Social Ties over the Life Cycle in Blue Monkeys

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Submitted in partial fulfillment of the
requirements for the degree of
Doctor of Philosophy
of the Graduate School of Arts and Sciences

COLUMBIA UNIVERSITY

2018

Abstract

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The ways that individuals socialize within groups have evolved to overcome challenges relevant to species-specific socioecology and individuals' life history state. Studying the drivers, proximate benefits, and fitness consequences of social interaction across life stages therefore helps clarify why and how social behavior has evolved. To date, juvenility is one life stage that field researchers have largely overlooked; however, individual experiences during development are relevant to later behavior and ultimately to fitness. Juvenile animals are subject to unique challenges related to their small size and relative inexperience. They are likely to employ behavioral strategies to overcome these challenges, while developing adult-like behavioral competence according to their species and sex. The research presented in this dissertation draws from long-term behavioral records of adult females and shorter-term behavioral records of juveniles from a population of blue monkeys (*Cercopithecus mitis stuhlmanni*) in western Kenya. I combine data on social behavior, demography, and biomarkers related to energetic and metabolic status, to assess both short and long term corollaries of social strategies in this gregarious Old World primate.

I first explored whether the quality of social ties predicted longevity among adult female blue monkeys. Controlling for any effects of dominance rank, group size, and life history strategy on survival, I used Cox proportional hazards regression to model the both the cumulative and current relationship of social ties and the hazard of mortality in 83 wild adult females of known age, observed 2-8 years each (437 subject-years) in 8 social

groups. The strength of bonds with close partners increased mortality risk under certain conditions: females that had strong bonds with partners that were inconsistent over multiple years had a higher risk of mortality than females adopting any other social strategy. Within a single year, females had a higher risk of mortality if they were strongly bonded with partners that were inconsistent from the previous year vs. with partners that were consistent. Dominance rank, number of adult female group-mates, and age at first reproduction did not predict the risk of death. This study demonstrates that costs and benefits of strong social bonds during adulthood can be context-dependent, relating to the consistency of social partners over time.

To understand the adaptive value of social behavior among juveniles, it was first necessary to understand the conditions under which their social behavior occurred and with which it co-varied. I examined the social behavior of 41 juvenile blue monkeys, using data collected over 8 consecutive months. I analyzed variation in social activity budgets and partner number related to life history characteristics, socio-demographic conditions, and seasonal environmental change. I examined partner preferences according to kinship, and relative age and rank. Lastly, I explored the stability of juvenile social tendencies over time. Males and females differed strongly in their social activity budgets and partner numbers: males spent more time playing with more partners than females, whereas females spent more time grooming and sitting close with more partners than males. Nevertheless, they were much more similar in terms of their partner preferences. Juveniles generally preferred to interact with partners with whom they were closely related and that were similar in age and maternal rank. Juveniles' affiliative and aggressive behavior varied seasonally, suggesting that these two types of behavior were related. Rates of agonism given and received were the only types of social behavior to demonstrate repeatable inter-individual differences. This analysis provides a comprehensive examination of juvenile behavior in blue monkeys, synthesizing findings with those in other primate and non-primate species.

I then explored the short-term costs and benefits of juveniles' sociality in terms of their effects on allostatic load. I examined variation in energy balance (as measured by urinary C-peptide), social style, and their influences on allostatic load (as measured by fecal glucocorticoid metabolites, fGCs). Juvenile energy balance varied according to sex, availability of ripe fruit, and rainfall. Both energy balance and social style predicted fGC levels, such that juveniles that had a higher energy balance, groomed less, and played more had lower fGCs. Time spent grooming interacted with energy balance in their effect on fGCs, such that individuals with higher energy balance actually had higher fGCs the more time they groomed. Neither maternal rank nor involvement in agonism corresponded with juvenile fGC levels. These results suggest that juvenile blue monkeys experience energetic stressors and that navigating the social environment via overt affiliative behavior, namely grooming, is a potentially stress-inducing endeavor.

Lastly, to further understand variation in social behavior during juvenility, I explored the role of mothers in shaping juveniles' affiliative tendencies. I examined whether the social behavior of juvenile animals resembled that of their mothers and whether their social behavior was subject to maternal effects, using data from the 41 juveniles and their 29 mothers. Juveniles' grooming time with peers corresponded with the amount of time they groomed with (primarily being groomed by) mothers as infants, and this relationship varied by sex. Females spent less time grooming with peers the more

maternal grooming they received during infancy, whereas males groomed with peers more. The time juveniles spent in other types of association with partners did not correspond with the same behavior in mothers, nor were other types of association subject to maternal effects. This exploratory study suggests limited effects of maternal behavior during infancy, but also that females and males respond differently to maternal investment during the first year.

The results of this dissertation emphasize the importance of long-term studies of natural populations in understanding the evolution of social behavior, particularly when examining the causes and consequences of social ties over the life cycle in a long-lived animal. Strategies of affiliation did indeed correspond with costs and benefits over the life cycle, as they were relevant both to mortality in female adults and metabolic hormones among juveniles. Further, individuals socialize during development according to their life trajectory as male or female, what seasonal changes in the physical environment require or allow, and early-life maternal effects.

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Acknowledgments

I have a long list of people to thank for their support, advice, patience, friendship, and comic relief. In the E3B department: Lourdes, Jae, Alex, and Kyle for so much guidance and behind the scenes work, and for being a breath of fresh air. My committee: Larissa Swedell, James Higham, James Curley, and Dorothy Cheney for their insights and encouragement. And to my lab mates past and present: Maressa Takahashi, Su-Jen Roberts, Michelle Brown, Holly Fuong, Lu Gao, and Jen Tinsman. Of course, I am deeply grateful to my advisor Marina Cords, who has been my Master Pai Mei. She is always ready to talk details, give it to me straight, and add insight and clarity to chaos. She asks a lot of me because, I think, she has believed in me. If I am in any way better at thinking and writing as a result of this whole PhD business, it is because of working with her.

I am very grateful I could spend the last 5+ years so close to my big sister Ivonne (Mufasa), because she's my oldest friend and doesn't have time for any B.S., which always has encouraged me to minimize it. Thanks to her and my brother-in-law Will for making a home for me in what would otherwise be a rushed, cramped, and transient place. It was important to me that I could see them almost every Sunday and that we could be a natural family amid a church family. Thanks to nephews and nieces, Diego and Lucia for helping me see the world with new eyes, to Joaquin for reminding me how to play, and Alba for making us all excited about tomorrow.

I probably would have been an insufferably chaotic character these past 5 years if it weren't for my dad, Pat Thompson. He was my sixth committee member, my alternate advisor, and the shoulder I cried on many times so that I could turn around and present a stronger face to everyone else. Thank you, Papa, for being there for me the past (near) 32 years, and for the last 5 in particular. I've been blessed beyond words to get to know you better during this program.

I am not sure if I could have handled all this very well without my church family. There have been many people along the way that taught me to be professional, generous, compassionate, and strong. Jaime Cecutti, thank you for being genuinely interested. Mike Zapata, thank you for showing me what an even keel looks like. Clara and Marcus, thanks for game nights and always being supportive. Pastors Stephen and Melissa Hickson, thank you for your messages and the opportunity to learn through service in your church. Much love and thanks to my dear friends: Heather Obasare, Hannah Omolade, Kim Wilson, Judith Rowland, Rita Makar, Angela Valco, Alexis Amann, and Danielle Tufts.

This entire analysis would not have been possible without the many, many hardworking teammates I had in Kenya. Thank you in particular to the team of fantastic women with whom I worked daily: Sylvia Khamuseini, Sheila Kasiti, Consolata Musanga, and Lewine Mutola. A deep and heartfelt thank you to the long-term assistants at the Kakamega Monkey Project for teaching me everything I needed to know about the monkeys and for working long hours to collect quality behavioral and plant phenological data: Joyce Munayi, Ernest Shikanga, Derick Shilavika, and Erick Widava. I am also indebted to all those involved in collecting data on adult females over the last several decades. Special thanks to camp managers Lauren McGee, Frances Hardy, Leah Pollack, piki driver Copeland Paul, and Pastors Mama and Baba Oade for helping me stay on the sunny side of life in Isecheno.

This work would not have been possible without the permission of the Government of Kenya, the Kenya Wildlife Association, the Kenya Forest Service, and the Kenya National Environment Management Authority to conduct research and collect samples in Kenya. I also thank Masinde Muliro University of Science and Technology (CEKATFOS) for local sponsorship.

I owe sincere thanks to the Leakey Foundation, the American Society of Primatologists, and the Animal Behavior Society for their financial support, which made the laboratory portion of this research possible. Also, thanks to the National Science Foundation for their support through my advisor and the NSF IGERT program. Thank you to Michael and Andrea Heistermann for their wonderful support and training during lab work at the German Primate Center, to Erin Vogel for the same at Rutgers University, and James Higham again at New York University.

Thanks, lastly, to various writers for creating some fantastic alternative worlds: J.R.R. Tolkein, George R.R. Martin, Quentin Tarantino, Beau Willimon, James Cameron, Ridley Scott, and writers of Homeland and X-Men 1-3. And special thanks to several fictional heroines for their inspiration: Beatrix Kiddo, Arya Stark, Mary Jane Paul, Ellen Ripley, Lara Croft, Storm, and Trinity.

All glory be to God.

Dedication

I dedicate this dissertation to my mama and papa, Alba Gonzalez Thompson and Patrick Thompson, because they instilled a sense of wonder and curiosity in me and never tried to snuff it out.

Chapter 1: Understanding the fitness benefits of social connectionover the life cycle.Introduction

In recent decades, research has focused on examining the adaptive benefits of long-term cooperative and affiliative relationships in animals, beyond the general benefits of social living (Lin & Michener, 1972; Silk, 2007). Studies of numerous gregarious and group-living mammals, including primates (Archie, Tung, Clark, Altmann, & Alberts, 2014; Gilby et al., 2013; Lehmann, Majolo, & McFarland, 2016; McFarland et al., 2015; McFarland & Majolo, 2013; McFarland et al., 2017; Silk et al., 2009; Silk et al., 2010b), rodents (Yee, Cavigelli, Delgado, & McClintock, 2008), cetaceans (Foster et al., 2012; Stanton & Mann, 2012), and ungulates (Cameron, Setsaas, & Linklater, 2009; Nuñez, Adelman, & Rubenstein, 2015; Vander Wal, Festa-Bianchet, Réale, Coltman, & Pelletier, 2014), have revealed that maintaining affiliative and cooperative relationships, both among same and opposite sex partners, corresponds with increased individual fitness, or increased survival and reproductive success. Despite the recent proliferation of findings that "social ties matter", the mechanisms by which relationships influence fitness are not altogether clear. The length and resolution of research projects, particularly on long-lived gregarious animals, are not always sufficient to understand the precise pathways by which long-term fitness outcomes come about.

This review focuses on evidence of *how* social ties influence individual fitness. Similar to previous reviews of "friendship" in animals (Bergman, 2010; Massen, Sterck, & De Vos, 2010; Seyfarth & Cheney, 2012), I touch on the description, evolution, and development of social ties in various social animals, with a focus on evidence from same-sex relationships in non-human primates. Unlike previous reviews, I concentrate on delineating pathways by which positive social interactions potentially influence fitness (expanding on those mentioned briefly in Cords and Thompson (2017)), while incorporating evidence from current literature. Importantly, the literature cited herein attempts to focus on the development and the effects of differentiated social relationships, rather than social living more broadly. I use the terms “ties” and “connections” interchangeably in reference to relationships (or the pattern of interactions) between individuals and their preferred social partners, and “bonds” to refer to an individual’s ties that are particularly strong relative to their other ties.

The review comprises three parts: 1) the definition and measurements of social ties, 2) the fitness outcomes associated with ties and the functional pathways by which they potentially enhance fitness, and 3) the physiological and developmental bases of social ties and their important links to early-life attachment to caregivers. In the first section, I address ways to quantify patterns in relationships and touch on the cognitive abilities that underlie them. In the second section, I outline seven functional pathways by which connections can benefit individuals and potentially influence their fitness, particularly given their life history stage, sex, and physical environment. These seven pathways include cooperative hunting, communal care of offspring, cooperative territorial defense, monopolizing mates and resources, establishing and maintaining social status, developing social and physical competence, and reducing exposure to risk and regulating homeostasis. In the final section, I describe the physiological underpinnings of connections and describe how early-life attachments, in part, are the evolutionary roots and strong ontogenetic influences on the physiology underlying ties later in life.

Issues Related to the Definition and Measurement of Social Connections

i. What are connections?

In the 1970's, Hinde pioneered the scientific description and classification of relationships in animals (Hinde, 1976a, 1976b). The impetus for such work was an accumulation of observations that individuals of many gregarious species associate in a non-random way, preferring to interact with certain conspecifics and avoiding others. A *relationship* between two individuals is formed when, after becoming known to one another, their interactions become patterned over time, and the quality of the interactions themselves define the quality of the relationship (e.g. cooperative, affiliative, agonistic (Hinde, 1976a). Friendships and associations are characterized by affiliative interactions, including spatial proximity, and non-aggressive physical contact and vocalizations. Alliances are characterized by cooperative interactions or joint efforts that achieve a mutual or reciprocated reward, such as access to food or a mate, and often occur in zero-sum contexts where individuals work together to outcompete a third party. Enemies and dominance relationships are characterized by agonistic and competitive interactions, including visual or vocal threats, physical aggression, chasing or fleeing, exclusion, and avoidance. In this review, I focus on the function of *connections* or ties, which I define as relationships that are characterized by association and cooperation rather than avoidance and competition. Connections herein are not related to reproduction (e.g. monogamous pairs), but do include the affiliative relationships among kin.

Typically, what are considered ties are relationships that are perpetuated because of the quality of the interactions that define them, and not by third variables such as individual personality or mutual attraction to particular microhabitats (Best, Dwyer, Seddon, & Goldizen, 2014; Dingemanse, Both, Drent, & Tinbergen, 2004; Godde, Humbert, Côté, Réale, & Whitehead, 2013). Male chimpanzees, for instance, maintain connections in that a dyad that maintains close spatial proximity in one period of observation is more likely to do the same in future (Mitani, 2009). The time that male chimpanzees spend in proximity to one another correlates positively with the quality of their interactions, as measured by the equitability of their grooming, suggesting that males are attracted to one another to affiliate (Mitani, 2009).

Despite controls for environmental variation, the line between the “dynamic stability” (Hinde, 1976a) of a relationship and the instability of interactions governed by third variables is not always clear. There are no universal criteria for either how stable or enduring a pattern must be to constitute a relationship. For instance, Henzi *et al.* (2009) argued that female baboons in two South African populations did not interact in ways that should be considered “relationships”, because the preference for dyad members to associate spatially increased when food was scarce and decreased when food was abundant. The majority of females in the study populations also did not demonstrate the same partner preferences from the first food-scarce season to the second. These findings resembled a previous report that the identity of a female’s top grooming associates changed from year to year over a four-year study (Barrett & Henzi, 2002). Silk *et al*. (2006; 2010a), by contrast, found that many of a baboon female’s closest spatial and grooming partners remained her closest partners for up to seven years. Unlike Barrett *et al.* (2002), Silk *et al*. (2006; 2010a) allowed a “one year gap” such that a female has a close partner for three years if her partner is close in year 1, not close in year 2, and reappears in year 3. However, the duration of strong ties did not change substantially whether excluding vs. including a one-year gap (Silk et al., 2010a). Although studies at both sites focused on grooming and spatial association behavior, differences in observation methods could account for differences in the length of female-female relationships among chacma baboons in South Africa vs. Botswana. For example, Henzi and Barrett (2002) based analyses on scan samples taken at 30 min intervals, whereas Silk *et al*. (2006, 2010) used 10-min focal follows, with point samples taken at 1 min intervals (Silk *et al.* 2006) or exact durations of grooming bouts recorded (Silk *et al.* 2010). While both sampling methods capture narrow windows on a female's social world, scans at 30 min intervals could be more prone to missing dyadic interactions that continuous focal follows capture. It is also possible that females actually associate in different ways between these two populations, particularly because the ecological environments of the two study sites differ (see McFarland et al., 2017).

ii. Quantifying individual social tendencies

In the literature today, measures of an individual's social ties fall into three major categories: measures of individual gregariousness, bondedness, and integration, each explained further below (Silk, Cheney, & Seyfarth, 2013).

