# The ecology and behavior of new chimpanzee mothers at Ngogo, Kibale National Park, Uganda

**by**

**Bethany Kaye Hansen**

A dissertation submitted in partial fulfillment
of the requirements for the degree of
Doctor of Philosophy
(Anthropology)
in the University of Michigan
2016

Doctoral Committee:

Professor John C. Mitani, Chair
Associate Professor Jacinta C. Beehner
Associate Professor Andrew J. Marshall
Professor David P. Watts, Yale University

## DEDICATION

To the chimpanzees of Ngogo, especially the females

# ACKNOWLEDGEMENTS

This dissertation would not have been possible without the help and support of several individuals and organizations. I thank… John Mitani for his expert guidance and mentorship, especially in the areas of critical thinking and scientific writing. I am honored to have had the opportunity to work with such a proficient and dedicated primatologist. David Watts, whose knowledge of primates, as well as his work ethic, are truly inspiring. Jacinta Beehner, who provided invaluable training during the writing process and who always knew when a few words of motivation were needed. Andy Marshall, who broadened my view of statistics and urged me to try new techniques. And Beverly Strassmann, Barb Smuts, Abby Bigham, and Laura MacLatchy, who all contributed to my understanding of evolution and biological anthropology.

I thank the late Jerry Lwanga, who not only provided logistical support at the Ngogo field site, but also shared much information about the forest, as well Ugandan culture. Tumusiime Alfred, Ndagizi Lawrence, Mbabazi Godfrey, and Twineomujuni Ambrozio assisted with data collection and provided training in the field. Alfred and ‘Ambrose’ went above and beyond their duties as field assistants, providing support for fundraising efforts for the Kyakagunga Community School. They also opened their homes to me, allowing me to spend time with their families. Tibisimwa James used his knowledge of the forest to lead anti-poaching efforts, along with his dedicated assistants. Businge Charles performed cooking and cleaning duties in camp, allowing me to spend so many hours observing chimpanzees. While in the field, Kevin

Langergraber, Carolyn Rowney, Michelle Brown, and Bryce Carlson provided much-needed companionship. I also thank the Uganda Wildlife Authority, the Uganda National Council for Science and Technology, and the Makerere University Biological Field Station for permission to work in Uganda's beautiful Kibale National Park.

I thank the many scientists whose research on the Ngogo chimpanzees provided invaluable background and context for this dissertation, particularly: Sylvia Amsler, Kevin Langergraber, Brent Pav, Kevin Potts, Lauren Sarringhaus, Marissa Sobolewski, and Monica Wakefield. Biological anthropology students at the University of Michigan provided support and mentorship, especially Marcela Benitez, Elizabeth Johnson, Aaron Sandel, and Rachna Reddy. The Center for Statistical Consulting and Research at the University of Michigan provided invaluable assistance with data analysis. This dissertation would not have been possible without financial support from several organizations at the University of Michigan: the College of Literature, Science, and the Arts; the Department of Anthropology, the International Institute; Rackham Graduate School; the African Studies Center; and the Department of Afroamerican and African Studies. The University Committee on Use and Care of Animals at the University of Michigan approved my research program.

Lastly, I extend the deepest and most heartfelt thanks to Kara C. Hansen and Ashley Lemke. Thank you for your friendship, wise words, and for always telling me, "You can do this."

# TABLE OF CONTENTS

# LIST OF FIGURES

# LIST OF TABLES

# ABSTRACT

Female mammals invest heavily in reproduction, and theory and empirical research indicate that two factors influence their fitness. First, females require food to reproduce and mothers should compete for access to food resources. Second, recent research indicates that in group-living species, females who form strong social bonds with each other reproduce more than do females who are unable to forge similar relationships. Therefore, females must meet both nutritional and social needs in order to reproduce successfully. Understanding the complex relationship between reproduction and socioecology promises to shed light on how evolution shapes the behavior of mothers.

Although mothers face a common set of challenges involving competition and affiliation, evidence indicates that within species, not all mothers are the same. One factor, parity, affects females in diverse taxa, including primates, carnivorans, and cetaceans. Due to their inexperience, primiparas, mothers raising their first offspring, face several challenges not experienced by multiparas, mothers with two or more offspring. As a result, primiparas behave differently than multiparas in several contexts.

Chimpanzees are an excellent species to investigate whether and how female behavior varies with parity. Chimpanzees have long life spans and first-time mothers live together with multiparas in multi-female, multi-male, fission-fusion communities. I investigated the relationship between parity and behavior by conducting a 15-month study of female chimpanzees living in a large community at Ngogo in the Kibale National Park, Uganda. The study took place during a period when the community grew in size due to several females giving birth to their first offspring. This produced an ideal situation to compare the behavior of mothers who differed in parity. Specifically, I tested the prediction that primiparas and multiparas behave differently. To determine how females compete with one another, I examined space use and intrasexual aggression, both of which influence access to food. To examine female social bonds, I analyzed observations of how females associated and groomed one another.

Females at Ngogo utilized small, overlapping home ranges within the larger community territory. Home ranges differed in size, but there was no evidence that parity affected this variation. As has been reported in several other chimpanzee communities, mothers were often aggressive toward adolescent nulliparas. Additional analyses revealed that female aggression varied with parity; primiparas displayed more aggression toward adolescents than did multiparas. Regarding affiliation, mothers mainly spent time and groomed with other mothers, rather than with adolescent nulliparas. A closer examination of mothers, who differed in parity, showed that primiparas groomed with nulliparas more often than did multiparas.

In sum, results of this thesis indicate that behavioral differences existed between primiparous and multiparous female chimpanzees. These differences involved mothers’ social interactions with adolescent nulliparas in competitive and affiliative contexts. These results emphasize the importance of examining parity because considering mothers as a single category can mask important behavioral variation. These results also indicate the importance of examining the lives of primiparas in order to understand how evolution has influenced the behavior of mothers.

# CHAPTER 1

# INTRODUCTION

Female primates invest heavily in reproduction via gestation, lactation, and providing extended care for dependent offspring. Because of this, female reproduction will be affected by the ability to convert food into offspring, and as a consequence, mothers should compete for access to food resources (Trivers 1972). In addition to feeding competition, group living poses challenges for female reproduction. In gregarious species, females must integrate themselves into the fabric of the group and develop and maintain social relationships to reproduce successfully. Recent research indicates that females obtain long-term fitness benefits by forging close affiliative bonds with other individuals (reviewed in Seyfarth & Cheney 2012). Together, ecological and social demands create selective pressures on mothers that involve competition and affiliation. To understand how evolution has shaped the behavior of primate mothers, it is necessary to explore the complex relationship between reproduction and socioecology.

While primate mothers face a common set of ecological and social challenges associated with reproduction, additional observations suggest that they differ in an important manner. Parity, or the number of offspring a female has borne, affects mothers in different ways across an array of species. Primiparas, mothers who have given birth to only one offspring, are negatively affected by processes that are not experienced by multiparas, mothers who have borne two or more offspring. First, primiparous females are young and are likely to be investing in their own growth and maturation (Bercovitch et al. 1998; Setchell et al. 2002; Rah et al. 2008). Second, primiparas are physiologically immature, which can reduce the efficiency of lactation (Hinde et al. 2009). As the result of their relatively poor quality, first-time mothers may forego investment in personal growth (humans, Rah et al. 2008; Pauli et al. 2013) or prolong lactation (rhesus macaques (*Macaca mulatta*), Hinde et al. 2009).

Studies of primates and nonprimate mammals show that behavioral differences also exist between primiparas and multiparas. These differences often involve primiparas' relative lack of experience. In some species, primiparas are less competent at interacting with their infants, and they provide reduced or inconsistent care compared to multiparas (prairie voles (*Microtus ochrogaster*), Wang & Novak 1994; domestic dogs (*Canis familiaris*), Guardini et al. 2015). Primiparas' lack of social experience may cause them to interact differently with peers than do multiparas. Primiparous female brown bears (*Ursus arctos*) have less knowledge of local dominance hierarchies compared to multiparas and may be less efficient in defending their cubs against infanticidal conspecifics (Zedrosser et al. 2009).

Understanding primiparity is important, as this life history stage marks the beginning of a female's reproductive career. In addition, experiences during primiparity can have consequences for lifetime reproductive success (Stearns 1992). Examining differences between primiparas and multiparas is informative because selection pressures and trade-offs between growth, maintenance, and reproduction are expected to change with maturation (Skogland 1989; Stearns 1992). Comparing the behavior of primiparas to multiparas can help reveal the challenges first-time mothers face. This area of study is particularly pertinent to gregarious species, where mothers both compete and affiliate with group-mates.

Chimpanzees provide an opportunity to examine how the behavior of primiparas differs from that of multiparas. Chimpanzees have long life spans and first-time mothers live together with multiparas in multi-female, multi-male, fission-fusion communities (Nishida 1968; Goodall 1986). This creates the possibility of comparing the behavior of females who differ in parity but otherwise experience similar ecological conditions. In the following, I set the stage for the questions addressed in this thesis by reviewing relevant aspects of female chimpanzee socioecology and life history.

## Female chimpanzee socioecology and life history

Female chimpanzees inhabit a communal territory, which is cooperatively defended by males against neighboring groups (Kawanaka & Nishida 1975; Goodall et al. 1979; Nishida 1979). As they move about their territories, female chimpanzees form temporary subgroups, or parties, that change in size and composition (Nishida 1968; Goodall 1986). Party size is influenced by food availability. Chimpanzees rely on a diet of ripe fruit (Nishida & Hiraiwa-Hasegawa 1987; Wrangham et al. 1998), a limited resource whose availability fluctuates in time and space (Wrangham 1979). Individuals form relatively large parties during periods of high fruit abundance (Wrangham 1977; Boesch 1996; Wrangham et al. 1992; Chapman et al. 1995; Matsumoto-Oda et al. 1998; Wrangham 2000).

Female chimpanzees typically disperse from their natal communities during adolescence when they are around 12-13 years old (Emery Thompson 2013). After a period of sub-fecundity of about two years, they begin to reproduce (Emery Thompson 2013). After giving birth for the first time, females bear additional offspring at approximately 5-6 year intervals. They continue to do so over their lifetimes, producing a total of 2-3 offspring on average (Emery Thompson 2013).

Long-term observations of female chimpanzees from several East African study sites have revealed a set of relationships between dominance rank, resource acquisition, and reproduction. These data indicate that female chimpanzees compete predominantly for space (Murray et al. 2007; Kahlenberg et al. 2008b; Miller et al. 2014). Mothers occupy small individual core areas within the communal territory. Core areas overlap extensively, and female fidelity to an area is high across years (Williams et al. 2002; Emery Thompson et al. 2007). Habitats are heterogeneous, and high-ranking females inhabit high quality core areas with more food than do low-ranking females, who occupy low-quality core areas. As a consequence, high-ranking females obtain access to more food compared to low-ranking females. High-ranking females are able to use this to their advantage and display shorter birth intervals and increased infant survivorship compared to low-ranking females (Emery Thompson et al. 2007).

Female chimpanzees rise in rank with both age (Nishida 1989; Greengrass 2005; Kahlenberg 2006; Murray et al. 2006) and tenure in the community (Kahlenberg et al. 2008a). Adolescent females, especially immigrants, occupy the lowest dominance ranks. Aggression between parous females, who have established core areas, occurs rarely (Muller et al. 2002; Wakefield 2008). In contrast, mothers often direct aggression toward adolescent nulliparas (Pusey 1980, 1990; Nishida 1989; Townsend et al. 2007; Kahlenberg et al. 2008a; Pusey et al. 2008). Nulliparas seek to establish their own core areas and represent a competitive threat to parous females.

Female chimpanzees have traditionally been characterized as asocial compared to male conspecifics (Wrangham & Smuts 1980; Goodall 1986; Wrangham et al. 1992). At several sites, females spend a large proportion of time alone, or for mothers, only with dependent offspring (reviewed in Watts 2012). Among female chimpanzees, those with dependent offspring are the least gregarious (Wrangham 2000; Williams et al. 2002). The social bonds between female chimpanzees have also been described as relatively weak compared to those between male chimpanzees (Nishida 1968; Goodall 1986; Wrangham et al. 1996). Kin selection theory predicts that social bonds are more likely to develop between individuals who are genetically related. As females are the dispersing sex in chimpanzees, pairs of females who live together are typically unrelated to each other (Vigilant 2001; Langergraber et al. 2009).

Recent research has refined the traditional view of female chimpanzee sociality showing that there is considerable variation in female affiliative behavior within and between chimpanzee communities (reviewed in Watts 2012). Several communities report that some pairs of unrelated female chimpanzees form strong social bonds with each other (Nishida 1989; Boesch & Boesch 2000; Wakefield 2008, 2013; Langergraber et al. 2009; Foerster et al. 2015). However, the factors that influence the formation of these bonds are presently unclear.

## Female chimpanzee parity

In literature on female chimpanzees, discussions of parity often involve comparing mothers to adolescent nulliparas (e.g., Muller et al. 2002; Kahlenberg et al. 2008a; Watts 2007). Although few studies have investigated whether mothers themselves differ, evidence suggests that they do. For example, in the Kasekela chimpanzee community at Gombe, primiparous female chimpanzees delayed subsequent births (Jones et al. 2010) and devoted more time to the care of young infants compared to multiparas (Stanton et al. 2014). At Mahale, primiparas and nulliparas engaged in aggression with one another more often than expected (Nishida 1989). In contrast, aggression between multiparas occurred less often than expected.

In addition, primiparas are typically lower-ranking than multiparas. As noted above, in some chimpanzee communities, females rise in rank with both age (Nishida 1989; Greengrass 2005; Kahlenberg 2006; Murray et al. 2006) and tenure in the community (Kahlenberg et al. 2008a). Primiparous chimpanzees may also be at a disadvantage as they lack familiarity with food resources in the community territory. Such knowledge is likely crucial to female chimpanzees (Wrangham & Smuts 1980; Williams et al. 2002), who appear to become more efficient foragers over time (Murray et al. 2006). Taken together, the preceding observations suggest that primiparous female chimpanzees face challenges not experienced by multiparous females in the contexts of feeding competition and aggression. As a result, these two types of females are expected to differ in their behavior.

I predict parity will influence the behavior of mothers in three specific ways: (1) Primiparas are likely inexperienced competitors and less efficient foragers compared to multiparas. Faced with feeding competition, primiparas may be forced to range more widely than multiparas to acquire food. If primiparas are unable to obtain adequate food, it is also possible that they may minimize their energy expenditure by ranging less widely as multiparas. In either scenario, the individual ranges of primiparas will differ in size compared to those of multiparas. (2) Adolescent nulliparas seek to establish individual ranges, and they likely increase feeding competition where they settle. If primiparas are disproportionately affected by this resource competition compared to multiparas, the former may be involved in intrasexual aggression more often than the latter. (3) Primiparas have had less time to integrate themselves socially with other females in the community. As a result, first-time mothers will show different patterns of intrasexual association and grooming compared to multiparas.

## The Ngogo study site

To investigate whether the behavior of mothers varied with parity, I conducted a 15-month field study of wild chimpanzees at Ngogo in the Kibale National Park, Uganda. The Kibale National Park is located in western Uganda (0°13′-0°41′N and 30°19′-30°32′E). The Ngogo chimpanzees range over a 35 $km^2$ territory near the center of the Park (Mitani et al. 2010). The first studies of the Ngogo chimpanzees took place between 1976 and 1981 (Ghiglieri 1984). Several additional short-term projects were conducted during the late 1980's and early 1990's (Wrangham et al. 1991, 1992; Grieser-Johns 1996). Long-term observations were initiated by D. Watts and J. Mitani in 1995 and the chimpanzees have been observed continuously since then (Mitani 2006; Mitani et al. 2000).

The Ngogo study site lies at a transition between lowland and montane rainforest and comprises moist, evergreen forest interspersed with patches of *Pennisetum purpureum* grassland (Struhsaker 1997). The Ngogo site contains large areas of old growth forest, the preferred habitat of chimpanzees (Lwanga 2006). This habitat contains a high abundance of fruiting trees, such as figs, which compose a large part of the Ngogo chimpanzees' diet (Watts et al. 2012a).

The high-quality habitat at Ngogo supports an exceptionally large chimpanzee community (Potts et al. 2009; Watts et al. 2012a). This provided a relatively large sample of chimpanzee mothers, making Ngogo an ideal site to conduct this study. In addition, an unusual demographic event took place, which provided a unique opportunity to observe the behavior of first-time mothers. Between 2010-2012 the already large community grew from 157 to 190 members, an increase of 20% over about 27 months. During this time, 31 surviving infants were born, 12 of them to first-time mothers. These circumstances permitted a comparison between females who differed in parity.

## Goals of this dissertation

In this dissertation I test the hypothesis that the lives of primiparous female chimpanzees differ from those of multiparas. In chapter 2, I investigate how females use space in the Ngogo community territory. I estimate the size of individual females' ranges and examine how these ranges are distributed throughout the community territory. Following this, I investigate whether parity and other reproductive factors predict the size of individual females' ranges. Transitioning from ranging behavior, in chapters 3 and 4 I focus on social interactions between unrelated females. In chapter 3 I begin by examining rates of female intrasexual aggression. I compare these rates to a prior study at Ngogo and to three studies from other wild chimpanzee communities. Following this, I examine how often mothers directed aggression toward partners in three different parity groups: nulliparas, primiparas, and multiparas. First, I consider mothers of different parity together to determine how parous females, as a group, behave. I then compare patterns of aggression between mothers of different parity to determine if primiparas and multiparas differ. In chapter 4, I analyze affiliative social interactions between females. I investigate how often mothers associated and groomed with partners in three parity groups: nulliparas, primiparas, and multiparas. I examine whether primiparas and multiparas display different patterns of affiliation with unrelated females to determine if social bonds vary with parity.

In chapter 5, I summarize the results from chapters 2, 3 and 4. I then discuss the implications of my findings. The specific goal of these chapters was to evaluate whether the behavior of first-time chimpanzee mothers differs from that of multiparas. Results of my analyses indicate that primiparous and multiparous mothers do, in fact, differ in their social interactions with other females. My findings highlight the importance of considering parity when examining the behavior of chimpanzee mothers. I conclude this dissertation by outlining some directions for future research.

# REFERENCES

Bercovitch, F. B., Lebron, M. R., Martinez, H. S., & Kessler, M. J. (1998). Primigravidity, body weight, and costs of rearing first offspring in rhesus macaques. *American Journal of Primatology*, *46*(2), 135–144. doi:10.1002/(SICI)1098-2345(1998)46:2<135::AID-AJP3>3.0.CO;2-X

Boesch, C. (1996). Social grouping in Taï chimpanzees. In: W. C. McGrew, L. F. Marchant, & T. Nishida (Eds.), *Great ape societies* (pp. 101–113). Cambridge: Cambridge University Press.

Boesch, C., & Boesch-Achermann, H. (2000). *The chimpanzees of the Taï Forest*. Oxford: Oxford University Press.

Chapman, C. A., Wrangham, R. W., & Chapman, L. J. (1995). Ecological constraints on group size: An analysis of spider monkey and chimpanzee subgroups. *Behavioral Ecology and Sociobiology*, *36*(1), 59– 70. doi:10.1007/BF00175729

Emery Thompson, M. (2013). Reproductive ecology of female chimpanzees. *American Journal of Primatology, 75*(3), 222–237. doi:10.1002/ajp.22084

Emery Thompson, M., Kahlenberg, S. M., Gilby, I. C., & Wrangham, R. W. (2007). Core area quality is associated with variance in reproductive success among female chimpanzees at Kibale National Park. *Animal Behaviour*, *73*(3), 501–512. doi:10.1016/j.anbehav.2006.09.007

Foerster, S., McLellan, K., Schroepfer-Walker, K., Murray, C. M., Krupenye, C., Gilby, I. C., & Pusey, A. E. (2015). Social bonds in the dispersing sex: Partner preferences among adult female chimpanzees. *Animal Behaviour*, *105*, 139-152. doi:10.1016/j.anbehav.2015.04.012

Ghiglieri, M. P. (1984). *The chimpanzees of Kibale Forest*. New York, NY: Columbia University Press.

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

Goodall, J., Bandora, A., Bermann, E., Busse, C., Matama, H., Mpongo, E., Pierce, A. & Riss, D. (1979). Intercommunity interactions in the chimpanzee population of the Gombe National Park. In: D. A. Hamburg & E. R. McCown (Eds.), *The great apes* (pp. 13–53). Menlo Park, CA: Benjamin/Cummings.

Greengrass, E. (2005). *Sociability and dominance among female chimpanzees at Gombe*. Ph.D. thesis. University of Bristol, Bristol, U.K.

Johns, B. G. (1996). Responses of chimpanzees to habituation and tourism in the Kibale Forest, Uganda. *Biological Conservation*, *78*(3), 257-262. doi:10.1016/S0006-3207(96)00044-4

Guardini, G., Bowen, J., Raviglione, S., Farina, R., & Gazzano, A. (2015). Maternal behaviour in domestic dogs: A comparison between primiparous and multiparous dogs. *Dog Behaviour*, *1*, 23-33. doi:10.4454/DOGB.V1I1.004

Hinde, K., Power, M. L., & Oftedal, O. T. (2009). Rhesus macaque milk: Magnitude, sources, and consequences of individual variation over lactation. *American Journal of Physical Anthropology, 138*(2), 148–157. doi:10.1002/ajpa.20911

Jones, J. H., Wilson, M. L., Murray, C., & Pusey, A. (2010). Phenotypic quality influences fertility in Gombe chimpanzees. *Journal of Animal Ecology*, *79*(6), 1262–1269. doi:10.1111/j.1365-2656.2010.01687.x

Kahlenberg, S. M. (2006). *Female-female competition and male sexual coercion in Kanyawara chimpanzees*. Ph.D. thesis. Harvard University, Cambridge, MA.

Kahlenberg, S. M., Emery Thompson, M., Muller, M. N., & Wrangham, R. W. (2008a). Immigration costs for female chimpanzees and male protection as an immigrant counterstrategy to intrasexual aggression. *Animal Behaviour*, *76*(5), 1497-1509. doi:10.1016/j.anbehav.2008.05.029

Kahlenberg, S. M., Emery Thompson, M., & Wrangham, R. W. (2008b). Female competition over core areas in *Pan troglodytes schweinfurthii*, Kibale National Park, Uganda. *International Journal of Primatology*, *29*(4), 931-947. doi:10.1007/s10764-008-9276-3

Kawanaka, K., & Nishida, T. (1975). Recent advances in the study of inter-unit-group relationships and social structure of wild chimpanzees of the Mahale Mountains. In: *The Proceedings from the Symposia of the 5th Congress of the International Primatological Society. Japan Science Press, Nagoya* (pp. 173-186).

Langergraber, K., Mitani, J., & Vigilant, L. (2009). Kinship and social bonds in female chimpanzees (*Pan troglodytes*). *American Journal of Primatology*, *71*(10), 840-851. doi:10.1002/ajp.20711

Lwanga, J. S. (2006). Spatial distribution of primates in a mosaic of colonizing and old growth forest at Ngogo, Kibale National Park, Uganda. *Primates*, *47*(3), 230-238. doi:10.1007/s10329-005-0173-5

Matsumoto-Oda, A., Hosaka, K., Huffman, M. A., & Kawanaka, K. (1998). Factors affecting party size in chimpanzees of the Mahale mountains. *International Journal of Primatology*, *19*(6), 999–1011. doi:10.1023/A:1020322203166

Miller, J. A., Pusey, A. E., Gilby, I. C., Schroepfer-Walker, K., Markham, A. C., & Murray, C. M. (2014). Competing for space: Female chimpanzees are more aggressive inside than outside their core areas. *Animal Behaviour*, *87*, 147-152.

doi:10.1016/j.anbehav.2013.10.023

Mitani, J. C. (2006). Demographic influences on the behavior of chimpanzees. *Primates*, *47*(1), 6-13. doi:10.1007/s10329-005-0139-7

Mitani, J. C., Merriwether, D. A., & Zhang, C. (2000). Male affiliation, cooperation and kinship in wild chimpanzees. *Animal Behaviour*, *59*(4), 885-893. doi:10.1006/anbe.1999.1389

Mitani, J. C., Watts, D. P., & Amsler, S. J. (2010). Lethal intergroup aggression leads to territorial expansion in wild chimpanzees. *Current Biology*, *20*(12), R507-R508. doi:10.1016/j.cub.2010.04.021

Muller, M. (2002). Agonistic relations among Kanyawara chimpanzees. In: C. Boesch, G. Hohmann, & L. F. Marchant (Eds.), *Behavioural diversity in chimpanzees and bonobos* (pp. 112–124). Cambridge: Cambridge University Press.

Murray, C. M., Eberly, L. E., & Pusey, A. E. (2006). Foraging strategies as a function of season and rank among wild female chimpanzees (*Pan troglodytes*). *Behavioral Ecology, 17*(6), 1020–1028. doi:10.1093/beheco/arl042

Murray, C. M., Mane, S. V., & Pusey, A. E. (2007). Dominance rank influences female space use in wild chimpanzees (*Pan troglodytes*): Towards an ideal despotic distribution. *Animal Behaviour*, *74*(6), 1795–1804. doi:10.1016/j.anbehav.2007.03.024

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: D. A. Hamburg, & E. R. McCown (Eds.), *The great apes* (pp. 72–121). Menlo Park, CA: Benjamin/Cummings.

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

Nishida, T., & Hiraiwa-Hasegawa, M. (1987). Chimpanzees and bonobos: Cooperative relationships among males. In: B. B. Smuts, D. L. Cheney, R. M. Seyfarth, R. W. Wrangham, & T. T. Struhsaker (Eds.), *Primate societies* (pp. 165–177). Chicago: University of Chicago Press.

Pauli, J., Lloyd, M., Kunselman, T., Stetter, A. R., Dodson, C. M., Legro, W. C., & Arch, R. S. (2013). Effect of adolescent pregnancy on final adult height in non-Hispanic white women. *Archives of Gynecology and Obstetrics*, *288*(3), 679-682. doi:10.1007/s00404-013-2781-4

Potts, K. B., Chapman, C. A., & Lwanga, J. S. (2009). Floristic heterogeneity between forested sites in Kibale National Park, Uganda: Insights into the fine-scale determinants of density in a large-bodied frugivorous primate. *Journal of Animal Ecology*, *78*(6), 1269-1277. doi:10.1111/j.1365-2656.2009.01578.x

Pusey, A. E. (1980). Inbreeding avoidance in chimpanzees. *Animal Behaviour*, *28*(2), 543–552. doi:10.1016/S0003-3472(80)80063-7

Pusey, A. E. (1990). Behavioural changes at adolescence in chimpanzees. *Behaviour*, *115*(3), 203-246.

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. *International Journal of Primatology, 29*(4), 949-973. doi:10.1007/s10764-008-9281-6

Rah, J. H., Christian, P., Shamim, A. A., Arju, U. T., Labrique, A. B., & Rashid, M. (2008). Pregnancy and lactation hinder growth and nutritional status of adolescent girls in rural Bangladesh. *Journal of Nutrition*, *138*(8), 1505-1511.

Seyfarth, R. M., & Cheney, D. L. (2012). The evolutionary origins of friendship. *Annual Review of Psychology*, *63*, 153-177. doi:10.1146/annurev-psych-120710-100337

Setchell, J. M., Lee, P. C., Wickings, E. J., & Dixson A. F. (2002). Reproductive parameters and maternal investment in mandrills (*Mandrillus sphinx*). *International Journal of Primatology*, *23*(1), 51–68. doi:10.1023/A:1013245707228

Skogland, T. (1989). Natural selection of wild reindeer life history traits by food limitation and predation. *Oikos*, 101-110. doi:10.2307/3565879

Stanton, M. A., Lonsdorf, E. V., Pusey, A. E., Goodall, J., & Murray, C. M. (2014). Maternal behavior by birth order in wild chimpanzees (*Pan troglodytes*): Increased investment by first-time mothers. *Current Anthropology*, *55*(4), 483-489. doi:10.1086/677053

Stearns, S. C. (1992). *The evolution of life histories* (Vol. 249). Oxford: Oxford University Press.

Struhsaker, T. T. (1997). *Ecology of an African rain forest*. Gainesville, FL: University Press of Florida.

Townsend, S. W., Slocombe, K. E., Emery Thompson, M., & Zuberbühler, K. (2007). Female-led infanticide in wild chimpanzees. *Current Biology*, *17*(10), 355–356. doi:10.1016/j.cub.2007.03.020

Trivers, R. L. (1972). Parental investment and sexual selection. In: B. Campbell (Ed.), *Sexual selection and the descent of man* (pp. 136–179). Chicago, IL: Aldine.

Vigilant, L., Hofreiter, M., Siedel, H., & Boesch, C. (2001). Paternity and relatedness in wild chimpanzee communities. *Proceedings of the National Academy of Sciences*, *98*(23), 12890-12895. doi:10.1073/pnas.231320498

Wakefield, M. (2008). Grouping patterns and competition among female *Pan troglodytes schweinfurthii* at Ngogo, Kibale National Park, Uganda. *International Journal of Primatology*, *29*(4), 907-929. doi:10.1007/s10764-008-9280-7

Wakefield, M. L. (2013). Social dynamics among females and their influence on social structure in an East African chimpanzee community. *Animal Behaviour*, *85*(6), 1303-1313. doi:10.1016/j.anbehav.2013.03.019

Wang, Z., & Novak, M. A. (1994). Alloparental care and the influence of father presence on juvenile prairie voles, *Microtus ochrogaster*. *Animal Behaviour*, *47*(2), 281-288. doi:10.1006/anbe.1994.1040

Watts, D. P. (2007). Effects of male group size, parity, and cycle stage on female chimpanzee copulation rates at Ngogo, Kibale National Park, Uganda. *Primates*, *48*(3), 222-231. doi:10.1007/s10329-007-0037-2

Watts, D. P. (2012). Long-term research on chimpanzee behavioral ecology in Kibale National Park, Uganda. In: P. M. Kappeler & D. P. Watts (Eds.), *Long-term field studies of primates* (pp. 313-338). New York, NY: Springer.

Watts, D. P., Potts, K. B., Lwanga, J. S., & Mitani, J. C. (2012). Diet of chimpanzees (*Pan troglodytes schweinfurthii*) at Ngogo, Kibale National Park, Uganda, 1. Diet composition and diversity. *American Journal of Primatology*, *74*(2), 114-129. doi:10.1002/ajp.21016

Williams, J. M., Pusey, A. E., Carlis, J. V., Farm, B. P., & Goodall, J. (2002). Female competition and male territorial behaviour influence female chimpanzees' ranging patterns. *Animal Behaviour*, *63*(2), 347–360. doi:10.1006/anbe.2001.1916

Wrangham, R. W. (1977). Feeding behaviour of chimpanzees in Gombe National Park, Tanzania. In: T. H. Clutton Brock (Ed.), *Primate ecology* (pp. 503–538). London: Academic Press.

Wrangham, R. W. (1979). On the evolution of ape social systems. *Social Science Information Sur Les Sciences Sociales*, *18*(3), 335–368. doi:10.1177/053901847901800301

Wrangham, R. W. (2000). Why are male chimpanzees more gregarious than mothers? A scramble competition hypothesis. In: P. M. Kappeler (Ed.), *Primate males* (pp. 248–258). Cambridge: Cambridge University Press.

Wrangham, R. W., & Smuts, B. B. (1980). Sex differences in the behavioral ecology of chimpanzees in the Gombe National Park, Tanzania. *Journal of Reproduction and Fertility*, *28*, 13–31.

Wrangham, R. W., Conklin, N. L., Chapman, C. A., & Hunt, K. D. (1991). The significance of fibrous foods for Kibale Forest chimpanzees. *Philosophical Transactions of the Royal Society of London. Series B, Biological Science*s, *334*(1270), 171–178. doi:10.1098/rstb.1991.0106

Wrangham, R. W., Clark, A., & Isabirye-Basuta, G. (1992). Female social relationships and social organization of Kibale Forest chimpanzees. In: T. Nishida, W. C. McGrew, P. Marler, M. H. Pickford, & F. B. M. de Waal (Eds.), *Topics in primatology, vol. 1: Human origins* (pp. 81–98). Tokyo: Tokyo University Press.

