41, 120

D
Delayed maturation, 257, 258, 274, 275
Demography, 5, 12, 16–18, 20, 23, 51, 82, 90, 108, 166, 185, 187, 217, 225, 238
Densities, 4, 5, 12, 49, 52, 54–56, 65, 66, 86, 92, 111, 112, 159, 186, 238
Dispersal
  age, 6, 7, 9, 10, 16–18
  barrier, 17
  cost, 4, 11, 12, 46, 75, 77, 79–90, 94–97, 215, 220, 223–225, 257, 260, 263, 269, 288
  opportunities, 4, 225, 288
  pattern, 3–20, 47, 54, 75–97, 105, 107, 118, 128, 173, 231–250, 271, 288–291
Dispersal trajectory(ies), 7
Division of labor, 257, 259, 267, 272–275
Dominance, 14, 35, 36, 40, 46, 47, 52, 63, 75, 77, 79–82, 84, 87, 89, 91–94, 105, 107, 109, 110, 113, 119, 128, 131, 146, 152–154, 156, 158, 159, 185, 207, 215–217, 220, 249, 255
Dominance relationship, 109, 110, 128, 146, 149–154, 156, 158, 220

E
Early weaning, 256, 258, 263, 265–269, 274, 275
Egalitarianism, 5, 158, 186, 207, 288
Eigenvector centrality, 30, 32, 34–37, 235, 238, 243–246, 248
Emigrate, 8, 9, 14, 16, 37, 78, 87, 89, 91, 107, 128, 140, 142, 143
Emotional mediation, 290
Encephalization, 259, 266–268, 274, 275
Encounter, 4, 10–12, 18, 35, 39, 40, 49, 64, 65, 67, 79–81, 87–91, 94, 96, 107, 118, 120, 128–130, 140, 142–143, 145, 149, 158, 159, 221
Endangered species, 4, 19, 20, 76
Energy availability, 218, 220, 288
Exogamy, 259
Extramarital sexual relationship, 187, 200–204, 206–208

F
Face-to-face interaction, 209
Fallback resource, 51
Familiarity, 4, 6, 12, 18, 19, 83, 94, 96, 165, 186
Fecundity, 258, 266, 267, 269, 271, 275
Feeding competition, 4, 5, 83–86, 88–91, 97, 109, 159, 260
Female association, 5, 18, 24, 37, 40, 45, 46, 54, 58, 67, 113, 114, 116, 117, 119, 120, 236
Female-bonded, 82, 83, 96, 235, 255
Female-dispersal, 3, 4, 11, 14, 17–19, 23, 46–47, 51, 66, 67, 75, 79–81, 83, 87, 88, 91, 92, 94, 96, 106, 107, 128, 132, 142, 158, 161, 165–180, 185, 208–209, 215–226, 231, 235, 236, 240, 243–248, 250, 255–256, 260, 264, 265, 269, 271, 287–291
Female kin, 3, 4, 77, 119, 215, 219–221, 250
Female-philopatric, 46, 82, 119, 215, 216, 219–221, 233, 235, 236, 238–240, 243–245, 247–250, 260, 289
Female transfer, 41, 79, 85, 91, 96, 107, 118–120, 128, 142–146, 158, 160, 161, 256, 260, 263, 275
First birth, 7, 128, 130, 142, 145–147, 149, 187
First menstrual, 193–197, 200
First reproduction, 11, 223
Fission and fusion, 5, 14, 25, 75, 77–79, 91, 93–94, 109, 128, 134–139, 142, 144, 158, 187, 189, 195, 207, 208
Fission-fusion dynamics, 4, 23, 24, 40, 47, 49, 105, 127, 216–217, 225, 226, 255, 256, 259, 263, 267, 274, 290–291
Flexibility, 47, 49, 106, 120, 165, 166, 168–170, 178–180, 186, 189, 215, 225, 247, 260, 288
Folivore paradox, 84–86, 88–90, 93, 96, 97, 102
Forager, 166–167, 194, 256, 272, 275, 276
Foraging, 47–49, 61, 64, 65, 86, 94, 110, 118, 120, 166, 186, 189, 198, 267, 275
Forest fragmentation, 5, 6, 9, 17, 19, 52, 54
Fossil evidence, 256, 257, 260, 265–269, 271, 272, 274, 275

G
Gender, 186, 207
Genito-genital (GG) rubbing, 131, 139, 141, 146, 154, 155, 157, 158, 161
Genitor, 207
Gorilla, 4, 75–97, 120, 159, 217, 255, 256, 259–266, 268, 271, 289, 291
Gorilla beringei (G. beringei), 76, 120
Gorilla gorilla (G. gorilla), 76
Great ape, 166, 219, 256–265, 267–272, 274, 275
Grooming, 38, 40, 52, 62–64, 105, 109, 119, 146, 153–155, 166, 201, 231–250, 267, 290
Grooming network, 234, 235, 237, 238, 243–247, 249, 250
Group cohesion, 224, 234, 235, 247, 250
Group fusion, 128, 134–139, 142, 158
Guacharos, 48, 50, 51, 53–55, 59–62, 65