Gregariousness is often measured simply by rates of affiliation given to and received from any partner relative to that of the average individual (e.g. composite sociality index, CSI, Sapolsky, Alberts, & Altmann, 1997) and/or by those rates relative to aggression given and received (e.g. relationship quality index, Weaver & de Waal, 2003). Although gregariousness is not a measure of one's precise strategy of connection, in species that associate non-randomly, one can predict that individuals distribute affiliation in a non-random manner.

Bondedness is fundamentally a quality of a dyad, but can be translated to describe the tendencies of an individual. Three particular measurable aspects of bondedness are bond strength, stability, and symmetry (Cairns & Schwager, 1987). Bond strength is usually calculated as the observed rate of affiliation and/or spatial association between two partners relative to their opportunities to encounter one another (Cairns & Schwager, 1987; Mitani, 2009), and is often further expressed in relation to the rates of an average dyad (e.g. dyadic CSI or DSI, Silk et al., 2013). One can characterize how strongly bonded an individual is by averaging the strength of an individual’s closest partners (Silk et al., 2013), where “closest” is determined by some reasonable threshold (Massen & Sterck, 2013; Silk et al., 2009). One can measure the stability of a bond as its duration over time or an individual’s bond stability by the consistency of the identities of its closest partners over time (Silk et al., 2013). The symmetry of a connection can be measured in several ways, such as the equitability of social exchange or the bias in responsibility for maintaining spatial proximity (Silk et al., 2013).

Integration is frequently measured as one’s total number of social partners (its network degree) and/or its position within a network (Hanneman & Riddle, 2005). Social networks are based on the rates of interaction within pairs of individuals, e.g. coalition formation and bond strength, and one can choose whether to filter connections such that they represent rates of interaction only above a given threshold (Hanneman & Riddle, 2005). Popular measures of an individual’s position within the network are its centrality, power, and local clustering coefficient (or local transitivity; Brent 2015) . There are several ways of expressing centrality, including betweenness or ability to link disparate cliques of individuals, closeness or number of connections required to reach certain individuals, and eigenvector centrality or the connectedness of an individual's connections. Centrality and power are generally considered to be useful measures of one's access to and ability to disseminate information and influence (and possibly disease). Local clustering coefficient is a measure of the connectedness (or connectivity) of one's social partners *with one another*. Hanneman and Riddle (2005) describe the connectivity of one's immediate network to be indicative of the "texture" one's regular social life. For example, an individual with high local transitivity may associate simultaneously with a consistent set of partners.

Closely related to integration is the idea of partner diversity (e.g. Shannon Weiner Diversity index; Silk et al. 2013) . In social contexts, the SWI in particular is most meaningful when one controls for group size, as it then represents how evenly an individual associates or distributes affiliative or cooperative behavior among its possible connections.

In measuring ties, one can control for spatial preferences, that are driven by non-social factors, by calculating spatial association according to the proportion of observations in which either individual were present in the same subgroup and the size of the subgroup (e.g. pairwise affinity index, Mitani, 2009). This approach is especially useful in species with fission-fusion social structures or poorly defined communities, such as dolphins or kangaroos. For example, some researchers have included the spatial overlap of individual home ranges as an analytical control variable when assessing the nature of social ties or propensity of two individuals to interact (e.g. Best et al., 2014; Mann, Stanton, Patterson, Bienenstock, & Singh, 2012).

To assess the influence of a dyadic attribute (e.g. kinship, age difference) on social ties that are independent of spatial preference, one can also randomly and repeatedly permute the underlying social matrices of the dyadic response, only swapping observations that occur in the same geographic areas, and then comparing permutation-based coefficients with observed (Farine, 2017). Indeed, apart from controlling for space use, there are many important methods to control for the general non-independence of dyadic measures as statistical responses (Farine, 2017; Farine & Whitehead, 2015; Gomes, Mundry, & Boesch, 2009). Permutation methods are less advisable when social ties are an independent or a predictor variable in a multiple regression, as permuting their underlying matrices may disrupt relationships between covariates if they are at all correlated (Anderson & Legendre, 1999; Dekker, Krackhardt, & Snijders, 2007).

In an experimental setting, one can manipulate available spaces and see if preferences for association hold (e.g. Durrell, Sneddon, O'connell, & Whitehead, 2004). Although less common, one can also control for the influence of individual personality in an association, such that interactions do not represent one individual's attraction to larger sub-groups (e.g. (Best et al., 2014) or lack of fear of novel environments (Dingemanse et al., 2004). Domestic pigs, for example, prefer particular resting areas within their sties, but not the company of particular sty-mates (Durrell et al., 2004). After the structure of the sty was changed, individuals did not prefer to associate spatially with their previous partners.

Several factors, apart from space use, can cause pronounced fluctuations in connections, such as seasonal availability of food, mates, or infants (Brent, MacLarnon, Platt, & Semple, 2012; Henzi et al., 2009), life history state including development and senescence (Almeling, Hammerschmidt, Sennhenn-Reulen, Freund, & Fischer; Berman, 1982), extraordinary climatic or demographic events (Sapolsky, 1986b), death via predation or infanticide (Engh, Beehner, Bergman, Whitten, Hoffmeier, et al., 2006; Wittig et al., 2008), and group fissioning (Cords, 2012). To assess the stability of ties despite these factors, behavioral data can be collated over periods that represent either stable environments, such as mating and non-mating seasons (Schülke, Bhagavatula, Vigilant, & Ostner, 2010), or simply cover all seasons in a year (Silk et al., 2009). One can also control for variation in the environment by clustering observations by habitat type (Silk, Alberts, & Altmann, 2003) or by building models that include the context of interaction (e.g. food vs. non-food, Smith et al., 2010) or an index of environmental quality (e.g. fruit availability) as analytical controls. Finally, observations potentially influenced by third variables could be omitted altogether. For example, in calculating a dyadic composite sociality index in female baboons, Silk *et al.* (2009) removed interactions when either female had an infant under 100 days old, because infants are attractive to adult females.

iii. Connections do not require but can involve advanced social cognition

A relationship, broadly, does not need to exist as a concept within the minds of its partners to be deemed as such by human observers. The formation and maintenance of connections, at most basic, requires cognitive abilities that mediate patterns of preference/avoidance and stability, i.e. individual recognition, social memory, and associative learning. The ability to recognize individuals either by sight or smell is widespread among social animals, indicating its fundamental value in social living, e.g. paper wasps (Sheehan & Tibbetts, 2011), octopuses (Tricarico, Borrelli, Gherardi, & Fiorito, 2011), storm petrels (Bonadonna & Sanz-Aguilar, 2012), dolphins (Bruck, 2013), elephants (McComb, Moss, Sayialel, & Baker, 2000), hyenas, several primates (Holekamp, Sakai, & Lundrigan, 2007), and many others (Frommolt, Goltsman, & Macdonald, 2003; Insley, Holt, Southall, & Atwood, 2014; Karavanich & Atema, 1998; Kirschel et al., 2011; Knörnschild, Feifel, & Kalko, 2013; Proops, McComb, & Reby, 2009)). Individuals of several gregarious species demonstrate long-term social memory, such as male hyenas that recognize former clan-mates after dispersing (Holekamp et al., 2007) and bottlenose dolphins that recognize individuals after 20 years of separation (Bruck, 2013). Associative learning in a social context is also common in animals. One example is social rank inheritance in spotted hyenas and several cercopithecine primates (Holekamp et al., 2007), in which a young female establishes a dominance rank immediately below her mother's via a series of interactions in which her mother or maternal kin intervene on her behalf in aggressive interactions, with other group-mates apparently learning this contingency (Holekamp & Smale, 1991).

Some animals demonstrate other, more advanced cognitive abilities that are necessary for certain social decisions. Individuals of some species demonstrate an awareness of triadic, or third party, social relationships. Male chimpanzees and female chacma baboons are more likely to avoid the close partners and the kin, respectively, of their recent opponents (Wittig, Crockford, Langergraber, & Zuberbuehler, 2014; Wittig, Crockford, Seyfarth, & Cheney, 2007), presumably to avoid any retaliatory harassment from them. Baboons pay more attention to an interaction that violates an expectation of triadic social relationships: individuals looked longer in the direction of a speaker when it played a threat signal from one group member that was followed it by a scream of another member who ranked higher than that of the threatener (Bergman, Beehner, Cheney, & Seyfarth, 2003; Cheney, Seyfarth, & Silk, 1995). Hyenas, corvids, and some fish also appear to understand the relative dominance status of other individuals (Emery, Seed, Von Bayern, & Clayton, 2007; Holekamp et al., 2007). In hyenas, a female increased her rate of aggression toward a target when joined by an ally that was lower-ranking to her but higher ranking to her target (Holekamp, 2007). This pattern ruled out the use of a rule of thumb such as "attack more when a dominant individual helps." Individuals of species that demonstrate triadic awareness may further apply this understanding when recruiting allies, intervening on the behalf of others, redirecting aggression, and reconciling (Holekamp et al., 2007). Lastly, theory of mind may inform social decision-making in some primates and corvids, but the debate of whether this ability is present in animals is extensive (e.g. Emery & Clayton, 2009) and beyond the scope of this review.

iv. Strategies of connection are adaptive

As Kummer (1978) envisioned it, individuals "invest" in connections because of their adaptive value, or the benefits that they confer on individuals either in the present or the future. The ability and propensity to recognize, seek, and invest in valuable connections evolves via kin selection, reciprocal altruism, or mutualism (Silk, 2007). In concrete terms, benefits of connections can be access to higher quality food (Holekamp et al., 2007; Peres, 1989), copulations (Connor, Read, & Wrangham, 2000), more rapid return to homeostasis (Wittig, 2010), protection from predators (Ron, Henzi, & Motro, 1996), or bodily warmth (McFarland et al., 2015). The actual value or importance of these benefits to individual fitness depends on the individual's experience of its environment, i.e. its state (e.g. old/young, large/small, male/female) and it access or exposure to some aspect of the environment (e.g. food, mates, shelter, warmth). As species represent some large-scale distinctions in state and environment, one would expect that the value of connections would vary among them.

Nevertheless, assessing the adaptive value of a behavioral strategy frequently involves many assumptions. As Grafen (1984) puts it, behavioral ecologists typically use a "phenotypic gambit." Instead of attempting to describe the genetic basis of a trait and its variation, one measures the trait phenotypically and assumes that its presence, absence or variation in degree represent alternative genetically-based strategies. Instead of measuring the fitness of a trait by the change in its gene frequency over time within a population, one measures an association between strategies and certain benefits (as listed above), and assumes that these benefits determine individual fitness. Indeed, field-based studies on long-lived animals are limited even when measuring more direct fitness-related outcomes, such as survival, reproductive output, and offspring survival, as even these may not always translate into lifetime reproductive success when measured over what may be a relatively short-term period.

Pathways of Connections' Benefits

Several studies present evidence that many or strong and consistent social ties correspond with better fitness-related outcomes. The seminal work of Silk and colleagues on two populations of savannah baboons brought the question "do social ties matter?" to the fore (Silk et al., 2003; Silk et al., 2009; Silk et al., 2010b) and in the following decade, several studies have examined links between either the quality or quantity of social ties and fitness outcomes, such as individual longevity (Archie et al., 2014; Brent, Ruiz-Lambides, & Platt, 2017; Foster et al., 2012; Stanton & Mann, 2012; Vander Wal et al., 2014), survival during or after a traumatic event (Lehmann et al., 2016; McFarland & Majolo, 2013; Nuñez et al., 2015), reproductive output (Gilby et al., 2013; McFarland et al., 2017; Schülke et al., 2010; Vander Wal et al., 2014), and infant survival to one year (Cameron et al., 2009; Kalbitzer et al., 2017; McFarland et al., 2017).

My goal is not to synthesize the findings of above studies, but rather to highlight that the studies provide one kind of evidence that connections influence fitness, i.e. different social strategies correspond with different patterns of fitness outcomes (e.g. survival, reproductive success). None demonstrate a clear functional pathway (excluding Cameron *et al.* 2009 and Stanton *et al.* 2012: avoiding harassment; McFarland & Majolo, 2013: thermoregulation) by which connections benefit individuals. Indeed, single studies rarely present both outcomes and the pathways by which they arise, because short-term projects are frequently unable to measure outcomes and long-term projects do not have the data to test pathways in hindsight. In the literature today, evidence of the functional pathways by which connections possibly influence fitness comprise the majority of evidence of connections' influence on fitness, therefore in the following paragraphs I review these pathways. When possible, I separately discuss strategies of connection by sex, and among same and mixed-sex connections, and by age classes to highlight how functional strategies differ based on these important state variables.

Pathway 1: Cooperative hunting

Hunting cooperatively is a strategy in which average individual energy intake is higher when hunting as a group than when hunting alone and occurs in a wide range of taxa including carnivores, cetaceans, primates, birds, and spiders (Bailey, Myatt, & Wilson, 2013; Ruch, Herberstein, & Schneider, 2014). Advantages of hunting cooperatively include capturing prey that is larger, in less time or distance covered, and with a lower variability in success over time (Bailey et al., 2013). Maintaining connections in the context of hunting thereby optimizes individual foraging efficiency (Bailey et al., 2013). Whether the bondedness of alliance members increases the efficiency of hunting is not clear, although hunting in family units vs. unrelated groups increased feeding efficiency in spiders (Ruch et al., 2014). Species that hunt cooperatively usually do so in extended family units, suggesting that familiarity may play a role in facilitating the cooperation of the hunt (Bailey et al., 2013). In some species, such as chimpanzees (Melis, Hare, & Tomasello, 2006) and hyenas (Drea & Carter, 2009), tolerance does appear to facilitate cooperation on experimental tasks that mimic foraging and hunting, respectively.

Pathway 2: Communal care of offspring

Individuals cooperate in rearing offspring when sharing the duties of care confers, on average, greater reproductive success than does rearing alone. Here, I refer to species that care communally for offspring and in which reproductive skew among females is low, i.e. not species classified as cooperative breeders. Female house mice are one example in which preferred social partners confer fitness benefits via communal rearing. In natural conditions, female house mice frequently provide milk to the offspring of others in a communal nest (CN), which enhances infant behavioral development (Curley & Branchi, 2012), growth, survival, and adult female lifetime reproductive success (Weidt, Lindholm, & Koenig, 2014). As adults, infants nursed communally show less anxiety, establish social roles among novel conspecifics more quickly, and are generally more sociable (Curley & Branchi, 2012). In an experimental study, females preferred certain spatial associates more than others and those that were allowed to rear litters with their preferred partners engaged in less overt aggression and enjoyed higher average individual reproductive success (number of offspring successfully weaned) than females paired with non-preferred partners (Weidt, Hofmann, & König, 2008). All pairs of females fought, but in the non-preferred pairs, one female delayed reproduction while the other had higher reproductive success than the average of preferred-partner pairs. Communal nursing was previously thought to be a product of social group living, but wild female mice appear to select their rearing partners (Weidt et al., 2014). Weidt *et al.* (2014) found that females in the wild formed communal nests in only 33% the cases in which a potential partner was present. Females were more likely to form communal nests when more partners were available, but less likely if population density was high, suggesting that females are not obligated to rear communally but choose it as a strategy given a suitable partner.