Wrangham, R. W., Chapman, C. A., Clark-Arcadi, A. P., & Isabirye-Basuta, G. (1996). Social ecology of Kanyawara chimpanzees: implications for understanding the costs of great ape groups. In: W.C. McGrew, L.F. Marchant, & T. Nishida (Eds.), *Great ape societies* (pp. 45-57). Cambridge: Cambridge University Press.

Wrangham, R. W., Conklin-Brittain, N. L., & Hunt, K. D. (1998). Dietary response of chimpanzees and cercopithecines to seasonal variation in fruit abundance. I. Antifeedants. *International Journal of Primatology*, *19*(6), 949–970. doi:10.1023/A:1020318102257

Zedrosser, A., Dahle, B., Støen, O. G., & Swenson, J. E. (2009). The effects of primiparity on reproductive performance in the brown bear. *Oecologia*, *160*(4), 847-854. doi:10.1007/s00442-009-1343-8

# CHAPTER 2

## Ranging behavior of female chimpanzees at Ngogo, Kibale National Park, Uganda

### INTRODUCTION

For female mammals, who invest heavily in reproduction through gestation, lactation, and offspring care, fitness is limited by the ability to acquire food and convert it into offspring (Emlen & Oring 1977; Trivers 1972). As they search for food, primate females restrict their movements to a specific area, the home range, defined as the area covered during normal day-to-day activities (Burt 1943). In heterogeneous habitats, food availability varies across the landscape, influencing the kinds of ranges occupied by females (Ostfeld 1990; Benson & Chamberlain 2007; Murray et al. 2007), and females are expected to compete for access to high quality areas (Sterck et al. 1997). Variation in home range location and size can lead to unequal division of resources among competitors, resulting in differential reproductive success (Adams 2001; Murray et al. 2007).

One important characteristic of a female's home range is the degree of overlap with ranges of same-sex competitors. This is greatly influenced by the abundance and distribution of resources. When food is plentiful, the costs of feeding competition are low, and home ranges of multiple individuals or groups can overlap (Bennett 1986; Rogers 1987). When food is limited, individuals (or groups) may differentiate their ranging to avoid potentially costly competition (e.g., red squirrels (*Sciurus vulgaris*), Wauters et al. 2005; elephant seals (*Mirounga leonina*), Field et al. 2005). For example, in high-quality habitats, individual female black bears (*Ursus americanus*) had extensively overlapping home ranges, while in low-quality habitats, female bears had little home range overlap (Powell 1986).

In addition to food availability, a female's reproductive status is another important factor influencing her space use. Female mammals face varying constraints during different stages of their reproductive careers. For example**,** sexually receptive females range more widely than females with dependent offspring, who are lactating (e.g., brown bears (*Ursus arctos*), Dahle & Swenson 2003; orangutans (*Pongo pygmaeus*), Wartmann et al. 2008; chimpanzees (*Pan troglodytes*), Wrangham & Smuts 1980; Goodall 1986; Hasegawa 1990; Bates & Byrne 2009). Because lactation is the most energetically expensive period in a female mammal's reproductive career, females who are nursing young may not be able to range as widely as females who do not have dependent infants. In contrast, it is also possible that females with dependent offspring are forced to range more widely than non-lactating females, in order to access enough food to meet their energetic requirements (e.g., roe deer (*Capreolus capreolus*), Tufto et al. 1996).

Traveling with dependent offspring may also influence a female's use of space. Female moose (*Alces alces*) restrict their ranging shortly after parturition. Moose mothers travel more over time as their calves become more mobile (van Beest et al. 2011). In many primate taxa, mothers carry young infants while traveling, which may force them to travel more slowly or range less widely (Altmann & Samuels 1992; Ross 2000; Boesch & Boesch-Achermann 2000; Williams et al. 2002a; Wrangham 2000). In contrast, one study of chimpanzees found that the presence of older dependent offspring, rather than a carried infant, impeded chimpanzee mothers' ranging (Pontzer & Wrangham 2006). Although older infants and juveniles can travel without being carried, they do not travel as efficiently as adults, which is likely related to their small stature (Pontzer & Wrangham 2006).

If the presence of infants and juveniles affects maternal ranging abilities, then it is reasonable to hypothesize that parity, more generally, may influence female movements. There are several reasons why it may be challenging for primiparous females ("primiparas", i.e., mothers who have given birth for the first time) to acquire food and nourish offspring compared to multiparous females (i.e., females who have borne more than one offspring). First, primiparas may not yet have completed growth, requiring them to continue investing in their own growth and maturation (Bercovitch et al. 1998; Setchell et al. 2002; Rah et al. 2008). Second, primiparas are also physiologically immature, which can reduce the efficiency of lactation (Hinde et al. 2009). Third, primiparas may be at a disadvantage compared to multiparas because they lack familiarity with food resources. Such knowledge is likely crucial to females in species that rely on a diet of fruit, a resource whose availability fluctuates in time and space (e.g., fruit bats (*Rousettus aegyptiacus*), Holland et al. 2005; gibbons (*Hylobates lar*), Asensio et al. 2011; Order Primates, Zuberbuhler & Janmaat 2010). Taken together, these observations suggest that, faced with the challenges of giving birth for the first time while obtaining adequate food, primiparous mothers may exhibit different patterns of space use than do multiparas. If primiparas are unable to obtain adequate food, they may minimize their energy expenditure by ranging less widely as multiparas. On the other hand, primiparas may be forced to range more widely than multiparas to obtain adequate food.

Chimpanzees (*Pan troglodytes*) provide an opportunity to investigate the effects of reproductive state on female ranging. Chimpanzees are frugivorous primates living in multi-female, multi-male communities, whose individuals form temporary subgroups or parties

(Nishida 1968). Community members share a territory, which males cooperatively defend against neighboring chimpanzee communities (Goodall et al. 1979; Watts & Mitani 2001). Females typically disperse from their natal communities during adolescence when they are around 12-13 years old, and they begin to reproduce about two years later after integrating themselves into their new communities (Emery Thompson 2013). Chimpanzees are long-lived, and it is not uncommon to find immigrant nulliparas together with primiparas and older multiparas.

Patterns of female space use vary across chimpanzee communities. In West African chimpanzee communities, females move across the entire territory and utilize different parts relatively uniformly (Taï: Lehmann & Boesch 2005; Bossou: Sugiyama 1988; Sakura 1994). In contrast, parous females in several East African chimpanzee communities occupy small individual ranges within the communal territory (Gombe: Williams et al. 2002b; Murray et al. 2007; Kanyawara: Wrangham et al. 1996; Kahlenberg et al. 2008a; Mahale: Hasegawa 1989). Individual ranges overlap and cluster into spatial neighborhoods (Williams et al. 2002b; Emery Thompson et al. 2007).

By concentrating space use in small individual ranges, females reduce the need for frequent and potentially costly competition (Wrangham 1979). This is supported by observations of female intrasexual aggression, which occurs rarely in East African chimpanzees, except in the context of establishing individual ranges. Aggression between parous female chimpanzees, who have established ranges, occurs rarely (Goodall 1986; Muller 2002; Kahlenberg et al. 2008a). In contrast, parous females behave aggressively toward immigrant nulliparas (Pusey 1980, 1990; Nishida 1989; Townsend et al. 2007; Kahlenberg et al. 2008a; Pusey et al. 2008), which may function to prevent nulliparas from settling. Immigrants likely increase feeding competition where they settle, making them the primary competitive threat to parous females.

Here, I investigate the ranging behavior of female chimpanzees at Ngogo in the Kibale National Park, Uganda. To date, relatively little is known about the ranging behavior of females in the Ngogo community, which lies within a productive habitat and is exceptionally large (Watts 1998; Watts & Mitani 2001; Mitani & Amsler 2003). This study took place during an unusual period of growth in the size of the community. Between 2010 and 2012, 31 surviving infants were born, 12 of them to first-time mothers. These circumstances permitted a comparison of space use across females who varied in reproductive state. In what follows, I examine two issues. First, I quantified individual ranges of nulliparous and parous females and examined how these ranges are distributed in the community territory. Specifically, I sought to determine whether individual females used the territory similarly or whether they displayed differences in their use of space. Second, I analyzed whether reproductive cycle stage, parity, and the presence of dependent offspring affected the size of females' home ranges.

## METHODS

### Study site and subjects

I observed chimpanzees at Ngogo in the Kibale National Park, Uganda. The Kibale Park is located in western Uganda (0°13′-0°41′N and 30°19′-30°32′E) and covers 795 $km^2$. The Ngogo chimpanzee community ranges over a 35 $km^2$ territory near the center of the Park (Mitani et al. 2010). Rain falls throughout the year with an annual mean of 1397 mm ± 174 mm (N=10 years, 1998-2007; Mitani 2009). Typically, September-December and March-May are wetter than average, while intervening months are drier (Butynski 1990; Struhsaker 1997). At an elevation of approximately 1350 m above sea level, the Ngogo study site lies at a transition between lowland and montane rainforest and comprises moist, evergreen forest interspersed with patches of *Pennisetum purpureum* grassland (Struhsaker 1997). Detailed descriptions of Ngogo and the ecology of the area can be found in Butynski (1990); Ghiglieri (1984); Struhsaker (1997); Lwanga et al. (2000).

I collected data over 12 months from August 2011 to July 2012. During this time the Ngogo chimpanzee community had 17-20 adolescents and 50-51 adult females. I observed 31 females with dependent offspring including 13 primiparas (mothers raising their first offspring), and 14 multiparas (mothers with two or more offspring). Four additional subjects gave birth during the study; one transitioned from adolescence to primiparity, and three transitioned from primiparity to multiparity, for a total of 14 primiparas and 17 multiparas by the end of the study.

In addition to the parous study subjects, I recorded observations on eight nulliparous adolescent females. I used the sample of nulliparous females as a comparison group for the parous female subjects. Six of the adolescent nulliparas were natal, and two of them were immigrants. The natal adolescent females ranged in age from 10-16 years. Because the immigrant females dispersed into the Ngogo community from elsewhere, their histories and ages were unknown. Although natal and immigrant adolescent females differ in several respects (Nishida et al. 2003; Kahlenberg et al. 2008a), I treated them as a single category because they neither lactate nor care for dependent offspring. While female chimpanzees typically disperse from their natal communities at adolescence (Nishida & Kawanaka 1972; Pusey & Packer 1987), some females at Ngogo do not disperse, instead remaining and reproducing there.

During the study period, the Ngogo chimpanzee community increased from 173 to 190 members. This growth was primarily due to births, but three immigrant females contributed to this increase by entering the Ngogo community during the course of this study. One infant died from an inferred intra-community infanticide (K. Langergraber, unpublished data) in the eighth month of the year-long study. The infanticide victim was a neonate born to a first-time mother. After the infanticide I continued to classify the female subject as an adolescent nullipara, not a primipara, because the majority of observations collected on this female took place prior to parturition, when she was an adolescent. Also, no observations were collected during the few days when her infant was alive. No other community members died during the study period.

### Data collection

During this study, I conducted approximately 1100 one-hour focal follows (Altmann 1974) on individual parous females. On a given day, I collected no more than two focals per individual, with observation sessions separated by at least two hours. I recorded observations of female space use in the community territory using a handheld global positioning system (GPS) device. During focal observations, I recorded a location point during the first and last minute of each focal follow. I considered a focal follow complete if the target female was in sight for at least 50 minutes. I also recorded the locations of non-focal females *ad libitum* as I encountered them throughout the day. When recording spatial locations I noted the geographic coordinates, date, time of day, and identity of all adult and adolescent females in association at that location. Association was defined as all chimpanzees that I judged to be within visual range of the focal female (Pepper et al. 1999; Mitani et al. 2002).

With the help of field assistants, I monitored adult and adolescent females’ reproductive cycles. Sexual swellings of females were scored daily based on turgidity, following Dahl et al. (1991). I considered females exhibiting maximally tumescent swellings to be sexually receptive (Tutin 1979).

### Spatial analyses

My goal was to determine how females utilized space within the community territory during normal daily activities. Female subjects sometimes participated in territorial boundary patrols and inter-group encounters with neighboring communities. These activities can be defined using spatial and behavioral criteria (see Watts & Mitani (2001) and Mitani & Watts (2005) for detailed descriptions). As chimpanzees generally move outside areas of typical use during these activities (Goodall 1986; Mitani & Watts 1999; Boesch & Boesch-Achermann 2000; Watts & Mitani 2001; Amsler 2009), I excluded observations of females recorded during these times.

I analyzed a subset of ranging data that included one location point per female per 50-minute time period, which was the minimum length of a focal follow. This approach is similar to prior studies at Ngogo (Amsler 2009; Langergraber et al. 2009) in which researchers utilized one point per individual per 30-minute time period. If I observed a female in multiple locations during a single 50-minute time period, I used the first recorded point. After restricting the dataset to one location per female per 50-minute period, I plotted each individual’s set of points on a map of the Ngogo territory to delineate the area utilized.

A home range is the area utilized by an individual during normal activities, while a core area represents the most frequently used part of the home range (Burt 1943). Studies of chimpanzees often report the size of a female’s core area, representing the smallest area where a female spends a subset of her time (e.g., 50% (Murray et al. 2007) or 80% of time (Wrangham & Smuts 1980)). However, as the present study took place over a relatively short time period (one year), I chose to calculate home range size, to avoid excluding valuable ranging information.

To estimate female home range size, I employed the minimum convex polygon (MCP) method, a procedure that has been utilized in previous studies of female primates (e.g., chimpanzees: Hasegawa 1990; Boesch & Boesch-Achermann 2000; Herbinger et al. 2001; Mitani & Amsler 2003; Williams et al. 2004; spider monkeys (*Ateles paniscus chamek*): Symington 1988; orangutans (*Pongo pygmaeus*): Singleton & van Schaik 2001). Minimum Convex Polygons are delineated by connecting the most peripheral ranging points in a sample with straight lines, creating a convex polygon whose internal angles measure less than 180 degrees (Worton 1987). Prior to computing MCPs, I examined each female's set of location points for spatial outliers, as these greatly affect the size of MCPs (Worton 1995). To detect outliers, I first calculated the centroid of each subject's set of ranging points. For a set of locations, the centroid is the arithmetic mean of all x and y values, which correspond to measurements of latitude and longitude. The centroid represents the 'average location' of a female's ranging points. Following this, I calculated the distance between an individual's centroid and each of her ranging points. I then computed the mean of these distances. For a given individual's location points, some spatial outliers had an unusually large distance to the centroid relative to other centroid-point distances. I defined outliers as points with a distance-to-centroid that exceeded the mean plus three standard deviations. Although the 'mean plus three standard deviations' is a rule of thumb (Sun & Chawla 2004), it approximates more complicated algorithms designed to detect spatial outliers (Knorr & Ng 1998). Following the exclusion of outliers, I constructed MCPs in ArcMap 10.2.2 using the minimum bounding geometry tool with a convex hull. I calculated each polygon's area in square kilometers, which corresponded to an individual female's home range.

### Home range overlap

Females in some East African chimpanzee communities form spatial subgroups known as 'neighborhoods' in which a subset of females have overlapping ranges located in the same part of their community's territory (Kanyawara: Emery Thompson et al. 2007; Mahale: Hasegawa 1990; Gombe: Williams et al. 2002b). I sought to determine whether females at Ngogo formed spatial subgroups. To do so, I examined home range overlap by overlaying individual MCPs two at a time on a map of the Ngogo trail system and measuring the area of overlap. I then calculated an index of range overlap, following Kernohan et al. (2001):

$$HR_{i,j} = A_{i,j} / A_i$$

where $HR_{ij}$ is the proportion of female *i*'s home range that is overlapped by female *j*'s home range, $A_{ij}$ is the area of overlap between the two females' home ranges, and $A_i$ is the area of female *i*'s home range. As individual home ranges vary in size (Williams et al. 2002b; Murray et al. 2007), typically $HR_{i,j} \neq HR_{j,i}$ (the indices are asymmetric). I measured the strength of association between the proportion of dyadic overlap from female *i's* and *j's* perspective. Upon inspection, I found the indices were bimodal, rather than normally distributed. As a result, I utilized Kendall's tau coefficient, a non-parametric correlation procedure, to compare overlap indices.

To identify subgroups of females with similar space use patterns, I used hierarchical cluster analyses implementing the unweighted pair-groups method using arithmetic averages (UPGMA, Sneath & Sokal 1973). I used the home range overlap indices to construct a similarity matrix between female subjects and computed squared Euclidean distances for the UPGMA analysis. The UPGMA approach is a simple, agglomerative (bottom-up) hierarchical clustering technique (Norušis 2012). At each step, the two clusters that are closest in distance are combined into a higher-level cluster. The distance between any two clusters is calculated as the mean distance between all pairs of objects in the different clusters. Here, a high index of ranging overlap indicates similarity and a short distance between individuals. The cluster analysis produces a dendrogram, a visual representation of the distance matrix, depicting spatial overlap between individual females. I identified clusters of females with similar space use by determining the cutoff points that produced well-defined clusters with the deepest branches, i.e., the greatest distance between subsequent splitting events or clusters (Romesburg 2004). I considered females assigned to the same cluster as belonging to a spatial neighborhood. I estimated the extent of each neighborhood by delineating a MCP from the combined location points of all females in a cluster (spatial outliers excluded).

Next, I sought to determine whether females used parts of the territory with varying intensity. I overlaid a map of the Ngogo trail system with 100x100-m grid cells. I projected the location points of all females onto the gridded map and summed the number of points that fell within each cell. I classified females' usage of each cell according to this sum, using the 'natural breaks' method (Jenks 1967). This resulted in three classes of intensity of use: low (1-12 points), medium (13-42 points), and high (43-138 points).

Following this, I investigated factors that might have affected the size of females' home ranges. I modeled home range size using a series of generalized linear models (GLM1). I included two predictor variables that apply to both adolescent nulliparas and parous females: reproductive cycle stage and parity (Table 1). I also included neighborhood affiliation as a predictor, as studies from other communities indicate that female ranging patterns and food availability can vary among neighborhoods (Williams et al. 2002b; Emery Thompson et al. 2007). Lastly, I included the number of location points per female as a predictor because home range estimates can be influenced by the number of observations in a sample (Bekoff & Mech 1984; Seaman et al. 1995).

**Table 2.1**. Summary of predictor variables for models predicting home range size (GLM1)

| | Variables | Categories |
|---|---|---|
| 1 | Reproductive cycle stage | Cycling; lactation 1 (0 – 6 months); lactation 2 (6 months – weaning); transition from pregnancy to lactation |
| 2 | Parity | Nulliparous, primiparous, multiparous |
| 3 | Neighborhood | Central, West |
| 4 | Number of location points | - |

I built GLMs representing all combinations of predictor variables and compared them using Akaike's Information Criterion with correction for small sample sizes (AICc). I also compared models using Akaike model weights (Burnham & Anderson 2002). I report model-averaged β coefficients and standard errors for each predictor across the three top models (i.e., for which summed AICc weight > 0.95).

I classified all adolescent nulliparas as 'cycling'. This included four natal adolescents who had not yet displayed maximal swelling size (see Pusey 1990). I classified parous subjects as ‘cycling’ only if they cycled during the majority of the study. The energetic burden of lactation is especially high in chimpanzees during the first six months following birth (Emery Thompson et al. 2012). As a result, I divided lactation into two stages: birth to six months (‘lactation 1’), and seven months to weaning (‘lactation 2’). I categorized mothers in the ‘lactation 1’ category only if the entire six-month period occurred during the study (i.e., only females who gave birth at the beginning or middle of the study year could exhibit lactation 1). I also conducted analyses with lactation condensed into a single category. Results of this analysis did not change the overall outcome of findings generated by dividing lactation into two categories. In what follows, I report results with lactation divided into two categories.

During the study, four females transitioned between parity groups. One primipara gave birth to her second infant in the third month of the study and I classified her as a multipara. Three additional females transitioned categories halfway through the study (one from nullipara to primipara, and two from primipara to multipara). I categorized these females in the parity category to which they transitioned (but utilized individual ranging data collected throughout the study). However, as the categorization of the three latter females is somewhat arbitrary, I repeated the analyses with the three “ambiguous” transitioning females in the parity group from which they transitioned. This did not change the overall outcome of results. I also investigated the effect of neighborhood affiliation, as it is possible that range size is influenced by factors specific to a neighborhood.

Next, I conducted a second set of GLMs (GLM2) examining the factors that influence home range size using only parous subjects. I sought to determine whether traveling with dependent offspring affected the ranging patterns of chimpanzee mothers. I included six predictor variables (Table 2.2) including the four variables utilized in the first set of GLMs (GLM1) and two variables that apply only to mothers: 1) presence of an infant age 0-2.9 years, and 2) presence of an infant older than three years and/or presence of a juvenile offspring. I coded each as a bivariate (yes/no) variable. Following Pontzer & Wrangham (2006), I chose three years as the cutoff between categories because observations from several chimpanzee communities indicate that by this age offspring start to travel independently, i.e., with the mother but without being carried (Goodall 1986; Doran 1992; Hiraiwa-Hasegawa 1990). Age designations for juvenile females were 5.0-9.9 years old. Juvenile males ranged from 5.0 years until the visible descent of testicles, which occurs between ages 10.0-11.0 years at Ngogo (Watts 2015).

I built GLMs representing all combinations of predictor variables and compared them using Akaike's Information Criterion with correction for small sample sizes (AICc) and Akaike model weights (Burnham & Anderson 2002). I report model-averaged β coefficients and standard errors for each predictor across the 22 top models (i.e., for which summed AICc weight > 0.95).

**Table 2.2**. Summary of predictor variables for models predicting home range size (GLM2)

| | Predictor variable | Categories |
|---|---|---|
| 1 | Reproductive cycle stage | Cycling; lactation 1 (0 – 6 months); lactation 2 (six months – weaning); transition from pregnancy to lactation |
| 2 | Parity | Nulliparas, primiparous, multiparous |
| 3 | Infant less than three years of age | Yes/no |
| 4 | Infant more than three years of age and/or a juvenile | Yes/no |
| 5 | Neighborhood | Central or West |
| 6 | Number of location points | - |

Spatial analyses were conducted using ArcMap, version 10.3.1 (© ESRI). Cluster and correlation analyses were conducted using SPSS for Macintosh, version 22 (© IBM

Corporation). Linear regression and model selection was conducted using the lme4 package in R, version 3.2.0 (R Core Team 2015).

## RESULTS

### Female space use

I recorded approximately 5300 locations of individual female subjects during the 12-month study. I detected 75 spatial outliers in the dataset with individuals having 0-4 outliers each. After excluding these outliers, individual females had an average of 140 location points (SD=37, range 59-222).

A MCP delineated from the location points of all female subjects indicated they ranged over 20.2 $km^2$ within the larger Ngogo community territory (Figure 2.1). Individual MCPs revealed that each female subject concentrated her space use to a home range within the Ngogo chimpanzee community territory (Figure 2.2). Home ranges were spread throughout the community territory and varied in size from 4.5-9.7 $km^2$ (mean=6.8, SD=1.3).

**Fig. 2.1** Minimum convex polygon estimating space use of female chimpanzee subjects. Polygon overlays the Ngogo trail system; dot denotes the centroid of the polygon and is in the same location on each figure for ease of comparison.

**Fig. 2.2** Minimum convex polygons estimating space use of individual female chimpanzees. Dot denotes the centroid of the minimum convex polygon delineated from all females' location points (see Fig 2.1).

Proportions of overlap between any two females' home ranges varied between 0.03-1.00. As home ranges differed in size, the proportion of overlap varied depending on the perspective of each female in a dyad. The two proportions of overlap from each dyad were correlated (N=703, Kendall's $\tau=0.61$, $P<0.01$). Overlap values were bimodally distributed indicating that dyadic similarity tended to be either high or low. Results of the cluster analysis based on dyadic home range overlap indicated that female subjects formed two distinct clusters representing subgroups of individuals with similar ranging patterns (Figure 2.3).

To reveal the extent of each neighborhood, I delineated MCPs from the ranging points of females assigned to each of the two clusters. One neighborhood was located in the central part of the territory, while the other was located in the western part (Figure 2.4). The central and western neighborhoods shared a 7.2 $km^2$ area of overlap. The two neighborhoods are compared in Table 2.3. It should be noted that subjects in the present study were a subset of the large number of females at Ngogo. I preferentially collected observations in the central and western neighborhoods, as females there were better habituated than those who ranged in the eastern part of the territory (personal observation). It is likely that an additional neighborhood existed in the eastern part of the territory.

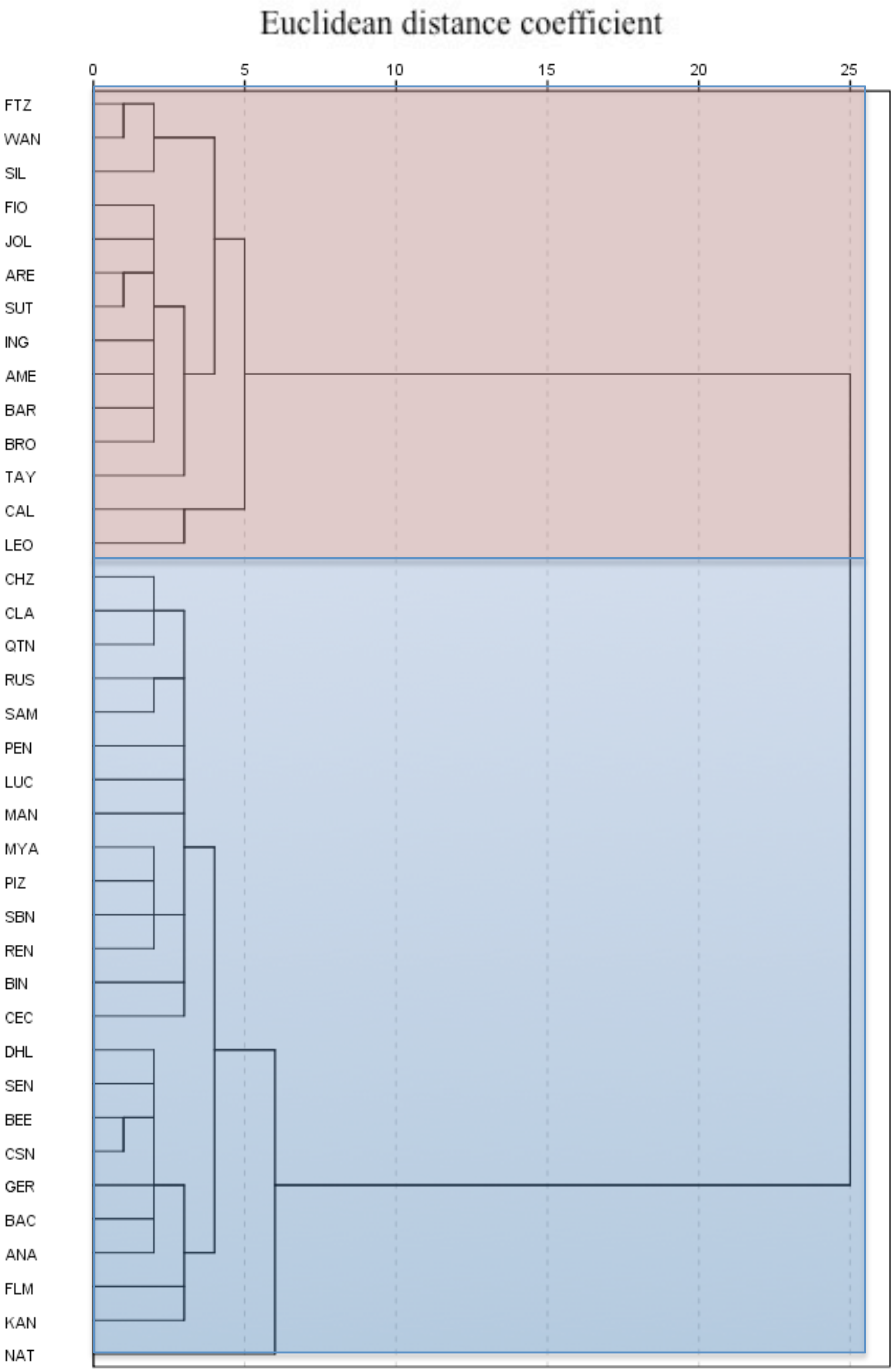

**Fig. 2.3** Dendrogram of the results of the UPGMA cluster analysis calculated from dyadic indices of ranging similarity for female study subjects. Two distinct clusters emerged representing subgroups of individuals with similar ranging patterns (represented by red and blue boxes).

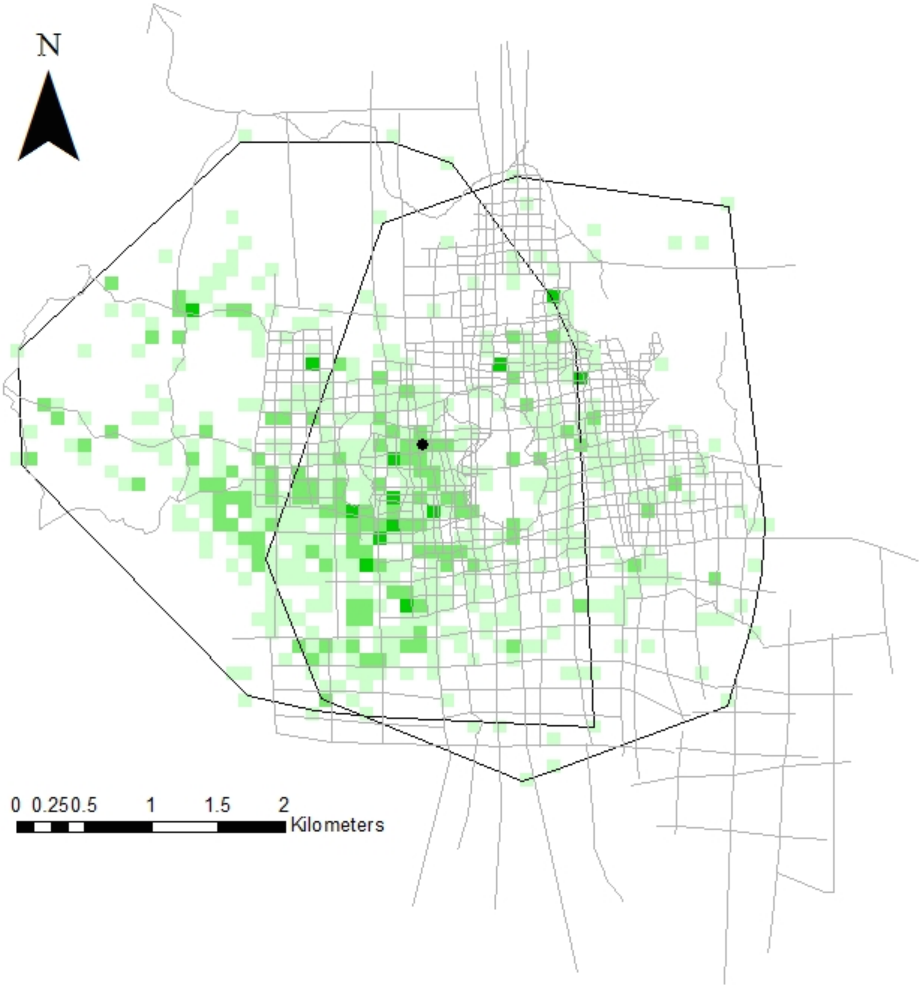

**Fig. 2.4** Space use of female subjects separated by neighborhood. Darker shades of green indicate areas of heavier use by subjects. Dot denotes centroid of the minimum convex polygon delineated from all females' location points (see Fig 2.1). Female subjects ranged in one of two neighborhoods, which shared an overlap zone containing several areas of heavy use.

**Table 2.3.** Comparison of attributes of two spatial neighborhoods of female chimpanzees

| Neighborhood | Central | Western |
|---|---|---|
| MCP area (km$^2$) | 13.0 | 14.2 |
| Proportion of neighborhood overlapped by the other | 0.55 | 0.51 |
| Total subjects | 14 | 22 |
| Adolescents (natal/immigrant) | 2(1/1) | 5(3/2) |
| Parous females (primiparous/ multiparous) | 13 (5/8) | 17 (8/6) |
| Primiparas | 5 | 7 |
| Multiparas | 8 | 7 |
| Transition | 1 A->P | 2 P->M |

Adolescent (A); primipara (P); multipara (M)

For dyads of females belonging to the same neighborhood (N=367), the mean proportion of home range overlap was 0.79. In contrast, for dyads in which the two females belonged to different neighborhoods (N=336), the mean proportion overlap of home ranges was 0.29. Considering dyads belonging to the central (N=91) and western (N=276) neighborhoods separately, the mean dyadic proportions of home range overlap were 0.69 and 0.83, respectively.