H
Habitat fragmentation, 17, 288
Habitat productivity, 65
Habitat quality, 15, 84, 89
Habituate, 17, 18, 24, 25, 45, 52, 54–57, 64–67, 77, 84, 89, 94, 96, 107, 109, 129, 216, 219, 258, 260, 274, 288
Home range, 36, 39, 47, 64, 65, 96, 109–112, 121, 129, 145, 159, 167, 186, 256
Hominidae, 231, 255, 256
Hominoid, 166, 259, 260
Homo erectus (H. erectus), 268, 272, 274
Homo habilis (H. habilis), 257, 267, 272
Homo neanderthalensis (H. neanderthalensis), 256, 266, 268, 272, 274, 275
Homo-Pan latest common ancestor (LCA), 257, 265, 269, 272, 275
Homo sapiens (H. sapiens), 268, 272, 275
Human ancestor, 167, 258, 259, 264–269, 271, 272, 274, 275
Human evolution, 166, 256–258, 265, 266, 272–274
Human family, 255–276
Hunter-gatherer, 165–180, 185–209, 271, 272

I
Immigrant female, 6, 12, 14, 24, 27, 32, 35, 37, 95, 108, 128–130, 145–158, 290
Immigration, 7–12, 14–16, 23, 27, 29, 35–37, 46, 87, 88, 107, 108, 128, 130, 135, 140–144, 146, 149, 155–157, 173, 287
Inbreeding, 75, 80–84, 159, 160, 219
Inbreeding avoidance, 75, 80–83, 96, 118, 128, 158, 160–161, 288
Incest taboo, 259
Individual recognition, 52, 53, 237
Infanticide, 34, 45, 75, 77, 79, 84–94, 158, 160, 220, 221, 225, 256, 261, 263–265, 269, 288
Interbirth interval, 87, 88, 90, 95, 96, 268
Intergroup transfer, 4, 40, 120, 121, 127–161
Inter-individual proximity, 45, 47–52, 55–61, 64–66
Intragroup competition, 47, 159–161

J
Jealousy, 193, 199–201, 203, 206, 207

K
Kin cooperation, 159–161
Kindred, 194
Kinship, 12, 38, 62–64, 105, 166, 169, 173–177, 195, 216, 217, 220, 221, 256, 257, 259

L
Lactating, 24, 26, 30, 33–34, 37, 38, 94, 198, 199, 220, 257
Lactational infertility, 199
Lagothrix lagothricha (L. lagothricha), 52
Life history(ies), 3–19, 23–41, 106–108, 128, 132, 135, 137, 177, 178, 185–209, 219, 222–226, 255–276, 287–289
Life span, 257, 259, 275
Long-term studies, 40, 41, 67, 117, 128, 169, 219, 264, 288, 291
Low-cost dispersal, 12

M
Male-bonded community model, 109, 110, 112, 121
Male dominance, 52, 105, 207
Male-male bond, 105
Male-only community model, 109, 110
Male-philopatric, 5, 47, 106, 118, 121, 158, 231, 235, 236, 240, 244, 248, 250, 289
Male philopatry, 23, 47, 52, 65, 83, 106, 107, 118, 128, 160, 161, 166, 185, 231, 233, 235–238, 240, 243, 244, 246–248, 250, 256, 271, 275, 287, 288, 291
Male quality, 86, 89, 97
Marital histories, 187
Marriage ritual, 194, 208

Maternal kin, 18, 64
Maternally related, 4, 19
Maternal relatedness, 12
Maternal sister, 12, 15, 16
Matriline, 3
Matrilineal, 3, 173, 179, 249
Matrilineal kin, 3
Maximal swelling, 107, 108
Menarche, 185, 187, 194, 208
Minimum reproductive unit, 232–238, 240, 247, 250
Modular social system, 240, 247
Modular society(ies), 235–237, 247–248, 269
Monogamous, 167, 190, 208, 221, 225, 256, 259, 265, 272–274
Mortality risk, 34, 220–221, 223, 225, 258
Mother-offspring, 63, 67
Multi-level community structure, 259, 274, 276
Multi-level social structure, 257, 271
Multilocality, 167, 169, 186, 208
Muriqui, 3–19, 46, 217, 255, 290, 291

N
Nasalis larvatus (N. larvatus), 238, 240, 244, 247, 249
Natal dispersal, 75, 80–84, 96
Natal group, 4, 6–19, 47, 52, 81, 83, 95, 97, 107, 108, 118–120, 128, 140, 143, 158–160, 225, 255, 260, 264, 271, 287, 288, 291
Neighborhood, 110, 113
Node, 28, 30, 38–40, 218
Northern muriquis, 3–19, 217

O
Oral history, 185, 187
Orangutans, 255, 256, 259–261, 263, 264, 266, 271
Oreonax, 46
Other-regarding, 273, 275
Outbreeding, 217–218, 224