Unlike female house mice that appear to seek an egalitarian rearing partnership, female eider ducks that communally rear young choose alliance partners based on negative assortment of physical condition (Öst, Ydenberg, Kilpi, & Lindström, 2003). Two or more un-related females often pool broods in crèches over the brood-rearing period (approx. 40 days) and share care duties, such as feeding and guarding young from predators. A cost to communal rearing arises if offspring fall low in a brood's dominance hierarchy. In general, females that choose to rear young communally are in poorer physical condition than those that rear alone, because high-quality females seem to feed and defend offspring well enough alone (Ost & Kilpi, 1999; Öst et al., 2003). Females that form alliances choose partners that have the optimal body condition relative to their own: for female B in poor physical condition, partner A is in good enough condition if the service she provides to B's offspring is better than if B's offspring are reared with only one mother. For female A in better physical condition, an optimal partner B is in poor enough physical condition such that B's offspring are unlikely to outrank A's. Similar negative assortment in body size or condition is seen in same sex associations of some invertebrates, such as male forked fungus beetles (Formica et al., 2011).

Pathway 3: Cooperative territorial defense

Among females, alliances to cooperatively defend territory can increase territory quality. Although the influence of the quality of *particular* social ties on the efficiency of cooperative territorial defense is largely unknown, the benefits of effective territorial defense could select for team-building social behavior such as increased tolerance (Sterck, Watts, & van Schaik, 1997), “pay-to-play” distributions of grooming from dominant to subordinate individuals (Kutsukake & Clutton-Brock, 2010), or more diverse and reciprocal grooming among group members (Cords, 2002; Majolo, de Bortoli Vizioli, & Lehmann, 2016). Cheney (1992) found that females in species that do not engage in territorial defense had exceptionally low grooming diversity; however, females’ grooming diversity was unrelated to the frequency of territorial disputes both across and within species in which territorial disputes did occur. Further, in Sifakas, individuals maintain stronger group cohesion in areas that overlap with neighboring groups’ home ranges, possibly in anticipation of territorial disputes (Benadi, Fichtel, & Kappeler, 2008).

While future studies should assess whether particular degrees of bondedness or social integration influence the outcome of territorial disputes, the benefits of female-female alliances in disputes are clear. Female golden lion tamarins that invest more time in cooperative territorial defense are able to maximize individual food intake and allow areas central to their territory to replenish themselves (Peres, 1989). Female lions are the primary defenders of territory and prides in the Serengeti: an increase in their number of adult females allowed a pride to gain disputed areas and improve territory quality in subsequent time periods (as determined by the distance of territory centroids to river confluences; Mosser & Packer, 2009). In general, larger groups often are more successful in territorial disputes (Cassidy, MacNulty, Stahler, Smith, & Mech, 2015; Markham, Alberts, & Altmann, 2012; Mosser & Packer, 2009; Roth & Cords, 2016; Sillero-Zubiri & Macdonald, 2001), and specific aspects of group composition can influence dispute outcomes (e.g. Sillero-Zubiri & Macdonald, 2001). Further studies could reveal how female-female relationships and alliances vary according to group size and how these contribute to outcomes of territorial disputes.

In some species, male territorial alliances appear to increase male reproductive success by enhancing the fertility of co-resident females (Williams, Oehlert, Carlis, & Pusey, 2004). Chimpanzee males form patrolling coalitions that raid neighboring community territories to harass both male and female neighbors (Williams et al., 2004). When male alliances increase the size of their community's territory, they do not gain more females, but inter-birth intervals of co-resident females become shorter and their reproductive rates increase (Williams et al., 2004). Male alliances thereby allow males to benefit from higher average individual paternity by increasing territory quality and female fertility (Williams et al., 2004). Male chimpanzees also increase female fertility within their communities by harassing older and non-cycling females in neighboring communities, who are more likely to compete with resident females and not sexually available to males. Male lions also attack neighbor females perhaps for the same reason (Mosser & Packer, 2009). It is further possible that male territorial behavior deters such harassment from neighboring males: in lion prides with a higher proportion of males relative to females, females were less likely to be wounded by neighbor males (Mosser & Packer, 2009).

Pathway 4: Monopolizing resources within social units

Males frequently form cooperative alliances to access and monopolize mates. The basis of mate-guarding alliances is that individuals achieve more copulations on average when in an alliance than when alone (Whitehead & Connor, 2005). Fertilizations are not a shareable resource, particularly in non-litter producing species, therefore males that mate-guard should benefit from some percentage of fertilizations over time. A classic example of mate-guarding alliances occurs in bottlenose dolphins (Whitehead & Connor, 2005), in which affiliative, non-kin partners form long-term alliances (up to 20 yrs, Connor, Heithaus, & Barre, 2001) that compete with other alliances to monopolize females in their communities. Formation of mate-guarding alliances varies by population and individuals are more likely to form alliances when individual body size is smaller, relative competitive abilities of alliance members are more similar, and the operational sex ratio of communities is male-biased (Whitehead & Connor, 2005). In Port Stephens, reproductive skew in alliances is not large and males that maintain larger alliances (e.g. 3-4 individuals) have higher individual reproductive success (Wiszniewski, Corrigan, Beheregaray, & Möller, 2012). In Shark Bay, males that participated in alliances whose members remained more constant over time (i.e. stable alliances) also participated in more multiple-day consortships, increasing average individual copulations (Connor et al., 2001). Males may also benefit from forming alliances by increasing access to females via mate choice. Male synchronous displays may attract females as a signal of male competitive ability (Connor, Smolker, & Bejder, 2006) and/or females perhaps prefer males in larger alliances (Wiszniewski et al., 2012).

Mate-guarding alliances occur in several other species. Male feral horses form alliances that are characterized by a strong affiliative bond that can last their lifetimes and they share fertilizations in a 3:1 ratio between the dominant and subordinate male (Feh, 1999). This scenario is better than either male would have alone, because allied males are globally low to middle ranking**.** Middle, but not low-ranking, male baboons in both Amboseli and Gilgil are more likely to form mate-guarding alliances, which steal females from their consortships with higher-ranking males (Noë & Sluijter, 1995). Allied male baboons do not appear to share an affiliative bond nor do they need to be co-resident for a long period to become familiar with one another; they do, however, appear to selectively choose their alliance partners (Noë & Sluijter, 1995). Although unexplored, authors predict that reproductive skew in baboon alliances should be low, as males are of similar competitive ability and should, in theory, take equal turns fertilizing females. This pattern of mutualism is apparent in mate-guarding alliances of male chimpanzees in which dominant and subordinate partners tolerate the other's consortships in turn (Watts, 1998).

Within-group alliances to monopolize food and nest sites occur primarily among females. The importance of such alliances for female fitness forms the basis of the socioecological model of female relationships, initially developed in regard to primates (Isbell & Young, 2002; Sterck et al., 1997) but applicable to other group-living species (see Archie, Morrison, Foley, Moss, & Alberts, 2006; Holekamp, Swanson, & Van Meter, 2013). According to the model, the formation of competitive alliances depends on the monopolizability of the resource defended, i.e. whether it is discrete, easily guarded, and/or easily consumed (Isbell & Young, 2002). A comparison of two subspecies of squirrel monkeys demonstrates this principle. In the subspecies whose foods were monopolizable, females formed friendships, alliances, and dominance hierarchies (Mitchell, Boinski, & Van Schaik, 1991). In the subspecies whose food was not monopolizable, female connections were undifferentiated. In many cases, female competitive alliances aim to secure *priority* of access to food and space via social status, rather than immediate access to resources themselves (Smith et al., 2010). For that reason, I continue to discuss within-group competitive alliances among females in the following section on dominance status.

Pathway 5: Establishing and maintaining social status

Connections are valuable for optimizing one's social power, or rank within a group's dominance hierarchy. This is particularly true in plural breeding species, where the single top-ranking male and female do not monopolize breeding and individuals tend to form highly linear dominance hierarchies. Among adult males dominance rank often translates to priority of access to mates and among females and juveniles rank translates to priority of access to food, space, and nesting sites (TH Clutton-Brock & E Huchard, 2013). In species with sex-typical roles of parental investment, these resources are integral to the fitness of the respective sex; therefore the benefits of securing a high dominance rank are clear. In a meta-analysis of several cercopithecine primates, male dominance rank accounted for 50% of the variance in mating success (Alberts, 2012; Altmann & Alberts, 2003). In females of several populations of matrifocal species, such as baboons and hyenas, high rank corresponds to shorter inter-birth intervals, earlier ages at reproductive maturity (Altmann & Alberts, 2003; Holekamp, Smale, & Szykman, 1996; Pusey, 2012; Pusey, Williams, & Goodall, 1997), and faster infant growth (Altmann & Alberts, 2005), although the differential benefits of rank are somewhat dependent on ecological (Holekamp et al., 1996) and demographic conditions (Silk, 2007).

Juveniles of species in which individuals inherit their mothers' dominance rank require the assistance of older allies to establish their optimal dominance status. Allies are typically mothers or maternal kin (Chapais & Gauthier, 2004). In female philopatric species where female dominance is unrelated to age, such as hyenas and many cercopithecine primates, maternal aid enables juvenile females to dominate all females subordinate to their mothers, or to "inherit" their mother's rank (or one just below mother's) for life (Chapais, 1988; Cheney, 1977; Datta, 1988; Engh, Esch, Smale, & Holekamp, 2000; Holekamp & Smale, 1991; Horrocks & Hunte, 1983; Pereira, 1989). For males too, such as bonobos, dominance rank correlates positively with maternal rank and male rank declines when mothers are no longer present in the community (Surbeck, Mundry, & Hohmann, 2011), suggesting that alliances with mothers are necessary for males to maintain their status. Similarly, in hyenas, juvenile males inherit a status just below their mothers for as long as they remain in their natal group (Holekamp et al., 2007). Although males' rank post-dispersal is not necessarily equal to their rank pre-dispersal (e.g. Smale, Frank, & Holekamp, 1993), the nutritional and social advantages of high rank in one's natal group could cause a male to disperse sooner rather than later and to groups offering optimal mating conditions, thereby potentially extending a male's reproductive career (e.g. Höner et al., 2010).

Adults of species in which individuals form dominance hierarchies also rely on allies to either maintain or rise in dominance rank. Females of such species are frequently philopatric and alliances that maintain the dominance hierarchy, or conservative alliances, are the most frequent kind among adults (Smith et al., 2010). In Japanese macaques, when a female's kin were removed from the group, she succumbed to revolutionary coalitions and rapidly fell in dominance rank, but was able to regain her former rank upon the reintroduction of her kin (Chapais, 1995). Patterns of rank inheritance also disappear in natural populations when supporting kin are absent. In a group of Japanese macaques with low relatedness, juveniles came to outrank females to whom their mothers were subordinate because target females lacked conservative support and juveniles opportunistically joined bridging coalitions with higher-ranking females (Chapais & Gauthier, 2004). The overall occurrence of rank-related coalitions are relatively rare, perhaps because single events are salient enough to reinforce developmentally established dominance relationships (Smith et al., 2010).

Males of species with dominance hierarchies frequently form alliances that they use to vie for top rank (Chapais, 1995). In such cases, the strength of affiliative ties with allies may be integral to alliance success. For example, Assamese macaque males maintain affiliative bonds with coalitionary allies and those with stronger bonds (measured by a CSI) with their top three affiliative partners were also more likely to rise in rank and sire more offspring in subsequent periods of observation (Schülke et al., 2010). Chimpanzee males form long-term, equitable ties with each other (Mitani, 2009) and also form coalitions to vie for alpha male status (Gilby et al., 2013); however, it is not yet clear if the strength of their affiliative connections translates into the success of their cooperative ones.

Pathway 6: Reducing exposure to risk and mediating HPA axis activity

In animals, both behavioral and endocrinological mediators help individuals avoid risk and maintain homeostasis (Romero, Dickens, & Cyr, 2009; Schulkin, 2011), which are centrally important for fitness in all organisms. While avoiding risks such as predation and aggression is a primary advantage of social ties, maintaining homeostasis can be considered a "secondary" benefit, as ties often confer this advantage only once the propensity to form ties has evolved. In the human medical and psychological literature, social ties that help individuals avoid risk and maintain homeostasis are collectively referred to as "social support" (Gunnar, 2017; Uchino, 2009), which is often partitioned into "instrumental" and "buffering" support. The former describes support that decreases or removes the risk or energetic challenge in the environment, such as sheltering individuals from predators and extreme cold, or increasing their access to food. The second refers to support that either reduces the psychological perception of risk and/or helps individuals return to homeostasis following their response to a challenge (i.e., their "stress response"). Reducing the psychological perception of risk is, of course, only beneficial if the risk is no longer present in the environment. Humans and laboratory animals, for example, are unlikely to be more exposed to a predator when alone, but feel the need to be more vigilant and alert for such a risk when alone (Hawkley & Cacioppo, 2010). In such cases, social support can "buffer" individuals from the perception of risk.

Evidence of the psychological component of buffering in non-human animals is obviously difficult to gather. However, monitoring sympathetic activity and important endocrinological mediators of homeostasis following a potential challenge is one way to gauge both individuals' perception of risk and their ability to return to homeostasis. Mediators prominently featured in studies of social buffering are glucocorticoid hormones (GCs). GCs catabolize glycogen into readily available glucose to respond to current and anticipated energetic needs, and dampen the activity of other physical processes that are less immediately important for survival, such as inflammatory immune responses and reproduction.(Sapolsky, Romero, & Munck, 2000). While long-term or “chronic” elevations in GCs are often characterized as maladaptive, causing permanent damage to their own negative feedback mechanism, individuals’ long-term memory, and fertility (Sapolsky, 2005; Sapolsky et al., 2000), it is unclear how relevant chronic GC levels are to the fitness of wild animals (Beehner & Bergman, 2017; Bonier, Martin, Moore, & Wingfield, 2009). In any case, variation in baseline GCs between individuals, and deviation from baseline within individuals, are useful signals of the challenges that an individual or population of individuals is experiencing (Beehner & Bergman, 2017).

a. Protection from isolation

Social isolation poses a physical threat to some social animals, particularly those that depend on a social group for defense from predators or territorial neighbors, and for maintaining hygiene or warmth (Cheney & Seyfarth, 2009; Hawkley, Cole, Capitanio, Norman, & Cacioppo, 2012). Captive individuals of various social species mount stress responses to experimentally induced isolation, including rats, piglets, and prairie voles, suggesting that the adaptive value of avoiding isolation is conserved across social animals (reviewed in Hawkley et al., 2012). In baboons, males that were more isolated, as measured by a CSI, had higher baseline GC concentrations than did more sociable males (Sapolsky et al., 1997). In humans, the perception of isolation increases one’s vigilance and expectancy of an impending threat, which increases sympathetic activity (Hawkley & Cacioppo, 2010). Prolonged increase in sympathetic activity results in increased peripheral resistance in blood vessels, hypertension, depression, risk of autoimmune disease, and myocardial infarction (Cacioppo, Hawkley, Norman, & Berntson, 2011). The over-activation of the HPA axis is the most likely cause these symptoms, as opposed to poor health practices (Cacioppo & Hawkley, 2003; Cohen, Gottlieb, & Underwood, 2000). In humans, the benefits of avoiding the negative consequences of isolation has selected for the neural pathways and brain regions used in the perception of physical pain to be co-opted in the perception of isolation, causing "social pain" and calling attention to weakened connections (Cacioppo et al., 2011).

b. Protection from harassment

Social partners can protect individuals from aggressive competition and sexual harassment. Baseline GC levels often correspond to individual's dominance status (reviewed in Sapolsky, 2005), however the social environments that correspond to status, and not necessarily status itself, appear to underlie observed patterns (Abbott et al., 2003). In a meta-analysis of Old and New World monkeys, Abbott *et al*. (Abbott et al., 2003) found that males in a given rank class (high or low) had lower baseline GC levels if they received more social support (i.e. grooming and interventions) and fewer attacks.