### Territory utilization and food

To examine how females utilized different parts of the Ngogo territory, I overlaid a map of the trail system with 100x100-m grid cells and counted the number of individual female location points that were contained in each cell. The natural breaks classification method (Jenks 1967) revealed 13 grid cells with the heaviest use. I examined focal observations that corresponded to the location points found within each grid cell to determine the activities females were engaged in at each location.

All 13 grid cells contained plant foods upon which I observed multiple females feeding. Twelve of the 13 grid cells contained one or two fruiting tree species (Table 2.4). The species found in the highest number of cells (eight of 13) was *Ficus mucuso*. This is in accordance with data indicating that chimpanzees at Ngogo devoted the highest amount of their feeding time (18%) to this fig species (Watts et al. 2012). Six additional fruiting tree species were fed upon in one or two grid cells. All six species ranked within the top 16 plant food species at Ngogo, based on the percentage of time spent feeding on each (Watts et al. 2012). Additionally, the tree, *Neoboutonia macrocalyx*, was fed upon in two grid cells. Chimpanzees at Ngogo wadge wood from the roots of this species (Watts et al. 2012), which may contain important micronutrients or medicinal compounds (Aruga et al. 2015).

**Table 2.4**. Major plant food species found in grid cells used most heavily by female chimpanzee subjects at Ngogo

| Grid cell | Plant food | Plant food |
|---|---|---|
| 1 | *Ficus mucuso* | *Uvariopsis congensis* |
| 2 | *Ficus mucuso* | - |
| 3 | *Ficus mucuso* | *Chrysophyllum albidum* |
| 4 | *Aningeria altissima* | *Neoboutonia macrocalyx* |
| 5 | *Ficus mucuso* | *Mimusops bagshawei* |
| 6 | *Ficus mucuso* | - |
| 7 | *Ficus mucuso* | *Mimusops bagshawei* |
| 8 | *Ficus mucuso* | *Uvariopsis congensis* |
| 9 | *Aningeria altissima* | - |
| 10 | *Neoboutonia macrocalyx* | - |
| 11 | *Ficus natalensis* | *Morus mesozygia* |
| 12 | *Ficus natalensis* | - |
| 13 | *Ficus mucuso* | - |

**Home range size**

I analyzed several factors that may have influenced the estimated home range size of individual female subjects. In the first set of models (GLM1), I included all subjects (parous and nulliparous) and investigated the effect of four variables on home range size: reproductive cycle stage, parity, neighborhood affiliation, and the number of location points. The model with the lowest AICc included the number of location points as the sole predictor and was assigned a model weight of 55% (Table 2.5). Model-averaged coefficient estimates (including 95% confidence intervals) for averaged models indicated that the intervals for all parameters, except number of location points, spanned zero (Table 2.6).

**Table 2.5**. Results of AICc analysis for three models of home range size in female chimpanzees

| Model | No. parameters | df | Parameters | AICc | ΔAIC | wAIC | Log likelihood |
|---|---|---|---|---|---|---|---|
| 1 | 1 | 3 | Points | 121.39 | 0.00 | 0.55 | -57.34 |
| 2 | 2 | 4 | Points, neighborhood | 122.03 | 0.64 | 0.40 | -56.41 |
| 3 | 2 | 5 | Points, parity | 125.88 | 4.49 | 0.06 | -57.00 |

**Table 2.6**. Model-averaged coefficient estimates (including 95% confidence intervals) for averaged models

|  | Estimate | Std. error | Adj. std. error | z value | Pr(>\|z\|) | Confidence intervals | |
|---|---|---|---|---|---|---|---|
|  |  |  |  |  |  | 2.5% | 97.5% |
| Intercept | 3.9039 | 0.7414 | 0.7671 | 5.089 | 4e-07 | 2.400 | 5.407 |
| Points | 0.0198 | 0.0051 | 0.0052 | 3.793 | 0.000149 | 0.010 | 0.030 |
| Neighborhood: west | 0.1987 | 0.3413 | 0.3472 | 0.572 | 0.567135 | -0.265 | 1.266 |
| Parity: multipara | 0.0004 | 0.1262 | 0.1308 | 0.003 | 0.997551 | -1.059 | 1.073 |
| Parity: primipara | -0.0172 | 0.1464 | 0.1506 | 0.114 | 0.908997 | -1.387 | 0.791 |

In the second set of analyses (GLM2), I included only parous subjects and examined the effect of six predictor variables on home range size: reproductive cycle stage, parity, presence of a carried infant (infant < three years), presence of a non-carried dependent offspring (infant > three years and/or a or juvenile), neighborhood affiliation, and number of location points. As in the first set of analyses (GLM1), the model with the lowest AICc had the number of location points as the sole predictor. The top model was assigned a model weight of only 21% (Table 2.7). Model-averaged coefficient estimates (including 95% confidence intervals) for averaged models indicated that the intervals for all parameters, except number of location points, spanned zero (Table 2.8).

**Table 2.7**. Results of AICc analysis for 22 models of home range size in parous female chimpanzees

| Model | No. parameters | df | Parameters | AICc | ΔAIC | wAIC | Log likelihood |
|---|---|---|---|---|---|---|---|
| 1 | 1 | 3 | Points | 104.86 | 0 | 0.21 | -48.99 |
| 2 | 2 | 4 | Points, neighborhood | 106.08 | 1.22 | 0.12 | -48.27 |
| 3 | 2 | 4 | Points, infant/juvenile | 106.13 | 1.26 | 0.11 | -48.29 |
| 4 | 2 | 4 | Points, infant < 3 | 106.44 | 1.57 | 0.10 | -48.45 |
| 5 | 2 | 4 | Points, parity | 106.99 | 2.13 | 0.07 | -48.73 |
| 6 | 3 | 5 | Points, neighborhood, infant/juvenile | 107.31 | 2.45 | 0.06 | -47.46 |
| 7 | 3 | 5 | Points, neighborhood, infant < 3 | 107.54 | 2.67 | 0.06 | -47.57 |
| 8 | 3 | 5 | Points, neighborhood, parity | 108.10 | 3.23 | 0.04 | -47.85 |
| 9 | 3 | 5 | Points, neighborhood, parity | 108.56 | 3.69 | 0.03 | -48.08 |
| 10 | 3 | 5 | Points, neighborhood, | 108.58 | 3.71 | 0.03 | -48.09 |

|  |  |  |  |  |  |  |  |
|---|---|---|---|---|---|---|---|
|  |  |  | infant/juvenile |  |  |  |  |
| 11 | 3 | 5 | Points, infant < 3, infant/juvenile | 108.91 | 4.05 | 0.03 | -48.26 |
| 12 | 4 | 6 | Points, neighborhood, infant/juvenile, infant < 3 | 109.82 | 4.96 | 0.02 | -47.16 |
| 13 | 4 | 6 | Points, parity, neighborhood, infant < 3 | 109.96 | 5.10 | 0.02 | -47.23 |
| 14 | 2 | 4 | Neighborhood, infant/juvenile | 110.02 | 5.16 | 0.02 | -50.24 |
| 15 | 1 | 3 | Neighborhood | 110.03 | 5.16 | 0.02 | -51.57 |
| 16 | 4 | 6 | Points, parity, neighborhood, infant/juvenile | 110.23 | 5.36 | 0.01 | -47.36 |
| 17 | Null | 2 | - | 110.52 | 5.66 | 0.01 | -53.05 |
| 18 | 1 | 3 | Infant/juvenile | 110.60 | 5.74 | 0.01 | -51.86 |
| 19 | 2 | 4 | Neighborhood, infant < 3 | 111.14 | 6.28 | 0.01 | -50.80 |
| 20 | 2 | 4 | Neighborhood, parity | 111.46 | 6.60 | 0.01 | -50.96 |
| 21 | 4 | 6 | Points, parity, infant < 3, infant/juvenile | 111.53 | 6.67 | 0.01 | -48.02 |
| 22 | 2 | 6 | Points, cycle | 111.69 | 6.83 | 0.01 | -48.10 |

**Table 2.8**. Model-averaged coefficient estimates (including 95% confidence intervals) for averaged models

|  | Estimate | Std. error | Adj. std. error | z value | Pr(>\|z\|) | Confidence intervals |  |
|---|---|---|---|---|---|---|---|
|  |  |  |  |  |  | 2.5% | 97.5% |
| Intercept | 4.23396 | 1.24041 | 1.28006 | 3.308 | 0.0009 | 1.725 | 6.743 |
| Points | 0.01881 | 0.00780 | 0.00741 | 2.538 | 0.0112 | 0.004 | 0.033 |
| Neighborhood: west | 0.58914 | 0.46947 | 0.49023 | 1.202 | 0.2295 | -0.372 | 1.550 |
| Infant/juvenile: yes | 0.60350 | 0.62991 | 0.65674 | 0.919 | 0.3581 | -0.684 | 1.891 |
| Infant < 3: yes | -0.52622 | 0.57890 | 0.60508 | 0.870 | 0.3845 | -1.712 | 0.660 |
| Parity: primipara | -0.12550 | 0.71443 | 0.73955 | 0.170 | 0.8652 | -1.575 | 1.324 |
| Cycle: lactation 1 | -1.26707 | 1.04659 | 1.09762 | 1.154 | 0.2483 | -3.418 | 0.884 |
| Cycle: | -0.83558 | 0.92581 | 0.97095 | 0.861 | 0.3895 | -2.739 | 1.067 |

| | | | | | | | |
|---|---|---|---|---|---|---|---|
| lactation 2 | | | | | | | |
| Cycle: transition from pregnancy to lactation | -1.00937 | 1.07981 | 1.13246 | 0.891 | 0.3728 | -3.229 | 1.210 |

## DISCUSSION

Results of this study indicate that females at Ngogo formed small, overlapping home ranges. Individual home ranges clustered into two neighborhoods based on ranging similarity. Additionally, individual ranges varied in size and this variation was greatly influenced by the number of location points recorded for each female during the study. No clear picture emerged regarding whether reproductive cycle stage, parity, or the presence of dependent offspring influenced home range size.

Female chimpanzees at Ngogo restricted their use of space use to small, overlapping home ranges. This accords with patterns of space use typical of East African chimpanzee communities, in which females use distinct areas that are smaller than the entire community territory (Gombe: Wrangham 1979; Wrangham & Smuts 1980; Goodall 1986, Williams et al. 2002b; Murray et al. 2007; Mahale: Hasegawa 1989; Kanyawara: Wrangham et al. 1996, Emery Thompson et al. 2007; Ngogo: Wakefield 2013). Ranging in small areas may decrease intrasexual competition by reducing the number of neighbors with whom each female must regularly compete (Wrangham 1979; Williams et al. 2002b). Additionally, by foraging in small areas, females likely gain specialized knowledge of food resources contained therein (Pusey et al. 1997), maximizing their foraging efficiency in the process (Wrangham & Smuts 1980; Williams et al. 2002b).

Despite potential benefits of differentiating individual ranges, in West African chimpanzee communities, females do not show this pattern and instead range more uniformly within the community's territory (Taï: Lehmann & Boesch 2005; Boussou: Sugiyama 1988; Sakura 1994). Specific to the Taï community, higher gregariousness and more uniform ranging patterns among females may be influenced by predation risk. Taï chimpanzees experience predation by leopards (Boesch 1991; Boesch & Boesch-Achermann 2000), whereas predation is low or absent at most other chimpanzee study sites (Boesch 1991, 2009). Taï chimpanzees likely avoid predation by spending time in groups, and it may be risky for females to travel alone and differentiate their space use (Boesch 1991; Boesch & Boesch-Achermann 2000). Instead of traveling alone, females at Taï may deal with intrasexual competition in a different way, by forming a linear dominance hierarchy (Wittig & Boesch 2003). In other chimpanzee communities, dominance relationships between females are less well defined (Goodall 1986; Pusey et al. 1997; Emery Thompson et al. 2007).

Although female chimpanzees in East Africa typically range in individual areas within a community, at Sonso in the Budongo Forest, Uganda, females instead maintain relatively uniform ranges (Emery Thompson et al. 2006). While the risk of predation may contribute to the pattern of uniform female ranging at Taï, this does not appear to be the case at Budongo, where this risk is low (Reynolds & Reynolds 1965).

A comparison between Ngogo and Sonso provides insight as these communities are similar in several ways, but have different patterns of female ranging. The two communities are located in Uganda, and separated by 180 km (Gruber et al. 2012). Both Ngogo and Sonso cover productive habitats that support high densities of chimpanzees (Sonso: 3.2-6.8 chimpanzees/km$^2$, (Newton-Fisher 2003); Ngogo: 5.1 chimpanzees/km$^2$, Potts et al. 2011). Chimpanzees in both communities devote a similar percentage of their feeding time to fruit, particularly figs (Watts et al. 2012). However, Sonso is unique in that it has a particularly diverse availability of chimpanzee foods (Gruber et al. 2012). This diversity may buffer chimpanzees at Sonso from experiencing periods of food scarcity, which occur infrequently there (Gruber et al. 2012). Future studies are needed to determine whether this diet diversity, or other factors result in the ranging differences observed between Ngogo and Sonso.

## Neighborhoods

Home ranges of female subjects at Ngogo formed two neighborhoods. Spatial neighborhoods have also been reported at Gombe (Williams et al. 2002b), and Kanyawara (Emery Thompson et al. 2007). Unlike neighborhoods at Kanyawara, which barely overlap, the two neighborhoods at Ngogo overlapped extensively. Further, the overlap zone of neighborhoods at Ngogo was used intensively by females. Why might this difference occur? While the Ngogo and Kanyawara communities are in close geographic proximity (10 km apart), Ngogo has a density of chimpanzees that is three times higher than at Kanyawara. This is likely due to the greater abundance of several species of fruiting trees, such as figs, found at Ngogo (Potts et al. 2009, 2011; Watts et al. 2011). It is possible that due to higher food availability, feeding competition is relaxed at Ngogo compared to Kanyawara, and sharing space may be less costly (see Murray et al. 2007). It is also possible that the high density of females at Ngogo makes it difficult to avoid space use overlap.

## Home range size

The size of individual female ranges varies within and between chimpanzee communities. In this study, home range size varied from approximately 4-9 $km^2$. This is similar to the ~5-10 $km^2$ home ranges reported for parous females in the Kanyawara community (Chapman & Wrangham 1993). Adult females at Gombe are reported to range over core areas of approximately 2 $km^2$ (Pusey et al. 1997), although areas of approximately 5 $km^2$ are reported by Williams et al. (2002b). In the Taï community, where females range widely across the territory, individual ranging areas exceed 10 $km^2$ (Lehmann & Boesch 2005). Inter-site comparison should be interpreted with caution, however, as territory size, habitat, and spatial analyses differed between studies.

The most important factor influencing home range size at Ngogo was the number of location points per female. The home range sizes reported here may underestimate actual ranges utilized by females during the study because individual range sizes did not reach an asymptote with the number of observations. The inability to properly characterize female range size affects my findings regarding the effect of reproductive factors on home range size, and as a consequence, these should be considered preliminary.

## Reproductive factors

I did not find evidence that reproductive variables (reproductive cycle stage, parity, presence of dependent offspring) predicted home range size. This is in contrast to several studies from chimpanzees and other taxa, which report that lactating females range less widely than non-lactating females (Wrangham 1979; Wrangham & Smuts 1980; Goodall 1986; Hasegawa 1990; Matsumoto-Oda & Oda 1998; Bates & Byrne 2009; Dahle & Swenson 2003; Wartmann et al. 2008). My ranging data are based mainly on observations of lactating mothers, as only two parous female subjects cycled throughout the majority of the study period. Sexually receptive female chimpanzees often associate with males, which can result in the formation of large parties (Watts 2007). As chimpanzee mothers with dependent offspring avoid associating with males (Otali & Gilchrist 2006) and large parties (Wrangham et al. 1993; Janson & Goldsmith 1995), I lack detailed observations of the spatial movements of sexually receptive females.

My observations did not support the hypothesis that parity affects home range size. Although primiparous chimpanzees probably lack the foraging skills of multiparas and may be lower-ranking, my results do not indicate that the first-time mothers are forced to range more widely. I also did not find evidence that the presence of dependent offspring influenced home range size. Indeed, between chimpanzee communities, no clear picture emerges concerning effect of dependent offspring on mothers' ranging. While infant carrying is hypothesized to be costly (Altmann & Samuels 1992; Ross 2000), several studies have failed to detect a relationship between the presence of dependent offspring and chimpanzee mothers' range size (Gombe: Murray et al. 2007; Taï: Lehmann & Boesch 2005). At Kanyawara, the presence of a carried infant did not affect mothers' daily travel distance, but the presence of a juvenile did (Pontzer & Wrangham 2006). In contrast, the presence of dependent offspring had no influence on female travel distance at Taï (Riedel 2011). Examining additional ranging metrics at Ngogo, such as daily distance traveled, would be useful in this context.

Interestingly, I did not find evidence that nulliparas, who neither lactate nor care for dependent offspring, ranged more widely than parous females. Other studies of chimpanzees have noted that immigrants may range widely over a community territory. Immigrants may be forced to forage away from dominant females, who have priority of access to resources (Murray et al. 2007). Immigrants also frequently spend time with adult males, who range widely across a territory (Kahlenberg et al. 2008b). Regarding the present study, the two immigrant subjects had been in the Ngogo community for one and four years at the study's inception. As such, these immigrants were somewhat familiar with food resources and other members of the community, potentially explaining why they did not need to range widely compared to parous females. In addition, one immigrant female was pregnant during most of the study and gave birth a few months before the study's end, which could have affected her ranging. To explore these possibilities, it will be necessary to examine how new immigrants to the community use space, and how this may change as immigrants spend more time and integrate themselves into a community.

Like the immigrant study subjects, natal adolescents also possessed home ranges of a similar size to those of parous females. All of the natal adolescents in this study spent at least some time traveling with their mothers. A mother's home range size and location thus can influence that of her daughter. In addition, most of the natal subjects had not yet displayed swellings reaching maximal size. Upon the onset of sexual receptivity, adolescent females decrease time spent with their mothers and begin associating with community males (Pusey 1983, 1990). As the natal adolescents in this study were likely not yet fully reproductively mature they might not have started ranging widely.

Observations from this study reinforce the assertion that ranging in small overlapping areas within a shared community territory is the typical pattern of space use for female chimpanzees in East Africa. By focusing space use in small individual areas spread throughout a territory, females may avoid potentially costly resource competition and maximize foraging efficiency. Further research is needed to resolve questions raised by this study. For example, how do patterns of space use interact with food availability at Ngogo? What factors influence patterns of female ranging over the long-term? Understanding relationships between reproduction and female space use at Ngogo, an unusually large community inhabiting a food-rich territory, is an important goal for future research.

# REFERENCES

Adams, E. S. (2001). Approaches to the study of territory size and shape. *Annual Review of Ecology and Systematics*, *32*, 277-303. doi:10.1146/annurev.ecolsys.32.081501.114034

Altmann, J. (1974). Observational study of behavior: Sampling methods. *Behaviour*, *49*(3), 227–267. doi:10.1163/156853974X00534

Altmann, J., & Samuels, A. (1992). Costs of maternal care: Infant carrying in baboons. *Behavioral Ecology and Sociobiology*, *29*(6), 391-398. doi:10.1007/BF00170168

Amsler, S. (2009). *Ranging behavior and territoriality in chimpanzees at Ngogo, Kibale National Park, Uganda*. Ph.D. thesis, University of Michigan, Ann Arbor, MI.

Aruga, N., Matsuo, H., Furuichi, T., & Hashimoto, C. (2015). Root eating by wild chimpanzees (*Pan troglodytes*) in the Kalinzu Forest, Uganda: Possible medicinal plant use. *Pan Africa News*, *22*(1), 7-10.

Asensio, N., Brockelman, W. Y., Malaivijitnond, S., & Reichard, U. H. (2011). Gibbon travel paths are goal oriented. *Animal Cognition*, *14*(3), 395-405. doi:10.1007/s10071-010-0374-1

Bates, L. A., & Bryne, R. (2009). Sex differences in the movement patterns of free-ranging chimpanzees (*Pan troglodytes schweinfurthii*). *Behavioral Ecology and Sociobiology*, *64*(2), 247–255. doi:10.1007/s00265-009-0841-3

Bekoff, M., & Mech, L. D. (1984). Simulation analyses of space use: Home range estimates, variability, and sample size. *Behavior Research Methods, Instruments, and Computers*, *16*(1), 32–37. doi:10.3758/BF03201046

Bennett, E. L. (1986). Environmental correlates of ranging behaviour in the banded langur, *Presbytis melalophos*. *Folia Primatologica*, *47*(1), 26-38. doi:10.1159/000156261

Benson, J. F., & Chamberlain, M. J. (2007). Space use and habitat selection by female Louisiana black bears in the Tensas River Basin of Louisiana. *Journal of Wildlife Management*, *71*(1), 117–126. doi:10.2193/2005-580

Bercovitch, F. B., Lebron, M. R., Martinez, H. S., & Kessler, M. J. (1998). Primigravidity, body weight, and costs of rearing first offspring in rhesus macaques. *American Journal of Primatology*, *46*(2), 135–144. doi:10.1002/(SICI)1098-2345(1998)46:2<135::AID-AJP3>3.0.CO;2-X

Boesch, C. (1991). The effects of leopard predation on grouping patterns in forest chimpanzees. *Behaviour*, *117*(3), 220-242. doi:10.1163/156853991X00544

Boesch, C. (2009). *The real chimpanzee: Sex strategies in the forest*. Cambridge: Cambridge

University Press.

Boesch, C., & Boesch-Achermann, H. (2000). *The chimpanzees of the Taï Forest*. Oxford: Oxford University Press.

Burnham, K. P., & Anderson, D. R. (2002). *Model selection and multimodel inference: A practical information-theoretic approach*, 2nd ed. New York, NY: Springer.

Burt, W. H. (1943). Territoriality and home range concepts as applied to mammals. *Journal of Mammalogy*, *24*(3), 346–352. doi:10.2307/1374834

Butynski, T. M. (1990). Comparative ecology of blue monkeys (*Cercopithecus mitis*) in high-density and low-density subpopulations. *Ecological Monographs*, *60*, 1–26. doi:10.2307/1943024

Chapman, C. A., & Wrangham, R. W. (1993). Range use of the forest chimpanzees of Kibale—implications for the understanding of chimpanzee social-organization. *American Journal of Primatology*, *31*(4), 263–273. doi:10.1002/ajp.1350310403

Dahl, J. F., Nadler, R. D., & Collins, D. C. (1991). Monitoring the ovarian cycles of *Pan troglodytes* and *P. paniscus*: A comparative approach. *American Journal of Primatology*, *24*(3-4), 195–209. doi:10.1002/ajp.1350240306

Dahle, B., & Swenson, J. E. (2003). Home ranges in adult Scandinavian brown bears (*Ursus arctos*): Effect of mass, sex, reproductive category, population density and habitat type. *Journal of Zoology*, *260*(4), 329-335. doi:10.1017/S0952836903003753

Doran, D. M. (1992). The ontogeny of chimpanzee and pygmy chimpanzee locomotor behavior: A case study of paedomorphism and its behavioral correlates. *Journal of Human Evolution, 23*(2), 139–158. doi:10.1016/0047-2484(92)90104-H

Doran, D. M. (1997). Influence of seasonality on activity patterns, feeding behavior, ranging, and grouping patterns in Taï chimpanzees. *International Journal of Primatology*, *18*(2), 183–206. doi:10.1023/A:1026368518431

Emery Thompson, M. (2013). Reproductive ecology of female chimpanzees. *American Journal of Primatology, 75*(3), 222–237. doi:10.1002/ajp.22084

Emery Thompson, M., & Wrangham, R. W. (2006). Comparison of sex differences in fission-fusion species: Reducing bias by standardizing for party size. In: N. E. Newton-Fisher, H. Notman, J. D. Paterson, & V. Reynolds (Eds.), *Primates of Western Uganda* (pp. 209–226). New York, NY: Springer.

Emery Thompson, M., Kahlenberg, S. M., Gilby, I. C., & Wrangham, R. W. (2007). Core area quality is associated with variance in reproductive success among female chimpanzees at Kibale National Park. *Animal Behaviour*, *73*(3), 501–512.

doi:10.1016/j.anbehav.2006.09.007

Emery Thompson, M., Muller, M. N., & Wrangham, R. W. (2012). The energetics of lactation and the return to fecundity in wild chimpanzees. *Behavioral Ecology*, *23*(6), 1234–1241. doi:10.1093/beheco/ars107

Emlen, S. T., & Oring, L. W. (1977). Ecology, sexual selection, and evolution of mating systems. *Science*, *197*(4300), 215–223. doi:10.1126/science.327542

Field, I. C., Bradshaw, C. J. A., Burton, H. R., Sumner, M. D., & Hindell, M. A. (2005). Resource partitioning through oceanic segregation of foraging juvenile southern elephant seals (*Mirounga leonina*). *Oecologia*, *142*(1), 127–135. doi:10.1007/s00442-004-1704-2

Ghiglieri, M. P. (1984). *The chimpanzees of Kibale Forest*. New York, NY: Columbia University Press.

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

Goodall, J., Bandora, A., Bergmann, E., Busse, C., Matama, H., Mpongo, E., Pierce, A., & Riss, D. (1979). Intercommunity interactions in the chimpanzee population of the Gombe National Park. In: D. Hamburg, & E. McCown (Eds.), *The great apes* (pp. 13-54). Menlo Park, CA: Benjamin/Cummings.

Gruber, T., Potts, K. B., Krupenye, C., Byrne, M., Mackworth-Young, C., McGrew, W. C., Reynolds, V., Zuberbühler, K. (2012). The influence of ecology on chimpanzee (*Pan troglodytes*) cultural behavior: A case study of five Ugandan chimpanzee communities. *Journal of Comparative Psychology*, *126*(4), 446-457. doi:10.1037/a0028702

Hasegawa, T. (1989). Sexual behavior of immigrant and resident female chimpanzees at Mahale. In: P. Heltne, & L. A. Marqardt (Eds.), *Understanding Chimpanzees* (pp. 90–103). Cambridge, MA: Harvard University Press.

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

Herbinger, I., Boesch, C., & Rothe, H. (2001). Territory characteristics among three neighboring chimpanzee communities in the Taï National Park, Côte d'Ivoire. *International Journal of Primatology*, *22*(2), 143–167. doi:10.1023/A:1005663212997

Hinde, K., Power, M. L., & Oftedal, O. T. (2009). Rhesus macaque milk: Magnitude, sources, and consequences of individual variation over lactation. *American Journal of Physical Anthropology 138*(2), 148–157. doi:10.1002/ajpa.20911

Hiraiwa-Hasegawa, M. (1990). Maternal investment before weaning. In: T. Nishida (Ed.), *The*

*Chimpanzees of the Mahale Mountains* (pp. 257–266). Tokyo: University of Tokyo Press.

Holland, R. A., Winter, P., & Waters, D. A. (2005). Sensory systems and spatial memory in the fruit bat *Rousettus aegyptiacus*. *Ethology*, *111*(8), 715-725. doi:10.1111/j.1439-0310.2005.01099.x

Janson, C. H., & Goldsmith, M. L. (1995). Predicting group size in primates: Foraging costs and predation risks. *Behavioral Ecology*, *6*(3), 326–336. doi:10.1093/beheco/6.3.326

Jenks, G. F. (1967). The data model concept in statistical mapping. *International Yearbook of Cartography*, *7*(1), 186–190.

Kahlenberg, S. M., Emery Thompson, M., Muller, M. N., & Wrangham, R. W. (2008a). Immigration costs for female chimpanzees and male protection as an immigrant counterstrategy to intrasexual aggression. *Animal Behaviour*, *76*(5), 1497-1509. doi:10.1016/j.anbehav.2008.05.029

Kahlenberg, S. M., Emery Thompson, M., & Wrangham, R. W. (2008b). Female competition over core areas in *Pan troglodytes schweinfurthii*, Kibale National Park, Uganda. *International Journal of Primatology*, *29*(4), 931-947. doi:10.1007/s10764-008-9276-3

Kernohan, B. J., Gitzen, R. A., Millspaugh, J. J. (2001). Analysis of animal space use and movements. In: J. J. Millspaugh, & J. M. Marzluff, (Eds.), *Radio tracking and animal populations* (pp. 126-168). San Diego, CA: Academic Press.

Knorr, E. M., & Ng, R. T. (1998). Algorithms for mining distance-based outliers in large datasets. In: *Proceedings of the VLDB Conference* (pp. 392–403). doi:10.1.1.55.8026

Langergraber, K., Mitani, J., & Vigilant, L. (2009). Kinship and social bonds in female chimpanzees (*Pan troglodytes*). *American Journal of Primatology*, *71*(10), 840-851. doi:10.1002/ajp.20711

Lehmann, J., & Boesch, C. (2005). Bisexually bonded ranging in chimpanzees (*Pan troglodytes verus*). *Behavioral Ecology and Sociobiology*, *57*(6), 525–535. doi:10.1007/s00265-004-0891-5

Lwanga, J. S., Butynski, T. M., & Struhsaker, T. T. (2000). Tree population dynamics in Kibale National Park, Uganda 1975–1998. *African Journal of Ecology*, *38*(3), 238–247. doi:10.1046/j.1365-2028.2000.00244.x

Matsumoto-Oda, A., & Oda, R. (1998). Changes in the activity budget of cycling female chimpanzees. *American Journal of Primatology*, *46*(2), 157-166.

Mitani, J. C. (2009). Male chimpanzees form enduring and equitable social bonds. *Animal Behaviour*, *77*(3), 633–640. doi:10.1016/j.anbehav.2008.11.021

Mitani, J. C., & Watts, D. P. (1999). Demographic influences on the hunting behavior of chimpanzees. *American Journal of Physical Anthropology*, *109*(4), 439–454. doi:10.1002/(SICI)1096-8644(199908)109:4<439::AID-AJPA2>3.0.CO;2-3

Mitani, J. C., & Amsler, S. J. (2003). Social and spatial aspects of male subgrouping in a community of wild chimpanzees. *Behaviour*, *140*(7), 869–884. doi:10.1163/156853903770238355

Mitani, J. C., Watts, D. P., & Lwanga, J, S. (2002). Ecological and social correlates of chimpanzee party size and composition. In: C. Boesch, G. Hohmann, & L. Marchant, (Eds.), *Behavioral diversity in chimpanzees and bonobos* (pp. 102–111). Cambridge: Cambridge University Press.

Mitani, J. C., Watts, D. P., Pepper, J. W., & Merriwether, D. A. (2002). Demographic and social constraints on male chimpanzee behaviour. *Animal Behaviour*, *64*(5), 727–737. doi:10.1006/anbe.2002.4014

Mitani, J. C., & Watts, D. P. (2005). Correlates of territorial boundary patrol behaviour in wild chimpanzees. *Animal Behaviour*, *70*(5), 1079–1086. doi:10.1016/j.anbehav.2005.02.012

Mitani, J. C., Watts, D. P., & Amsler, S. J. (2010). Lethal intergroup aggression leads to territorial expansion in wild chimpanzees. *Current Biology*, *20*(12), R507-R508. doi:10.1016/j.cub.2010.04.021

Muller, M. (2002). Agonistic relations among Kanyawara chimpanzees. In: C. Boesch, G. Hohmann, & L. F. Marchant (Eds.), *Behavioural diversity in chimpanzees and bonobos* (pp. 112–124). Cambridge: Cambridge University Press.

Murray, C. M., Mane, S. V., & Pusey, A. E. (2007). Dominance rank influences female space use in wild chimpanzees (*Pan troglodytes*): Towards an ideal despotic distribution. *Animal Behaviour*, *74*(6), 1795–1804. doi:10.1016/j.anbehav.2007.03.024

Newton-Fisher, N. E. (2003). The home range of the Sonso community of chimpanzees from the Budongo Forest, Uganda. *African Journal of Ecology*, *41*(2), 150-156. doi:10.1046/j.1365-2028.2003.00408.x

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

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

Nishida, T., & Kawanaka, K. (1972). Inter-unit-group relationships among wild chimpanzees of the Mahale mountains. *Kyoto University African Studies*, *7*(131), 131-169.