P
Paedomorphic, 161
Pan paniscus (P. paniscus), 83, 127–161
Pan troglodytes (P. troglodytes), 47, 83, 127
Paradox, 11, 84–86, 88–90, 97
Parallel cousin, 195
Paranthropus robustus, 256
Party size, 4, 23–24, 26, 28, 32, 39, 113–115, 118, 119, 290
Pater, 207
Patrilineal, 165, 166, 169, 170, 194, 204
Patrilineal-patrilocal band model, 165, 185
Patrilineal-patrilocal model, 169–170
Phylogenetic, 3, 46, 90, 91, 128, 186, 217–219, 222, 223, 267, 272
Piliocolobus tephrosceles, 237–238, 243, 244, 246–248, 250
Polyandrous, 190, 208
Polygamous, 190, 200, 204, 208
Population, 4, 5, 7–9, 11, 12, 14, 16–19, 47–59, 61, 62, 65–67, 75, 76, 80, 83, 86, 88–94, 96, 97, 114, 119, 130, 169, 173, 176, 178, 190, 215, 224, 225, 260, 264, 266–267, 276, 289, 291
  density, 5, 12, 52, 54, 65, 66, 86, 92, 159, 186
  persistence, 4
Post-marital co-residence pattern, 185
Post-marital residence, 168, 169, 177–178, 185, 190, 194, 208
Post-marital residential pattern, 190, 194
Post-reproductive period, 257, 268, 275, 276
Predation, 34, 45, 46, 66, 75, 84, 85, 87, 88, 90, 91, 94, 97, 119, 215, 221, 225, 234, 256, 258, 260, 264–267, 269, 271, 274, 275, 288
Pregnant, 24, 26, 27, 34, 65, 94, 191, 198, 207
Presbytis femoralis, 238, 244, 247
Promiscuity, 5, 271, 272
Provisioning, 115, 119, 129, 158, 221, 264, 265, 267, 272–276
Proximity, 7, 14, 15, 40, 48, 52, 54–61, 64, 66, 67, 93, 216, 219, 290
Pygmy(ies), 168–180, 186, 187, 288

R
Ranging, 4, 16, 39, 47, 91, 105–121, 143, 190, 238
Reciprocal basis, 208
Remarriage, 200–201, 204
Reproduction, 4, 11, 15–17, 19, 40, 75, 84, 89, 95, 207, 216, 220, 221, 223, 225, 256, 258, 260, 261, 263, 264, 288
Reproductive energetics, 220, 225, 226
Reproductive function, 199
Reproductive rate, 47, 216, 223, 289
Reproductive skew, 5, 89, 216
Reproductive status, 24, 26, 27, 29, 32–35, 37–40, 52, 155

Reproductive success, 18, 39, 46, 51, 66, 84, 86–88, 94, 97, 110, 118, 216, 220, 255, 263, 269
Residential group, 186–189, 208
Residential pattern, 166, 168–171, 173–180, 187–190, 194
Resource competition, 54, 216
Rhinopithecus roxellana (R. roxellana), 238, 244, 247

S
Savanna, 235, 258, 259, 266, 267
Seasonal dispersal, 12, 18
Seasonality, 4, 11–12, 18, 19, 24
Secondary dispersal, 4, 7, 12, 19, 47, 75, 88, 219
Second transfer, 142, 145–146, 156, 158–160
Self-handicapping, 154, 158
Semnopithecus entellus, 238
Sex difference, 105–121, 243–246
Sexual coercion, 79, 263, 269
Sexual maturity, 4, 107, 120, 275
Sexual relationships, 185–209, 257
Sharing, 166, 170, 186, 189, 194, 202, 205, 206, 208, 267, 271, 273, 274, 276, 290
Social association, 34, 62–64, 106, 128, 130, 148, 157
Social behavior, 45, 57, 64, 65, 117, 154, 273
Social embeddedness, 216
Social environment, 65
Social grooming, 131, 132, 146, 153–155, 231
Social interactions, 40, 45–67, 109, 128, 129, 131, 146, 157, 173, 225, 231, 234, 248, 250, 268, 272, 274, 276, 289–291
Social network, 5, 24, 28, 30–32, 34, 35, 40, 167, 180, 231–250
Social network analysis, 235, 237–239
Social organization, 45, 109, 118, 165–180, 215, 235, 247, 271
Social play, 131, 139, 146, 153–158, 161
Social preference, 4, 12–15, 18
Social relationship, 14, 15, 18, 23, 35, 37, 38, 40, 41, 45, 54, 77, 105, 109, 117, 118, 127–161, 170, 173, 179, 203, 209, 231, 235, 247, 255, 287, 289–290
Social state, 217, 225
Socio-ecological model, 260
Space requirement, 66, 67
Spacing, 45–67
Specific senior female, 157
Spider monkey, 23–41, 46, 47, 49, 64, 65, 255, 288–291
Strength of association, 12, 24, 30, 32–35, 37, 39, 113, 119, 223, 224

T
Temporary visit, 142–145
Territoriality, 64, 166, 180, 186, 260, 263
Tinigua, 24, 25, 47, 49–52, 54, 55, 57–61, 65, 66
Trachypithecus pileatus, 238
Transfer, 3, 40, 51, 75, 107, 127, 221, 256
Translocation, 17–19

V
Variation
  in female dispersal, 17, 18, 118
  in individual dispersal, 12
Virilocality, 185, 194

W
Woolly monkey, 45–67, 290