In feral horses, mothers that were more sociable with female peers (high CSI) were better shielded from harassment from adult males, perhaps leading to the higher survival of their foals (Cameron et al., 2009). Alternatively, the bond a female has with a male may increase his tolerance of her and lower the rate at which he harasses her, as seen in Assamese macaques (Haunhorst, Heesen, Ostner, & Schülke, 2017). Such patterns within dyads may demonstrate a more general pattern of "paying" potentially threatening or dominant individuals for social tolerance (Kutsukake & Clutton-Brock, 2010; Seyfarth, 1977).

Male dolphins, rather than females appear to benefit from higher social centrality early in life perhaps because it helps them avoid harassment from larger juveniles, who are targeting their future competitors. Juvenile male bottlenose dolphins that are more central (eigenvector centrality) in spatial association networks during their infancy survive longer than males that are less central (Stanton & Mann, 2012). There was no influence of centrality on female survival nor did the sheer number (binary degree) of a male's connections predict his survival. An association with a well-connected mother may be at the root of this effect, such that a male that associates more frequently with its mother has higher eigenvector centrality. As another example, female langurs frequently form coalitions to defend one another from the harassment of potentially infanticidal males (Sterck et al., 1997).

c. Coping with trauma and instability

Associating with social partners often appears to help individuals cope with traumatic events. Among female baboons in the Okavango Delta, GC levels increased in response to various events, including infanticide, losing a close partner to predation (Engh, Beehner, Bergman, Whitten, Hoffmeier, et al., 2006), and instability in the male or female dominance hierarchy (Engh, Beehner, Bergman, Whitten, Hoffmeiers, et al., 2006; Wittig et al., 2008). Wittig et al. (2008) found that female GC levels rose at the onset of instability in the alpha male position. Females that subsequently focused, or decreased the diversity, of their grooming connections to a smaller subset of individuals, presumably their closest associates, showed a more rapid decline in GC concentrations than females that did not focus their networks or did so to a lesser degree. By contrast, individual rates of grooming did not change from before to after the onset of instability. Focusing networks then perhaps provided females with a dependable source of grooming, or with partners with whom females felt most familiar, such as kin.

Females baboons that maintained grooming networks that were more focused had lower baseline GC levels even during periods of rank stability (Crockford, Wittig, Whitten, Seyfarth, & Cheney, 2008). It is possible therefore that simply associating regularly with bond partners attenuates HPA reactivity. Indeed, chimpanzees that groomed with a strong vs. weakly bonded partner for a single bout, regardless of bout length or quality, demonstrated a drop in urinary GC levels relative to before grooming, and did so both after a challenging event (intergroup encounter) and in the absence of challenges (Wittig et al., 2016).

Affiliative contact may mediate HPA responses by stimulating the release of oxytocin (OT, Crockford et al., 2013; Seyfarth & Cheney, 2013), which can counteract the effects of GCs and reduce GC levels (Curley, 2011). In Barbary macaques, giving grooming, but not receiving grooming, was shown to associate with lower baseline GC levels (Shutt, MacLarnon, Heistermann, & Semple, 2007). Among female rats, the equitability of grooming relationships appears to lowers GC levels (Yee et al., 2008). Among trios of sisters, those that groomed most equitably in response to a stressor had the lowest levels of GCs (Yee et al., 2008) and in adulthood, these females had the lowest risk of mortality and were the least likely to develop mammary tumors.

The most supportive social strategy is not always a small and close set of connections. Among female rhesus macaques, females that had more ties, and partners with more ties themselves (i.e. proximity reach), had lower GC levels if they were low-ranking (Brent, Semple, Dubuc, Heistermann, & MacLarnon, 2011). High-ranking females, however, had lower GC levels when they were less connected. This variation could result from psychological stressors perhaps being condition-dependent. For example, following the immigration of a new male baboon, elevation in GC levels were highest among females that were at greatest risk of infanticide, i.e. lactating females (Engh, Beehner, Bergman, Whitten, Hoffmeiers, et al., 2006). Nevertheless, why patterns of direct and indirect ties within a spatial association network predicted GC levels of rhesus females is not clear.

d. Protection from environmental variation and predation

Social partners can help defend individuals from challenges in the physical environment, such as food scarcity and cold temperatures. The intensity of a tie in a non-competitive context often translates into tolerance in contexts where individuals potentially compete for a limited resource, such as food or warmth. The strength of a bond between female baboons in the arid Namibian savannah significantly predicted their likelihood to co-feed with one another and predicted co-feeding more strongly than relatedness (King, Clark, & Cowlishaw, 2011). Tolerant or preferential co-feeding also increases among affiliative partners in domestic dairy cows and Assamese macaques (Haunhorst et al., 2017; Val-Laillet, Guesdon, von Keyserlingk, de Passillé, & Rushen, 2009). Simply having more social ties may also increase the number of tolerant spatial associates. Vervets in South Africa huddle together at night to help maintain homeothermy (McFarland et al., 2015). Temperatures fall below freezing during winter and individuals that had more spatial and/or grooming partners throughout the day maintained a higher minimum body temperature and varied less in temperature from day to night (as measured by a subcutaneous thermometer). Number of social ties appeared to translate, too, into thermal efficiency for male and female adult and subadult Barbary macaques in the Atlas Mountains, where individuals with more ties were more likely to survive an intense winter (Lehmann et al., 2016; McFarland & Majolo, 2013). In both species, more social ties during the day perhaps allowed individuals to occupy key huddling locations among group members to stay warm at night.

Social ties and their corresponding tolerance and familiarity can also influence exposure to predators. In some primates, a lack of tolerance between dominant and subordinate females appears to cause the lowest-ranking females to be located peripherally to the group, leaving them exposed to higher rates of predation (Ron et al., 1996; van Schaik & Van Noordwijk, 1986). In reverse, being tolerated by a larger number of potential neighbors could increase spatial integration in a group and reduce exposure to predators. For example, eigenvector centrality in spatial association networks of adult ewes increases their survival, reproductive output, and infant survival (Vander Wal et al., 2014). Interestingly, rams do not incur these benefits of high eigenvector centrality, perhaps because they are at lower risk of being preyed upon (Vander Wal, Gagné-Delorme, Festa-Bianchet, & Pelletier, 2015). Stronger connections may help individuals to avoid predators because the familiarity between partners increases the efficiency of communication. In crested macaques, for example, adult females follow others' eye movements more frequently and quickly when they are more strongly connected (Micheletta & Waller, 2012). In dwarf mongooses, too, individuals respond more readily, for longer, and are more likely to approach a caller with whom they are strongly vs. weakly bonded when the caller emits a recruitment call to mob predatory snakes (Kern & Radford, 2016). In both macaques and mongooses, one can see how differentiated social ties mediate the increased vigilance that is often cited as a primary cause of the evolution of sociality, particularly in primates (Sterck et al., 1997). Females are more responsive to their strongest connections perhaps because strong connections have proved themselves trustworthy or perhaps because the physiological basis of their bond increases their behavioral synchrony (e.g. Arueti et al., 2013). More fundamentally, bonded partners may be more responsive to one another than are weakly bonded partners simply because they more easily recognize one another's cues. Pairs of social mite larvae that are familiar with one another react more quickly than unfamiliar pairs to the larvae of a predatory mite (Strodl & Schausberger, 2012).

Pathway 7: Developing social and physical competence

Social ties during development may benefit individuals immediately, e.g. by defending them from harassment, and/or in the future by either persisting in themselves or preparing individuals for adult-typical behavior (Fairbanks, 2003). The social environment during development can become ingrained in several aspects of physiology if perceived as a signal for the environment to come in adulthood (Bateson, Gluckman, & Hanson, 2014; Sachser, Kaiser, & Hennessy, 2013). According to evolutionary theory, signals that accurately portray the adult environment are beneficial because they may provide better physio- and psychological preparation for future environments, causing a predictive adaptive response (PAR, Bateson et al., 2014; Gluckman, Hanson, Spencer, & Bateson, 2005). Evidence of PARs to the physical environment is limited (e.g. Berghänel *et al.*, 2017), and may be more likely to occur in wild animals with short vs. long lifespans (Douhard et al., 2014). PARs to the social environment, however, have not been well studied in either short or long-lived wild animals. Nevertheless, laboratory studies suggest that social experience during development can lead to behavioral profiles that are more likely to be successful in their adult environment. For example, guinea pig males raised in colonies with several adult males during adolescence demonstrate behavior as adults that is likely better adapted to intense competition for mates than males raised with a single male: they are less aggressive and follow a queuing strategy, rather than a contest strategy, to achieve reproductive dominance (Kaiser, Harderthauer, Sachser, & Hennessy, 2007). Similarly, in cichlids, individuals raised with older conspecifics are better able to navigate an intense adult competitive environments than those raised without (Taborsky & Oliviera, 2012). The ability to assess social stimuli and respond optimally (i.e. with predefined optimal behavior) is termed "social competence" (Taborsky & Oliveira, 2012) and the motor skills required for those responses add its physical component.

a. Benefit of learning

Maintaining particular individuals as regular social partners can be key to developing competence in various physical or social tasks, like foraging or defending territory. In captive ravens, the trained behavior required to open a food box spread more readily between individuals that affiliated more often, and more readily between affiliative than antagonistic partners (Kulahci et al., 2016). Cichlids raised with (vs. without) older conspecifics seem to learn socially appropriate behavior by experiencing the varied social roles and competitive abilities of other individuals in their unit: those raised with older conspecifics required fewer trials to respond appropriately (i.e. submissively) when experimentally introduced to a territory-holding individual (Arnold & Taborsky, 2010). They also required fewer trials to develop proper aggressive responses to intruders when they were territory-holders, themselves.

Studies of individual variation in social network centrality may also demonstrate the importance of experiential diversity in social competence. Juvenile male long-tailed manakins that were more central (information centrality) within networks based on non-aggressive contact were more likely as adults to rise to alpha status within their leks. Interestingly, the centrality of *adult* males did not predict rise to alpha status, suggesting that network centrality during development was key. McDonald (2007) argued that high juvenile connectivity represents investment in several leks and the development of proper dominant and submissive behavior that built individual social capital.

Experiential diversity possibly primes individual social competence in adulthood, too. Adult male cowbirds whose aviary members were regularly rotated, rather than held constant, sang more to court females than to intimidate males when competing with males of all treatments within a mating tournament condition (White, Gersick, Freed-Brown, & Snyder-Mackler, 2010). This behavior perhaps does not reflect competence, as the authors did not predefine appropriate behavior in the competitive mating condition. Nevertheless, males with a diversity of social experience were more successful in the mating tournament by copulating at higher rates than males held in aviaries with constant membership (White et al., 2010).

b. Benefit of social play

Connections that occur in the context of social play may have a particularly important role in the development of competence. Play predominantly occurs during development and among peers, and is hypothesized to develop competence by its ability to provide “practice for the unexpected” and “self-assessment” (Spinka, Newberry, & Bekoff, 2001). Social play consists of friendly interactions that nevertheless involve acute social and physical challenges that are easily overcome and typically low risk. In this way, play allows individuals to gain cognitive and physical experience of unexpected situations and of their own abilities and limitations. In support of the self-assessment hypothesis, both male and female juveniles of several species, including sable antelope (Thompson, 1996) and ground squirrels, prefer to play with partners that are similar to them in size and age. In some species, however, play appears to be more asymmetric: domestic dogs, for example, prefer partners that they can dominate and demonstrate more offensive than self-handicapping behavior (Ward, Bauer, & Smuts, 2008). This inequality between social partners may serve as practice for maintaining social status later in life. For example, juvenile male marmots that win more play fights also rise to higher social ranks later in adulthood (Blumstein, Chung, & Smith, 2013). Nevertheless, play is not universal preparation for later fighting. Among male meerkats, rates of winning in play during development do not correspond to fighting success in adulthood (Sharpe, 2005b).

Social play during immaturity appears critical in developing some of the neuroanatomical and hormonal pathways necessary for competence. In rats, juveniles that are deprived of play partners (but not other social partners) do not develop normal neural circuitry in the medial prefrontal cortices of the brain, which is associated with motor-skills (Bell, Pellis, & Kolb, 2010). As these areas are functionally linked in the production of social behavior, their proper development is key to social competence (Bell et al., 2010). In another experiment, male rats isolated during a period of development when play is most abundant were delayed in demonstrating appropriate submissive behavior to a dominant, resident male (van den Berg et al., 1999), much like socially incompetent cichlids that were raised without older conspecifics (Arnold & Taborsky, 2010). These males also had higher baseline GCs and adrenaline levels than males that did play during development (van den Berg et al., 1999). In marmosets, too, individuals that engaged in more social play had lower baseline GCs and lower GC reactivity (Mustoe, Taylor, Birnie, Huffman, & French, 2014). The negative effect of social play on GC concentrations was stronger than the positive effect of prenatal exposure on GCs, suggesting that social play is one way to compensate for potentially deleterious GC exposure in the womb.

The competence developed by social play may also be linked to fitness outcomes. In Belding ground squirrels, males and females that played more showed faster development of motor skills (Nunes, Muecke, Sanchez, Hoffmeier, & Lancaster, 2004) and in adulthood females that played more defended their territory more intensely and were more likely to successfully wean their first litter (Nunes, 2014). This analysis is perhaps incomplete in demonstrating the effect of play on fitness because individual body size possibly influenced both play rates and adult aggression independently (Nunes, 2014). In brown bears, litters with higher average play rates had a larger proportion of cubs survive the winter season (Fagen & Fagen, 2004). The effect of play on survival held even after controlling for the abundance of salmon, the bears' primary food. Fagen and Fagen (2004) argue that this result demonstrates how play prepared the cubs' physiology to overcome the stressors faced during the long and harsh winter season. Because play behavior is energetically costly and access to food can increase play rates (e.g. Sharpe, Clutton-Brock, Brotherton, Cameron, & Cherry, 2002), this study is important in demonstrating that experience in play rather than access to food influences fitness (Fagen & Fagen, 2004).

The Physiological and Developmental Bases of Connections

In mammals, affiliation and cooperation are linked evolutionarily and developmentally by their common roots in the biological mechanisms of parent-offspring attachment, or the connection between an early-life dependent and its caregiver. Also in mammals, an attachment is typically strongest between an offspring and its mother (Curley & Keverne, 2005) and in birds between a hatchling and its caregiver (Hinde, 1961). Attachment theory, as developed by Bowlby and Ainsworth from the 1950's to 1980's, emphasizes the importance of the mother-infant relationship in the normal social and emotional development of mammalian young (Bretherton, 1992). At its heart, the theory maintains that a dependent young mammal requires a secure and stable attachment to its mother or caregiver that provides a base from which the individual explores, develops autonomy, and acquires decision-making skills, each of which bear on the development of later life social connections. Although not all social ties are best characterized as attachments *per se* (Bergman, 2010; Suomi, 2005), they share many behavioral commonalities. For example, while rat pups will nurse from any lactating dam, they develop recognition of their mother's odor and form a strong preference for her (Moriceau, Roth, & Sullivan, 2010). An attachment is an emotional linkage that motivates one individual to maintain proximity or to interact with another, and causes it to express distress upon forced separation, pleasure upon reunion, and grief upon permanent loss (Ainsworth & Parkes, 1991).

i. Common neurochemical pathways of attachment and connections

Two predominant neurochemical systems appear to mediate both caregiver-dependent attachment and later-life social connections: the cerebral endorphin and oxytocin/vasopressin systems. The cerebral administration of beta-endorphin opioids reduces the distress behavior of offspring when separated from mothers in chicks, puppies, and guinea pigs (in Keverne, Martensz, & Tuite, 1989). Keverne *et al.* therefore hypothesized that social ties, too, may be mediated by the reward of beta-endorphins. The authors pair-housed talapoin monkeys that were more affiliative than aggressive with one another and manipulated a barrier to unite and separate them for constant amounts of time. Pairs received one of three treatments: morphine injections, opioid blockers, or nothing (controls). Among controls, pairs that groomed more reciprocally upon reunion had higher central (CSF) concentrations of beta-endorphins. Pairs that were administered morphine were more indifferent upon reunion, grooming and soliciting grooming less than other treatments. Finally, pairs administered an opioid blocker sought more contact, grooming and soliciting grooming more than other treatments. These results demonstrated that beta-endorphins are indeed a driving reward in affiliative behavior.