Nishida, T., Corp, N., Hamai, M., Hasegawa, T., Hiraiwa-Hasegawa, M., Hosaka, K., Hunt, K., Itoh, N., Kawanaka, K., Matsumoto-Oda, A., Mitani, J., 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. *American Journal of Primatology*, *59*(3), 99-121. doi:10.1002/ajp.10068

Norušis, M. J. (2012). *IBM SPSS Statistics 19 Advanced Statistical Procedures Companion*. Upper Saddle River, NJ: Prentice Hall.

Ostfeld, R.S. (1990) The ecology of territoriality in small mammals. *Trends in Ecology & Evolution*, *5*(12), 411–415. doi:10.1016/0169-5347(90)90026-A

Otali, E., & Gilchrist, J. S. (2006). Why chimpanzee (*Pan troglodytes schweinfurthii*) mothers are less gregarious than nonmothers and males: The infant safety hypothesis. *Behavioral Ecology and Sociobiology*, *59*(4), 561–570. doi:10.1007/s00265-005-0081-0

Pepper, J. W., Mitani, J. C., & Watts, D. P. (1999). General gregariousness and specific social preferences among wild chimpanzees. *International Journal of Primatology*, *20*(5), 613–632. doi:10.1023/A:1020760616641

Pontzer, H., & Wrangham, R. W. (2006). Ontogeny of ranging in wild chimpanzees. *International Journal of Primatology*, *27*(1), 295-309. doi:10.1007/s10764-005-9011-2

Potts, K. B., Chapman, C. A., & Lwanga, J. S. (2009). Floristic heterogeneity between forested sites in Kibale National Park, Uganda: Insights into the fine-scale determinants of density in a large-bodied frugivorous primate. *Journal of Animal Ecology*, *78*(6), 1269-1277. doi:10.1111/j.1365-2656.2009.01578.x

Potts, K. B., Watts, D. P., & Wrangham, R. W. (2011). Comparative feeding ecology of two communities of chimpanzees (*Pan troglodytes*) in Kibale National Park, Uganda. *International Journal of Primatology*, *32*(3), 669–690. doi:10.1007/s10764-011-9494-y

Powell, R. A. (1986). Home-range overlap of black bears in North Carolina. *International Conference on Bear Research and Management*, *7*, 235-242.

Pusey, A. E. (1980). Inbreeding avoidance in chimpanzees. *Animal Behaviour*, *28*(2), 543–552. doi:10.1016/S0003-3472(80)80063-7

Pusey, A. E. (1983). Mother-offspring relationships in chimpanzees after weaning. *Animal Behaviour*, *31*(2), 363–377. doi:10.1016/S0003-3472(83)80055-4

Pusey, A. E. (1990). Behavioural changes at adolescence in chimpanzees. *Behaviour*, *115*(3), 203-246. doi:10.1163/156853990X00581

Pusey, A. E., & Packer, C. (1987). Dispersal and philopatry. In: B. B. Smuts, D. L. Cheney, R. M. Seyfarth, R. W. Wrangham, & T. T. Struhsaker (Eds.), *Primate societies* (pp. 250–

266). Chicago, IL: Chicago University Press.

Pusey, A. E., Williams, J., & Goodall, J. (1997). The influence of dominance rank on the reproductive success of female chimpanzees. *Science*, *277*(5327), 828–831. doi:10.1126/science.277.5327.828

Pusey, A. E., Murray, C., Wallauer, W., Wilson, M., Wroblewski, E., & Goodall, J. (2008). Severe aggression among female *Pan troglodytes schweinfurthii* at Gombe National Park, Tanzania. *International Journal of Primatology*, *29*(4), 949-973. doi:10.1007/s10764-008-9281-6

R Development Core Team. (2015). R: A language and environment for statistical computing. Vienna, Austria: R Foundation for Statistical Computing.

Rah, J. H., Christian, P., Shamim, A. A., Arju, U. T., Labrique, A. B., & Rashid, M. (2008). Pregnancy and lactation hinder growth and nutritional status of adolescent girls in rural Bangladesh. *Journal of Nutrition*, *138*(8), 1505-1511.

Reynolds, V. (1965). *Budongo: An African forest and its chimpanzees*. Garden City, NY: Natural History Press.

Riedel, J., Franz, M., & Boesch, C. (2011). How feeding competition determines female chimpanzee gregariousness and ranging in the Taï National Park, Côte d'Ivoire. *American Journal of Primatology*, *73*(4), 305-313. doi:10.1002/ajp.20897

Rogers, L. L. (1987). Effects of food supply and kinship on social behavior, movements, and population growth of black bears in northeastern Minnesota. *Wildlife Monographs*, *97*, 3–72.

Romesburg, C. H. (2004). *Cluster analysis for researchers*. Morrisville, NC: Lulu Press.

Ross, C. (2001). Park or ride? Evolution of infant carrying in primates. *International Journal of Primatology*, *22*(5), 749-771. doi:10.1023/A:1012065332758

Sakura, O. (1994). Factors affecting party size and composition of chimpanzees (*Pan troglodytes verus*) at Bossou, Guinea. *International Journal of Primatology*, *15*(2), 167–183. doi:10.1007/BF02735272

Seaman, D. E., Millspaugh, J. J., Kernohan, B. J., Brundige, G. C., Raedeke, K. J., & Gitzen, R. A. (1999). Effects of sample size on kernel home range estimates. *The Journal of Wildlife Management*, *63*(2), 739-747. doi:10.2307/3802664

Setchell, J. M., Lee, P. C., Wickings, E. J., & Dixson A. F. (2002). Reproductive parameters and maternal investment in mandrills (*Mandrillus sphinx*). *International Journal of Primatology*, *23*(1), 51–68. doi:10.1023/A:1013245707228

Singleton, I., & van Schaik, C.P. (2001). Orangutan home range size and its determinants in a Sumatran swamp forest. *International Journal of Primatology*, *22*(6), 877– 911. doi:10.1023/A:1012033919441

Sneath, P. H. A., & Sokal, R. R. (1973). *Numerical taxonomy: The principles and practice of numerical classification*. San Francisco, CA: W.H. Freeman.

Sterck, E. H. M., Watts, D. P., & van Schaik, C. P. (1997). The evolution of female social relationships in nonhuman primates. *Behavioral Ecology and Sociobiology*, *41*(5), 291–305. doi:10.1007/s002650050390

Struhsaker, T. T. (1997). *Ecology of an African rain forest*. Gainesville, FL: University Press of Florida.

Sugiyama, Y. (1988). Grooming interactions among adult chimpanzees at Bossou, Guinea, with special reference to social structure. *International Journal of Primatology*, *9*(5), 393-407. doi:10.1007/BF02736216

Sun, P., & Chawla, S. (2004). On local spatial outliers. In: *Proceedings of 4th IEEE International Conference on Data Mining*. 209–216.

Symington, M. M. (1988). Food competition and foraging party size in the black spider monkey (*Ateles paniscus chamek*). *Behaviour*, *105*(1), 117–134. doi:10.1163/156853988X00476

Townsend, S. W., Slocombe, K. E., Emery Thompson, M., & Zuberbühler, K. (2007). Female-led infanticide in wild chimpanzees. *Current Biology*, *17*(10), 355–356. doi:10.1016/j.cub.2007.03.020

Trivers, R. L. (1972). Parental investment and sexual selection. In: B. Campbell (Ed.), *Sexual selection and the descent of man* (pp. 136–179). Chicago, IL: Aldine.

Tufto, J., Andersen, R., & Linnell, J. (1996). Habitat use and ecological correlates of home range size in a small cervid: The roe deer. *Journal of Animal Ecology*, *65*(6), 715-724. doi:10.2307/5670

Tutin, C. E. G. (1979). Mating patterns and reproductive strategies in a community of wild chimpanzees (*Pan troglodytes schweinfurthii*). *Behavioral Ecology and Sociobiology*, *6*(1), 29–38. doi:10.1007/ BF00293242

Van Beest, F. M., Rivrud, I. M., Loe, L. E., Milner, J. M., & Mysterud, A. (2011). What determines variation in home range size across spatiotemporal scales in a large browsing herbivore?. *Journal of Animal Ecology*, *80*(4), 771-785. doi:10.1111/j.1365-2656.2011.01829.x

Wakefield, M. L. (2013). Social dynamics among females and their influence on social structure in an East African chimpanzee community. *Animal Behaviour*, *85*(6), 1303-1313. doi:10.1016/j.anbehav.2013.03.019

Wartmann, F. M., Purves, R. S., & van Schaik, C. P. (2010). Modelling ranging behaviour of female orang-utans: a case study in Tuanan, Central Kalimantan, Indonesia. *Primates*, *51*(2), 119-130. doi:10.1007/s10329-009-0186-6

Watts, D. P. (1998). Coalitionary mate guarding by male chimpanzees at Ngogo, Kibale National Park, Uganda. *Behavioral Ecology and Sociobiology*, *44*(1), 43–55. doi:10.1007/s002650050513

Watts, D. P. (2007). Effects of male group size, parity, and cycle stage on female chimpanzee copulation rates at Ngogo, Kibale National Park, Uganda. *Primates*, *48*(3), 222-231. doi:10.1007/s10329-007-0037-2

Watts, D. P. (2015). Mating behavior of adolescent male chimpanzees (*Pan troglodytes*) at Ngogo, Kibale National Park, Uganda. *Primates*, *56*(2), 163-172. doi:10.1007/s10329-014-0453-z

Watts, D. P., & Mitani, J. C. (2001). Boundary patrols and intergroup encounters in wild chimpanzees. *Behaviour*, *138*(3), 299–327. doi:10.1163/15685390152032488

Watts, D. P., Potts, K. B., Lwanga, J. S., & Mitani, J. C. (2012). Diet of chimpanzees (*Pan troglodytes schweinfurthii*) at Ngogo, Kibale National Park, Uganda, 2. Temporal variation and fallback foods. *American Journal of Primatology*, *74*(2), 130-144. doi:10.1002/ajp.21015

Wauters, L. A., Bertolino, S., Adamo, M., Van Dongen, S., & Tosi, G. (2005). Food shortage disrupts social organization: The case of red squirrels in conifer forests. *Evolutionary Ecology*, *19*(4), 375-404. doi:10.1007/s10682-005-8311-5

Williams, J. M., Hsien-Yang, L., & Pusey, A. E. (2002a). Costs and benefits of grouping for female chimpanzees at Gombe. In: C. Boesch (Ed.), *Behavioural Diversity in Chimpanzees and Bonobos* (pp. 192-203). Cambridge: Cambridge University Press. doi:10.1017/CBO9780511606397.019

Williams, J. M., Pusey, A. E., Carlis, J. V., Farm, B. P., & Goodall, J. (2002b). Female competition and male territorial behaviour influence female chimpanzees' ranging patterns. *Animal Behaviour*, *63*(2), 347–360. doi:10.1006/anbe.2001.1916

Williams, J. M., Oehlert, G., Carlis, J. & Pusey, A. E. (2004). Why do male chimpanzees defend a group range? Reassessing male territoriality. *Animal Behaviour*, *68*(3), 523-532. doi:10.1016/j.anbehav.2003.09.015

Wittig, R. M., & Boesch, C. (2003). Food competition and linear dominance hierarchy among female chimpanzees of the Taï National Park. *International Journal of Primatology*, *24*(4), 847–867. doi:10.1023/A:1024632923180

Worton, B. J. (1987). A review of models of home range for animal movement. *Ecological modelling*, *38*(3), 277-298. doi:10.1016/0304-3800(87)90101-3

Worton, B. J. (1995). A convex hull-based estimator of home-range size. *Biometrics*, *51*(4), 1206-1215. doi:10.2307/2533254

Wrangham, R. W. (1979). On the evolution of ape social systems. *Social Science Information Sur Les Sciences Sociales*, *18*(3), 335–368. doi:10.1177/053901847901800301

Wrangham, R. W. (2000). Why are male chimpanzees more gregarious than mothers? A scramble competition hypothesis. In: P. M. Kappeler (Ed.), *Primate males* (pp. 248–258). Cambridge: Cambridge University Press.

Wrangham, R. W., & Smuts, B. B. (1980). Sex differences in the behavioral ecology of chimpanzees in the Gombe National Park, Tanzania. *Journal of Reproduction and Fertility*, *28*, 13–31.

Wrangham, R. W., Conklin, N. L., Etot, G., Obua, J., Hunt, K. D., Hauser, M. D., & Clark, A. P. (1993). The value of figs to chimpanzees. *International Journal of Primatology*, *14*(2), 243-256. doi:10.1007/BF02192634

Wrangham, R. W., Chapman, C. A., Clark-Arcadi, A. P., & Isabirye-Basuta, G. (1996). Social ecology of Kanyawara chimpanzees: Implications for understanding the costs of great ape groups. In: W. C. McGrew, L. F. Marchant, & T. Nishida (Eds.), *Great ape societies* (pp. 45-57). Cambridge: Cambridge University Press.

Zuberbühler, K., & Janmaat, K. R. L. (2010). Foraging cognition in non-human primates. In: M. L. Platt, & A. A. Ghazanfar (Eds.), *Primate Neuroethology* (pp. 64-83). Oxford: Oxford University Press.

# CHAPTER 3

## Aggression between wild female chimpanzees varies with parity

## INTRODUCTION

Parental investment and sexual selection theory provide a framework to investigate female competition (Trivers 1972). Because females tend to invest more in reproduction than do males, female fitness is limited by the ability to acquire food and convert it into offspring, while male fitness is limited by mating opportunities. Consequently, females typically compete for access to food, and males compete for mates.

Chimpanzees (*Pan troglodytes*) provide a model species in which to investigate female competition. These animals live in multi-female, multi-male, fission-fusion communities in which individuals form temporary subgroups, or parties (Nishida 1968). Females usually disperse from their natal communities during adolescence when they are around 12-13 years old and start to reproduce about two years later (Emery Thompson 2013). Chimpanzees rely on a diet of ripe fruit (Nishida & Hiraiwa-Hasegawa 1987; Wrangham et al. 1998), a limited resource whose availability fluctuates in time and space (Wrangham 1979). Given the aforementioned constraints imposed by parental care, female chimpanzees compete for food, albeit subtly and indirectly. Recent research has revealed that this competition has attendant effects on female reproduction (Pusey et al. 1997; Emery Thompson et al. 2007a). In East Africa, female chimpanzees compete for space (Murray et al. 2007; Kahlenberg et al. 2008b; Miller et al. 2014). Chimpanzee mothers occupy small individual core areas within the communal territory. Core areas overlap extensively, and female fidelity to an area is high across years (Williams et al. 2002; Emery Thompson et al. 2007a). Habitats are heterogeneous, and observations from the Gombe and Kanyawara chimpanzee communities indicate that high-ranking females inhabit high quality core areas with more food than do low-ranking females, who occupy low-quality core areas (Murray et al. 2007; Emery Thompson et al. 2007; Kahlenberg et al. 2008). As a consequence, high-ranking females obtain access to more food compared with low-ranking females. High-ranking females are able to use this to their advantage and display shorter birth intervals and increased infant survivorship compared with low-ranking females (Emery Thompson et al. 2007a).

Female chimpanzees behave aggressively toward each other as they compete for resources, including space, which are required to successfully reproduce. In East African chimpanzee communities, female intrasexual aggression tends to be sustained, but of low intensity (Pusey et al. 2008). This is likely due to potential risks associated with behaving aggressively, such as injury to dependent offspring, and because winning a single aggressive interaction rarely has a high payoff. However, aggression between female chimpanzees has been observed to intensify when access to resources is threatened. This has occurred during times of community growth when infants are born and when new females transfer into a community. In cases involving the latter, aggression tends to be directed by parous females towards immigrant nulliparas (Goodall 1986; Muller 2002; Kahlenberg et al. 2008). Nulliparas, who seek to establish their own core areas, represent a competitive threat to parous females.

While reproductive status has been shown to influence aggression between parous and nulliparous female chimpanzees, the parity of mothers is likely to affect matters in additional ways. Primiparous females ("primiparas"), mothers who have given birth for the first time, are young and may be continuing to invest in their own growth and maturation (Bercovitch et al. 1998; Setchell et al. 2002; Rah et al. 2008). Primiparas are also physiologically immature, which can reduce the efficiency of lactation (Hinde et al. 2009). The relatively poor quality of first-time mothers is displayed in several ways. Primiparas may forego investment in personal growth (humans, Rah et al. 2008; Pauli et al. 2013) or prolong lactation (rhesus macaques (*Macaca mulatta*), Hinde et al. 2009). Primiparous female chimpanzees delay subsequent births (Jones et al. 2010) and devote more time to the care of young infants than do multiparous females (i.e., "multiparas") (Stanton et al. 2014). Primiparas may be lower-ranking than multiparas as female chimpanzees in some communities rise in rank with both age (Nishida 1989; Greengrass 2005; Kahlenberg 2006; Murray et al. 2006) and tenure in the community (Kahlenberg et al. 2008b). Primiparous chimpanzees may also be at a disadvantage as they lack familiarity with food resources in the community territory. Such knowledge is likely crucial to female chimpanzees (Wrangham & Smuts 1980; Williams et al. 2002), who appear to gain foraging knowledge over time (Murray et al. 2006). Taken together, the preceding observations suggest that, faced with the challenges of first time motherhood, primiparous female chimpanzees will be affected by competition for resources to a greater extent than multiparas. To compete effectively, primiparas may engage in more frequent intrasexual aggression compared to multiparas.

Here, I investigate whether female parity influences rates of aggression between female chimpanzees. To do so, I took advantage of an unusual situation at Ngogo in the Kibale National Park, Uganda. The Ngogo chimpanzee community is exceptionally large (Watts 1998; Watts &

Mitani 2001; Mitani & Amsler 2003) and contains many females. Between 2010-2012 the community experienced considerable growth, increasing 20% over about 27 months. During this time, 31 surviving infants were born, 12 of them to first-time mothers. These circumstances permitted a comparison of primiparous and multiparous mothers during a period when competition for resources was likely very high. In what follows I examine two questions. First, I investigated whether females experienced heightened levels of aggression in the large and expanding community at Ngogo. I compared levels of female aggression to those reported in previously published studies of chimpanzees. Second, I asked whether primiparas directed higher rates of aggression toward adolescent nulliparas than did multiparas. My aim is to clarify how parity affects aggressive behavior between females in our closest living relatives.

## METHODS

### Study site and subjects

I observed chimpanzees at Ngogo in the Kibale National Park, Uganda. The Kibale Park (795 km$^2$) is located in western Uganda (0°13′-0°41′N and 30°19′-30°32′E), and lies at an elevation of approximately 1350 m above sea level. The Ngogo chimpanzee community ranges over a 35 km$^2$ territory (Mitani et al. 2010) near the center of the Park. Rain falls throughout the year with an annual mean ± SD of 1397 ± 174 mm (N=10 years, 1998-2007; Mitani 2009). Typically, September-December and March-May are wetter than average, while intervening months are drier (Butynski 1990; Struhsaker 1997). The study site lies at a transition between lowland and montane rainforest and comprises moist, evergreen forest interspersed with patches of

*Pennisetum purpureum* grassland (Struhsaker 1997). Detailed descriptions of Ngogo and the ecology of the surrounding area can be found in Butynski (1990); Ghiglieri (1984); Struhsaker (1997) and Lwanga et al. (2000).

I collected data over 15 months, May-July 2010 and August 2011-July 2012. During this time the Ngogo community had 17-24 adolescent and 41-51 adult female chimpanzees. I divided adult females into two groups based on parity: primiparas (mothers raising their first offspring) and multiparas (mothers with two or more offspring). My primary study subjects included 15 primiparas, 17 multiparas, and 6 mothers who transitioned between these parity categories during the study, for a total of 38 individuals.

I observed how subjects interacted with both parous and nulliparous females. My 16 nulliparous adolescent subjects included 7 natal and 9 immigrant females. In addition to these recognizable nulliparas, parous subjects sometimes interacted with ‘unknown’ adolescents who could not be identified as individuals. During the study, five adolescents from other areas immigrated into the Ngogo community, and they were not always recognizable as individuals during the first months following immigration. In addition, several peripheral parous females at Ngogo had adolescent daughters, who I also could not easily identify as individuals. Due to this, I treated adolescents as a single category. I considered natal females to be adolescents at 10 years of age (Nishida et al. 2003; cf. Pusey 1980), approximately the time female chimpanzees begin to exhibit sexual swellings (Goodall 1986; Nishida et al. 2003). During the study, two natal juvenile females transitioned to adolescence.

I collected observations at a time when the Ngogo chimpanzee community grew from 157 to 190 members. This growth was primarily due to births. Twelve adolescent females gave birth to their first surviving infant either during the study period or within four months prior to the start.

Additionally, six primiparas gave birth to a second infant, transitioning to multiparous status, and 13 multiparas gave birth. Two infants (less than one year old) died during the study, one from an inferred intra-community infanticide (K. Langergraber, unpublished data) and one of unknown causes. The infanticide victim was a neonate born to a first-time mother. Subsequent to the infanticide, I classified the female subject as an adolescent, not a primipara. This is because most observations made on this female took place prior to parturition, when she was an adolescent. Also, no observations were made during the few days her infant was alive. The other infant was born to a multipara, and thus its death did not affect my classification of the mother's reproductive status. No additional deaths occurred in the community.

## Behavioral Observations

During the 15-month study period, I completed approximately 1100 one-hour focal follows (Altmann 1974) of individual parous females, the main study subjects. In 2010, I also collected approximately 100 hours of focal observations on adolescent females. During the study, individual females varied greatly in their degree of habituation to human presence. Due to this, relatively short (one-hour) focal sessions were conducted, maximizing the amount of data that could be consistently collected from a large sample of females.

On a given day, I collected no more than two focal samples of a particular individual, with observation sessions separated by at least two hours. During each focal session, six instantaneous scan samples were conducted at 10-minute intervals (Altmann 1974). During each scan, the identity of all adult and adolescent females judged to be within visual range of the focal female was recorded. Chimpanzees within this visual range were considered to be ‘in association’ (Pepper et al. 1999; Mitani et al. 2002).

With the help of field assistants, I monitored adult and adolescent females’ reproductive cycles. Sexual swellings of females were scored daily based on turgidity, following Dahl et al. (1991). I considered females exhibiting maximal tumescent swellings to be sexually receptive (Tutin 1979). I did not include maximally tumescent females as focal subjects because females are known to alter their association patterns during this time (Pepper et al. 1999; Matsumoto-Oda 1999), and I was only interested in intrasexual relationships. In 2010, I conducted focal sessions on adolescent females opportunistically, both during and outside periods of sexual receptivity.

During focal sessions, I recorded observations of aggression that occurred between adolescent nulliparas and adult females *ad libitum*. I considered aggression to include behaviors such as threats, charging displays, and physical contact, which were directed toward one or more recipients. Mild aggression involved threats, such as shaking a branch at or flapping arms at an opponent. Threats could constitute an entire aggressive episode, but more often they were incorporated into charging displays, the most common type of aggression observed. During charging displays chimpanzees direct exaggerated body motions and/or move rapidly toward recipients (Bygott 1979; Goodall 1986). Female chimpanzees at Ngogo typically lunged, stomped toward, or chased opponents during charging displays. When physical contact occurred it was usually brief, involving hitting an opponent with hands or feet. Extended physical contact, including grappling or biting, occurred rarely.

I defined an aggressive interaction as a sequence of aggressive behaviors that occurred between female participants. Bouts of aggression involving the same participants were defined as separate interactions after more than 10 minutes elapsed between aggressive behaviors

(Kahlenberg et al. 2008b). For each interaction I recorded the identity and parity of all females involved and their roles directing and/or receiving aggression. Most aggressive interactions involved two females, but some involved three or more. I considered an interaction to be 'decided' when a recipient submitted to an aggressor, but did not retaliate. Submissive behaviors include screaming, physical avoidance, and pant grunting, a vocal signal of submission in chimpanzees (de Waal 1978; Bygott 1979; Noë et al. 1980).

I evaluated females' involvement in aggression on a dyadic level, considering each unique director-recipient dyad separately in a given interaction. I counted only the initial act of aggression between each director-recipient dyad in an interaction. For example, a coalition of two females chasing a single recipient two times in less than a minute was counted as one act for each aggressor. Although some female chimpanzees at Ngogo clearly dominated others, agonistic interactions between them did not occur with sufficient frequency to permit detection of a dominance hierarchy.

### Analyses

Prior studies have quantified aggression between female chimpanzees in different ways (Nishida 1989; Muller 2002; Kahlenberg et al. 2008a; Wakefield 2008; Miller et al. 2014). To permit comparison with these studies, I quantified rates of female aggression in three ways. First, I calculated an overall rate of aggression by dividing the total number of dyadic aggressive interactions recorded during focal sessions by the total number of hours females spent in association. This allowed me to compare rates of aggression at Ngogo to previously published reports from two other East African communities, Mahale (Nishida 1989) and Kanyawara

(Muller 2002). Second, I computed an overall rate of decided aggressive interactions for comparison to the only published rate of female aggression at Ngogo (Wakefield 2008). To do this, I divided the number of times females were involved in decided aggressive interactions during focal sessions by the total number of hours females spent in association. Third, I calculated the mean rate of aggression directed by individual mothers for comparison to a rate based on long-term data from Kasekela community at Gombe (Miller et al. 2014). For each subject, I divided the number of aggressive acts she directed during her focal sessions by the number of focal hours she associated with other females.

To determine whether patterns of female aggression varied as a function of parity, I conducted analyses using observations in which the parity of both the aggressor (mother) and recipient were known. I employed these analyses to test the predictions that: (1) mothers direct aggression more often toward adolescent nulliparas than toward other mothers, and (2) primiparas direct aggression more often toward adolescent nulliparas than do multiparas. To do this, I compared rates of aggression directed by mothers toward three types of females: adolescent nulliparas, primiparas, and multiparas, using general linear models (GLMs). To answer the first question (do mothers direct more aggression towards adolescents than toward other mothers), I conducted a GLM with the number of aggressive acts directed by individual mothers as the outcome variable (GLM1). For this model, I considered mothers a single group, regardless of parity. The main predictor variable was the parity of the recipient of aggression.

To answer the second question (do primiparas direct more aggression towards adolescents than do multiparas), I conducted a second GLM (GLM2). As in GLM1, the number of aggressive acts directed by individual mothers was the outcome variable. However, for this model I considered both the parity of the aggressor (parous subjects) and the recipients of aggression (adolescent nulliparas, primiparas, and multiparas) as predictors. The interaction of these two predictors involved six aggressor-recipient (AR) combinations: primipara-adolescent (PA), primipara-primipara (PP), primipara-multipara (PM), multipara-adolescent (MA), multipara-primipara (MP), and multipara-multipara (MM) [Table 1]. In both models, I counted aggressive acts separately in each year of the study (2010-2012) and included 'year of study' as a predictor variable to account for changes in rates of aggression between periods.

**Table 3.1** Schematic of potential interactions between two types of chimpanzee mothers and three types of female recipients

| Parity group | | Aggressor-recipient dyad (AR) |
|---|---|---|
| Aggressor | Recipient | |
| Primipara | Adolescent | PA |
| | Primipara | PP |
| | Multipara | PM |
| Multipara | Adolescent | MA |
| | Primipara | MP |
| | Multipara | MM |

My data on female aggression violate assumptions of independence because there are repeated measures of individual females within and between years of data collection. Violation of assumptions of independence can increase the frequency of type I errors (Clifford et al. 1989). To address this, I utilized generalized estimating equations (GEEs), which account for potential unknown correlation within outcomes of a GLM (Liang & Zeger 1986). Specifically, GEEs use a quasi-likelihood estimation approach, adjusting the standard error to account for the correlation within observations from the same group, in this case repeated observations of an individual female chimpanzee.

For each GLM, I numbered repeated observations from the same female with a dummy variable. I fit both models with an exchangeable working correlation matrix, which assumes that the correlation between any two observations from the same female is the same $\alpha$ (Jang 2011). A benefit of GEEs is that parameter estimates and standard errors are robust to misspecification of the correlation matrix (Overall & Tonidandel 2004). However, if data are not missing at random, pooling observations across study subjects may bias results towards frequently observed individuals (Gillies et al. 2006; Aarts et al. 2008). I implemented two procedures to avoid this: an exchangeable working correlation matrix, as mentioned above, and robust standard errors (Koper & Manseau 2009).

For each parous female subject, I counted the number of aggressive acts she directed toward three groups of opponents who differed in parity: adolescent nulliparas, primiparas, and multiparas. In both GLMs I utilized counts of directed aggression as the response variable and ‘year of study’ as a predictor variable. Because count data of directed aggression were overdispersed, I fit both GLMs with a negative binomial distribution and a log link function.

To account for individual differences in association, I quantified the number of opportunities each focal female had to interact aggressively with individuals from each of the three parity groups. For each year, I calculated “female-scans” per parity group by counting the number of adolescent nulliparas, primiparas, and multiparas that the focal female associated with across all scans. Counts of female-scans were right skewed so I applied a natural log transformation. I divided each female’s yearly count of directed aggressive acts by the natural logarithm of the yearly sum of scan samples in which she was observed associating with at least one female of the parity group of interest. I multiplied raw rates by six to obtain hourly rates because scan samples were made at 10-minute intervals. I compared rates of aggression using rate ratios (R) where:

$$R = \frac{\text{rate of aggression in aggressor-recipient group A (reference category)}}{\text{rate of aggression in aggressor-recipient group B}}$$

Statistical analyses were conducted using SPSS for Macintosh, version 22 (© IBM Corporation). I set the level of significance at $P < 0.05$.

## RESULTS

### Rates of female intrasexual aggression

To test my first prediction that rates of female chimpanzee aggression were higher in this study compared to other sites, I calculated three rates. First, females at Ngogo engaged in intrasexual aggression at a rate of 8.3 interactions per 100 hours. This is 2-12 times more often than the rates reported from two other East African communities (Table 3.2).

Second, I found decided aggressive interactions between females occurred at a rate of 3.5 per 100 hours. This is two times higher than the previously published rate of female aggression at Ngogo (Table 3.3). Based on observations of mainly parous and a few adolescent females between 2003 and 2005, Wakefield (2008) observed 1.7 decided aggressive interactions per 100 focal hours.

**Table 3.2** Rates of aggressive interactions between female chimpanzees in three East African communities

| Community | Aggressive interactions per 100 hours | Rate ratio[a] (Ngogo: other) | Community size |
|---|---|---|---|
| Kibale-Ngogo[b] | 8.3 | - | 157-190 |
| Mahale, M Group[c] | 4.6 | 1.8 | ~100-110 |
| Kibale-Kanyawara[d] | 0.7 | 11.9 | 48-50 |

[a] Kibale-Ngogo study is the reference category for rate ratios
[b] This study
[c] Nishida 1989 (p. 75; 39 incidences of aggression during 844.2 hours of focal observation)
[d] Muller 2002 (Tables 8.1 and 8.3; 5 incidences of aggression during 679.8 hours of observation)

**Table 3.3** Rates of decided aggressive interactions between female chimpanzees in the Ngogo community

| Years of study | Decided aggressive interactions per 100 hours | Rate ratio[a] (Wakefield:other) | Community size |
|---|---|---|---|
| 2003-2005[b] | 1.7 | - | 145-156 |
| 2010-2012[c] | 3.5 | 2.1 | 157-190 |

[a] Wakefield 2008 study is the reference category for rate ratios
[b] Wakefield 2008 (p. 917; 18 incidences of aggression during 1080 hours of focal observation)
[c] This study

Third, overall rates of aggression (number of interactions per 100 hours) did not account for the number of competitors in a group. If overall rates of aggression at Ngogo were elevated due to the large female population, this does not necessarily indicate that individual females experience high rates of aggression compared to females in other communities. To examine this possibility, I compared the mean individual rate of aggression directed by mothers at Ngogo to a rate based on long-term data from Gombe-Kasekela (Miller et al. 2014; Table 3.4). Mothers at Ngogo directed intrasexual aggression at a mean rate of 3.0 acts per 100 hours ± standard error 0.6. This is 12 times more often than mothers at Gombe-Kasekela (Table 3.4).