The oxytocin (OT) pathway of social reward likely evolved in some of the earliest mammals as a reward pathway to facilitate bonding and increased coordination (Curley & Keverne, 2005). OT has simultaneous central and peripheral functions: peripherally, OT is released to stimulate the contraction of the uterus for parturition, the tactile stimulation of which releases a flood of OT within the brain to serve as a reward for the individual recognition of one's offspring, usually via olfactory stimuli (Curley & Keverne, 2005). OT acts in the brain as a general anxiolytic (Campbell, 2010), therefore its release is calming and pleasurable. The central release of OT is adaptive in initiating and reinforcing the bond between mother and offspring and also the responsiveness of mothers to infant signals (Churchland & Winkielman, 2012). In later life connections, OT levels increase in response to contact with a recognized and valuable individual, although likely to much a lesser extent, thereby reinforcing the social connection with a pleasurable reward much like that between mothers and offspring (Curley & Keverne, 2005). Crockford *et al*. (2013) found that urinary concentrations of OT were higher in chimpanzees immediately after they groomed with individuals with whom they were more strongly bonded. One should note with caution that the accuracy and validity of using peripheral concentrations of OT to assess central concentrations is not altogether certain, because OT does not pass the blood/brain barrier (Churchland & Winkielman, 2012). Nevertheless, peripheral and central levels often appear related in wild animals (Crockford, Deschner, Ziegler, & Wittig, 2014), and an effect of peripherally administered OT is visible for some social tasks. In humans, OT administered by nasal spray increased coordination in a cooperative drawing task (Arueti et al., 2013), possibly paralleling the coordination necessary in mother-offspring interactions.

ii. Influence of attachment for later life connections

The quality of early-life attachments determines the development of many aspects of the above reward systems and the HPA axis and so influences the formation of later life social connections. Studies of rodents and non-human primates have demonstrated the importance of secure attachments early in life, mostly by observing the consequences of insecure attachments. In rats, licking and grooming (LG) alters methylation patterns in hippocampal cells to increase the expression of GC receptors (GRs), making the negative feedback of the stress response more efficient and decreasing neophobic behavior (Champagne et al., 2006). In reverse, human victims of childhood abuse decrease expression of GRs (Champagne, 2010), resulting in higher baseline GC levels and possibly the degeneration of hippocampal neurons that leads to depression (Sapolsky, 2000). Both neophobia and depressive symptoms impede the formation and maintenance of later life connections.

Behavioral evidence also demonstrates that secure mother-offspring attachment enhances the development of basic emotional competence, or emotional regulation, which may later underlie the social and physiological competence necessary to maintain valuable connections. Compared to orphans, bonobo infants that were raised by mothers regulated their emotional responses to social distress more effectively, i.e. by screaming for shorter bouts, not continuing to scream after a 30 second pause, and taking less time overall to recover from distress (Clay & de Waal, 2013). As juveniles, securely attached individuals were more sociable (CSI), played more frequently and in longer bouts, and were more likely to demonstrate the social skill of consolation towards distressed peers (Clay & de Waal, 2013). Similarly, immature brown capuchins (during infancy, weaning, and juvenescence) that were securely attached to their mothers regulated their emotions more efficiently in response to social conflict and were more likely to initiate reconciliation with their former opponents (Weaver & de Waal, 2003), thereby potentially restoring valuable connections (Cords & Thurnheer, 1993). Even in humans, adolescents that reported a sense of secure attachment with their mothers in childhood demonstrated a stronger propensity to regulate their emotions by seeking support from peers than adolescents that reported insecure attachments (Allen, Porter, McFarland, McElhaney, & Marsh, 2007). Adolescents that had secure attachments also demonstrated higher quality social connections, as measured by self-rated degrees of trust, communication, and alienation among peers (Allen et al., 2007).

The influence of early-life attachments on later-life strategies of connection underscores the potential legacy that one generation of social ties leaves for the next. The epigenetic inheritance of behavioral profiles is well demonstrated in the context of maternal care: low maternal affect begets low maternal affect in house mice, via changes in estrogen receptor mediated expression of OT receptors (Champagne, 2008). Here, one can see that strategies of social connection may also be heritable epigenetically, particularly if maternal sociality corresponds strongly with maternal attachment behavior. This possibility adds another perspective to studies that demonstrate that maternal connectedness influences offspring survival (e.g. Cameron et al., 2009; Silk et al., 2003;

Silk et al., 2009), namely, that maternal strategies of connection influence those of offspring, and offspring strategies themselves influence offspring fitness.

Summary and Future Directions

Across social species, the evidence for the benefits of social connections comes in two types of patterns: 1) links between variation in social ties and variation in fitness outcomes and 2) links between social ties and short-term advantages conferred along pathways that likely influence fitness. This review outlines and evaluates seven functional pathways: cooperative hunting, communal care of offspring, cooperative territorial defense, monopolizing mates and resources, establishing and maintaining social status, developing of social and physical competence, and mediating exposure to risk and HPA axis activity. This list is not exhaustive and pathways are certainly not mutually exclusive.

The purpose of this review is to synthesize and frame evidence of the adaptive value of social connections for two reasons: 1) to encourage testing of alternative hypotheses about which social strategies are most important for individuals of a given species, sex, and age and 2) to facilitate the formation of these hypotheses with a clear list of functional pathways. To further aid the understanding of mechanisms by which social ties influence fitness, this review also outlines how life history and environmental variables influence the patterns of interaction that characterize ties. Also, this review highlights that the external environment can shape intrinsic states, particularly during the important life stage of immaturity.

The optimal strategies of connectedness appear often to depend on nuanced variables such as individual condition (e.g. eider ducks, Öst et al., 2003) or competitive ability (e.g. rhesus macaque females Brent et al., 2011; female mice, Weidt et al., 2008; male dolphins Whitehead & Connor, 2005; male baboons Nöe & Sluijter, 1995). Broadly, it appears that affiliative behavior and various degrees of diversity in connections can be beneficial to both adult and immature males and females in a wide array of social species. There still remains much to be understood about what intrinsic life history and external challenges in the social and physical environment drive and select for patterns of social ties. Similarly, studies must consider how the challenges, or costs, of social living generally and of particular population and group structures counterbalance the benefits of social ties and shape patterns of social interaction.

Chapter 2: Stronger Social Bonds Do Not Always Predict Greater Longevity in A Gregarious Primate

Accepted for publication in *Ecology and Evolution*
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Figure 2.1. Two adult female blue monkeys grooming. Photo: M. Cords

Abstract

In group-living species, individuals often have preferred affiliative social partners, with whom ties or bonds can confer advantages that correspond with greater fitness. For example, in adult female baboons and juvenile horses, individuals with stronger or more social ties experience greater survival. We used detailed behavioral and life history records to explore the relationship between tie quality and survival in a gregarious monkey (Cercopithecus mitis stuhlmanni), while controlling for dominance rank, group size, and life history strategy. We used Cox proportional hazards regressions to model the cumulative (multi-year) and current (single year) relationships of social ties and the hazard of mortality in 83 wild adult females of known age, observed 2-8 years each (437 subject-years) in 8 social groups. The strength of bonds with close partners was associated with increased mortality risk under certain conditions: females that had strong bonds with close partners that were inconsistent over multiple years had a higher risk of mortality than females adopting any other social strategy. Within a given year, females had a higher risk of death if they were strongly bonded with partners that changed from the previous year vs. with partners that remained consistent. Dominance rank, number of adult female group-mates, and age at first reproduction did not predict the risk of death. This study demonstrates that costs and benefits of strong social bonds can be context-dependent, relating to the consistency of social partners over time.

Key-words: fitness, social relationships, social ties, social partner consistency, survival.

Introduction

Among social animals, individuals commonly have differentiated relationships, or ties, with others. Particularly intriguing are close social bonds, which are characterized by especially high rates of affiliative behavior, including amicable physical contact, and/or particularly close spatial association (Cords & Thompson, 2017). To understand social differentiation from an evolutionary perspective, it is essential to examine its fitness consequences. In humans, for instance, decades of research have shown that the quality and patterning of social ties predict important fitness-related variables like disease risk (Uchino, 2006) and mortality (Holt-Lunstad, Smith, & Layton, 2010). Human studies also suggest that the short-term effects of social ties accumulate over the long-term to influence health outcomes (Uchino, 2006).

More recently, research on non-human animals has also linked social relations to direct and indirect measures of fitness, such as reproductive rate (Farine & Sheldon, 2015; Formica et al., 2011; Formica et al., 2012; Gilby et al., 2013; McDonald, 2007; Schülke et al., 2010; Vander Wal et al., 2014), offspring survival (Cameron et al., 2009; Kalbitzer et al., 2017; Silk et al., 2003; Silk et al., 2009; Vander Wal et al., 2014), and longevity (Archie et al., 2014; Brent et al., 2017; Fagen & Fagen, 2004; Foster et al., 2012; Lehmann et al., 2016; McFarland et al., 2017; Nuñez et al., 2015; Silk et al., 2010b; Stanton & Mann, 2012; Yee et al., 2008). Among these measures, longevity, or survival, is a particularly important fitness measure in long-lived mammals, like primates, that have relatively low reproductive rates (Jones, 2011; Morris et al., 2011). Adult female baboons (Papio hamadryas ursinus) in Botswana lived longer if they maintained stronger, more consistent bonds with each other (Silk et al., 2010b). Similarly, female baboons in Kenya (Papio hamadryas cynocephalus) lived longer if they were more connected to either adult male or female group-mates (Archie et al., 2014).

Affiliative relationships can influence fitness in several ways (Cords & Thompson, 2017). The general benefits of group living may be amplified by living with especially tolerant and familiar partners. Such partners may work together more efficiently in cooperative hunting (Ruch et al., 2014), communal care of offspring (Weidt et al., 2014), or attending to predators (Micheletta et al., 2012). In several species, affiliative partners, often kin, compete more effectively as allies, and alliances help to maintain dominance rank (Chapais, 1995; Mitani, Merriwether, & Zhang, 2000; Schülke et al., 2010) or increase access to mates (Connor et al., 2000; Feh, 1999). Affiliative partners may also provide psychosocial support that attenuates prolonged stress responses to events like infanticide or the loss of close social partners (Engh, Beehner, Bergman, Whitten, Hoffmeier, et al., 2006; Wittig et al., 2008), although links between chronically elevated glucocorticoids and fitness may not be as direct or as prevalent in wild animals as in humans (Beehner & Bergman, 2017). More general integration in social groups, e.g. having more affiliative partners, may also provide such a buffering effect and protect individuals from environmental risks like cold temperatures (Lehmann et al., 2016; McFarland et al., 2015; McFarland & Majolo, 2013), enhance access to relevant social and environmental information (Archie, Moss, & Alberts, 2006; Templeton, Reed, Campbell, & Beecher, 2012), and help individuals survive traumatic population-wide events (Nuñez et al., 2015).

Although most studies emphasize the effects of affiliative and cooperative relations on fitness outcomes, agonistic interactions may also be important. In Barbary macaques, individuals that either received or directed aggression to more partners, and whose aggressive partners were not aggressive towards one another, were more likely to survive a hard winter (Lehmann et al., 2016). Similarly, yellow-bellied marmots (Marmota flaviventris) lived longer if they initiated aggression towards more recipients, although the benefits of aggression here likely derived from its association with social dominance (Lea, Blumstein, Wey, & Martin, 2010).

Indeed, dominance status or rank, derived from agonistic interactions, has a pervasive influence on fitness-related variables in female mammals, as rank frequently corresponds with priority of access to food (T. Clutton-Brock & E. Huchard, 2013). Dominance rank can predict survival (Pusey et al., 1997; Silk et al., 2010b), possibly because high-ranking individuals are able to access safer microhabitats and avoid predation (van Schaik & Van Noordwijk, 1986), better access nutrients (Foerster, Cords, & Monfort, 2011), and avoid harassment during development (Silk, Samuels, & Rodman, 1981). In our study species, the blue monkey, rank has no effect on conception probability (Roberts & Cords, 2013), but higher-ranking females had lower baseline glucocorticoid levels during an energetically challenging period when lactation overlapped with low food availability (Foerster et al., 2011).

Variables other than the quality of social ties and rank can also influence survival in group-living animals. Large group size may enhance survival by providing benefits similar to those of maintaining particularly affiliative relationships, such as more effective vigilance for predators (Elgar, 1989; Lehtonen & Jaatinen, 2016; Roberts, 1996; van Schaik & Van Noordwijk, 1986), defense of young offspring (Grinnell & McComb, 1996; Wolff & Peterson, 1998), or defense of feeding territories (Radford & du Plessis, 2004; Roth & Cords, 2016). Nevertheless, living in larger groups may also exact costs by increasing within-group competition for food (Roberts & Cords, 2013; VanderWaal, Mosser, & Packer, 2009), or by increasing the risk of male takeovers and subsequent infanticide (Steenbeek & van Schaik, 2001). In some cases, the way the cost-benefit balance changes in larger social groups means that intermediate group sizes are optimal for individual fitness (Markham, Gesquiere, Alberts, & Altmann, 2015; Roberts & Cords, 2013). Finally, at a basic life history level, individuals may trade off energetic investment in somatic growth and maintenance (survival) for reproduction (Descamps, Boutin, Berteaux, & Gaillard, 2006; Hamel et al., 2010).

In this study, we used survival analyses to examine the link between affiliative social ties and lifespan of wild adult female blue monkeys, while also controlling for the influence of other socio-demographic factors and a potential life history trade-off. We examined both the cumulative (multi-year) and current (annual) effect of social experience on survival, using fixed-effect and time-dependent Cox models to test for each, respectively. We focused mainly on affiliative relations because agonistic interactions occur at low rates in this species (Klass & Cords, 2015).

Although blue monkeys differ from other cercopithecines in multiple ways, we expected to confirm patterns documented in certain macaques (Lehmann et al., 2016) and baboons (Archie et al., 2014; Silk et al., 2010b), namely, that more or higher-quality social ties, either cumulatively over multiple years or in one's current environment, correspond with higher survival. Unlike these other species, blue monkeys are highly arboreal, live in a less seasonal (rainforest) environment, seem to experience relatively strong feeding competition between groups but relatively weak competition within groups (Cords, 2007; Klass & Cords, 2015), and live in groups with a single male. Despite these differences, we hypothesized that strong and stable female-female affiliative ties would enhance longevity in female blue monkeys because, like other cercopithecines, they have a female-philopatric and matrilineally structured society in which grooming is the most obvious form of affiliation. We combine long-term life history data with detailed behavioral observations from an 8-year period on a wild population. We predicted specifically that females that maintained consistent and strong bonds with their closest partners would have a survival advantage relative to females with weak and inconsistent bonds, and that the benefits of strong and consistent bonds would be more pronounced over the long-term.

Materials and methods

(a) Study Site and Population

The study population inhabits the Isecheno area of Kakamega Forest in western Kenya (0˚19´ N, 34˚52´ E; elevation 1580 m, mean annual rainfall 1997–2011 1942 mm; Mitchell 2009). Natural predators occur here, including the African crowned eagle (Stephanoaeutus coronatus) and Gaboon viper (Bitis gabonica, Gaynor & Cords 2012). The ca. 2 km2 study area supports a high density of blue monkeys, with approximately 192 individuals/km2 in old secondary forest and fewer in mixed indigenous plantations (Fashing et al., 2012). Between-group territorial disputes are common, occurring about every other day (Cords, 2007). Blue monkey groups usually comprise a single adult male, multiple adult philopatric females and their young. This population has been monitored since 1979 and all study group members were identifiable based on natural physical variation (Cords, 2012).

During the period of data collection for this study (2006-2014), we observed 83 adult (parous) female subjects in eight study groups, four of which resulted from two fission events that occurred in 2008 and 2009 (Fig. 1 in Klass & Cords 2015). In addition, in one group, three juveniles of unknown provenance joined the group in 2010 and became adult subjects in our analysis.

Long-term monitoring of demographic events (Cords 2012) allowed us to specify birth and death dates; females alive at the end of the study (N=63) were right-censored. For 12 of the oldest adult females and 3 who had immigrated as juveniles, we estimated birthdates based on changes in juvenile body size (average precision ± 0.75 years, range: 0.08-2). We inferred most deaths based on permanent disappearances as observers rarely found carcasses of missing animals. Female dispersal from the natal group is extremely rare in this species (two possible events in 111 group-years of monitoring, though these may have been small group fusions, author MC pers. obs.), and several females that disappeared either left behind young offspring (<2 years) or were in poor physical condition prior to disappearance. Cause of death was seldom known, but most deaths probably resulted from intrinsic factors or predation.

(b) Behavioral data collection

Detailed records of adult female social behavior, based on focal animal sampling, were available from October 2006. A team of observers trained by and including MC conducted 30 min samples on subjects approximately once every 3 days throughout the year (mean ± SD observation hours per subject-year = 67 ± 20, N = 437). On a given day, observers chose focal subjects so as to even out the sampling rate across individuals and to balance observation time across the hours of the day. Subjects were observed for 2-8 years each (mean = 5.26). We considered a subject to be present in a given observation year if she was a subject for >10% of the year (69 of 467 subject-years < full year, mean days observed if < full year = 310).

During focal samples, observers made instantaneous records at 1 min intervals of subject activity (including grooming, resting, feeding, and moving) and the identity of all "neighbors" within 1 m whenever the subject was grooming or resting, or within 7 m if she was feeding. Because of the dense vegetation, subjects sometimes went out of sight. If observers relocated the subject within 15 min, they continued the sample until they achieved 30 min of observation; otherwise, the sample was terminated. Samples lasting < 20 min were discarded.

Data on agonism, used to calculate dominance rank, came from focal and ad libitum observations (Klass & Cords 2015). Observers recorded winners and losers in all decided agonistic interactions (in which one and only one opponent showed submission).

Data analysis

i. Social predictors of survival

In many primates, mothers of young infants attract extra social attention. To measure social interaction that was not driven by short-term attraction to infants (Henzi & Barrett, 2002), we removed observation records when a subject or her partner had an infant <100 days old. Infant blue monkeys begin to spend a substantial time away from their mothers at this age (Förster & Cords, 2005).

To see how the quality of social bonds affected survival we first calculated bond strength for a given subject and all her adult female social partners in a given year. For this we used an annual dyadic sociality index (DSI, Silk, Cheney & Seyfarth 2013) based on grooming and time spent resting in proximity (1 m), each expressed as a proportion of total dyad observation time (which was the sum of time observed for each dyad member as a subject). Grooming and resting within 1 m are two measures of affiliation known to be strongly biased toward maternal kin (Cords & Nikitopoulos, 2015). Matrices of dyadic proportions of time spent grooming or resting in proximity were correlated in 28 of 43 group-years, so their combination in a composite index seemed justified (electronic supplementary material, Table S2.1). We calculated the index as follows:

$$\text{DSI} = \frac{1}{2}\left(\frac{G_{ij}}{G_{med}}\right) + \frac{1}{4}\left(\frac{R_{ij}}{R_{med}} + \frac{R_{ji}}{R_{med}}\right)$$

where G_{ij} represents the proportion of time that the dyad members spent grooming, R_{ij} and R_{ji} represent the proportion of time each dyad member i and j, as focal subjects, spent resting within 1 m of the other (without grooming or feeding), and G_{med} and R_{med} are the median values of all within-group dyads across social groups in the same year. We divided the resting association data for a given dyad into two equal components based on focal subject identity to account for the fact that resting-proximity was not symmetrical within the dyad (i.e., a resting focal subject might have a neighbor who was feeding, when observers scored proximity partners within a larger 7 m distance). A DSI of 1 would represent a typical dyad, while values >1 represent a dyad with stronger than median social ties.

To characterize each subject's bondedness over multiple years, we first averaged DSIs with her top three partners in a given year, and then averaged over her annual values. We chose to average the DSIs of a female's top 3 partners for two reasons. First, across several species of social mammals, individuals tend to associate with decreasing intensity across social partners in tiers that scale by a multiple 3 – 3.15 (e.g. tier1 = individual, tier2 = grooming clique, Zhou et al. 2005; Hill, Bentley & Dunbar 2008). Second, averaging over top 3 partners allowed us to compare results with previous landmark studies on closely-related primates (Silk et al., 2003; Silk et al., 2009). Nevertheless, to assess whether ties with top 3 partners specifically were meaningful, we also explored the influence of DSIs averaged over the top 6 closest partners.

To measure partner consistency over multiple years, we first identified those individuals among the top three partners that were "consistent", and then asked what proportion of a female's top 3 partner "slots", across the years in which she was observed, were occupied by such consistent partners. We considered a top partner in a given year to be consistent if her DSI continued to place her in the top three positions at least once in the next two years (Silk et al. 2009). In a subject's second to last year of observation, we counted a top partner as consistent if she was among the top 3 in the next year only. We then determined what fraction of a female's top three "slots", summed across years, were occupied by a consistent partner. The number of "slots" was 3Y-3, where Y is the total number of observation-years; we subtracted 3 because we could not assess consistency status of partners in the last year. This fraction varied from 0 (low consistency) to 1 (high consistency). Partner consistency was not related to number of years observed. To correspond with our alternative measure of bond strength with top 6 partners, we also calculated consistency in top 6 partners over time. During a few years, some subjects lived in groups with fewer than 6 or even 3 adult female groupmates. These comprised 7% and 1% of 437 subject-years, respectively.

To measure current partner consistency (i.e. within a given year), we counted the proportion of a female's top 3 or 6 partners that were present among her top partners at least once in the previous 2 years. For a female's second year of observation, we counted the proportion of top partners present from the previous year of observation alone. As the consistency of partners in a female's first year of observation could not be measured, annual partner consistencies were calculated for 354 of 437 subject-years. We calculated annual partner consistency retrospectively because we considered current (not future) partner stability relative to previous years to be most relevant to survival in the same year. Although prospective and retrospective measures of multi-year partner consistency do not differ greatly, measuring multi-year consistency prospectively assesses whether a female invested in partners that then remained consistent, and perhaps whether current partner choices would pay off over time.

Similar to a previous study (Silk et al. 2010), we wished to condense bond strength and partner consistency into a single measure of relationship quality. Multi-year bond strength and partner consistency were correlated (N = 83, r = 0.23, p = 0.03), however they were not correlated so closely as to load on a single principal component (Table S2.2). The relative independence of these variables led us to categorize females in one of four classes of above (+) and below (-) population mean bond strength and partner consistency, where class 1 = - strength & - consistency (N = 29), 2 = - strength & + consistency (N = 20), 3 = + strength & - consistency (N = 11), and 4 = + strength & + consistency (N = 23). We also categorized females using measures of bond strength and partner consistency among her top 6 partners (classes 1 -/- N = 39, 2 -/+ N = 11 +/- N = 16, 3 +/+ N = 17). To better understand if females were forced into particular multi-year classes because of the deaths of social partners, we calculated how often deaths were responsible for partner changes, and whether the proportion of death-induced changes differed among females by class.

To characterize current relationship quality, we again created an index in which females were placed in 4 classes of above or below average annual bond strength and above or below average annual partner consistency. These classes were populated relative to one another in a similar way as multi-year strength-consistency classes (top 3 class 1 -/- N = 112 subject-years, 2 -/+ N = 94, 3 +/- N = 60, 4 +/+ N = 88; top 6 class 1 N = 150, 2 N = 65, 3 N = 84, 4 N = 55).

We calculated dominance ranks from records of decided agonistic interactions among adult females using the I&SI method as implemented in DomiCalc (Schmid & de Vries, 2013). We expressed ranks as the proportion of adult female group-mates a female out-ranked in each year. For multi-year analyses, we averaged subjects' annual ranks over all years in which she was observed.

ii. Demographic and environmental predictors of survival

Long-term records allowed us to specify females' age at first birth and the number of adult female group-mates (Cords 2012). Average number of adult female groupmates closely approximated a female's average number of adult female grooming partners (N =

83, $r = 0.8$, $p < 0.001$), as annual grooming networks among female groupmates were saturated or nearly so. We therefore included only number of adult female groupmates, and not number of grooming partners (which would provide no additional information), as a predictor of survival.

Statistical Analysis

i. Repeatability of social behavior

To assess the validity of averaging bond strength, dominance rank, and adult female groupmates over time to derive single, multi-year values for each subject, we tested the repeatability of inter-individual differences in each predictor by calculating the intra-class correlation coefficient from a linear mixed effects model (function rpt in R package "rptR", Nakagawa & Schielzeth 2010). The model calculates the proportion of total variance among all annual measures of a given variable that is attributed to variation between individuals, which are modeled as random effects, while controlling for variance explained by other social or environmental variables, modeled as fixed effects.

ii. Survival analysis

We used both fixed-time and time-dependent Cox Proportional Hazards regressions (function coxph in R package "survival", Therneau & Grambsch 2000; Therneau 2015) to assess the cumulative (fixed-time) and current (time-dependent) influence of social tie quality (bond strength and consistency class with top partners), dominance relationships (rank), group size (number of adult female groupmates), and life history strategy (age at first birth) on a subject's instantaneous risk of death. Survival intervals were left truncated at a subject's age when focal animal sampling began in

October 2006 (if she was an adult then) or at the subject's age at first birth (if she became an adult later). In all models, we used standardized covariates (Schielzeth, 2010).

We considered a predictor to influence the hazard if the 95% confidence interval of its parameter estimate did not include zero (Nakagawa & Cuthill, 2007). Because bond strength-partner consistency classifications were based on dyadic data, we additionally examined their influence on the hazard according to permutation tests, comparing observed effects of strength-consistency class to a null model based on 1000 random node permutations of annual DSI matrices (Croft, Madden, Franks, & James, 2011; Farine, 2017). We chose node permutations to test the null hypothesis based on the possibility that females could maintain any position within a social group's annual network. Because of a lack of consensus in the literature as to whether permutation tests are appropriate when relational social measures are independent variables (Anderson & Legendre, 1999; Dekker et al., 2007; Lehmann et al., 2016; VanderWaal, Atwill, Hooper, Buckle, & McCowan, 2013), we compared 95% CIs and permutation to assess their agreement, and if significance based on 95% CIs disagreed with permutation tests, we gave prominence to 95% CI results.

For fixed-time covariate Cox models, we averaged annual measures across all years in which the subject was observed, effectively testing the cumulative effect of multiple years of social conditions on survival. Survival models have sufficient power when each variable corresponds with 5—10 events (Vittinghoff & McCulloch, 2007). Given our sample size of 20 deaths in 83 females, we created two models with 3 predictors each. Both tested the influence of social ties (strength-consistency class) on survival and controlled for the effects of a potential life history trade-off (age at first reproduction). One model included adult female dominance rank and the other included number of adult female groupmates as measures of social competition. We report model-averaged parameters of strength-consistency class and age at first birth, as their effects did not differ qualitatively between the model including dominance rank and the model including number of adult female groupmates ("modavg" function in R package "AICcModavg", Mazerolle, 2016). To assess the possibility that female survival was highest in groups of intermediate size, we also explored two additional models testing the significance of a quadratic relationship between survival and number of adult female groupmates, alongside subjects' strength-consistency class for top 3 and top 6 partners and her age at first reproduction. We tested that all models, with either dominance rank or number of female groupmates, met the proportional hazards assumption by assessing the correlation of their Schoenfeld residuals to transformed time (cox.zph function in R package "survival", Therneau & Grambsch 2000; Therneau 2015).

In the time-dependent covariate model, variables per subject-year appeared as separate observations to predict a female's risk of death in the same year. This approach effectively tested the time-dependent relationship between current social conditions and survival. We constructed separate models for measures with top 3 and 6 partners, which included annual values of strength-consistency class, dominance rank, and number of adult female groupmates.

Results

Averaging annual measures of social predictor variables appeared to be a valid approach, as each predictor showed repeatable inter-individual differences (electronic supplementary material, Table S2.3). Nevertheless, as the lower confidence limit of bond strength's repeatability statistic was close to zero, a female's bond strength did appear to vary from year to year. Such intra-individual variation supported our analysis of time-dependent predictors.

Across 83 females, the average female's bond strength with her top three partners was 7.6 ± 2.5, i.e. 7.6 times greater than the median bond-strength between any two adult co-resident females, and 51 ± 18% of the top three partner identities remained consistent (as per definition) during her observation period (electronic supplementary material, Table S2.4). Females lived with an average of 13.6 ± 4.2 adult female groupmates (range 3 – 21).

Measures of bond strength and partner consistency with top 3 partners were each highly correlated with their corresponding measure including top 6 partners (Table S2.4). Each multi-year measure decreased as group size increased, such that females had weaker and less consistent close partners in larger social groups (Table S2.4). Indeed, average number of adult female groupmates varied by strength-consistency class with top 3 partners, such that females that had strong and consistent partners (class 4, + / +) lived on average in smaller groups than females that had weak and inconsistent bond partners (class 1, - / - ; Tukey's HSD, difference classes 4 - 1 = -3.89, 95% range = - 6.82 – - 0.96, p = 0.004 ; Figure 2.2). Number of adult female groupmates did not differ between any other classes of relationship quality.

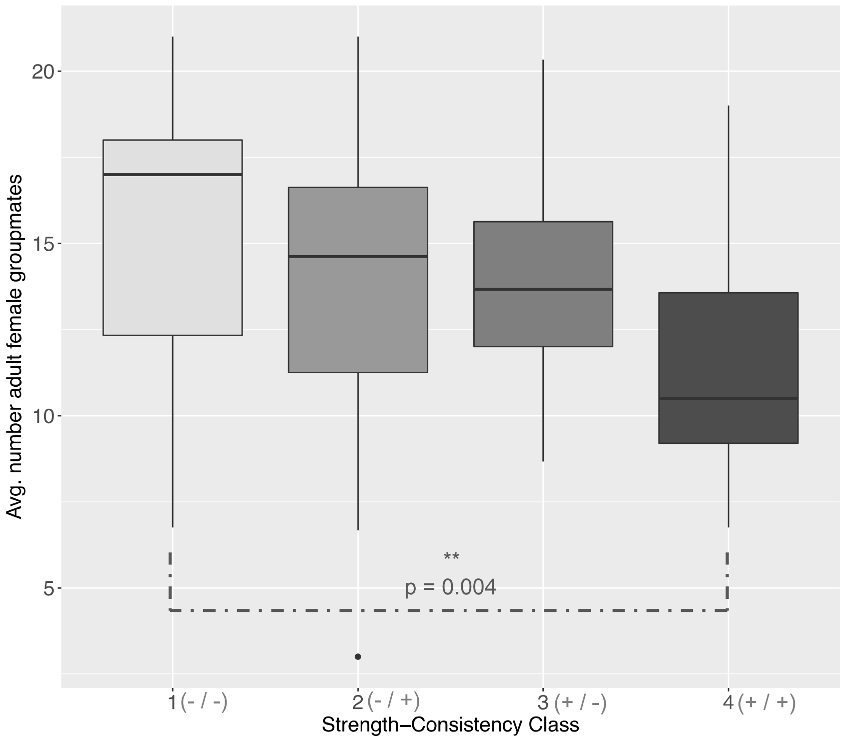

Figure 2.2. Number of adult female groupmates per female (median and IQR, N = 83) by multi-year strength-consistency class of top 3 partners.Group sizes were significantly different for females in Class 1 vs. 4 (see text).