**Table 3.4** Individual rates of intrasexual aggression directed by chimpanzee mothers in two East African communities

| Community | Acts of directed aggression per 100 hours | Standard error | Rate ratio[a] (Ngogo: other) | Community size |
|---|---|---|---|---|
| Kibale-Ngogo[b] | 3.0 | 0.6 | - | 157-190 |
| Gombe-Kasekela[c] | 0.26 | 0.04 | 12 | 41-62 |

[a] Kibale-Ngogo study is the reference category for rate ratios
[b] This study
[c] Miller et al. 2014

### Rate of aggression by mothers: variation with recipient parity

To test the prediction that mothers were more aggressive toward adolescent females than toward mothers, I compared individual rates of aggression directed by parous females towards adolescent nulliparas, primiparas, and multiparas. The parity of recipients was a highly significant predictor of the rate of aggressive acts directed by mothers (GLM1: $X^2 = 34.958$, $P<0.001$). Year of data collection was a non-significant predictor and excluded from the final model.

Figure 1 shows mean individual rates of aggressive acts directed by mothers toward recipients who differed in reproductive status. Mothers directed aggression toward adolescent nulliparas significantly more often than toward either primiparas or multiparas (Table 3.5). I did not detect a significant difference in rates of aggressive acts directed by parous females toward primiparas versus multiparas (GLM1: estimate 0.421; standard error 0.3249, $X^2 = 1.682$, P=0.195). Comparing rates indicated that parous females directed aggression towards adolescents 3-4 times more often than towards primiparas and multiparas, respectively (mean rate: adolescent nulliparas: 2.5; primiparas: 0.8; multiparas: 0.6 acts/100 hours).

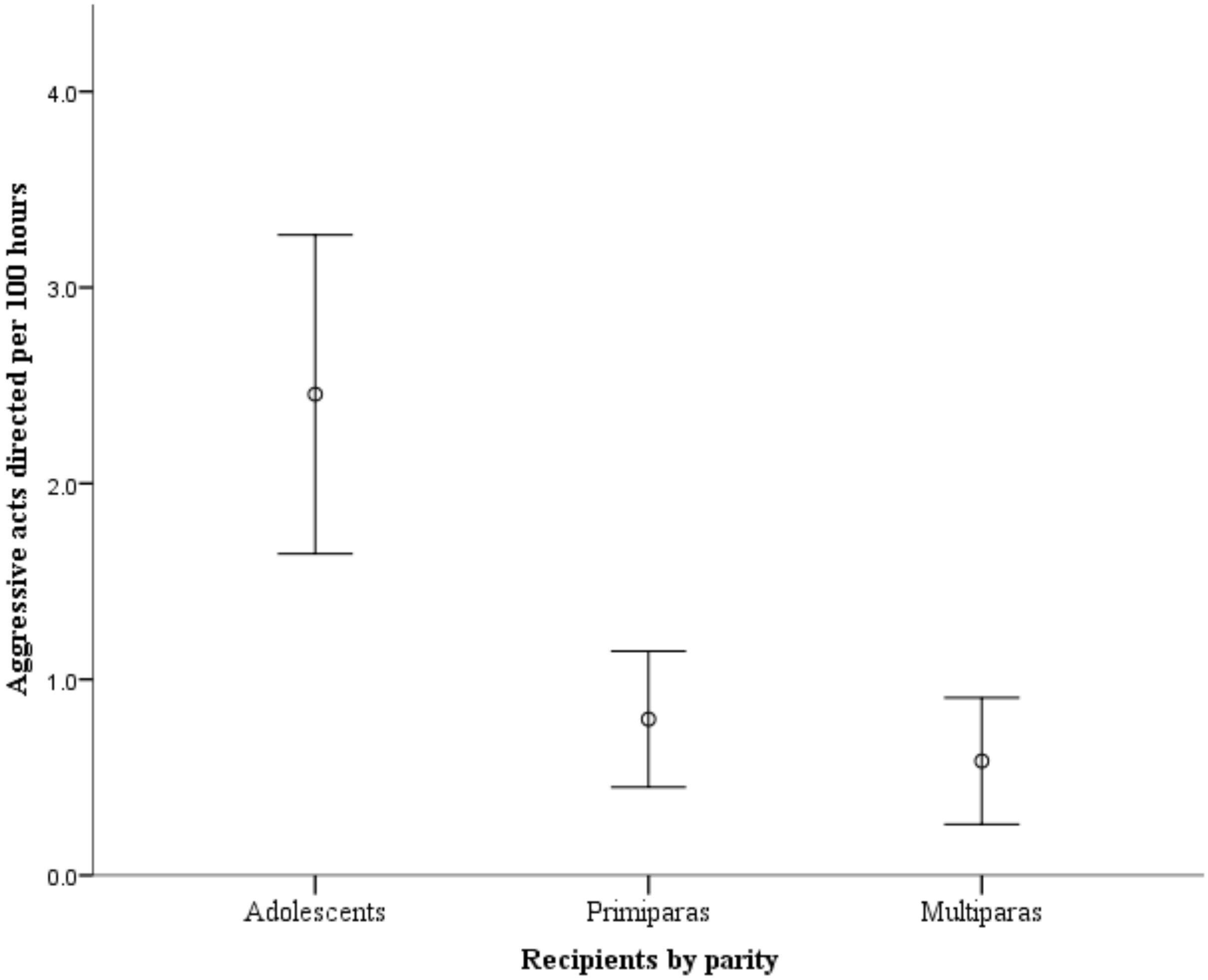

**Fig. 3.1** Rates of aggression directed by chimpanzee mothers toward females in three reproductive categories. Means ± 2 standard errors are shown; see text for statistics.

**Table 3.5** Results of GLM1, a test of the effect of recipient parity on the rate of intrasexual aggression directed by chimpanzee mothers

| Effect | Estimate | Standard error | $X^2$ | P |
|---|---|---|---|---|
| Intercept | -5.462 | 0.1618 | 1139.784 | <0.001 |
| Multipara | -1.423 | 0.2800 | 25.828 | <0.001 |
| Primipara | -1.002 | 0.2428 | 17.028 | <0.001 |
| Adolescent[a] | 0 | . | . | . |

[a] Adolescent is the reference category

### Rates of aggression directed by mothers: comparing primiparas and multiparas

To test the prediction that primiparas directed more aggression toward adolescents than did multiparas, I compared the rates primiparas and multiparas directed aggression toward adolescent nulliparas, primiparas, and multiparas. Here I found that the interaction of aggressor and recipient parity (AR) predicted the rate of intrasexual aggressive acts directed by mothers (GLM2: $X^2 = 45.220$, $P<0.001$). Year of the study was a non-significant predictor and excluded from the final model. Figure 3.2 shows individual rates of aggressive acts directed by two groups of mothers toward recipients of three parity groups.

Primiparas directed aggression toward adolescent nulliparas more often than did multiparas. In fact, the rate primiparas directed aggression toward adolescents was significantly greater than rates that occurred between all other aggressor-recipient groups (Table 3.6). Primiparas targeted adolescents with aggression 3-6 times more often than rates between other aggressor-recipient groups.

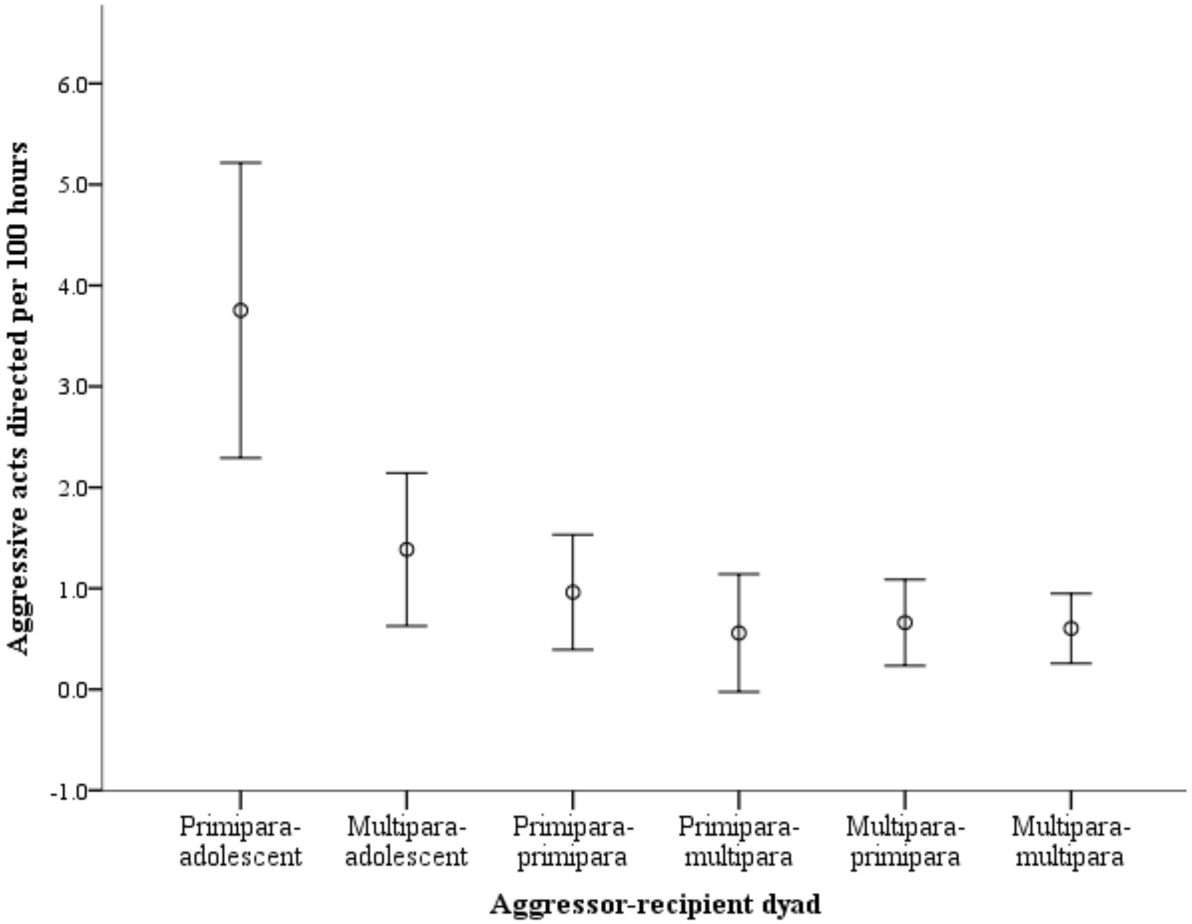

**Fig. 3.2** Individual rates of aggression directed by primiparas and multiparas to females of varying reproductive status. Means ± 2 standard errors are shown; see text for statistics.

I conducted multiple iterations of the model, using each AR dyad as the reference category. Excluding primiparas' direction of aggression toward adolescent nulliparas, I detected no significant differences in rates of aggression between aggressor-recipient groups.

**Table 3.6** Results of GLM2, a test of the effect of the interaction of aggressor and recipient parity (AR) on the rate of intrasexual aggression directed by chimpanzee mothers

| Parameter | Estimate | Standard error | $X^2$ | P value | Mean rate (acts/100 hours) | Rate ratio[a] (other:PA) |
|---|---|---|---|---|---|---|
| Intercept | -5.158 | 0.1827 | 797.117 | <0.001 | | |
| Primipara-adolescent (PA) | 0 | . | . | . | 3.8 | - |
| Multipara-adolescent (MA) | -0.664 | 0.2753 | 5.818 | 0.016 | 1.4 | 0.37 |
| Primipara-primipara (PP) | -1.235 | 0.3644 | 11.492 | 0.001 | 1.0 | 0.26 |
| Primipara-multipara (PM) | -1.887 | 0.4405 | 18.355 | <0.001 | 0.6 | 0.16 |
| Multipara-primipara (MP) | -1.371 | 0.3467 | 15.631 | <0.001 | 0.7 | 0.18 |
| Multipara-multipara (MM) | -1.602 | 0.2857 | 31.454 | <0.001 | 0.6 | 0.16 |

[a] Primipara-adolescent (PA) is the reference category for rate ratios

## DISCUSSION

In this study, I have shown that rates of female intrasexual aggression at Ngogo were higher than those previously reported in East African communities. My findings concur with results reported from other chimpanzee communities, indicating that most of this aggression is directed by mothers toward adolescent nulliparas. Additional analyses revealed that not all mothers behaved the same. Primiparous mothers were more aggressive toward adolescents than were multiparas. Pooling observations of aggressive behavior across mothers therefore masks important variation. In the following, I discuss the two major findings from this research.

## Rates of female chimpanzee intrasexual aggression

Few publications report rates of aggression between wild female chimpanzees. Those that do vary methodologically, making comparisons difficult. I calculated three different rates of female aggression for comparison with other studies. I documented higher rates of female aggression in this study compared to a previous study at Ngogo and reports from three other East African chimpanzee communities.

Relatively high rates of aggression at Ngogo are expected for several reasons. In this unusually large community (Watts 1998; Watts & Mitani 2001; Mitani & Amsler 2003), females live together at high density (Wakefield 2008). In primates, rates of female agonism increase with the number of female competitors in a group (Wheeler et al. 2013). Further, female chimpanzees at Ngogo are more gregarious than are females in other East African chimpanzee communities (Wakefield 2008, 2013); thus they associate often with potential competitors.

Demographic change probably also contributed to the high rates of female aggression observed during this study. In 2003-2005, there were 145-157 community members at Ngogo (Wakefield 2008). When this study began in 2010, the community was similar in size, but grew 20% over the following two years (Table 3.7). Compared to 2003-2005, during the present study there were a greater number of adult and adolescent females. As 31 infants were born, there were many lactating females experiencing the most energetically expensive period in a female mammal's reproductive career (Hanwell & Peaker 1977; Gittleman & Thompson 1988; Clutton-Brock et al. 1989). Taken together, these observations suggest that female chimpanzees at Ngogo likely displayed high rates of aggression to compete for scarce resources during the course of this study.

**Table 3.7** Demographic characteristics of the Ngogo chimpanzee community during two studies

| Years of study | Community size | Adolescent females | Adult females |
|---|---|---|---|
| 2003-2005[a] | 145-157 | 6-14 | 42-43 |
| 2010-2012[b] | 157-190 | 17-24 | 41-51 |

[a] Wakefield 2008
[b] This study

Previous studies have demonstrated an association between demographic change and aggression between female chimpanzees. In the Mahale chimpanzee community, female aggression increased when several females immigrated into the community (Nishida 1989). Similarly, in the Kanyawara chimpanzee community, female intrasexual aggression increased four-fold when immigrants entered the community, peaking when multiple immigrants were present (Kahlenberg et al. 2008b). At Budongo, the Sonso community nearly doubled in size over a decade, leading to a highly female-biased sex ratio (Townsend et al. 2007). Three female-led infanticides, a rare behavior, likely took place near the end of this period. Female-led infanticide in chimpanzees is considered an extreme response to feeding competition whereby females eliminate vulnerable competitors (Pusey 1983; Townsend et al. 2007). These observations, together with the present study, suggest that East African female chimpanzees intensify aggression when competition for resources is exacerbated.

## Aggression by mothers toward adolescent nulliparas

Chimpanzee mothers at Ngogo regard adolescent nulliparas, who seek to establish their own core areas, as competitors. As a consequence, mothers at Ngogo directed higher rates of aggression toward adolescent females than towards other mothers. Specifically, mothers behaved aggressively to adolescent nulliparas 2-3 times more often than they did towards mothers.

During the study, five adolescent females emigrated into the Ngogo community. This is a higher rate than reported in a previous study at Ngogo (Wakefield 2008) and studies from other East African communities (Gombe: Goodall 1983; Kanyawara: Kahlenberg et al. 2008a). The presence of several natal adolescents during the study is also relevant. Female chimpanzees typically disperse from their natal community at adolescence (Nishida & Kawanaka 1972; Pusey & Packer 1987). However, some females at Ngogo do not disperse, instead remaining and reproducing in their natal community. Eight of the 38 parous study subjects have been identified as natal females via genetic analysis (Langergraber et al. 2009).

Although mothers at Ngogo often directed aggression toward adolescent females, this pattern was not consistent across all classes of mothers. Primiparas directed more aggression toward adolescent nulliparas than did multiparas. Primiparas targeted adolescent females with aggression often; they did so three times more often than did multiparas and 3-6 times more often than mothers targeted mothers. Furthermore, I found that multiparas did not target adolescent females with aggression more often than they targeted primiparas or multiparas. Thus, the high rates of aggression directed by mothers towards adolescent females was mainly driven by primiparas.

Several factors may explain why primiparas engaged so often in potentially costly aggression with adolescent nulliparas. Primiparas are at the start of potentially long reproductive careers and early dominance acquisition may influence their subsequent reproduction in important ways. At Gombe, a female chimpanzee’s rank at age 21 strongly predicts her rank a decade later (Pusey et al. 1997). Young mothers who behave aggressively, whether to defend a new core area or establish dominance rank, benefit by reducing feeding competition (Nishida 1989). Evidence indicates that by increasing access to food, female chimpanzees gain reproductive benefits. In the Kanyawara chimpanzee community, females inhabiting areas with more preferred foods had elevated ovarian hormone production, shorter birth intervals, and higher infant survivorship compared to females inhabiting areas with fewer preferred foods (Emery Thompson et al. 2007a).

Evidence also suggests that multiparas may be buffered from intrasexual competition, as they likely outrank other females in the community. High-ranking female chimpanzees at Gombe forage more efficiently and have a higher quality diet than do subordinate females (Murray et al. 2006). Additionally, immigrants there settle in parts of the territory rarely used by high-ranking females (Williams 2000; Murray et al. 2007). How do dominant female chimpanzees outcompete others in the absence of frequent aggression? A study of captive chimpanzees described female dominance relationships as characterized by “respect from below rather than intimidation and a show of strength from above” (de Waal 1982, pp. 179). This also appears to describe dominance relationships between wild female chimpanzees. Subordinate behavior tends to be directed from young to old females and from females whose tenure in the community has been short compared to those who have been residents for longer (Nishida 1989; Kahlenberg et al. 2008b; Wakefield 2008). In the same manner, relatively frequent competition between primiparas and adolescent nulliparas at Ngogo could result from the latter avoiding aggression from multiparas, who have been in the community longer and are likely to be higher ranking.

The finding that primiparas, but not multiparas, often directed aggression toward adolescents differs from other published reports. At Mahale, Nishida (1989) considered primiparas and adolescent nulliparas a single group. There, these females directed more aggression towards each other than expected. However, multiparas also gave more aggression to primiparas and adolescent nulliparas than expected. In the Kanyawara chimpanzee community, Kahlenberg et al. (2008b) found that high-ranking mothers who occupied high quality core areas were the most aggressive toward immigrants. Currently, it is not well understood why patterns of intrasexual aggression displayed by mothers vary between chimpanzee communities.

In sum, observations from this study and others indicate that intrasexual aggression is a tool female chimpanzees use flexibly to compete with others. Because female chimpanzees must balance the costs and benefits of competition, they direct intrasexual aggression strategically at specific opponents (e.g., adolescent nulliparas, infants) during periods of resource scarcity (e.g., population growth). However, it is also clear that competition between female chimpanzees varies over time and between communities. Further research is needed to resolve several questions raised by this study. For example, will the high rates of aggression directed toward adolescents by primiparas, but not multiparas, persist over time at Ngogo? Does this pattern of aggression occur in other chimpanzee communities? Answers to these questions will continue to enrich our understanding of the subtle way females chimpanzees compete with each other in the wild.

# REFERENCES

Aarts, G., MacKenzie, M., McConnell, B., Fedak, M. & Matthiopoulos, J. (2008). Estimating space-use and habitat preference from wildlife telemetry data. *Ecography*, *31*(1), 140–160. doi:10.1111/j.2007.0906-7590.05236.x

Altmann, J. (1974). Observational study of behavior: sampling methods. *Behaviour*, *49*(3), 227–267. doi:10.1163/156853974X00534

Bercovitch, F. B., Lebron, M. R., Martinez, H. S., & Kessler, M. J. (1998). Primigravidity, body weight, and costs of rearing first offspring in rhesus macaques. *American Journal of Primatology*, *46*(2), 135–144. doi:10.1002/(SICI)1098-2345(1998)46:2<135::AID-AJP3>3.0.CO;2-X

Butynski, T. M. (1990). Comparative ecology of blue monkeys (*Cercopithecus mitis*) in high-density and low-density subpopulations. *Ecological Monographs*, *60*, 1–26. doi:10.2307/1943024

Bygott, D. (1979). Agonistic behaviour and dominance in wild chimpanzees. In: D. Hamburg, & E. R. McCown (Eds.), *The great apes* (pp. 405–427). Menlo Park, CA: Benjamin/Cummings.

Clark, C. (1977). A preliminary report on weaning among chimpanzees of the Gombe National Park, Tanzania. In: S. Chevalier-Skolnikoff, & F. Poirier (Eds.), *Primate bio-social development: biological, social and ecological determinants* (pp. 235-260). New York, NY: Garland Press.

Clifford, P., Richardson, S., & Hémon, D. (1989). Assessing the significance of the correlation between two spatial processes. *Biometrics*, *45*, 123–134. doi:10.2307/2532039

Clutton-Brock, T., Albon S., & Guinness, F. (1989). Fitness costs of gestation and lactation in wild mammals. *Nature, 337*(6204), 260–262. doi:10.1038/337260a0

Dahl, J. F., Nadler, R. D., & Collins, D. C. (1991). Monitoring the ovarian cycles of *Pan troglodytes* and *P. paniscus*: A comparative approach. *American Journal of Primatology*, *24*(3-4), 195–209. doi:10.1002/ajp.1350240306

Emery Thompson, M. (2013). Reproductive ecology of female chimpanzees. *American Journal of Primatology, 75*(3), 222–237. doi:10.1002/ajp.22084

Emery Thompson, M., Kahlenberg, S. M., Gilby, I. C., & Wrangham, R. W. (2007). Core area quality is associated with variance in reproductive success among female chimpanzees at Kibale National Park. *Animal Behaviour*, *73*(3), 501–512. doi:10.1016/j.anbehav.2006.09.007

Ghiglieri, M. P. (1984). *The chimpanzees of Kibale Forest*. New York, NY: Columbia University

Press.

Gillies, C. S., Hebblewhite, M., Nielsen, S. E., Krawchuk, M. A., Aldridge, C. L., Frair, J. L., Saher, D. J., Stevens, C. E., & Jerde, C. L. (2006). Application of random effects to the study of resource selection by animals. *Journal of Animal Ecology*, *75*(4), 887–898. doi:10.1111/j.1365-2656.2006.01106.x

Gittleman, J. L., & Thompson, S. D. (1988). Energy allocation in mammalian reproduction. *American Zoologist*, *28*(3), 863–875. doi:10.1093/icb/28.3.863

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

Greengrass, E. (2005). *Sociability and dominance among female chimpanzees at Gombe*. Ph.D. thesis. University of Bristol, Bristol, U.K.

Hanwell, A., & Peaker, M. (1977). Physiological effects of lactation on the mother. *Symposia of the Zoological Society of London*, *41*, 297–311.

Hinde, K., Power, M. L., & Oftedal, O. T. (2009). Rhesus macaque milk: Magnitude, sources, and consequences of individual variation over lactation. *American Journal of Physical Anthropology 138*(2), 148–157. doi:10.1002/ajpa.20911

Jang, M. J. (2011). *Working correlation selection in generalized estimating equations*. Ph.D. thesis, University of Iowa, Iowa City, IA.

Jones, J. H., Wilson, M. L., Murray, C., & Pusey, A. E. (2010). Phenotypic quality influences fertility in Gombe chimpanzees. *Journal of Animal Ecology*, *79*(6), 1262–1269. doi:10.1111/j.1365-2656.2010.01687.x

Kahlenberg, S. M. (2006). *Female-female competition and male sexual coercion in Kanyawara chimpanzees*. Ph.D. thesis. Harvard University, Cambridge, MA.

Kahlenberg, S. M., Emery Thompson, M., Muller, M. N., & Wrangham, R. W. (2008a). Immigration costs for female chimpanzees and male protection as an immigrant counterstrategy to intrasexual aggression. *Animal Behaviour*, *76*(5), 1497-1509. doi:10.1016/j.anbehav.2008.05.029

Kahlenberg, S. M., Emery Thompson, M., & Wrangham, R. W. (2008b). Female competition over core areas in *Pan troglodytes schweinfurthii*, Kibale National Park, Uganda. *International Journal of Primatology*, *29*(4), 931-947. doi:10.1007/s10764-008-9276-3

Koper, N., & Manseau, M. (2009). Generalized estimating equations and generalized linear mixed-effects models for modelling resource selection. *Journal of Applied Ecology*, *46*(3), 590–599. doi:10.1111/j.1365-2664.2009.01642.x

Langergraber, K., Mitani, J., & Vigilant, L. (2009). Kinship and social bonds in female chimpanzees (*Pan troglodytes*). *American Journal of Primatology*, *71*(10), 840-851. doi:10.1002/ajp.20711

Liang, K. Y., & Zeger, S. L. (1986). Longitudinal data-analysis using generalized linear-models. *Biometrika*, *73*, 13-22. doi:10.1093/biomet/73.1.13

Lwanga, J. S., Butynski, T. M., & Struhsaker, T. T. (2000). Tree population dynamics in Kibale National Park, Uganda 1975–1998. *African Journal of Ecology*, *38*(3), 238–247. doi:10.1046/j.1365-2028.2000.00244.x

Matsumoto-Oda, A. (1999). Mahale chimpanzees: Grouping patterns and cycling females. *American Journal of Primatology*, *47*(3), 197–207. doi:10.1002/(SICI)1098-2345(1999)47:3<197::AID-AJP2>3.0.CO;2-3

Miller, J. A., Pusey, A. E., Gilby, I. C., Schroepfer-Walker, K., Markham, A. C., & Murray, C. M. (2014). Competing for space: Female chimpanzees are more aggressive inside than outside their core areas. *Animal Behaviour*, *87*, 147-152. doi:10.1016/j.anbehav.2013.10.023

Mitani, J. C. (2009). Male chimpanzees form enduring and equitable social bonds. *Animal Behaviour*, *77*(3), 633–640. doi:10.1016/j.anbehav.2008.11.021

Mitani, J. C., & Watts, D. P. (1999). Demographic influences on the hunting behavior of chimpanzees. *American Journal of Physical Anthropology*, *109*(4), 439–454. doi:10.1002/(SICI)1096-8644(199908)109:4<439::AID-AJPA2>3.0.CO;2-3

Mitani, J. C., Watts, D. P., Pepper, J. W., & Merriwether, D. A. (2002). Demographic and social constraints on male chimpanzee behaviour. *Animal Behaviour*, *64*(5), 727–737. doi:10.1006/anbe.2002.4014

Mitani, J. C., & Amsler, S. J. (2003). Social and spatial aspects of male subgrouping in a community of wild chimpanzees. *Behaviour*, *140*(7), 869–884. doi:10.1163/156853903770238355

Mitani, J. C., Watts, D. P., & Amsler, S. J. (2010). Lethal intergroup aggression leads to territorial expansion in wild chimpanzees. *Current Biology*, *20*(12), R507-R508. doi:10.1016/j.cub.2010.04.021

Muller, M. (2002). Agonistic relations among Kanyawara chimpanzees. In: C. Boesch, G. Hohmann, & L. F. Marchant (Eds.), *Behavioural diversity in chimpanzees and bonobos* (pp. 112–124). Cambridge: Cambridge University Press.

Murray, C. M., Eberly, L. E., & Pusey, A. E. (2006). Foraging strategies as a function of season and rank among wild female chimpanzees (*Pan troglodytes*). *Behavioral Ecology, 17*(6), 1020–1028. doi:10.1093/beheco/arl042

Murray, C. M., Mane, S. V., & Pusey, A. E. (2007). Dominance rank influences female space use in wild chimpanzees (*Pan troglodytes*): Towards an ideal despotic distribution. *Animal Behaviour, 74*(6), 1795–1804. doi:10.1016/j.anbehav.2007.03.024

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

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

Nishida, T., & Kawanaka, K. (1972). Inter-unit-group relationships among wild chimpanzees of the Mahale mountains. *Kyoto University African Studies*, *7*(131), 131-169.

Nishida, T., & Hiraiwa-Hasegawa, M. (1987). Chimpanzees and bonobos: Cooperative relationships among males. In: B. B. Smuts, D. L. Cheney, R. M. Seyfarth, R. W. Wrangham, & T. T. Struhsaker (Eds.), *Primate societies* (pp. 165–177). Chicago, IL: University of Chicago Press.

Nishida, T., Corp, N., Hamai, M., Hasegawa, T., Hiraiwa-Hasegawa, M., Hosaka, K., Hunt, K., Itoh, N., Kawanaka, K., Matsumoto-Oda, A., Mitani, J., 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. *American Journal of Primatology*, *59*(3), 99-121. doi:10.1002/ajp.10068

Noë, R., de Waal, F. B. M., & van Hoof, J. (1980). Types of dominance in a chimpanzee colony. *Folia Primatologica*, *34*(1-2), 90–110. doi:10.1159/000155949

Overall, J. E., & Tonidandel, S. (2004). Robustness of generalized estimating equation (GEE) tests of significance against misspecification of the error structure model. *Biometrical Journal*, *46*(2), 203–213. doi:10.1002/bimj.200210017

Pauli, J., Lloyd, M., Kunselman, T., Stetter, A. R., Dodson, C. M., Legro, W. C., & Arch, R. S. (2013). Effect of adolescent pregnancy on final adult height in non-Hispanic white women. *Archives of Gynecology and Obstetrics*, *288*(3), 679-682. doi:10.1007/s00404-013-2781-4

Pepper, J. W., Mitani, J. C., & Watts, D. P. (1999). General gregariousness and specific social preferences among wild chimpanzees. *International Journal of Primatology*, *20*(5), 613–632. doi:10.1023/A:1020760616641

Pusey, A. E. (1980). Inbreeding avoidance in chimpanzees. *Animal Behaviour*, *28*(2), 543–552. doi:10.1016/S0003-3472(80)80063-7

Pusey, A. E. (1983). Mother-offspring relationships in chimpanzees after weaning. *Animal*

*Behaviour*, *31*(2), 363–377. doi:10.1016/S0003-3472(83)80055-4

Pusey, A. E., & Packer, C. (1987). Dispersal and philopatry. In: B. B. Smuts, D. L. Cheney, R. M. Seyfarth, R. W. Wrangham, & T. T. Struhsaker (Eds.), *Primate societies* (pp. 250–266). Chicago, IL: Chicago University Press.

Pusey, A. E., Williams, J., & Goodall, J. (1997). The influence of dominance rank on the reproductive success of female chimpanzees. *Science*, *277*(5327), 828–831. doi:10.1126/science.277.5327.828

Rah, J. H., Christian, P., Shamim, A. A., Arju, U. T., Labrique, A. B., & Rashid, M. (2008). Pregnancy and lactation hinder growth and nutritional status of adolescent girls in rural Bangladesh. *Journal of Nutrition*, *138*(8), 1505-1511.

Rijt-Plooij, H. H. C., & Plooij, F. X. (1987). Growing independence, conflict and learning in mother-infant relations in free-ranging chimpanzees. *Behaviour*, *101*(1), 1-86. doi:10.1163/156853987X00378

Setchell, J. M., Lee, P. C., Wickings, E. J., & Dixson, A. F. (2002). Reproductive parameters and maternal investment in mandrills (*Mandrillus sphinx*). *International Journal of Primatology*, *23*(1), 51–68. doi:10.1023/A:1013245707228

Stanton, M. A., Lonsdorf, E. V., Pusey, A. E., Goodall, J., & Murray, C. M. (2014). Maternal behavior by birth order in wild chimpanzees (*Pan troglodytes*): Increased investment by first-time mothers. *Current Anthropology*, *55*(4), 483-489. doi:10.1086/677053

Struhsaker, T. T. (1997). *Ecology of an African rain forest*. Gainesville, FL: University Press of Florida.

Townsend, S. W., Slocombe, K. E., Emery Thompson, M., & Zuberbühler, K. (2007). Female-led infanticide in wild chimpanzees. *Current Biology*, *17*(10), 355–356. doi:10.1016/j.cub.2007.03.020

Trivers, R. L. (1972). Parental investment and sexual selection. In: B. Campbell (Ed.), *Sexual selection and the descent of man* (pp. 136–179). Chicago, IL: Aldine.