Deaths accounted for 13.8% of the average female's changes in top 3 partners (N = 82 females with changes in top 3) and 19.6% of changes among her top 6 partners (N = 80 females with changes in top 6). Proportion of partner changes resulting from death did not differ among females according to their multi-year, top 3 strength-consistency classes (ANOVA F3,78 = 1.99, p = 0.12). However, females that were weakly bonded to a consistent set of top 6 partners (class 2) experienced a higher proportion of death-related partner changes than females with weak and inconsistent (class 1; N = 80, Tukey's HSD, difference classes 2 - 1 = 0.29, range = 0.10 – 0.48, p = 0.001) and strong and inconsistent top 6 partners (class 3, difference classes 3 - 2 = -0.31, range = -0.52 – -

0.094, p = 0.002). It is likely that females with few partner changes consequently had a higher proportion of changes resulting from deaths.

Influences on risk of death

Risk of death among adult females varied according to multi-year relationship quality with their top 3 partners (Table 2.1, Figure 2.3). Females that had above average strength bonds with less than average consistency in partners (class 3, + / -) had a higher risk of death than females in all other strength-consistency classes, according to both 95% CI's of parameter estimates and permutation tests (Table 2.1, Figure 2.3). The difference in the hazards of classes 1 (- / -), 2 (- / +), and 4 (+ / +) did not reach significance according to 95% CIs (Tables S2.5–6). Yet according to permutation tests, the hazard ratio of females with weak and inconsistent bonds (class 1, - / -) vs. females with strong and consistent bonds (class 4, + / +) was significantly higher than expected by chance. There were no differences in risk between intermediate-risk classes 1 and 2 according to either 95% CIs or permutation tests.

When we considered a females' multi-year relationship quality with top 6 partners, there were no significant contrasts in the hazards among strength-consistency classes according to 95% CIs. According to permutation tests, however, classes 1 (- / -) and 3 (+ / -) had similar hazards that were significantly higher than classes 2 (- / +) and 4 (+ / +, Tables S2.7–9). Permutation tests therefore emphasized a positive influence on survival of consistency among top 6 partners.

The significant effects according to permutation tests are potentially false positives, which may arise as a result of breaking ancillarity (Anderson & Legendre

1999; Dekker, Krackhardt & Snijders 2007). Permuting values of a predictor variable in a multiple regression breaks ancillarity if there is any collinearity among predictor variables, as it removes any relationships between them. Indeed, there were several unavoidable correlations among bond strength, partner consistency, rank, and group size (Table S2.4), although collinearity among them in linear regression Cox models was not problematically high (max VIF all models, excluding model with quadratic term = 1.23). These contrasts in results according to parametric vs. permutation-based null hypotheses may contribute further to discussion in the ecological literature about the suitability of permuting an independent social variable when estimating its partial regression coefficient.

Neither multi-year dominance rank's nor group size's influence on survival reached significance (Table 2.1, fixed-time models). Group size also did not demonstrate a quadratic relationship with survival (Tables S2.10–11). Age at first reproduction did approach significance in the expected direction, such that later ages at maturity would increase longevity (Table 2.1). All models including either dominance rank or number of adult female groupmates as a competition variable did not depart from proportional hazards (all global $p > 0.10$).

Table 2.1. Influence of (standardized) fixed-time predictors on risk of death.

N=83 females, 20 deaths.

Predictor class	Predictor of hazard	Factor level	ß	95% CI	Hazard Ratio	Proportion of permutation coefficients < observed
Social ties	Strength – Consistency Class (reference class: 3, +/-)	1 (- / -)	-2.1 †	**-3.53, -0.62** *	0.13	**0.001[1], 0.02[2]**
		2 (- /+)	-1.5 †	**-2.91, -0.13** *	0.22	**0.01[1,2]**
		4 (+/+)	-3.0 †	**-4.83, -1.2** *	0.05	**0[1,2]**
Competition	Dominance rank	n/a	0.06	-0.52, 0.64	1.06	n/a
	Number adult female groupmates	n/a	-0.23	-0.77, 0.31	0.80	n/a
Life history	Age at first birth	n/a	-0.52 †	-1.12, 0.07	0.59	n/a

† Model averaged coefficient

* 95% CI does not include zero

1From model 1: including dominance rank as competition variable.

2From model 2: including number of adult female groupmates as competition variable.

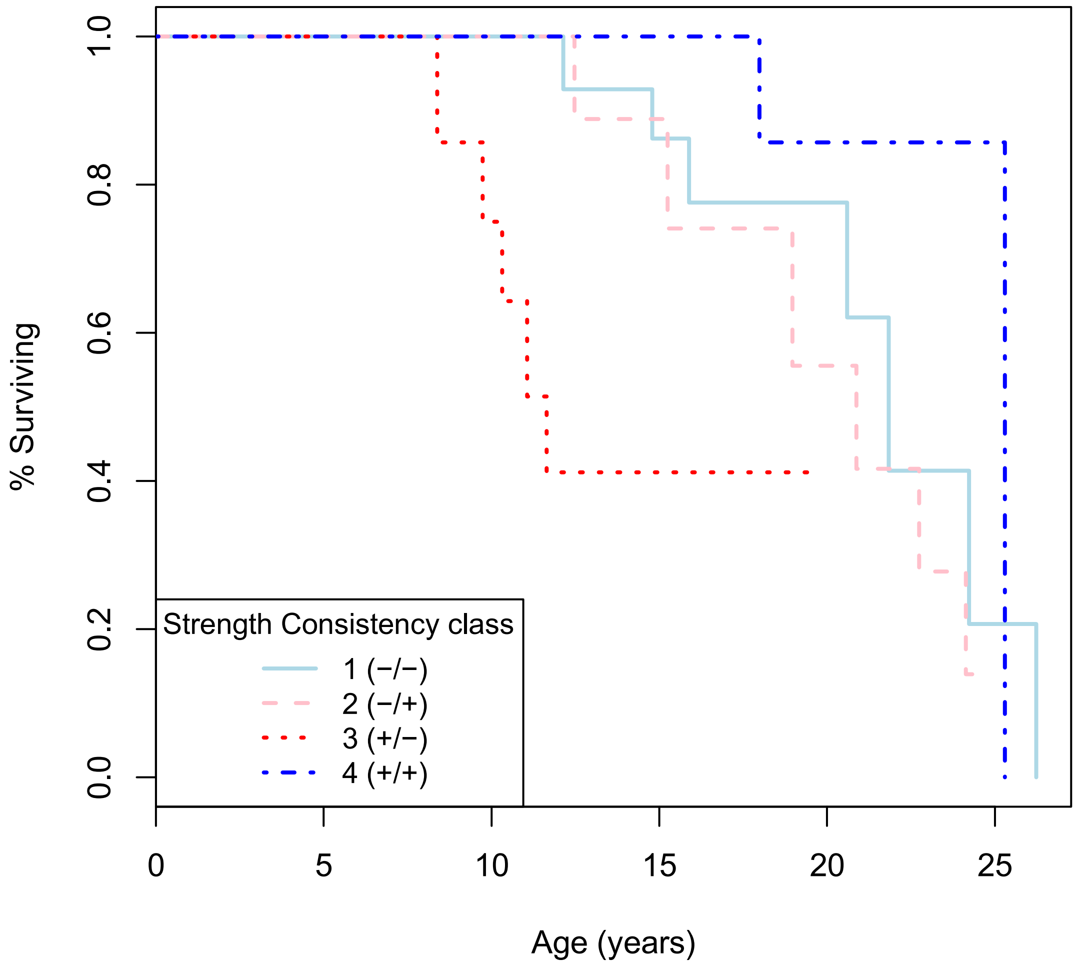

Figure 2.3. Survival curve of subjects in four multi-year bond strength – partner consistency classes : Class 1) below average bond strength and below average partner consistency (light blue, solid line). Class 2) below average bond strength and above average consistency (pink, dashed line). Class 3) above average bond strength and below average consistency (red, small dotted line). Class 4) above average strength and above average consistency (dark blue, dashed and dotted line).

Time-dependent covariate models revealed patterns similar to those of fixed-time models. Strong bonds with few top 3 partners from the previous two years (class 3: +

strength / - consistency) was associated with a higher risk of death than having strong bonds with consistent partners from previous years (class 4 +/+, Cox proportional hazards, N = 354, ß class 3 vs. 4 = -1.52, hazard ratio = 0.22, 95% CI = -3.03 – - 0.01; electronic supplementary material, Tables S2.12 –13, Fig. S2.2 – S2.3). However, no other comparison between annual strength-consistency classes was more or less hazardous than the other. Fewer between-class comparisons reached significance in time-dependent models and the lower 95% confidence limit of the coefficient of class 3 vs. 4 was very near zero, suggesting that annual strength-consistency class had a weaker effect on survival than strength-consistency classes based on multiple years. The effects of annual dominance rank and annual group size on survival did not reach significance in models of either top 3 or top 6 partners. Strength-consistency class with top 6 partners also did not significantly influence survival in a time-dependent way.

Discussion

(a) Influences on the risk of death

The quality of a female's social ties with her closest 3 partners, assessed both over multiple and single years, predicted survival in adult female blue monkeys. Specifically, over multiple years of observation, a female's risk of death was highest if she had strong bonds with a set of top 3 partners that was inconsistent from year to year. Females that were weakly bonded over multiple years, with either consistent or inconsistent partners, or strongly bonded with consistent partners all had similarly lower risks of death than females with strong and inconsistent partners. Similarly, a female that was strongly bonded in a given year with partners that had changed from previous years had a higher risk of dying in that same year than females that were strongly bonded with consistent partners. Neither multi-year nor current annual relationship quality with her closest 6 partners influenced female survival.

We did not find clear evidence of a life history trade-off between survival and reproduction (Table 2.1, fixed-time analysis). If early investment in reproduction does compromise somatic maintenance, these results emphasize the greater influence of cumulative social relationship quality vs. physical condition on survival in blue monkeys. Similarly in bighorn ewes, social ties had a stronger effect than body mass on survival (Vander Wal et al. 2014). We also found no evidence of an effect of dominance rank and group size on survival, either over multiple years or in a particular year.

Maintaining strong bonds when partners are inconsistent from year to year (highest risk multi-year strategy, Table 2.1 Figure 2.3) may represent an investment that outweighs the return, i.e. females invest in partners that are too inconsistent to reciprocate or cooperate as allies. In general, consistent partners help to create a stable social environment, and the loss of important partners can elicit a stress response (Engh et al. 2006). Affiliative partners that persist over time may also promote reciprocal grooming (Taborsky 2013) or provide coalitionary or affiliative support on a subject’s behalf during or after an aggressive encounter (Silk et al. 2010a). More passively, consistent partners may tolerate a subject’s presence during feeding (Marshall et al. 2012). The benefits of consistent partners are presumably amplified when partners affiliate more intensely (Silk et al. 2010b). The fact that strong bonds over multiple years actually decreased survival when partners were inconsistent, rather than having a neutral influence, suggests that maintaining strong bonds may be costly to blue monkey females.

The effects of current relationship quality on immediate survival (in a time-dependent model) also suggested that strong bonds were costly. Maintaining currently strong bonds with few close partners from previous years was riskier than being strongly bonded with many previously close partners. This finding emphasizes that if a female maintains strong bonds, she should do so with partners that are relatively consistent. It also suggests that females may not only lose the return on investment in strong bonds with future inconsistent partners, but they may also pay a cost when associating most frequently with "new" partners.

The stronger effect of multi- vs. single-year strength-consistency class on survival further suggests that the cost of maintaining strong bonds with inconsistent partners is cumulative. Only after several years of investment in partners that change from year to year are females disadvantaged relative to females maintaining any other strategy of bondedness with close partners (i.e. even being weakly bonded with inconsistent partners or weakly bonded with consistent partners is a better strategy).

If maintaining bonds is costly, being weakly bonded may actually be a beneficial strategy over multiple years. In fact, maintaining weak bonds with either consistent or inconsistent partners were both lower risk than maintaining strong bonds with inconsistent partners over time. Females that are weakly bonded spend less time and energy on partners, and so perhaps never pay the cost of maintaining strong bonds.

Demographic constraints such as group size, but not partner deaths, may underlie the uncoupling of bond strength and partner consistency in blue monkeys. Females with the most hazardous combinations of strong bonds with inconsistent partners over multiple years tended to live in groups of intermediate size. Meanwhile, females that lived with relatively more or fewer females had weak and inconsistent or strong and consistent partners, respectively. While the greater availability of different social partners may understandably decrease the consistency of close partners from year to year, extreme (vs. intermediate) group sizes may facilitate females' beneficial tendency to maintain either strong bonds with consistent or weak bonds with inconsistent partners. Although the riskiest social strategy tended to occur in groups of intermediate size, number of adult female group-mates did not appear to have a quadratic relationship with female survival.

Comparison with other social species

This study is the first survival analysis to examine how social connections influence longevity in an arboreal primate (Yee et al. 2008; Silk et al. 2010b; Foster et al. 2012; Stanton & Mann 2012; Archie et al. 2014; Nuñez, Adelman & Rubenstein 2015; Brent, Ruiz-Lambides & Platt 2017; McFarland et al. 2017) and to compare the cumulative vs. current effects of relationship quality. Results both concur with and differ from these and other previous studies of how social relations influence other direct fitness measures (Silk, Alberts & Altmann 2003; McDonald 2007; Cameron, Setsaas & Linklater 2009; Silk et al. 2009; Schülke et al. 2010; Brent et al. 2013; Gilby et al. 2013; Vander Wal et al. 2014; Kalbitzer *et al.* 2017).

Similar to all the above studies, we found that greater sociality in the form of stronger top bonds can indeed correspond with higher survival in blue monkey females. However, in contrast to several previous studies, strong bonds actually correspond with lower survival in certain situations (i.e., when bond partners change from year to year), suggesting that maintaining bonds is costly. Indeed, over multiple years, females that were weakly bonded had a lower risk of death than females that were strongly bonded to partners that were inconsistent over time.

Blue monkey females seem to receive a return on their social investment only if bond partners are relatively consistent. Somewhat similarly, affiliation appears to be costly to female marmots because strongly affiliating females produced fewer offspring (although the causal relationship between affiliation and reproduction was not clear, Wey & Blumstein 2012) and are more likely to die during hibernation (Yang, Maldonado-Chaparro, & Blumstein, 2016). Also similarly, in white-faced capuchin, the costs and benefits of females' strong bonds depend on male behavior (Kalbitzer *et al.* 2017). The offspring of strongly bonded females were more likely to fall victim to infanticide during alpha male replacements, but during periods of alpha male stability, they were more likely to survive. As the strongest bonds of blue monkey females are not necessarily with a consistent set of partners (unlike in baboons, Silk, Alberts & Altmann 2006a,b; Silk et al. 2010b), females may actually benefit by saving the time and energy spent on cultivating strong bonds. Those savings and their benefits remain to be quantified on a mechanistic level. Because within-group agonism and alliances are rare in blue monkeys (Klass & Cords 2015), the function of social bonds in general may be to maintain group cohesiveness rather than orchestrating competitive power relations within groups. Group-wide cohesion may not require particularly strong bonds.

Conclusions

We found that stronger bonds do not necessarily increase survival in females in a matrilocal, gregarious species. In adult female blue monkeys, stronger bonds with close social partners decreased survival when close partners were inconsistent over time. When strong bonds were consistent over multiple years, survival was high relative to all other strategies. It appears, then, that strong bonds may be costly to adult females and are a productive "investment" only in situations where their benefit outweighs their cost. Other longitudinal, individual-based studies that examine the influence of social ties on fitness may find it useful to incorporate variables that capture variation in the potential costs and benefits of social ties.