Tutin, C. E. G. (1979). Mating patterns and reproductive strategies in a community of wild chimpanzees (*Pan troglodytes schweinfurthii*). *Behavioral Ecology and Sociobiology*, *6*(1), 29–38. doi:10.1007/ BF00293242

Wakefield, M. (2008). Grouping patterns and competition among female *Pan troglodytes schweinfurthii* at Ngogo, Kibale National Park, Uganda. *International Journal of Primatology*, *29*(4), 907-929. doi:10.1007/s10764-008-9280-7

Wakefield, M. L. (2013). Social dynamics among females and their influence on social structure in an East African chimpanzee community. *Animal Behaviour*, *85*(6), 1303-1313. doi:10.1016/j.anbehav.2013.03.019

de Waal, F. B. M. (1978). Exploitative and familiarity-dependent support strategies in a colony of semi-free living chimpanzees. *Behaviour*, *66*(3), 268-311. doi:10.1163/156853978X00143

de Waal, F. B. M. (1982). *Chimpanzee politics*, Baltimore, MD: Johns Hopkins University Press.

Watts, D. P. (1998). Coalitionary mate guarding by male chimpanzees at Ngogo, Kibale National Park, Uganda. *Behavioral Ecology and Sociobiology*, *44*(1), 43–55. doi:10.1007/s002650050513

Watts, D. P. (2000). Grooming between male chimpanzees at Ngogo, Kibale National Park. I. Partner number and diversity and grooming reciprocity. *International Journal of Primatology*, *21*(2), 189–210. doi:10.1023/A:1005469302911

Watts, D. P., & Mitani, J. C. (2001). Boundary patrols and intergroup encounters in wild chimpanzees. *Behaviour*, *138*(3), 299–327. doi:10.1163/15685390152032488

Wheeler, B. C., Scarry, C. J., & Koenig, A. (2013). Rates of agonism among female primates: A cross-taxon perspective. *Behavioral Ecology*, *24*(6), 1369-1380. doi:10.1093/beheco/art076

Williams, J. M. (2000). *Female strategies and reasons for territoriality in chimpanzees: Lessons from three decades of research at Gombe*. Ph.D. thesis, University of Minnesota, Minneapolis, MN.

Williams, J. M., Pusey, A. E., Carlis, J. V., Farm, B. P., & Goodall, J. (2002). Female competition and male territorial behaviour influence female chimpanzees' ranging patterns. *Animal Behaviour*, *63*(2), 347–360. doi:10.1006/anbe.2001.1916

Williamson, E. A., & Feistner, A. T. C. (2003). Habituating primates: Processes, techniques, variables and ethics. In: J. M. Setchell, & D. J. Curtis, (Eds.), *Field and laboratory methods in primatology: A practical guide* (pp. 25–39). Cambridge: Cambridge University Press.

Wrangham, R. W. (1979). On the evolution of ape social systems. *Social Science Information Sur Les Sciences Sociales*, *18*(3), 335–368. doi:10.1177/053901847901800301

Wrangham, R. W., Conklin-Brittain, N. L., & Hunt, K. D. (1998). Dietary response of chimpanzees and cercopithecines to seasonal variation in fruit abundance. I. Antifeedants. *International Journal of Primatology*, *19*(6), 949–970. doi:10.1023/A:1020318102257

Wrangham, R. W., & Smuts, B. B. (1980). Sex differences in the behavioral ecology of chimpanzees in the Gombe National Park, Tanzania. *Journal of Reproduction and Fertility*, *28*, 13–31.

# CHAPTER 4

# Primiparous and multiparous female chimpanzees differ in patterns of intrasexual affiliation

## INTRODUCTION

Females in several primate species form strong social bonds with each other. Recent studies indicate that females who forge these bonds obtain short-term physiological and long-term fitness benefits by doing so. For example, female baboons (*Papio* spp.) who form strong social bonds with others display lower glucocorticoid levels, produce more surviving offspring, and live longer than do females who are unable to establish similar bonds (Silk et al. 2003; Silk et al. 2010; Wittig et al. 2008).

Thus far, these findings have largely been derived from studies of two species of baboons in which females are the philopatric sex. In these cases, strong bonds are often forged between closely related females, and as a consequence, kinship plays an important role in determining who befriends whom and who benefits. Female primates, however, do not always live together with close kin because in some species females disperse from their natal groups. After females disperse, they are likely to live with unrelated females with whom they maintain weak affiliative relationships (e.g., mountain gorillas (*Gorilla beringei beringei*), Watts 2002; hamadryas baboons (*P. hamadryas hamadryas*), Barton et al. 1996, but see Swedell 2002; woolly monkeys

(*Lagothrix poeppigii*), Di Fiore & Fleischer 2005). In some cases, however, unrelated females form close social bonds that confer physiological benefits, such as reduced stress (spider monkeys (*Ateles geoffroyi*), Rodrigues 2013).

Chimpanzees provide an opportunity to investigate whether unrelated females establish social bonds and the factors that influence the formation of such bonds. Female chimpanzees typically disperse from their natal communities (Nishida & Kawanaka 1972; Pusey 1979), and as a result, pairs of females who live together are typically unrelated (Vigilant et al. 2001; Langergraber et al. 2009). Previous research indicates that some pairs of unrelated female chimpanzees forge strong social bonds (Nishida 1989; Boesch & Boesch 2000; Wakefield 2008, 2013; Langergraber et al. 2009; Foerster et al. 2015), but the factors affecting the formation of these bonds are presently unclear.

Affiliative relationships often occur between individuals who are similar in some way ("the similarity principle," de Waal & Luttrell 1986; homophily, reviewed in McPherson et al. 2001). Unrelated individuals frequently select social partners of similar age or dominance rank (e.g., rhesus macaques (*Macaca mulatta*), de Waal & Luttrell 1986; humans, Kapsalis & Berman 1996; hyenas (*Crocuta crocuta*), Smith et al. 2007). Female reproductive status is also likely to affect affiliative relationships. Mothers face a particular set of challenges due to reproduction and they may benefit from associating with other parous females. Doing so may reduce the risk of predation through the dilution effect (e.g., order *Cetacea*, Whitehead & Mann 2000; mouflon (*Ovis aries*), Pipia et al. 2009). In species where mothers and offspring receive aggression from male conspecifics, associating with other mothers may create a safer environment in which to socialize (Connor & Peterson 1994; Otali & Gilchrist 2006). Creating opportunities for offspring to develop and maintain relationships is especially important in long-lived, social species, whose members must compete and cooperate to reproduce successfully (Poirier & Smith 1974; Burghardt 2014).

Although the challenges of motherhood can unite females, there is also evidence that mothers differ. Primiparas, or first-time mothers, differ in many ways from multiparas, mothers who have given birth multiple times. Primiparas may be young and physiologically immature, which can reduce the efficiency of lactation (rhesus macaques, Hinde et al. 2009; brown rats (*Rattus norwegicus*), Künkele & Kenagy 1997). Compared to multiparas, primiparas may invest more time interacting with or caring for infants (Stanton et al. 2014; Dettmer et al. 2015). This increased investment may be due to first-time mothers' inexperience caring for offspring or it could be a strategy primiparas use to compensate for their relative youth, immaturity, and inability to compete effectively with multiparas. Differences between primiparas and multiparas can extend beyond mothers and their offspring. Compared to multiparous brown bear (*Ursus arctos*) mothers, primiparas are socially inexperienced and may be less able to defend cubs against infanticidal conspecifics (Zedrosser et al. 2009). In a population of bottlenose dolphins (*Tursiops truncatus*), primiparas associated with nulliparous females or females without dependent calves while multiparas associated with other mothers with dependent calves (Owen 2000).

Here, I investigate whether the social bonds formed between female chimpanzees varied as a function of parity. To do so, I examine patterns of association and grooming between females at Ngogo in the Kibale National Park, Uganda. The Ngogo chimpanzee community is exceptionally large (Watts 1998; Watts & Mitani 2001; Mitani & Amsler 2003) and contains many females. Between 2010-2012, 31 surviving infants were born in the community, 12 of them to first-time mothers. This allowed me to investigate the affiliative behavior of primiparous and multiparous mothers. In what follows I address two questions. First, do mothers of different parity associate more with parous females or with non-mothers (i.e., nulliparous adolescents)? Answering this question will reveal whether parous females preferentially spend time with females of a similar reproductive status. Second, do primiparas and multiparas display different patterns of grooming with unrelated females? Answering this question will reveal whether patterns of intrasexual grooming vary as a function of mothers' parity.

## METHODS

### Study site and subjects

I observed chimpanzees at Ngogo in the Kibale National Park, Uganda. The Kibale Park is located in western Uganda (0°13′-0°41′N and 30°19′-30°32′E) and covers 795 $km^2$. The Ngogo chimpanzee community ranges over a 35 $km^2$ territory (Mitani et al. 2010) near the center of the Park. Rain falls throughout the year with an annual mean ± standard error of 1397 ± 174 mm (N=10 years, 1998-2007; Mitani 2009). Typically, September-December and March-May are wetter than average, while intervening months are drier (Butynski 1990; Struhsaker 1997). At an elevation of approximately 1350 m above sea level, the Ngogo study site lies at a transition between lowland and montane rainforest and comprises moist, evergreen forest interspersed with patches of *Pennisetum purpureum* grassland (Struhsaker 1997). Detailed descriptions of Ngogo and the ecology of the surrounding area can be found in Butynski (1990); Ghiglieri (1984); Struhsaker (1997) and Lwanga et al. (2000).

I collected data over 15 months, May-July 2010 and August 2011-July 2012. During this time the Ngogo community had 17-24 adolescent and 41-51 adult female chimpanzees. My analyses on how parity is involved in female social relationships took advantage of the known reproductive histories of females at Ngogo, which have been continuously recorded since study began there in 1995. I divided adult females into two groups based on parity: primiparas (mothers raising their first offspring) and multiparas (mothers with two or more offspring). My primary study subjects were females with dependent offspring and included 15 primiparas, 18 multiparas, and five mothers who transitioned between these parity categories during the study.

I recorded observations of female chimpanzees interacting with both parous females and nulliparous adolescents. Here, I use 'nullipara' to refer only to adolescent females who have not yet produced a surviving offspring. Nulliparas comprised 16 individuals: seven natal females and nine immigrants. Natal adolescent female subjects ranged in age from 10–16 years. Because the immigrant females dispersed into the Ngogo community from elsewhere, their histories and ages were unknown.

In addition to these 16 nulliparas, parous subjects sometimes interacted with 'unknown' adolescents who could not be identified as individuals. During the study, five adolescents from other communities immigrated into Ngogo, and they were not always recognizable during the first few months following immigration. In addition, several peripheral parous females at Ngogo had adolescent daughters who I also could not easily identify as individuals. Due to this, I treated adolescents as a category and not as individuals. Although female chimpanzees typically disperse from their natal community at adolescence (Nishida & Kawanaka 1972; Pusey & Packer 1987), some females at Ngogo do not disperse, instead remaining and reproducing in their natal community. Eight of the 38 parous study subjects were identified as natal females using long-term behavioral observations and genetic analyses (Langergraber et al. 2009).

During the study period, the Ngogo chimpanzee community increased from 157 to 190 individuals, primarily due to births. Twelve adolescent females gave birth to their first surviving infant either during the study period or within four months prior to the start. Additionally, six primiparas gave birth to a second infant, transitioning to multiparous status, and 13 multiparas gave birth. Two infants (less than one year old) died during the study, one from an inferred intra-community infanticide (K. Langergraber, unpublished data) and one of unknown causes. The infanticide victim was a neonate born to a first-time mother. Subsequent to the infanticide I considered the female subject to be an adolescent, not a primipara. This is because the majority of observations collected on this female took place prior to parturition, when she was an adolescent. Also, no observations were made during the few days when her infant was alive. The other infant was born to a multipara, and thus its death did not affect the mother's reproductive status.

## Behavioral Observations

During the study, I conducted approximately 1100 one-hour focal follows (Altmann 1974) of individual parous females. On any given day, I conducted no more than two focal follows per individual, with observation sessions separated by at least two hours. During focal observation sessions, I made six instantaneous scan samples at 10-minute intervals (Altmann 1974). During each scan I recorded the composition of the party, noting the identity of adults and adolescents that I judged to be within visual range of the focal female. I considered all chimpanzees within this visual range to be 'in association' (Pepper et al. 1999; Mitani et al. 2002). I recorded grooming involving focal subjects and unrelated parous and adolescent females *ad libitum*, noting the duration of grooming to the nearest 15 seconds. Females usually groomed in pairs, but focal subjects sometimes groomed with two females simultaneously. In the latter cases, I recorded these as two separate grooming interactions. During each interaction, I recorded the identity of participants and whether the focal subject was the groomer or recipient of grooming.

With the help of field assistants, I monitored adult and adolescent females' reproductive cycles. The sexual swellings of females were scored daily based on turgidity following Dahl et al. (1991). I considered females exhibiting maximally tumescent swellings to be sexually receptive (Tutin 1979). I did not include maximally tumescent females as focal subjects because females are known to alter their association patterns during this time (Pepper et al. 1999; Matsumoto-Oda 1999), and I was only interested in intrasexual relationships.

### Data analyses

### Association patterns

Chimpanzees live in a fission–fusion society, and party composition reflects association preferences (Newton-Fisher 1999). To determine whether association patterns varied with parity, for each female dyad I calculated a pairwise affinity index (PAI) based on party association (Pepper et al. 1999). Numerically, this index is:

$$\frac{I_{\mathrm{ab}} * \sum s_{\mathrm{i}}(s_{\mathrm{i}} - 1)}{\sum a_{\mathrm{i}}(s_{\mathrm{i}} - 1) * \sum b_{\mathrm{i}}(s_{\mathrm{i}} - 1)}$$

where $I_{ab}$ = the number of scan samples where individuals $a$ and $b$ are in the same party, $a_i$ = the total number of scan samples of $a$, $b_i$ = the total number of scan samples of $b$, and $S_i$ = the size of group $i$, where a "group" is defined as the number of individuals in the same party. I normalized the observed indices by dividing them by their expected values. To generate expected values and provide a statistical test of the null hypothesis that all individuals behaved the same way, I used a randomization technique. This procedure repeatedly re-shuffled the membership of observed parties, while retaining the number of times each individual was observed and the observed distribution of party sizes. After each randomization, the PAI was calculated for each dyad. I repeated this process 10,000 times, using the average of the randomized values to generate an expected value for each pair. I log transformed the observed/expected ratios to ensure that dyadic interactions above and below expected levels would have equal weight. After log transformation, $x$ and $1/x$ have the same magnitude but the opposite sign. To avoid undefined values resulting from observed or expected values of zero, I truncated the range of the log-transformed values to $-2 \leq x \leq 2$, corresponding to a floor of 0.01 and a ceiling of 100 for observed/expected ratios. As the composition of females in the community changed over time and not all subjects were observed each year, I calculated three separate PAIs – one for each year of the study (2010, 2011, and 2012).

To examine whether females formed subgroups based on associations, I conducted hierarchical cluster analyses implementing the unweighted pair-groups method using arithmetic averages (UPGMA, Sneath & Sokal 1973). The UPGMA approach is a simple, agglomerative (bottom-up) hierarchical clustering technique (Norušis 2012). At each step, the two clusters that are closest in distance are combined into a higher-level cluster. The distance between any two clusters is calculated as the mean distance between all pairs of objects in the different clusters.

For the analysis, I used PAIs to construct distance matrices between female subjects and used squared Euclidean distances. As such, a high PAI is associated with a small inter-female distance.

The cluster analysis produced a dendrogram, a visual representation of the distance matrix depicting association patterns of individual females. I identified associative clusters of females by determining the cutoff points that produced well-defined clusters with the deepest branches, i.e., the greatest distance between subsequent splitting events or clusters (Romesburg 2004). These clusters represent subgroups of females who were observed in association often.

Following cluster analysis, an examination of PAIs revealed females belonging to different clusters rarely or never associated. I therefore used PAIs from females belonging to the same cluster for the subsequent analysis of parity and association. I amalgamated within-cluster PAIs across the three years of study to create a single dataset. Using a generalized linear model (GLM) I compared PAIs between females in five dyadic combinations based on parity: primiparas and adolescent nulliparas, multiparas and adolescent nulliparas, primiparas and primiparas, primiparas and multiparas, and multiparas and multiparas. In this analysis (GLM1), I utilized PAIs as the dependent variable and parity of associates as the predictor. Because I was interested only in affiliation between non-kin, I excluded PAIs between mothers and daughters and sisters to produce this model. I excluded PAIs involving parous females who were not focal subjects (due to too few observations) and PAIs involving adolescent nulliparas who were observed in fewer than 20 association scans in each year of the study.

## Grooming

I investigated whether grooming varied as a function of parity, considering both the focal mother and three categories of non-kin who themselves differed in parity: adolescent nulliparas, primiparas, and multiparas. I assessed grooming involvement separately for each year of the study as some female subjects changed parity status between years. I did not restrict analyses to within-cluster grooming for two reasons: (1) female chimpanzees groom one another infrequently (Goodall 1986; Wrangham et al. 1992; Wheeler et al. 2013) and therefore to do so would overly restrict my sample size; and (2) some adolescent grooming partners of focal subjects could not be identified as individuals, and therefore they could not be accurately assigned to a cluster.

In the first grooming model, GLM2, I compared how often individual primiparous and multiparous mothers were involved in intrasexual grooming. The dependent variable was the annual amount of time (represented by counts of 15-second segments) that individual mothers were involved in intrasexual grooming (either as the director and/or recipient of grooming). I included two predictor variables, the parity of the mother and the parity of the grooming partner (adolescent nullipara, primipara, or multipara). I also examined the interaction between these two variables, which involved the same five categories as in GLM1 (see previous description).

Counts of grooming segments were overdispersed, therefore I fit GLM2 with a negative binomial distribution and a log link function. To account for individual differences in association, I quantified the number of opportunities each focal female had to groom with individuals from each of the three parity groups. For each year, I calculated "female-scans" per parity group by counting the number of adolescent nulliparas, primiparas, and multiparas that the focal female associated with across all her focal scans. Counts of female-scans were right skewed so I applied a natural log transformation. I offset each female's yearly count of grooming segments by the natural logarithm of the yearly sum of scan samples in which she was observed associating with at least one female of the parity group of interest.

Because scan samples were made at 10-minute intervals, I multiplied the resulting rates by six to obtain hourly rates. I compared rates of grooming using rate ratios (R) where:

$$R = \frac{\text{rate of grooming in group A (reference category)}}{\text{rate of grooming in group B}}$$

Grooming involves two individuals who participate in the interaction in different ways. The preceding analysis on grooming involvement (GLM2) does not reveal whether mothers were grooming other females or being groomed by them. To address this, I conducted additional GLMs examining how often mothers directed and received intrasexual grooming (GLM3 and GLM4, respectively).

For directed grooming (GLM3), the dependent variable was the annual amount of time (represented by counts of 15-second segments) that each mother groomed other females. I included a single predictor variable, the parity of the mother. As I did not observe mothers groom females in all parity groups, I could not include the parity of grooming partners in GLM3. Lastly, for GLM4, I examined how much grooming mothers received from females in each of the three parity groups. The dependent variable was the amount of grooming each mother received from other females. I included two predictor variables, the parity of the mother, and the parity of the grooming partner (adolescent nullipara, primipara or multipara). I also examined the interaction between these two variables, which involved six director-recipient combinations: adolescent-primipara, adolescent-multipara, primipara-primipara, primipara-multipara, multipara-primipara, and multipara-multipara. As directionality is pertinent in the receipt of grooming, there is an additional category of grooming partners in this analysis (here, multipara-primipara and the reverse, primipara-multipara are separate categories), compared to the analysis on grooming involvement.

For both grooming directed and received, counts of grooming segments were overdispersed, therefore I fit GLMs 3 and 4 with a negative binomial distribution and a log link function. As with GLM2, I offset each female's yearly count of grooming segments by the natural logarithm of the yearly sum of scan samples in which she was observed associating with at least one female of the parity group of interest.

Statistical analyses were conducted using SPSS for Macintosh, version 22 (© IBM Corporation). I set the $\alpha$-level of significance at $P < 0.05$.

## Generalized estimating equations

My observations of female chimpanzee social interactions violate assumptions of independence for several reasons. Most notably, there are repeated measures within and between years of data collection (a female observed in all three years of the study would have three rates per year per GLM). Also, five study subjects transitioned from primiparous to multiparous status during the study and are represented in more than one parity group. Violation of assumptions of independence can increase the frequency of type I errors (Clifford et al. 1989). To circumvent these problems, I utilized generalized estimating equations (GEEs), which account for potential unknown correlation among outcomes of a GLM (Liang & Zeger 1986). Specifically, GEEs use a quasi-likelihood estimation approach, adjusting the standard error to account for the correlation within observations from the same group, in this case repeated observations of an individual female chimpanzee. GEEs are favorable as parameter estimates and empirical standard errors are robust to misspecification of the correlation structure (Dobson 2002; Overall & Tonidandel 2004). In addition, GEEs are usually less analytically complex than generalized linear mixed models (Agresti 2002), making model convergence more likely (Koper & Manseau 2009).

For PAI data, there are repeated observations from the same female in different dyads within the same cluster. In GLM1, I numbered dyads from the same yearly cluster with a dummy variable. For grooming data, there were repeated observations of individual females within and between years. In GLMs 2 through 4, I numbered observations from the same focal female with a dummy variable. I fit all GLMs with an ‘exchangeable’ working correlation matrix, which assumes that the correlation between any two observations from the same group is the same $\alpha$ (Jang 2011).

## RESULTS

### Association

Pairwise affinity indices between female chimpanzees ranged from -2.0 to 1.5. Distributions of PAIs were similar across the three years of study, although fewer female subjects were observed in 2010. In all years different female dyads associated more and less than expected, based on the null hypothesis that individuals associate randomly (Figure 4.1). In each year several female dyads were never observed in association (represented by PAIs of -2.0).

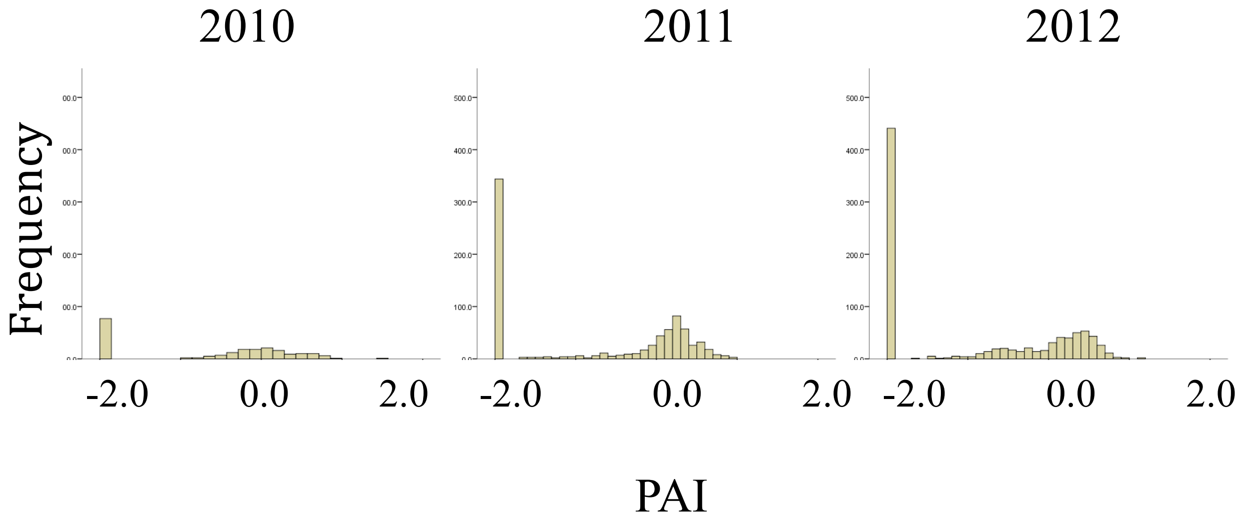

**Fig. 4.1.** Frequency of pairwise affinity indices of female chimpanzee association during three years of study. Positive values indicate association greater than expected, while negative values indicate association less than expected.

Results of cluster analysis using PAIs indices indicate that in each year of the study, females formed two distinct clusters representing subgroups of individuals who associated frequently (Figures 4.2, 4.3, 4.4). Each association cluster contained 12-24 study subjects and at least two females from each parity group. The topology of the dendrogram from 2010 differs from the other two years, revealing large inter-individual differences. This is likely due to the fact that the duration of data collection was shorter in 2010 compared to 2011 and 2012, and fewer female dyads were observed. Despite these differences, cluster membership was stable across the three-year study period. Of 43 females who were subjects in multiple years of the study, only three (two natal adolescents, one natal primipara) associated with different clusters across years.

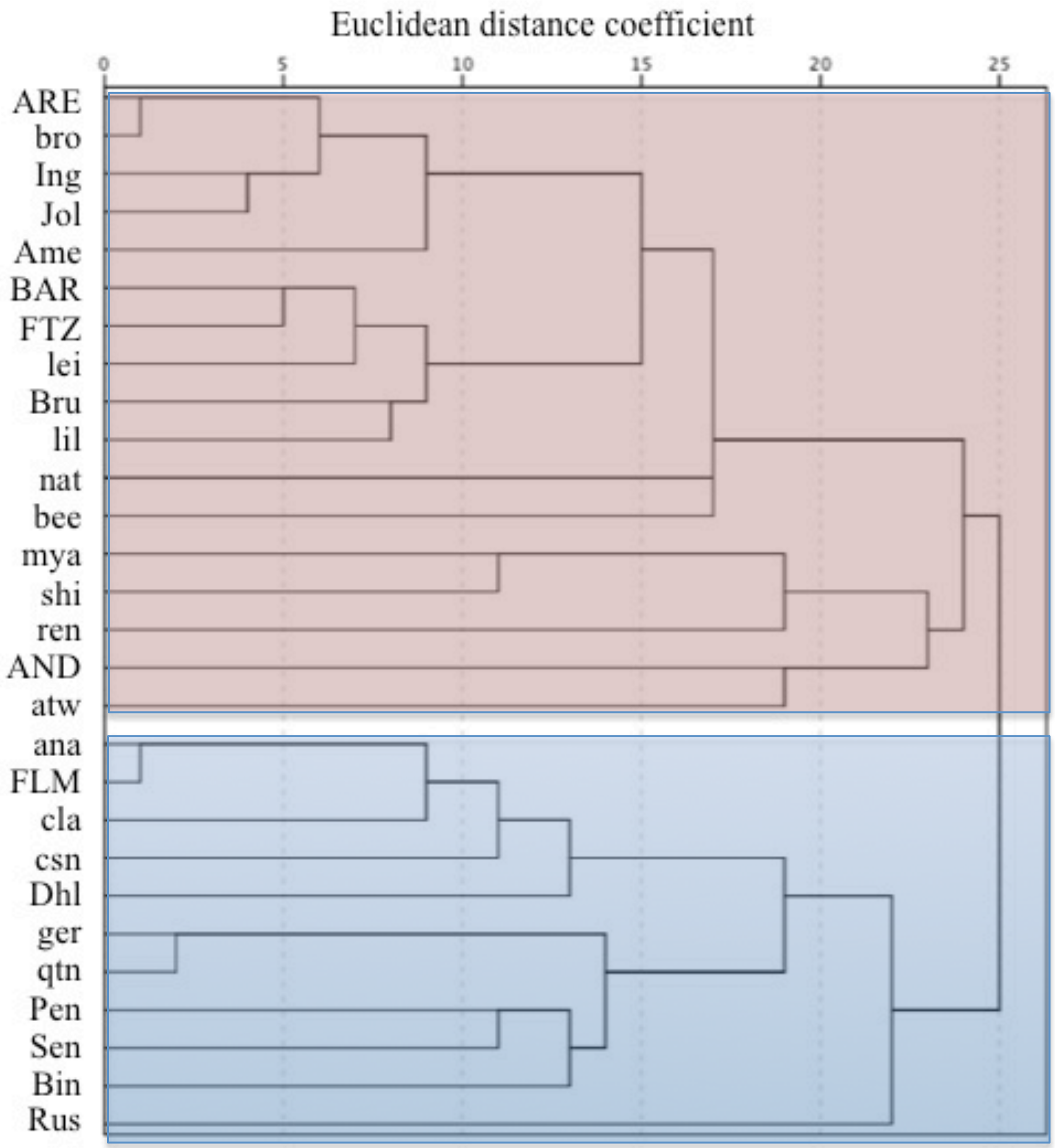

**Fig 4.2.** Dendrogram of the results of the UPGMA cluster analysis calculated from the pairwise affinity indices for females in 2010. Each three-letter code represents a female subject (adolescent nulliparas are indicated by lowercase letters, primiparas by only the first letter capitalized, and multiparas by all letters capitalized). Females formed two clusters, which represent association cliques (red and blue squares).

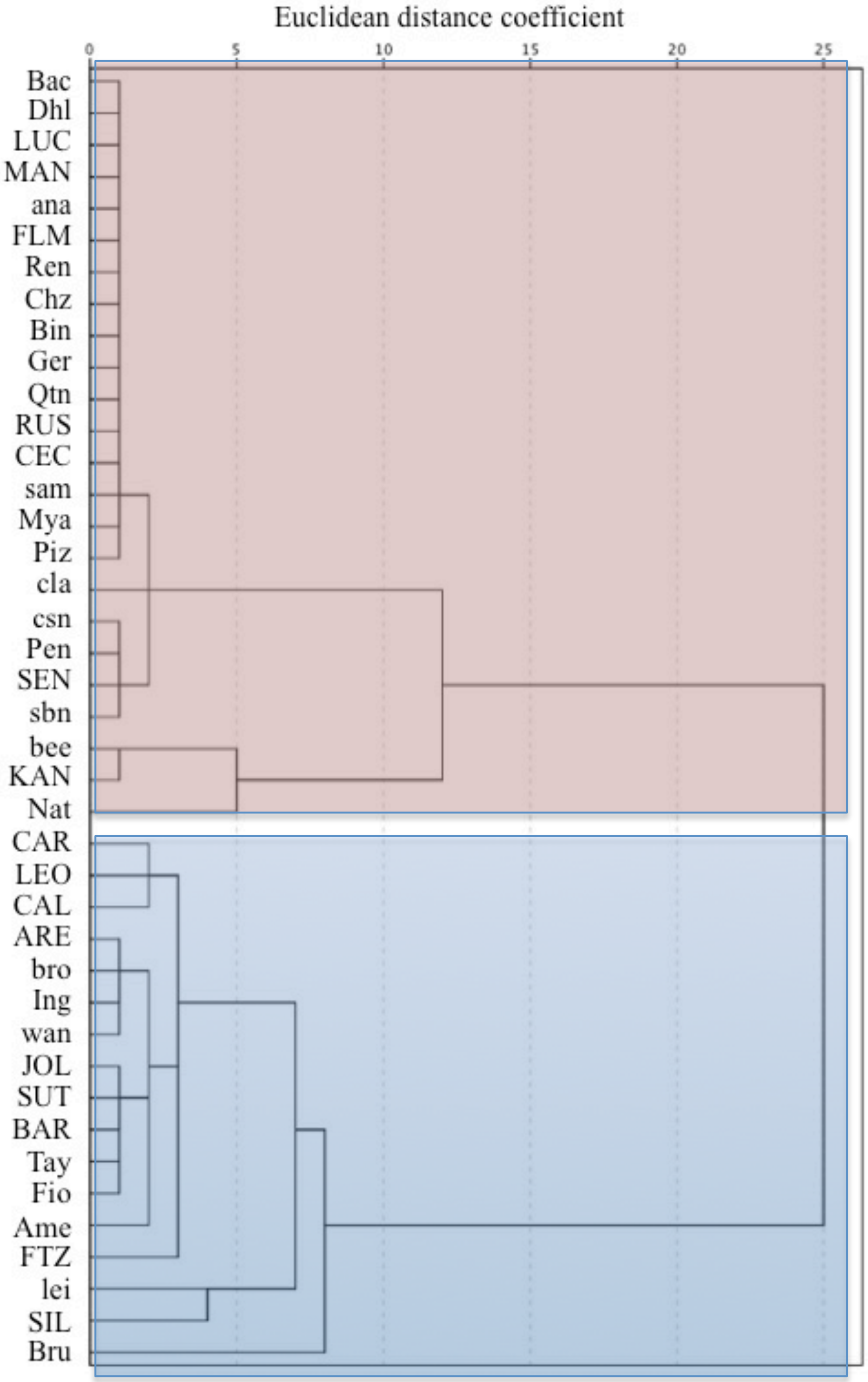

**Fig 4.3.** Dendrogram of the results of the UPGMA cluster analysis calculated from the pairwise affinity indices for females in 2011. Each three-letter code represents a female subject (adolescent nulliparas are indicated by lowercase letters, primiparas by only the first letter capitalized, and multiparas by all letters capitalized). Females formed two clusters, which represent association cliques (red and blue squares).

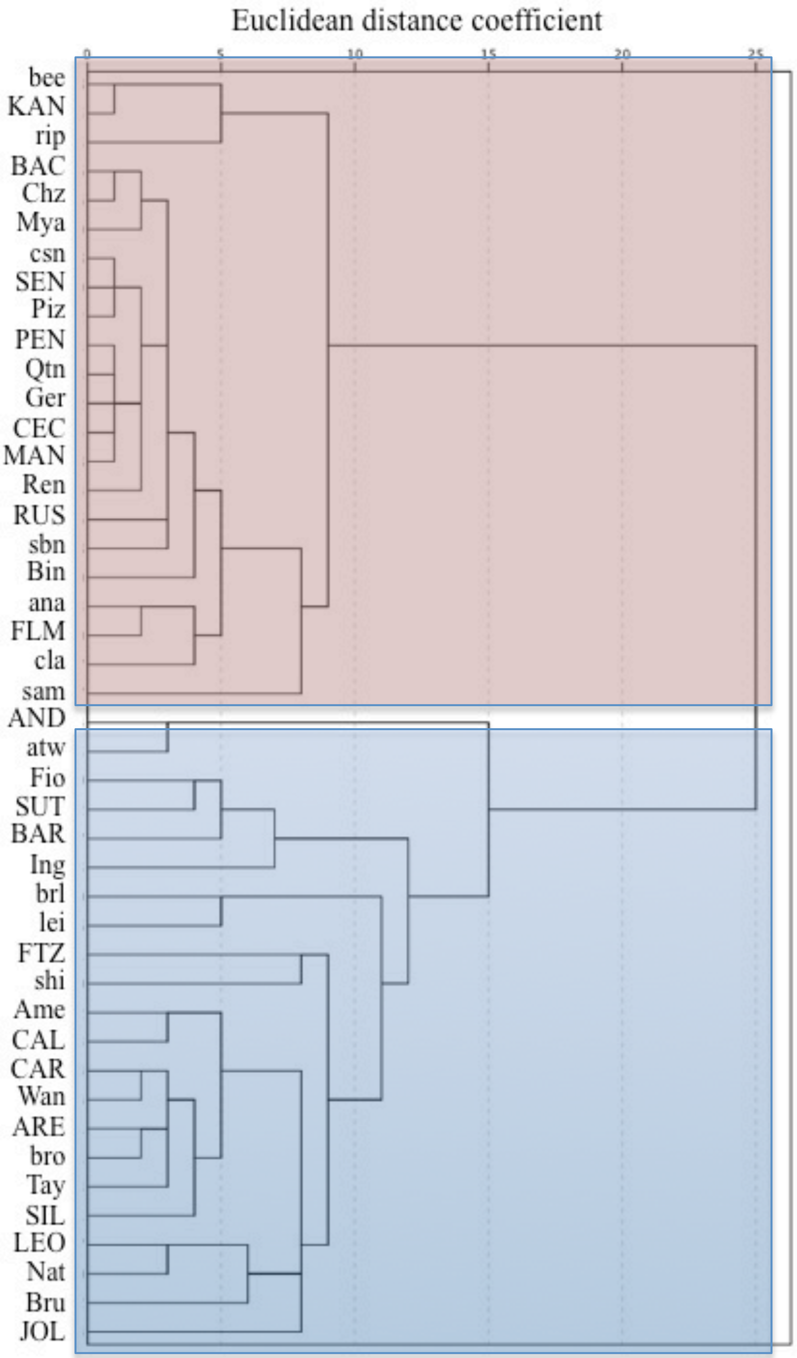

**Fig 4.4.** Dendrogram of the results of the UPGMA cluster analysis calculated from the pairwise affinity indices for females in 2012. Each three-letter code represents a female subject (adolescent nulliparas are indicated by lowercase letters, primiparas by only the first letter capitalized, and multiparas by all letters capitalized). Females formed two clusters, which represent association cliques (red and blue squares).

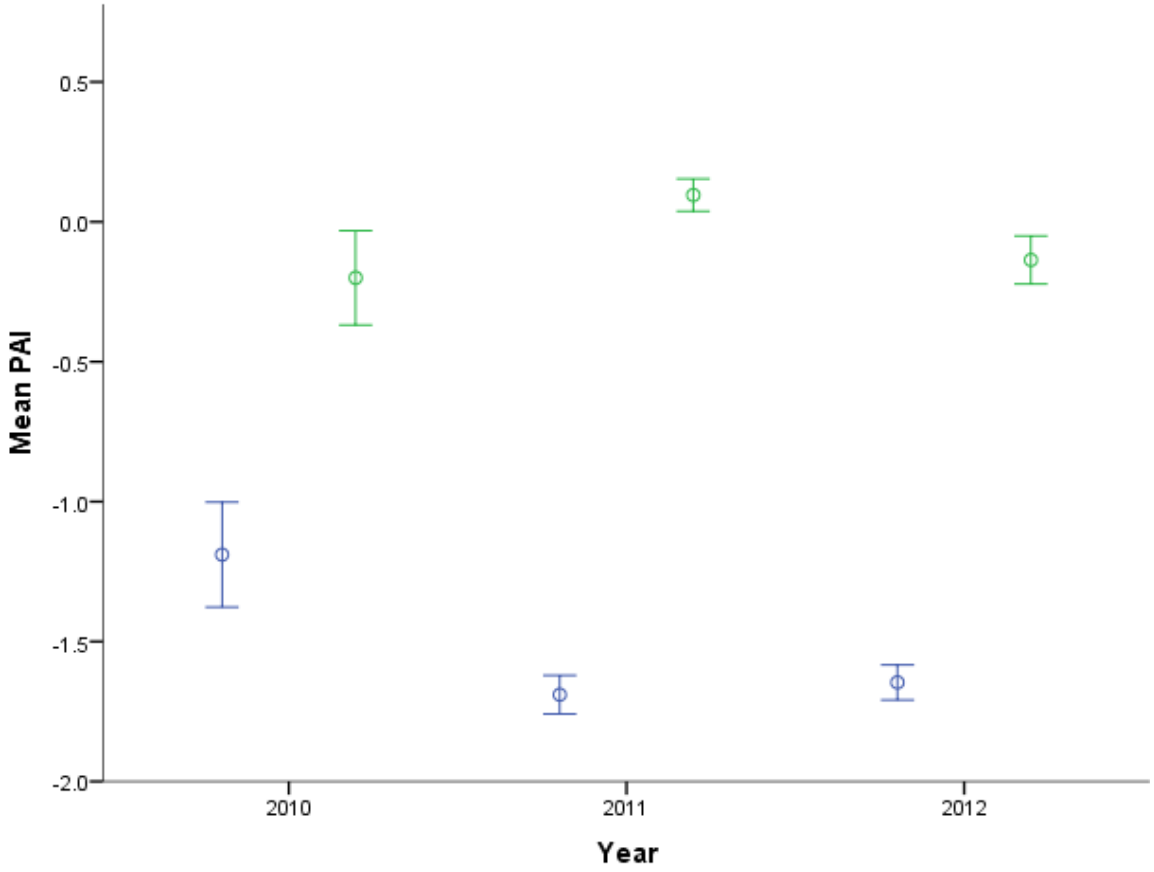

**Fig 4.5**. Pairwise affinity indices between parous female chimpanzees and female associates during three years of study. Means ± 2 standard errors are shown for indices of females in different (blue) or the same (green) associative clusters.

To investigate whether female association varied with parity, I compared PAIs between five groups of females who differed in parity. For females in the same yearly cluster, the parity of associates was a significant predictor of PAI (GLM1, $X^2$=17.547, df=4, P=0.002). Primiparas and multiparas had higher PAIs with mothers than they did with adolescent nulliparas (Table 4.3). Primiparas and multiparas did not differ in PAIs with adolescent nulliparas. Additional comparisons indicated that there were no differences in PAIs between the three groups involving only parous females (primipara-primipara, primipara-multipara, and multipara-multipara).

**Table 4.1** Results of GLM1, a test of the effect of parity of associates on pairwise affinity index (PAI)

| Parameter | Estimate | Standard error | $X^2$ | P value | Mean PAI | PAI ratio[a] (other:AM) |
|---|---|---|---|---|---|---|
| Intercept | -0.248 | 0.0713 | 12.066 | 0.001 | | |
| Adolescent-primipara | 0.073 | 0.0916 | 0.0642 | 0.423 | 0.15 | 0.93 |
| Adolescent-multipara | 0 | . | . | . | 0.16 | - |
| Primipara-primipara | 0.320 | 0.0967 | 10.923 | 0.001 | 0.29 | 1.80 |
| Multipara-primipara | 0.288 | 0.0856 | 11.368 | 0.001 | 0.22 | 1.36 |
| Multipara-multipara | 0.227 | 0.1011 | 5.024 | 0.025 | 0.22 | 1.38 |

[a] Adolescent-multipara (AM) is the reference category for PAI ratios

## Grooming

Chimpanzee researchers define grooming interactions in different ways (Goodall 1986; Lehmann & Boesch 2009; Newton-Fisher 2011; Wakefield 2013). Considering only one bout of grooming per dyad daily, I observed 179 interactions between mothers and unrelated parous or adolescent females during 1052 focal hours of females in association. This equates to approximately one grooming interaction per five hours of observation. There was considerable inter-individual variation in grooming behavior. In each year of the study, some subjects were never observed engaged in intrasexual grooming while others groomed with several partners (range: 0-10 partners per year, mean and median: 2, SD: 2.2). Additionally, parous female subjects predominantly groomed with partners within their associative cluster. Of 179 grooming interactions, 145 occurred in dyads for which partners could be assigned to a cluster (not all females who groomed with focal subjects were observed often enough to be included in cluster analysis, and sometimes the identity of adolescent grooming partners could not be ascertained). Only 11 (8%) of grooming interactions occurred between females assigned to different clusters.

### Grooming involvement

To determine whether grooming behavior varied with parity, I compared the amount of time individual mothers were involved in grooming interactions with adolescent nulliparas, primiparas, and multiparas. A mother's parity did indeed predict how often she was involved in grooming (GLM2, $X^2$=4.016, df=1, P=0.045). Primiparas groomed with other females nearly three times more often than did multiparas (mean of individual minutes spent per 100 hours ± SD: 30.0 ± 73.0 and 10.7 ± 28.7 respectively). Partner parity, on the other hand, did not predict how often mothers were involved in grooming (GLM2: $X^2$=2.168, df=2, P=0.338).

The interaction of mother and partner parity showed a trend toward predicting mothers' grooming involvement (GLM2: $X^2$=9.140, df=2, P=0.058). This indicates that the parity of both the mother and her grooming partner predicted grooming involvement. Of the five parity combinations, multiparas and adolescent nulliparas spent the least amount of time grooming with each other (Table 4.2). A comparison of rates indicated primiparas groomed with adolescent females seven times more often than did multiparas and that this difference was statistically significant. Additional iterations of the model did not reveal any other differences in duration of grooming involvement between groups.

**Table 4.2** Results of GLM2, a test of the effect of the interaction of parity of associates on the duration of intrasexual grooming involving chimpanzee mothers

| Parameter | Estimate | Standard error | $X^2$ | P value | Mean minutes/100 hours | Rate ratio[a] (other:AM) |
|---|---|---|---|---|---|---|
| Intercept | -3.171 | 0.5674 | 31.238 | <0.001 | | |
| Adolescent-primipara | 1.308 | 0.6771 | 3.732 | 0.053 | 24.1 | 6.5 |
| Adolescent - multipara | 0 | . | . | . | 3.7 | - |
| Primipara-primipara | 1.681 | 0.6969 | 5.818 | 0.016 | 39.3 | 10.6 |
| Primipara-multipara | 1.091 | 0.6218 | 3.080 | 0.079 | 18.3 | 4.9 |
| Multipara-multipara | 1.347 | 0.5719 | 5.545 | 0.019 | 19.4 | 5.2 |

[a] Adolescent-multipara (AM) is the reference category for rate ratios

### Grooming given

Grooming involves two individuals who participate in the interaction in different ways. The preceding results do not make clear whether patterns of grooming resulted from mothers' involvement as groomers or recipients. To examine this, I conducted a series of additional analyses. First, I examined whether the amount of grooming mothers gave to other females varied with parity. Primiparas groomed females more than did multiparas (mean of individual minutes given per 100 hours ± SD: 16.3 ± 52.6 and 6.8 ± 25.8 respectively). However, this difference was not significant (GLM3, $X^2$=1.447, df=1, P=0.229). Partner parity was a significant predictor of an individual mother's rate of directed grooming (GLM3, $X^2$=15.902, df=2, P<0.001). Mothers groomed primiparas and multiparas similar amounts (mean of individual minutes given per 100 hours ± SD, respectively: 15.8 ± 61.8 and 15.0 ± 35.7). However, mothers groomed adolescents (mean of individual minutes ± SD: 4.4 ± 14.7 minutes per 100 hours) less than they groomed primiparas ($P<0.001$) or multiparas ($P=0.006$). Because I did not observe multiparas grooming adolescent nulliparas during focal observation, I could not investigate the interaction between groomer and recipient parity.

### Grooming received

After I examined grooming mothers gave to other females, I analyzed the receipt of grooming by mothers. I compared amounts of grooming individual mothers received from adolescent nulliparas, primiparas, and multiparas. Primiparas received three times more grooming than did multiparas (mean of individual minutes received per 100 hours ± SD: 11.5 ± 22.7 and 4.4 ± 13.3 respectively). However, this difference was not significant (GLM4: $X^2=3.336$, df=1, $P=0.068$). Although the amount of grooming mothers received did not vary as a function of partner parity (GLM4: $X^2=4.636$, df=1, $P=0.098$), mothers received significantly less grooming from multiparas than they did from adolescent nulliparas (GLM4: $X^2=4.636$, df=1, $P=0.038$). The mean ± SD minutes of grooming individual mothers received per 100 hours from adolescents and multiparas were 10.0 ± 23.8 and 5.1 ± 11.3 minutes, respectively.

The interaction of groomer and recipient parity did not predict how often mothers received grooming (GLM4: $X^2=7.958$, df=2, $P=0.159$). Out of all parity combinations, primiparas received grooming from adolescent nulliparas most often (Table 4.3). However, this rate was not significantly different than those between other parity combinations. I conducted multiple iterations of the model, using each parity group as the reference category and detected no significant differences in how often mothers groomed mothers.

**Table 4.3** Results of GLM4, a test of the effect of the interaction of groomer and recipient parity on the rates of intrasexual grooming received by chimpanzee mothers

| Parameter | Estimate | Standard error | $X^2$ | P value | Mean minutes/100 hours | Rate ratio[a] (other:AM) |
|---|---|---|---|---|---|---|
| Intercept | -3.333 | 0.6595 | 25.539 | 0.000 | | |
| Adolescent-primipara | 1.134 | 0.7614 | 2.219 | 0.136 | 15.7 | 4.2 |
| Adolescent - multipara | 0 | . | . | . | 3.7 | - |
| Primipara-primipara | 0.745 | 0.7622 | 0.955 | 0.328 | 12.4 | 3.4 |
| Primipara-multipara | 0.269 | 0.8579 | 0.098 | 0.754 | 6.0 | 1.6 |
| Multipara-primipara | 0.300 | 0.7238 | 0.172 | 0.678 | 6.6 | 1.8 |
| Multipara-multipara | -0.215 | 0.3437 | 0.392 | 0.531 | 3.4 | 0.9 |

[a] Adolescent-multipara (AM) is the reference category for rate ratios. The parity of the groomer is listed first followed by the parity of the recipient.

## DISCUSSION

Results of this study indicated that female chimpanzees did affiliate with non-kin females, and that patterns of affiliation varied with parity. Mothers associated mainly with other mothers, rather than with adolescent nulliparas. Mothers of different parity groups also varied in their grooming interactions. Primiparas were involved in more intrasexual grooming than were multiparas. This was due, in part, to the high rates of grooming between adolescent nulliparas and primiparas. In contrast, adolescents and multiparas did not groom often.

**With whom do chimpanzee mothers form intrasexual social bonds?**

Chimpanzee mothers at Ngogo associated primarily with other parous females. This finding is consistent with reports from several other chimpanzee communities. When in association, mothers are often in nursery parties, groups of mothers and dependent offspring (Kortlandt 1962; Goodall 1968, Halperin 1979; Boesch 1996; Pepper et al. 1999; but see Wrangham et al. 1992). Observations from several species suggest that mothers benefit by affiliating with other parous females. Mothers and their dependents are vulnerable to predation and intersexual aggression, threats that are stressful and potentially lethal (Corkeron et al. 1987; Boonstra et al. 1998; Taylor et al. 2000). Gathering together in groups affords mothers protection against such threats (Möller & Harcourt 2008; Pipia et al. 2009).

In chimpanzees, nursery parties also provide a relatively safe environment in which to socialize (see Otali & Gilchrist 2006) because aggression between parous female chimpanzees is rare (Muller 2002; Wakefield 2008). In the Taï chimpanzee community, close intrasexual bonds are associated with reduced aggression between female partners (Lehmann & Boesch 2009). Also, in nursery parties mothers gain opportunities to groom same-sex peers. Subsequent to grooming each other, closely bonded female chimpanzee partners in the Budongo Forest experienced elevated levels of oxytocin, regardless of their genetic relatedness (Crockford et al. 2013). Oxytocin is a hormone that facilitates bonding in social mammals (Curley & Keverne 2005).

In addition to providing opportunities for mothers to interact with conspecifics, nursery parties allow dependent offspring to develop relationships and practice social skills (Poirier & Smith 1974; Watts & Pusey 1993; Williams et al. 2002). This is especially important in species with complex social systems and an extended maturation period (Pellis et al. 2014), as experiences in youth influence future reproductive success (Cameron et al. 2008; Blumstein et al. 2013; Nunes 2014). For example, social play behavior influences social development in several species (Fagen 1981; Beckhoff & Byers 1998). In chimpanzees, there is evidence that young individuals seek particular social partners (Watts & Pusey 1993), thus influencing the association patterns of their mothers (Murray et al. 2014).

While chimpanzee mothers likely benefit from associating with one another, affiliation between nulliparous and parous chimpanzees is constrained for several reasons. First, while mothers avoid associating with males (Pepper et al. 1999) due to the risk of aggression (Otali & Gilchrist 2006), nulliparas, especially immigrants, seek the company of males (Pusey 1980; Kahlenberg et al. 2008a). Second, nulliparas represent feeding competitors to parous females. Parous female chimpanzees feed in small, overlapping core areas (Williams et al. 2002; Murray et al. 2007; Kahlenberg et al. 2008; Hasegawa 1989; Emery Thompson et al. 2007). To successfully reproduce, adolescent nulliparas must establish a core area, and this likely increases feeding competition. Thus, parous females are likely to shun adolescents (Nishida 1989; Kahlenberg et al. 2008; Pusey et al. 2008), rather than affiliate with them. Lastly, from the perspective of parous females, nulliparas are not desirable social partners, as they may not be permanent residents of the community and are likely low-ranking (Nishida 1989; Kahlenberg et al. 2008).

**Do the intrasexual social bonds of primiparas and multiparas differ?**

As described above, there are several reasons why mothers, regardless of parity, may benefit from affiliating with other mothers. My findings on association patterns support this. However, my results regarding grooming indicate that interactions differed as a function of a female parity. Primiparas groomed with unrelated females more than did multiparas. Why might primiparas and multiparas differ in their grooming interactions? One possibility involves the availability of partners. Chimpanzee mothers preferentially groom offspring, especially dependents (Nishida 1988; Goodall 1986; Sugiyama 1988; Wrangham et al. 1992; Boesch & Boesch 2000). While primiparas have only one offspring, multiparas may have two dependents, as well as adolescent and adult offspring. As a consequence, primiparas may have more time available to groom with non-kin than do multiparas. In the Mahale Mountains chimpanzee community, multiparas devoted over 85% of their grooming time to offspring while primiparas devoted only around 45% (Nishida 1988[1]).

At Ngogo, differences in mothers' grooming involvement were related to their interactions with adolescent nulliparas. Primiparas groomed more often with adolescent nulliparas than did multiparas. Primiparas sometimes directed grooming toward adolescent females while multiparas were not observed to do so during focal observation sessions. I observed multiparas grooming unrelated adolescents a few times outside of focal following episodes, which indicates that these two types of females do groom each other, but only very rarely. In contrast, the parity

---

[1] Values based on data reported in Table II. For individuals with multiple measurements within a parity category, I calculated a mean. I then calculated a mean of all individuals within each parity class, and these are the percentages I report.

combination with highest rate of received grooming was primiparas receiving grooming from adolescents.

Several reasons may explain why primiparas groomed more with adolescents than did multiparas. As discussed previously, one reason relates to parity; compared to multiparas, primiparas likely have more time available for grooming because they only have one offspring. Observations from several taxa suggest that, for a variety of reasons, primiparity is a particularly challenging period. If these challenges induce stress, it is possible that first-time mothers invest in intrasexual grooming relationships as a coping mechanism (see Taylor et al. 2000). Adolescent nulliparas, who lack offspring and are in the process of integrating themselves socially into a new community, may be willing partners (e.g., Idani 1991; Guan et al. 2013).

In addition to parity, demographic factors specific to Ngogo may have contributed to the relatively close social bonds between primiparas and nulliparas. When this study began in 2010, there was a large cohort of 20 adolescents in the community. Ten of these individuals transitioned to motherhood over 27 months, while eight (five natal, three immigrant) remained nulliparous. Affiliative bonds between female chimpanzees may form during adolescence (Nishida 2012; Foerster et al. 2015), and studies indicate that social bonds between female chimpanzees are stable across years (Nishida 1989; Boesch & Boesch 2000; Wakefield 2008, 2013; Langergraber et al. 2009; Lehmann & Boesch 2009). Females who forge bonds as adolescents may retain those bonds, even if one individual transitions to motherhood before the other. Thus, the high rates of grooming between primiparas and adolescents in this study may reflect social bonds formed as adolescents. This is supported by the observation that nearly all grooming interactions between mothers and adolescents at Ngogo involved familiar adolescents, natal and immigrant, rather than new immigrants to the community.

One limitation of this study is that the variable of interest, parity, is positively correlated with age, which may also play an important role in influencing affiliation between female chimpanzees. Additional research will be required to tease apart the influences of parity and age on female association patterns. Several other questions about female chimpanzee sociality remain unanswered. For example, it is not clear whether the differences observed between primiparas and multiparas in this study are specific to Ngogo, or whether they apply to other communities. In addition, we do not yet know whether differences in female chimpanzee affiliation have any implications for their health and reproductive success. As primiparity is an important life history event (Stearns 1992) and female social bonds influence fitness in other species, this is a critical area that warrants further study.

## REFERENCES

Agresti, A. (2002). *Categorical data analysis*. Hoboken, NJ: John Wiley & Sons.

Altmann, J. (1974). Observational study of behavior: Sampling methods. *Behaviour*, *49*(3), 227–267. doi:10.1163/156853974X00534

Barton, R. A., Byrne, R. W., & Whiten, A. (1996). Ecology, feeding competition and social structure in baboons. *Behavioral Ecology and Sociobiology*, *38*(5), 321-329. doi:10.1007/s002650050248

Beckoff, M., & Byers, J. A. (1998). *Animal play: Evolutionary, comparative, and ecological perspectives*. Cambridge: Cambridge University Press.

Blumstein, D. T., Chung, L. K., & Smith, J. E. (2013). Early play may predict later dominance relationships in yellow-bellied marmots (*Marmota flaviventris*). *Proceedings of the Royal Society of London B: Biological Sciences*, *280*(1759), 20130485. doi:10.1098/rspb.2013.0485

Boesch, C. (1996). Social grouping in Taï chimpanzees. In: W. C. McGrew, L. F. Marchant, & T. Nishida (Eds.), *Great ape societies* (pp. 101–113). Cambridge: Cambridge University Press.

Boesch, C., & Boesch-Achermann, H. (2000). *The chimpanzees of the Taï Forest*. Oxford: Oxford University Press.

Boonstra, R., Hik, D., Singleton, G. R., & Tinnikov, A. (1998). The impact of predator-induced stress on the snowshoe hare cycle. *Ecological Monographs*, *68*(3), 371-394. doi:10.1890/0012-9615(1998)068[0371:TIOPIS]2.0.CO;2

Burghardt, G. M. (2014). A brief glimpse at the long evolutionary history of play. *Animal Behavior and Cognition*, *1*(2), 90-98. doi:10.12966/abc.05.01.2014

Butynski, T. M. (1990). Comparative ecology of blue monkeys (*Cercopithecus mitis*) in high-density and low-density subpopulations. *Ecological Monographs*, *60*, 1–26. doi:10.2307/1943024

Cameron, E. Z., Linklater, W. L., Stafford, K. J., & Minot, E. O. (2008). Maternal investment results in better foal condition through increased play behaviour in horses. *Animal Behaviour*, *76*(5), 1511-1518. doi:10.1016/j.anbehav.2008.07.009

Clifford, P., Richardson, S., & Hémon, D. (1989). Assessing the significance of the correlation between two spatial processes. *Biometrics*, *45*, 123–134. doi:10.2307/2532039

Connor, R. C., & Peterson, D. M. (1994). *The lives of whales and dolphins.* New York, NY: Holt.

Corkeron, P. J., Morris, R. J., & Bryden, M. M. (1987). Interactions between bottlenose dolphins and sharks in Moreton Bay, Queensland. *Aquatic Mammals*, *13*(3), 109-113.

Crockford, C., Wittig, R. M., Langergraber, K., Ziegler, T. E., Zuberbühler, K., & Deschner, T. (2013). Urinary oxytocin and social bonding in related and unrelated wild chimpanzees. *Proceedings of the Royal Society of London B: Biological Sciences*, *280*(1755), 20122765. doi:10.1098/rspb.2012.2765

Curley, J. P., & Keverne, E. B. (2005). Genes, brains and mammalian social bonds. *Trends in Ecology & Evolution*, *20*(10), 561-567. doi:10.1016/j.tree.2005.05.018

Dahl, J. F., Nadler, R. D., & Collins, D. C. (1991). Monitoring the ovarian cycles of *Pan troglodytes* and *P. paniscus*: A comparative approach. *American Journal of Primatology*, *24*(3-4), 195–209. doi:10.1002/ajp.1350240306

Dettmer, A. M., Kaburu, S. S., Byers, K. L., Murphy, A. M., Soneson, E., Wooddell, L. J., & Suomi, S. J. (2015). First-time rhesus monkey mothers, and mothers of sons, preferentially engage in face-to-face interactions with their infants. *American Journal of Primatology*, *78*(2), 238–246. doi:10.1002/ajp.22503

Di Fiore, A., & Fleischer, R. C. (2005). Social behavior, reproductive strategies, and population genetic structure of *Lagothrix poeppigii*. *International Journal of Primatology*, *26*(5), 1137-1173. doi:10.1007/s10764-005-6462-4

Dobson, A. J. (2002). *An introduction to generalized linear models*. Boca Raton, FL: Chapman & Hall/CRC.

Emery Thompson, M., Kahlenberg, S. M., Gilby, I. C., & Wrangham, R. W. (2007). Core area quality is associated with variance in reproductive success among female chimpanzees at Kibale National Park. *Animal Behaviour*, *73*(3), 501–512. doi:10.1016/j.anbehav.2006.09.007

Fagen, R. (1981). *Animal play behavior*. New York, NY: Oxford University Press.

Foerster, S., McLellan, K., Schroepfer-Walker, K., Murray, C. M., Krupenye, C., Gilby, I. C., & Pusey, A. E. (2015). Social bonds in the dispersing sex: Partner preferences among adult female chimpanzees. *Animal Behaviour*, *105*, 139-152. doi:10.1016/j.anbehav.2015.04.012

Ghiglieri, M. P. (1984). *The chimpanzees of Kibale Forest*. New York, NY: Columbia University Press.

Goodall, J. (1968). The behavior of free-living chimpanzees in the Gombe Stream Reserve. *Animal Behaviour Monographs*, *1*, 163–311.

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

Guan, Z. H., Huang, B., Ning, W. H., Ni, Q. Y., Sun, G. Z., & Jiang, X. L. (2013). Significance of grooming behavior in two polygynous groups of western black crested gibbons: Implications for understanding social relationships among immigrant and resident group members. *American Journal of Primatology*, *75*(12), 1165-1173. doi:10.1002/ajp.22178

Halperin, S. D. (1979). Temporary association patterns in free ranging chimpanzees: An assessment of individual grouping preferences. In: D. A. Hamburg, & E. R. McCown, (Eds.), *The great apes* (pp. 491-499). Menlo Park, CA: Benjamin/Cummings.

Hasegawa, T. (1989). Sexual behavior of immigrant and resident female chimpanzees at Mahale. In: P. Heltne & L. A. Marqardt (Eds.), *Understanding Chimpanzees* (pp. 90–103). Cambridge, MA: Harvard University Press.

Hinde, K., Power, M. L., & Oftedal, O. T. (2009). Rhesus macaque milk: Magnitude, sources, and consequences of individual variation over lactation. *American Journal of Physical Anthropology 138*(2), 148–157. doi:10.1002/ajpa.20911

Idani, G. I. (1991). Social relationships between immigrant and resident bonobo (*Pan paniscus*) females at Wamba. *Folia Primatologica*, *57*(2), 83-95. doi:10.1159/000156568

Jang, M. J. (2011). *Working correlation selection in generalized estimating equations*. Ph.D. thesis, University of Iowa, Iowa City, IA.

Kahlenberg, S. M., Emery Thompson, M., Muller, M. N., & Wrangham, R. W. (2008a). Immigration costs for female chimpanzees and male protection as an immigrant counterstrategy to intrasexual aggression. *Animal Behaviour*, *76*(5), 1497-1509. doi:10.1016/j.anbehav.2008.05.029

Kahlenberg, S. M., Emery Thompson, M., & Wrangham, R. W. (2008b). Female competition over core areas in *Pan troglodytes schweinfurthii*, Kibale National Park, Uganda. *International Journal of Primatology*, *29*(4), 931-947. doi:10.1007/s10764-008-9276-3

Kapsalis, E., & Berman, C. M. (1996). Models of affiliative relationships among free-ranging rhesus monkeys (*Macaca mulatta*). *Behaviour*, *133*(15), 1235-1263.

Koper, N., & Manseau, M. (2009). Generalized estimating equations and generalized linear mixed-effects models for modelling resource selection. *Journal of Applied Ecology*, *46*(3), 590–599. doi:10.1111/j.1365-2664.2009.01642.x

Kortlandt, A. (1962). Chimpanzees in the wild. *Scientific American*, *206*, 128-138.

Künkele, J., & Kenagy, G. J. (1997). Inefficiency of lactation in primiparous rats: The costs of first reproduction. *Physiological and Biochemical Zoology*, *70*(5), 571-577. doi:10.1086/515862

Langergraber, K., Mitani, J., & Vigilant, L. (2009). Kinship and social bonds in female chimpanzees (*Pan troglodytes*). *American Journal of Primatology*, *71*(10), 840-851. doi:10.1002/ajp.20711

Lehmann, J., & Boesch, C. (2009). Sociality of the dispersing sex: The nature of social bonds in West African female chimpanzees, *Pan troglodytes*. *Animal Behaviour*, *77*(2), 377-387. doi:10.1016/j.anbehav.2008.09.038

Liang, K. Y., & Zeger, S. L. (1986). Longitudinal data-analysis using generalized linear-models. *Biometrika*, *73*, 13-22. doi:10.1093/biomet/73.1.13

Lwanga, J. S., Butynski, T. M., & Struhsaker, T. T. (2000). Tree population dynamics in Kibale National Park, Uganda 1975–1998. *African Journal of Ecology, 38*(3), 238–247. doi:10.1046/j.1365-2028.2000.00244.x

Matsumoto-Oda, A. (1999). Mahale chimpanzees: Grouping patterns and cycling females. *American Journal of Primatology*, *47*(3), 197–207. doi:10.1002/(SICI)1098-2345(1999)47:3<197::AID-AJP2>3.0.CO;2-3

McPherson, M., Smith-Lovin, L., & Cook, J. M. (2001). Birds of a feather: Homophily in social networks. *Annual Review of Sociology*, *27*, 415-444. doi:10.1146/annurev.soc.27.1.415

Mitani, J. C. (2009). Male chimpanzees form enduring and equitable social bonds. *Animal Behaviour*, *77*(3), 633–640. doi:10.1016/j.anbehav.2008.11.021

Mitani, J. C., Watts, D. P., Pepper, J. W., & Merriwether, D. A. (2002). Demographic and social constraints on male chimpanzee behaviour. *Animal Behaviour*, *64*(5), 727–737. doi:10.1006/anbe.2002.4014

Mitani, J. C., & Amsler, S. J. (2003). Social and spatial aspects of male subgrouping in a community of wild chimpanzees. *Behaviour*, *140*(7), 869–884. doi:10.1163/156853903770238355

Mitani, J. C., Watts, D. P., & Amsler, S. J. (2010). Lethal intergroup aggression leads to territorial expansion in wild chimpanzees. *Current Biology*, *20*(12), R507-R508. doi:10.1016/j.cub.2010.04.021

Möller, L. M., & Harcourt, R. G. (2008). Shared reproductive state enhances female associations in dolphins. *International Journal of Ecology*, *2008*. doi:10.1155/2008/498390

Muller, M. (2002). Agonistic relations among Kanyawara chimpanzees. In: C. Boesch, G. Hohmann, & L. F. Marchant (Eds.), *Behavioural diversity in chimpanzees and bonobos* (pp. 112–124). Cambridge: Cambridge University Press.

Murray, C. M., Mane, S. V., & Pusey, A. E. (2007). Dominance rank influences female space use in wild chimpanzees (*Pan troglodytes*): Towards an ideal despotic distribution. *Animal Behaviour*, *74*(6), 1795–1804. doi:10.1016/j.anbehav.2007.03.024

Murray, C. M., Lonsdorf, E. V., Stanton, M. A., Wellens, K. R., Miller, J. A., Goodall, J., & Pusey, A. E. (2014). Early social exposure in wild chimpanzees: Mothers with sons are more gregarious than mothers with daughters. *Proceedings of the National Academy of Sciences*, *111*(51), 18189-18194. doi:10.1073/pnas.1409507111

Newton-Fisher, N. E. (1999). Association by male chimpanzees: A social tactic? *Behaviour*, *136*(6), 705-730. doi:10.1163/156853999501531

Newton-Fisher, N. E., & Lee, P. C. (2011). Grooming reciprocity in wild male chimpanzees. *Animal Behaviour, 81*(2), 439-446. doi:10.1016/j.anbehav.2010.11.015

Nishida, T. (1988). Development of social grooming between mother and offspring in wild chimpanzees. *Folia Primatologica*, *50*(1-2), 109-123. doi:10.1159/000156335

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

Nishida, T. (2012). *Chimpanzees of the lakeshore: Natural history and culture at Mahale*. New York, NY: Cambridge University Press.

Nishida, T., & Kawanaka, K. (1972). Inter-unit-group relationships among wild chimpanzees of the Mahale mountains. *Kyoto University African Studies*, *7*(131), 131-169.

Norušis, M. J. (2012). *IBM SPSS Statistics 19 Advanced Statistical Procedures Companion*. Upper Saddle River, NJ: Prentice Hall.

Nunes, S. (2014). Juvenile social play and yearling behavior and reproductive success in female Belding's ground squirrels. *Journal of Ethology*, *32*(3), 145-153. doi:10.1007/s10164-014-0403-7

Otali, E., & Gilchrist, J. S. (2006). Why chimpanzee (*Pan troglodytes schweinfurthii*) mothers are less gregarious than nonmothers and males: The infant safety hypothesis. *Behavioral Ecology and Sociobiology*, *59*(4), 561–570. doi:10.1007/s00265-005-0081-0

Overall, J. E., & Tonidandel, S. (2004), Robustness of generalized estimating equation (GEE) tests of significance against misspecification of the error structure model. *Biometrical Journal*, *46*(2), 203–213. doi:10.1002/bimj.200210017

Owen, C. (2001). *A comparison of maternal care by primiparous and multiparous bottlenose dolphins* (*Tursiops truncatus*)—*does parenting improve with experience*? MSc thesis, University of California Santa Cruz, Santa Cruz, CA.

Pellis, S. M., Pellis, V. C., & Himmler, B. T. (2014). How play makes for a more adaptable brain. *American Journal of Play*, *7*(1), 73-98.

Pepper, J. W., Mitani, J. C., & Watts, D. P. (1999). General gregariousness and specific social preferences among wild chimpanzees. *International Journal of Primatology*, *20*(5), 613–632. doi:10.1023/A:1020760616641

Pipia, A., Ciuti, S., Grignolio, S., Luchetti, S., Madau, R., & Apollonio, M. (2009). Effect of predation risk on grouping pattern and whistling behaviour in a wild mouflon *Ovis aries* population. *Acta Theriologica*, *54*(1), 77-86. doi:10.1007/BF03193139

Poirier, F. E., & Smith, E. O. (1974). Socializing functions of primate play. *American Zoologist*, *14*(1), 275-287. doi:10.1093/icb/14.1.275

Pusey, A. E. (1979). Intercommunity transfer of chimpanzees in Gombe National Park. In: D. A. Hamburg, & E. R. McCown (Eds.), *The great apes* (pp. 464–479). Menlo Park, CA: Benjamin/Cummings.

Pusey, A. E. (1980). Inbreeding avoidance in chimpanzees. *Animal Behaviour*, *28*(2), 543–552. doi:10.1016/S0003-3472(80)80063-7

Pusey, A. E., & Packer, C. (1987). Dispersal and philopatry. In: B. B. Smuts, D. L. Cheney, R. M. Seyfarth, R. W. Wrangham, & T. T. Struhsaker (Eds.), *Primate societies* (pp. 250–266). Chicago, IL: Chicago University Press.

Pusey, A. E., Murray, C., Wallauer, W., Wilson, M., Wroblewski, E., & Goodall, J. (2008). Severe aggression among female *Pan troglodytes schweinfurthii* at Gombe National Park, Tanzania. *International Journal of Primatology*, *29*(4), 949-973. doi:10.1007/s10764-008-9281-6

Rodrigues, M. A. (2013). *Stress and sociality in a patrilocal primate: Do female spider monkeys tend-and-befriend?* Ph.D. thesis, The Ohio State University, Columbus, OH.

Romesburg, C. H. (2004). *Cluster analysis for researchers*. Morrisville, NC: Lulu Press.

Silk, J. B., Alberts, S. C., & Altmann, J. (2003). Social bonds of female baboons enhance infant survival. *Science*, *302*(5648), 1231-1234. doi:10.1126/science.1088580

Silk, J. B., Beehner, J. C., Bergman, T. J., Crockford, C., Engh, A. L., Moscovice, L. R., Wittig, R. M., Seyfarth, R. M., & Cheney, D. L. (2010). Strong and consistent social bonds enhance the longevity of female baboons. *Current Biology*, *20*(15), 1359-1361.

doi:10.1016/j.cub.2010.05.067

Smith, J. E., Memenis, S. K. & Holekamp, K. E. 2007. Rank-related partner choice in the fission-fusion society of the spotted hyena (*Crocuta crocuta*). *Behavioral Ecology and Sociobiology*, *61*(5), 753-765. doi:10.1007/s00265-006-0305-y

Sneath, P. H. A., & Sokal, R. R. (1973). *Numerical taxonomy: The principles and practice of numerical classification*. San Francisco, CA: W.H. Freeman.

Stanton, M. A., Lonsdorf, E. V., Pusey, A. E., Goodall, J., & Murray, C. M. (2014). Maternal behavior by birth order in wild chimpanzees (*Pan troglodytes*): Increased investment by first-time mothers. *Current Anthropology*, *55*(4), 483-489. doi:10.1086/677053

Stearns, S. C. (1992). *The evolution of life histories* (Vol. 249). Oxford: Oxford University Press.

Struhsaker, T. T. (1997). *Ecology of an African rain forest*. Gainesville, FL: University Press of Florida.

Sugiyama, Y. (1988). Grooming interactions among adult chimpanzees at Bossou, Guinea, with special reference to social structure. *International Journal of Primatology*, *9*(5), 393-407. doi:10.1007/BF02736216

Swedell, L. (2002). Affiliation among females in wild hamadryas baboons (*Papio hamadryas hamadryas*). *International Journal of Primatology*, *23*(6), 1205-1226. doi:10.1023/A:1021170703006

Taylor, S. E., Klein, L. C., Lewis, B. P., Gruenewald, T. L., Gurung, R. A., & Updegraff, J. A. (2000). Biobehavioral responses to stress in females: Tend-and-befriend, not fight-or-flight. *Psychological Review*, *107*(3), 411-429. doi:10.1037/0033-295X.107.3.411

Tutin, C. E. G. (1979). Mating patterns and reproductive strategies in a community of wild chimpanzees (*Pan troglodytes schweinfurthii*). *Behavioral Ecology and Sociobiology*, *6*(1), 29–38. doi:10.1007/BF00293242

Vigilant, L., Hofreiter, M., Siedel, H., & Boesch, C. (2001). Paternity and relatedness in wild chimpanzee communities. *Proceedings of the National Academy of Sciences*, *98*(23), 12890-12895. doi:10.1073/pnas.231320498

de Waal, F. B. M., & Luttrell, L. M. (1986). The similarity principle underlying social bonding among female rhesus monkeys. *Folia primatologica*, *46*(4), 215-234. doi:10.1159/000156255

Wakefield, M. (2008). Grouping patterns and competition among female *Pan troglodytes schweinfurthii* at Ngogo, Kibale National Park, Uganda. *International Journal of Primatology*, *29*(4), 907-929. doi:10.1007/s10764-008-9280-7

Wakefield, M. L. (2013). Social dynamics among females and their influence on social structure in an East African chimpanzee community. *Animal Behaviour*, *85*(6), 1303-1313. doi:10.1016/j.anbehav.2013.03.019

Watts, D. P. (1998). Coalitionary mate guarding by male chimpanzees at Ngogo, Kibale National Park, Uganda. *Behavioral Ecology and Sociobiology*, *44*(1), 43–55. doi:10.1007/s002650050513

Watts, D. P. (2002). Gorilla social relationships: A comparative overview. In: A. B. Taylor, & M. L. Goldsmith (Eds.), *Gorilla biology: A multidisciplinary perspective* (pp. 302-327). New York, NY: Cambridge University Press.

Watts, D. P., & Pusey, A. E. (1993). Behavior of juvenile and adolescent great apes. In: M. E. Pereira, & L.A. Fairbanks (Eds.), *Juvenile primates: Life history, development, and behavior* (pp. 148-167). Chicago, IL: University of Chicago Press.

Watts, D. P., & Mitani, J. C. (2001). Boundary patrols and intergroup encounters in wild chimpanzees. *Behaviour, 138*(3), 299–327. doi:10.1163/15685390152032488

Wheeler, B. C., Scarry, C. J., & Koenig, A. (2013). Rates of agonism among female primates: A cross-taxon perspective. *Behavioral Ecology*, *24*(6), 1369-1380. doi:10.1093/beheco/art076

Whitehead, H., & Mann, J. (2000). Female reproductive strategies of cetaceans. In: J. Mann, R. C. Connor, P. L. Tyack, & H. Whitehead (Eds.), *Cetacean societies: Field studies of dolphins and whales* (pp. 219-246). Chicago, IL: University of Chicago Press.

Williams, J. M., Pusey, A. E., Carlis, J. V., Farm, B. P., & Goodall, J. (2002). Female competition and male territorial behaviour influence female chimpanzees' ranging patterns. *Animal Behaviour*, *63*(2), 347–360. doi:10.1006/anbe.2001.1916

Wittig, R. M., Crockford, C., Lehmann, J., Whitten, P. L., Seyfarth, R. M., & Cheney, D. L. (2008). Focused grooming networks and stress alleviation in wild female baboons. *Hormones and Behavior*, *54*(1), 170-177. doi:10.1016/j.yhbeh.2008.02.009

Wrangham, R. W., Clark, A., & Isabirye-Basuta, G. (1992). Female social relationships and social organization of Kibale Forest chimpanzees. In: T. Nishida, W. C. McGrew, P. Marler, M. H. Pickford, & F. B. M. de Waal (Eds.), *Topics in primatology, Vol. 1: Human origins* (pp. 81–98). Tokyo: Tokyo University Press.

Zedrosser, A., Dahle, B., Støen, O. G., & Swenson, J. E. (2009). The effects of primiparity on reproductive performance in the brown bear. *Oecologia*, *160*(4), 847-854. doi:10.1007/s00442-009-1343-8

# CHAPTER 5

# CONCLUSION

In this thesis I examined the question: do the lives of first-time chimpanzee mothers differ from those of mothers with two or more offspring? To address this question I conducted a systematic study of the behavior of wild female chimpanzees at Ngogo in the Kibale National Park, Uganda. Specifically, I compared patterns of ranging, aggression, and affiliation between primiparous and multiparous mothers.

## Female ranging patterns

In chapter 2 I quantified how females used space in the Ngogo territory. I found that individuals restricted their movements to small overlapping home ranges that are embedded within the larger community territory. These observations support prior research from several other chimpanzee communities (Gombe: Williams et al. 2002; Murray et al. 2007; Kanyawara: Wrangham et al. 1996; Kahlenberg et al. 2008b; Mahale: Hasegawa 1989). The additional data from Ngogo provided in this dissertation therefore strengthen the assertion that this pattern of space use is typical for female chimpanzees in East Africa. Ranging over a small area likely allows females to gain specialized knowledge of food resources and maximize their foraging efficiency (Wrangham & Smuts 1980; Pusey et al. 1997; Williams et al. 2002). This differential use of space may also prevent potentially costly competition by reducing the number of females with whom each individual must regularly compete (Wrangham 1979; Williams et al. 2002).

The data presented in Chapter 2 also demonstrate that the home ranges of Ngogo females clustered into two neighborhoods based on ranging similarity. Spatial neighborhoods have also been reported in communities at Gombe (Williams et al. 2002) and Kanyawara (Emery Thompson et al. 2007). The two neighborhoods at Ngogo overlapped extensively and contained food resources utilized intensively by females. The degree of neighborhood overlap at Ngogo differs from Kanyawara, where neighborhoods barely overlap. Compared to Kanyawara, high neighborhood overlap at Ngogo may relate to the relatively abundant food there, which may make sharing space less costly for females (see Murray et al. 2007). It is also possible that the high density of females at Ngogo makes it difficult to avoid space use overlap. At Gombe and Kanyawara, neighborhood affiliation is important as it affects a female's ability to access food, her behavior, and ultimately her fitness (Williams et al. 2002; Emery Thompson et al. 2007). Future studies will be necessary to evaluate whether similar relationships exist at Ngogo.

Finally in chapter 2, I investigated whether parity, reproductive cycle stage, and the presence of dependent offspring influenced female home range size. Some studies report that female chimpanzees experiencing the burdens of energetically costly lactation and traveling with dependent offspring restrict their ranging compared to other females (Wrangham & Smuts 1980; Goodall 1986; Hasegawa 1990; Boesch & Boesch-Achermann 2000; Wrangham 2000; Williams et al. 2002; Bates & Byrne 2009). Based on these findings, I was particularly interested in determining if parity, more generally, influenced female space use at Ngogo.

I did not find evidence that parity, reproductive cycle stage, or the presence of dependent offspring affected the size of individual female home ranges. However, my results did indicate that the number of observations per female influenced estimates of home range size. Therefore, these results should be considered preliminary. Additional research will be required to obtain larger samples of observations. These samples, in turn, can be used to test the relationships between these factors and individual female home range size. As there is no consensus in the literature regarding the influence of reproductive factors on female ranging patterns, future research of space use at Ngogo, which possesses both a dense population of females and abundant food resources, is likely to provide novel insights.

### Female intrasexual aggression

Evidence from several communities indicates that female chimpanzees compete aggressively for resources (Williams et al. 2002; Murray et al. 2007; Kahlenberg et al. 2008a,b; Miller et al. 2014), and that this behavior influences fitness (Pusey et al. 1997; Emery Thompson et al. 2007). In chapter 3, I examined patterns of female aggression at Ngogo and found that aggression between females occurred more often than has been reported in other East African communities. There are several reasons that may explain the high rates of female intrasexual aggression observed at Ngogo. First, among primates, rates of female agonism increase with the number of female competitors in a group (Wheeler et al. 2013). The Ngogo community is large and group members live at relatively high density (Watts 1998; Watts & Mitani 2001; Mitani & Amsler 2003; Potts et al. 2009). Second, females at Ngogo are gregarious compared to females in other East African chimpanzee communities (Wakefield 2008, 2013), and thus they frequently associate with potential competitors. Third, during this study, the number of chimpanzees at Ngogo increased both due to births and the immigration of adolescent nulliparas into the community. It is likely that this increase in community size exacerbated competition for resources. Observations from several East African chimpanzee communities indicate nulliparous adolescent females seek to establish individual ranges, and increased feeding competition ensues where they settle (reviewed in Pusey at al. 2013). As a result, chimpanzee mothers regard adolescents as competitors and target them with aggression to prevent them from settling (Nishida 1989; Kahlenberg et al. 2008a; Pusey et al. 2008). In accord with results reported from other chimpanzee communities, I found that female aggression at Ngogo was most often directed by mothers toward adolescent nulliparas. However, when I considered primiparas and multiparas separately, I found that first-time mothers drove this pattern. Why did primiparas engage in potentially costly aggression so often?

First, primiparas are beginning potentially long reproductive careers. Utilizing aggression to resist the presence of nulliparous competitors may be especially beneficial for first-time mothers. In this way, they can increase the amount of food available to themselves over the long-term. Secondly, if the challenges of being a mother for the first time cause primiparas to experience relatively high levels of resource competition, this could explain why primiparas directed high rates of aggression towards adolescents. These two scenarios are supported by observations from Gombe, which indicate that female chimpanzees appear to escalate aggression when the potential benefits of doing so are high (Pusey et al. 2008). Lastly, the relatively high rates of aggression between primiparas and adolescent nulliparas at Ngogo could result from the latter avoiding aggression from multiparas, who may be higher ranking.

The high rates of aggression directed toward adolescents by primiparas documented in this study differ from findings reported in prior research. At Mahale, Nishida (1989) considered primiparas and adolescent nulliparas a single group and found that they directed more aggression towards each other than expected. However, multiparas also directed more aggression towards primiparas and adolescents than expected, which contrasts with my observations. Additionally, in the Kanyawara chimpanzee community, high-ranking mothers ranging in high quality areas were the most aggressive toward immigrant nulliparas (Kahlenberg et al. 2008a). At Kanyawara, females rise in rank with age, and thus the dominant females are likely multiparous. These comparisons suggest that inter-community variation exists in the aggressive behavior of mothers who vary in parity. However, methodological differences between studies and demographic and ecological variations between sites (e.g. community size, food availability) make it difficult to interpret intercommunity differences in female aggression.

Observations from Ngogo support the assertion that female chimpanzees utilize intrasexual aggression to compete. By considering primiparas and multiparas separately, I showed that females displayed different patterns of aggression. This suggests that competition affects mothers in different ways. These results expand our knowledge regarding how female chimpanzees compete in the wild.

## Female affiliative relationships

While females compete directly with each other, as explored in Chapter 3, they must also invest in forging social bonds. Females in several primate species form strong social bonds with each other, and research indicates they obtain short-term physiological and long-term fitness benefits by doing so (Seyfarth & Cheney 2012). These findings have been derived from species in which females are the philopatric sex. In these cases, females form bonds with other closely related females, and kinship strongly influences who does what with whom. Less is known about female social bonds in species, such as chimpanzees, where females are dispersing sex.

I began chapter 4 by investigating whether unrelated female chimpanzees at Ngogo formed social bonds with one another. Results indicated that mothers most often associated and groomed with other mothers, rather than with adolescent nulliparas. This mirrors the results from prior studies of chimpanzees and several other species, which indicate affiliative social interactions between parous females benefit mothers and their dependent offspring (Taylor et al. 2000; Boesch & Boesch-Achermann 2000; Cameron et al. 2009).

Subsequently in chapter 4, I examined whether primiparas and multiparas displayed different patterns of affiliation with unrelated females. Similar to the results on aggression in chapter 3, different patterns emerged when mothers were classified by parity. Primiparas were more often involved in grooming interactions with adolescent nulliparas than were multiparas. This was driven by the relatively high rates of grooming that primiparas received from adolescent females. Several factors may help explain this pattern. First, primiparas, who have only one offspring, have more time available to groom non-kin compared to multiparas, who may have several offspring to attend and care for. Second, affiliative bonds between female chimpanzees may begin forming in adolescence (Nishida 2012; Foerster et al. 2015). Bonds between female chimpanzees have been observed to persist across years (Nishida 1989; Boesch & Boesch-Achermann 2000; Wakefield 2008; Langergraber et al. 2009; Lehmann & Boesch 2009). These observations suggest that females who forge bonds as adolescents may retain those bonds, even if one individual transitions to motherhood before the other.

## Future directions

This thesis reveals the importance of considering parity when investigating the behavior of chimpanzee mothers, as primiparas and multiparas differ. The results presented here also highlight several important areas in need of further study. In the following, I discuss three of these areas.

First, it will be instructive to compare the results of this study with additional studies at Ngogo that take place during a time of population stability. Compared with longer-studied communities such as those at Gombe, Mahale, and Kanyawara, less is known about the lives of female chimpanzees at Ngogo. The paucity of data makes it impossible to determine whether the patterns of behavior observed in this study are generalizable. Were these patterns a reflection of what is typical in this extremely large community, or do they stem from the increase in community size and the large cohort of females who gave birth for the first time? Studying the behavior of females at Ngogo during a period of population stability or even decline would provide the necessary data to address and resolve these questions.

Second, this thesis provides insight into female behavior from the perspective of mothers. While I have shown that mothers’ social interactions vary with parity, the influence of parity extends beyond these females. The results presented here indicate that behavioral differences between primiparas and multiparas involved their interactions with adolescent nulliparas. Examining matters from the perspective of adolescent females and how they range and interact with other females in the Ngogo community would complement the results presented in this thesis.

Third, in this thesis I focused on one variable, a mother's parity. However, parity is positively correlated with female age, which can make it challenging to disentangle the individual effects of each (e.g., Fessler et al. 2005). As mentioned previously, reports from some other chimpanzee communities indicate that as females age, they also tend to rise in dominance rank (Nishida 1989; Pusey et al. 1997; Greengrass 2005; Kahlenberg 2006; Murray et al. 2006). Thus, rank and parity are also likely to be positively correlated. In this study, I focused on parity because the ages of many female subjects, as well as their dominance relationships, were not well known. Depending on the specific research questions asked, one variable may a better predicator than another. Ideally, as data on parity, age, and dominance relationships become known, they can all be analyzed together to tease apart their effects as explanatory mechanisms.

While previous research on female chimpanzees has emphasized differences between parous and nulliparous females, this dissertation reveals that the parity of mothers is also important. A major contribution of my research is that I have shown that primiparous and multiparous mothers differed in their aggressive and affiliative behavior. Thus, if mothers are considered a single category, this may mask important behavioral variation. Building on previous work (e.g., Nishida 1989; Stanton et al. 2014), my findings highlight the importance of examining how females navigate the unique challenges of primiparity. In doing so, added insight has been provided into how evolution has shaped the behavior of primate mothers.

## REFERENCES

Bates, L. A., & Bryne, R. (2009). Sex differences in the movement patterns of free-ranging chimpanzees (*Pan troglodytes schweinfurthii*). *Behavioral Ecology and Sociobiology*, *64*(2), 247–255. doi:10.1007/s00265-009-0841-3

Boesch, C., & Boesch-Achermann, H. (2000). *The chimpanzees of the Taï Forest*. Oxford: Oxford University Press.

Cameron, E. Z., Setsaas, T. H., & Linklater, W. L. (2009). Social bonds between unrelated females increase reproductive success in feral horses. *Proceedings of the National Academy of Sciences*, *106*(33), 13850-13853. doi:10.1073/pnas.0900639106

Emery Thompson, M., Kahlenberg, S. M., Gilby, I. C., & Wrangham, R. W. (2007). Core area quality is associated with variance in reproductive success among female chimpanzees at Kibale National Park. *Animal Behaviour*, *73*(3), 501–512. doi:10.1016/j.anbehav.2006.09.007

Fessler, D. M., Navarrete, C. D., Hopkins, W., & Izard, M. K. (2005). Examining the terminal investment hypothesis in humans and chimpanzees: Associations among maternal age, parity, and birth weight. *American Journal of Physical Anthropology*, *127*(1), 95-104. doi:10.1002/ajpa.20039

Foerster, S., McLellan, K., Schroepfer-Walker, K., Murray, C. M., Krupenye, C., Gilby, I. C., & Pusey, A. E. (2015). Social bonds in the dispersing sex: Partner preferences among adult female chimpanzees. *Animal Behaviour*, *105*, 139-152. doi:10.1016/j.anbehav.2015.04.012

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

Greengrass, E. (2005). *Sociability and dominance among female chimpanzees at Gombe*. Ph.D. thesis. University of Bristol, Bristol, U.K.

Hasegawa, T. (1989). Sexual behavior of immigrant and resident female chimpanzees at Mahale. In: P. Heltne & L. A. Marqardt (Eds.), *Understanding chimpanzees* (pp. 90–103). Cambridge, MA: Harvard University Press.

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

Kahlenberg, S. M. (2006). *Female-female competition and male sexual coercion in Kanyawara chimpanzees*. Ph.D. thesis. Harvard University, Cambridge, MA.

Kahlenberg, S. M., Emery Thompson, M., Muller, M. N., & Wrangham, R. W. (2008a).

Immigration costs for female chimpanzees and male protection as an immigrant counterstrategy to intrasexual aggression. *Animal Behaviour*, *76*(5), 1497-1509. doi:10.1016/j.anbehav.2008.05.029

Kahlenberg, S. M., Emery Thompson, M., & Wrangham, R. W. (2008b). Female competition over core areas in *Pan troglodytes schweinfurthii*, Kibale National Park, Uganda. *International Journal of Primatology*, *29*(4), 931-947. doi:10.1007/s10764-008-9276-3

Langergraber, K., Mitani, J., & Vigilant, L. (2009). Kinship and social bonds in female chimpanzees (*Pan troglodytes*). *American Journal of Primatology*, *71*(10), 840-851. doi:10.1002/ajp.20711

Lehmann, J., & Boesch, C. (2009). Sociality of the dispersing sex: The nature of social bonds in West African female chimpanzees, *Pan troglodytes*. *Animal Behaviour*, *77*(2), 377-387. doi:10.1016/j.anbehav.2008.09.038

Miller, J. A., Pusey, A. E., Gilby, I. C., Schroepfer-Walker, K., Markham, A. C., & Murray, C. M. (2014). Competing for space: Female chimpanzees are more aggressive inside than outside their core areas. *Animal Behaviour*, *87*, 147-152. doi:10.1016/j.anbehav.2013.10.023

Mitani, J. C., & Amsler, S. J. (2003). Social and spatial aspects of male subgrouping in a community of wild chimpanzees. *Behaviour*, *140*(7), 869–884. doi:10.1163/156853903770238355

Murray, C. M., Eberly, L. E., & Pusey, A. E. (2006). Foraging strategies as a function of season and rank among wild female chimpanzees (*Pan troglodytes*). *Behavioral Ecology, 17*(6), 1020–1028. doi:10.1093/beheco/arl042

Murray, C. M., Mane, S. V., & Pusey, A. E. (2007). Dominance rank influences female space use in wild chimpanzees (*Pan troglodytes*): Towards an ideal despotic distribution. *Animal Behaviour*, *74*(6), 1795–1804. doi:10.1016/j.anbehav.2007.03.024

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

Nishida, T. (2012). *Chimpanzees of the lakeshore: Natural history and culture at Mahale*. New York, NY: Cambridge University Press.

Potts, K. B., Chapman, C. A., & Lwanga, J. S. (2009). Floristic heterogeneity between forested sites in Kibale National Park, Uganda: Insights into the fine-scale determinants of density in a large-bodied frugivorous primate. *Journal of Animal Ecology*, *78*(6), 1269-1277. doi:10.1111/j.1365-2656.2009.01578.x

Pusey, A. E., Williams, J., & Goodall, J. (1997). The influence of dominance rank on the reproductive success of female chimpanzees. *Science*, *277*(5327), 828–831. doi:10.1126/science.277.5327.828

Pusey, A. E., Murray, C., Wallauer, W., Wilson, M., Wroblewski, E., & Goodall, J. (2008). Severe aggression among female *Pan troglodytes schweinfurthii* at Gombe National Park, Tanzania. *International Journal of Primatology*, *29*(4), 949-973. doi:10.1007/s10764-008-9281-6

Pusey, A. E., & Schroepfer-Walker, K. (2013). Female competition in chimpanzees. *Philosophical Transactions of the Royal Society of London B: Biological Sciences*, *368*(1631), 20130077. doi:10.1098/rstb.2013.0077

Stanton, M. A., Lonsdorf, E. V., Pusey, A. E., Goodall, J., & Murray, C. M. (2014). Maternal behavior by birth order in wild chimpanzees (*Pan troglodytes*): Increased investment by first-time mothers. *Current Anthropology*, *55*(4), 483-489. doi:10.1086/677053

Seyfarth, R. M., & Cheney, D. L. (2012). The evolutionary origins of friendship. *Annual Review of Psychology*, *63*, 153-177. doi:10.1146/annurev-psych-120710-100337

Taylor, S. E., Klein, L. C., Lewis, B. P., Gruenewald, T. L., Gurung, R. A., & Updegraff, J. A. (2000). Biobehavioral responses to stress in females: Tend-and-befriend, not fight-or-flight. *Psychological Review*, *107*(3), 411-429. doi:10.1037/0033-295X.107.3.41

Wakefield, M. (2008). Grouping patterns and competition among female *Pan troglodytes schweinfurthii* at Ngogo, Kibale National Park, Uganda. *International Journal of Primatology*, *29*(4), 907-929. doi:10.1007/s10764-008-9280-7

Wakefield, M. L. (2013). Social dynamics among females and their influence on social structure in an East African chimpanzee community. *Animal Behaviour*, *85*(6), 1303-1313. doi:10.1016/j.anbehav.2013.03.019

Watts, D. P. (1998). Coalitionary mate guarding by male chimpanzees at Ngogo, Kibale National Park, Uganda. *Behavioral Ecology and Sociobiology*, *44*(1), 43–55. doi:10.1007/s002650050513

Watts, D. P., & Mitani, J. C. (2001). Boundary patrols and intergroup encounters in wild chimpanzees. *Behaviour*, *138*(3), 299–327. doi:10.1163/15685390152032488

Wheeler, B. C., Scarry, C. J., & Koenig, A. (2013). Rates of agonism among female primates: A cross-taxon perspective. *Behavioral Ecology*, *24*(6), 1369-1380. doi:10.1093/beheco/art076

Williams, J. M., Pusey, A. E., Carlis, J. V., Farm, B. P., & Goodall, J. (2002). Female competition and male territorial behaviour influence female chimpanzees' ranging patterns. *Animal Behaviour*, *63*(2), 347–360. doi:10.1006/anbe.2001.1916

Wrangham, R. W. (1979). On the evolution of ape social systems. *Social Science Information Sur Les Sciences Sociales*, *18*(3), 335–368. doi:10.1177/053901847901800301

Wrangham, R. W. (2000). Why are male chimpanzees more gregarious than mothers? A scramble competition hypothesis. In: P. M. Kappeler (Ed.), *Primate males* (pp. 248–258). Cambridge: Cambridge University Press.

Wrangham, R. W., & Smuts, B. B. (1980). Sex differences in the behavioral ecology of chimpanzees in the Gombe National Park, Tanzania. *Journal of Reproduction and Fertility*, *28*, 13–31.

Wrangham, R. W., Chapman, C. A., Clark-Arcadi, A. P., & Isabirye-Basuta, G. (1996). Social ecology of Kanyawara chimpanzees: Implications for understanding the costs of great ape groups. In: W. C. McGrew, L. F. Marchant, & T. Nishida (Eds.), *Great ape societies* (pp. 45-57). Cambridge: Cambridge University Press.