In general, studies such as ours that find a correlation between the quality of social ties and survival in animals are only a first step in understanding the actual mechanisms by which social ties influence fitness. Although it is a regular challenge of long-term field studies to obtain high-resolution data on individuals' physiological status and social interactions simultaneously, future studies should aim to resolve the three-part connection between social ties, physiological status, and fitness outcomes whenever possible. Consideration of social measures and time scales relevant to study species will help us to understand how social ties influence fitness.

Acknowledgments

We thank the Government of Kenya for research approval, Masinde Muliro University of Science and Technology (CEKATFOS) for local sponsorship, and Kenya Forest and Wildlife Services for cooperation. We are grateful to field assistants, too many to list individually, that helped with data collection, especially C. Abungu, P. Akelo, M. Atamba, S. Foerster, C. Makalasia, J. Munayi, C. Oduor, E. Shikanga, D. Shilabiga, and

E. Widava, who contributed over multiple years (see also https://plhdb.org/Acknowledgments).

Funding: To MC, Columbia University, the Leakey, Wenner-Gren and National Science Foundations (SBR 95-23623, BCS 98-08273, 05–54747, 10-2847, DGE 09-66166) and AAAS-WISC.

Authors’ contributions

NT and MC conceived the ideas and designed methods; MC collected the data; NT and MC analysed the data; NT led manuscript writing. Both authors contributed critically to the drafts and gave final approval for publication.

Competing interests: The authors have no competing interests.

Supplementary data: The datasets supporting this article will be made available in Dryad.

Supplemental Information

Table S2.1. QAP Matrix correlations of annual matrices of proportion of dyads' shared observation time spent grooming and resting within 1 m.

Year*	Group	test value	p value**	significant alpha < 0.05
2006-2007	GN	0.41	0	TRUE
2007-2008	GN	0.4	0	TRUE
2008-2009	GN	0.38	0	TRUE
2009-2010	GN	0.11	0.12	FALSE
2010-2011	GN	0.5	0	TRUE
2011-2012	GN	0.54	0	TRUE
2012-2013	GN	0.47	0	TRUE
2013-2014	GN	0.56	0	TRUE
2006-2007	GS	0.31	0	TRUE
2007-2008	GS	0.56	0	TRUE
2008-2009	GSB	0.11	0.31	FALSE
2008-2009	GSA	0.09	0.21	FALSE
2009-2010	GSB	0.01	0.44	FALSE
2009-2010	GSAA	0.88	0	TRUE
2009-2010	GSC	-0.07	0.52	FALSE
2010-2011	GSB	0.79	0.06	FALSE
2010-2011	GSAA	0.25	0.06	FALSE
2010-2011	GSC	0.56	0.03	TRUE
2011-2012	GSB	0.94	0.16	FALSE
2011-2012	GSAA	0.61	0	TRUE
2011-2012	GSC	0.5	0.01	TRUE
2012-2013	GSB	0.39	0.4	FALSE
2012-2013	GSAA	0.36	0.01	TRUE
2012-2013	GSC	0.51	0	TRUE
2013-2014	GSB	0.41	0.39	FALSE
2013-2014	GSAA	0.77	0	TRUE
2013-2014	GSC	0.68	0	TRUE
2006-2007	TWN	0.37	0.08	FALSE
2007-2008	TWN	0.01	0.44	FALSE
2008-2009	TWN	0.43	0.08	FALSE
2009-2010	TWN	0.09	0.35	FALSE
2010-2011	TWN	0.31	0.17	FALSE
2011-2012	TWN	0.5	0.01	TRUE
2012-2013	TWN	0.66	0	TRUE

2013-2014	TWN	0.38	0.01	TRUE
2006-2007	TWS	0.31	0	TRUE
2007-2008	TWS	0.39	0	TRUE
2008-2009	TWS	0.44	0	TRUE
2009-2010	TWS	0.26	0.01	TRUE
2010-2011	TWS	0.31	0	TRUE
2011-2012	TWS	0.3	0	TRUE
2012-2013	TWS	0.31	0	TRUE
2013-2014	TWS	0.49	0	TRUE
	percentage years correlated:			28/43 = %65

*Each 12-month year ran from October to October

** p value of 0 is <0.001

Table S2.2. Loadings of multi-year bond strength and consistency with top 3 partners on principal components.

	PC1	**PC2**
% Variance explained	99.48%	0.52%
strength.3	0.9998	0.0176
consistency.3	0.0176	-0.9998

Table S2.3. LMER Repeatability statistics for variables with annual measures * (rptR package) N = 437 subject-years

Variable	Fixed effect in model (control variable)	R	95% CI	p**
Bond strength (top 3)	Number adult female groupmates	0.15	0.06 - 0.23	< 0.001
Dominance rank		0.82	0.75 - 0.86	< 0.001
Number adult female groupmates		0.73	0.65 - 0.79	< 0.001

*Subject included as random effect.

**1000 bootstrap iterations used to calculate 95% CI and 1000 matrix randomizations used to calculate p.

Table S2.4. Mean and standard deviation across all subjects of multi-year variables used to predict survival, and correlations[1] between variables (N = 83 subjects). Columns 1-9 correspond to predictors listed in the left-most column.

Predictor	$\bar{x}$	SD	Range	1	2	3	4	5	6	7	8
1. Age at entry	10.1	± 3.9	5.8 – 22.6	-	-0.22 *	-0.27 *	-	-			
2. Bond strength top 3 partners	7.6	± 2.49	2.9 – 15.9		-	0.95 ***	0.27*	0.32**	-	-0.35**	-
3. Bond strength top 6	5.4	± 1.91	2.12 – 12.7			-	0.26*	0.27*	-	-0.29**	-
4. Partner consistency top 3	0.51	± 0.18	0 – 1				-	0.45***	0.22*	-0.38***	-
5. Partner consistency top 6	0.67	± 0.13	0.17 – 1					-	-	-0.59***	-
6. Dominance rank	0.49	± 0.29	0 – 1						-	-	-
7. Number adult female groupmates	13.6	± 4.2	3 – 21							-	-
8. Age at first birth	7.3	± 1.2	4.6 – 10.9								-

[1] - no correlation, * $p < 0.05$, ** $p < 0.01$, *** $p < 0.001$. There were no p values 0.10 -- 0.05.

Multi-year strength-consistency class with top 3 partners: comparisons between different reference classes:

Table S2.5. Average influence of multi-year strength-consistency class (top 3 partners) in fixed-time survival models, where reference class = 4, strong and consistent bonds. N=83 females, 20 deaths.

Predictor of hazard	Factor level	ß	95% CI	Hazard Ratio	Proportion of permutation coefficients < observed	Proportion of permutation coefficients > observed
Strength – Consistency Class (reference class: 4, + / + lowest risk)	1 (- / -)	0.93 †	-0.72, 2.6	2.55	**1[1], 0.999[2]**	**0[1], 0.001[2]**
	2 (- /+)	1.49 †	-0.2, 3.18	4.45	0.958[1], 0.961[2]	0.042[1], 0.039[2]
	3 (+/ -)	3.01 †	**1.2, 4.83 ***	20.39	**1[1,2]**	**0[1,2]**

† Model averaged coefficient
* 95% CI does not include zero
[1] From model 1: including dominance rank as competition variable.
[2] From model 2: including number of adult female groupmates as competition variable.

Table S2.6. Average influence of multi-year strength-consistency class (top 3 partners) in fixed-time survival models, where reference class = 1, weak and inconsistent bonds. N=83 females, 20 deaths.

Predictor of hazard	Factor level	ß	95% CI	Hazard Ratio	Proportion of permutation coefficients < observed	Proportion of permutation coefficients > observed
Strength – Consistency Class (reference class: 1, - / - second to lowest risk)	2 (- / +)	0.56 †	-0.73, 1.84	1.74	0.069[1], 0.065[2]	0.931[1], 0.935[2]
	3 (+/ -)	2.1 †	**0.62, 3.53 ***	8.0	**0.999[1], 0.984[2]**	**0.001[1], 0.016[2]**
	4 (+/+)	-0.93 †	-2.6, 0.72	0.39	**0[1], 0.01[2]**	**1[1], 0.99[2]**

† Model averaged coefficient
* 95% CI does not include zero
[1] From model 1: including dominance rank as competition variable.
[2] From model 2: including number of adult female groupmates as competition variable.

Multi-year strength-consistency class with top 6 partners results:

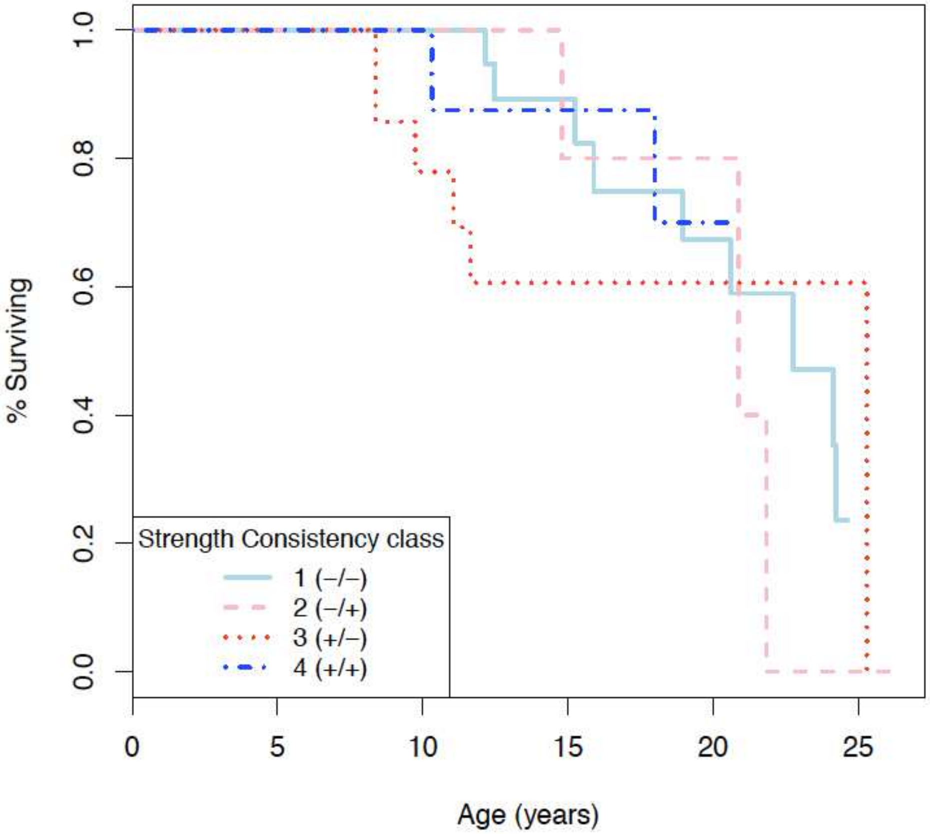

Figure S2.1. Survival curve of subjects falling into a given multi-year bond strength – partner consistency (with top 6 partners) class. Class 1) below average bond strength and below average partner consistency (light blue, solid line). Class 2) below average bond strength and above average consistency (pink, dashed line). Class 3) above average bond strength and below average consistency (red, small dotted line). Class 4) above average strength and above average consistency (dark blue, dashed and dotted line). Female survival did not significantly vary by class according to coefficients' 95% CI.

Table S2.7. Average influence of multi-year strength-consistency class (<u>top 6 partners</u>) in fixed-time survival models, where <u>reference class = 3</u>, strong and inconsistent bonds (highest risk class). N=83 females, 20 deaths.

	Predictor of hazard	Factor level	ß	95% CI	Hazard Ratio	Proportion of permutation coefficients < observed	Proportion of permutation coefficients > observed
Social ties	Strength – Consistency Class (reference class: 3, + / - highest risk)	1 (- / -)	-0.39†	-1.56, 0.79	0.68	0.517[1], 0.625[2]	0.549[1], 0.409[2]
		2 (- /+)	-0.47†	-2.07, 1.13	0.62	**0.005[1], 0.002[2]**	**0.995, 0.998[1,2]**
		4 (+/ +)	-0.82†	-2.68, 1.05	0.44	**0.011[1], 0.01[2]**	**0.989[1], 0.99[2]**
Competition	Dominance rank	n/a	0.13	-0.37, 0.62	1.14	n/a	n/a
	Number adult female groupmates	n/a	-0.44	-0.97, 0.29	0.64	n/a	n/a
Life history	Age at first birth	n/a	-0.46	-1.01, 0.09	0.63	n/a	n/a

† Model averaged coefficient
* 95% CI does not include zero
[1] From model 1: including dominance rank as competition variable.
[2] From model 2: including number of adult female groupmates as competition variable.

Table S2.8. Average influence of multi-year strength-consistency class (<u>top 6 partners</u>) in fixed time survival models, where <u>reference class = 4</u>, strong and consistent bonds (lowest risk class). N=83 females, 20 deaths.

Predictor of hazard	Factor level	ß	95% CI	Hazard Ratio	Proportion of permutation coefficients < observed	Proportion of permutation coefficients > observed
Strength – Consistency Class (reference class: 4, + / + lowest risk)	1 (- / -)	0.43†	-1.33, 2.19	1.54	**0.985[1], 0.987[2]**	**0.015[1], 0.013[2]**
	2 (- /+)	0.34†	-1.54, 2.23	1.41	0.481[1], 0.513[2]	0.519[1], 0.487[2]
	3 (+/ -)	0.82†	-1.05, 2.68	2.26	**0.989[1], 0.99[2]**	**0.011[1], 0.01[2]**

† Model averaged coefficient
* 95% CI does not include zero
[1] From model 1: including dominance rank as competition variable.
[2] From model 2: including number of adult female groupmates as competition variable.

Table S2.9. Average influence of multi-year strength-consistency class (top 6 partners) in fixed-time survival models, where reference class = 1, weak and inconsistent bonds. N=83 females, 20 deaths.

Predictor of hazard	Factor level	ß	95% CI	Hazard Ratio	Proportion of permutation coefficients < observed (more likely to decrease hazard)	Proportion of permutation coefficients > observed
Strength – Consistency Class (reference class: 1, - / - second to *highest* risk)	2 (- / +)	-0.90†	-1.59, 1.42	0.92	**0.008^1, 0.005^2**	**0.992^1, 0.995^2**
	3 (+/ -)	0.39†	-0.79, 1.56	1.47	0.483^1, 0.375^2	0.517^1, 0.615^2
	4 (+/+)	-0.43†	-2.19, 1.33	0.65	**0.015^1, 0.013^2**	**0.985^1, 0.987^2**

† Model averaged coefficient
* 95% CI does not include zero
[1] From model 1: including dominance rank as competition variable.
[2] From model 2: including number of adult female groupmates as competition variable.

Table S2.10. Test quadratic relationship of number adult female groupmates on survival in fixed-time Cox model (including multi-year st.co classes with top 3 partners, reference level 3 + st / - cons)

	coef	Hazard ratio	lowerCI	upperCI
st.co3 (class 1 -/-)	-1.793	0.167	-3.382	-0.204
st.co3 (class 2 -/+)	-1.371	0.254	-2.751	0.009
st.co3 (class 4 +/+)	-2.956	0.052	-4.773	-1.14
af.groupmates	-0.355	0.701	-1.048	0.337
af.groupmates^2	-0.239	0.788	-0.967	0.489
age.first.rep	-0.495	0.609	-1.099	0.109

Table S2.11. Test quadratic relationship of number adult female groupmates on survival in fixed-time Cox model (including multi-year st.co classes with top 6 partners, reference level 3 + st /- cons)

	coef	Hazard ratio	lowerCI	upperCI
st.co6 (class 1 -/-)	-0.324	0.723	-1.508	0.861
st.co6 (class 2 -/+)	-0.103	0.903	-2.144	1.939
st.co6 (class 4 +/+)	-0.592	0.553	-2.643	1.46
af.groupmates	-0.381	0.683	-1.041	0.279
af.groupmates^2	-0.321	0.726	-1.196	0.555
age.first.rep	-0.461	0.63	-1.019	0.096

Annual strength-consistency class with top 3 partners results:

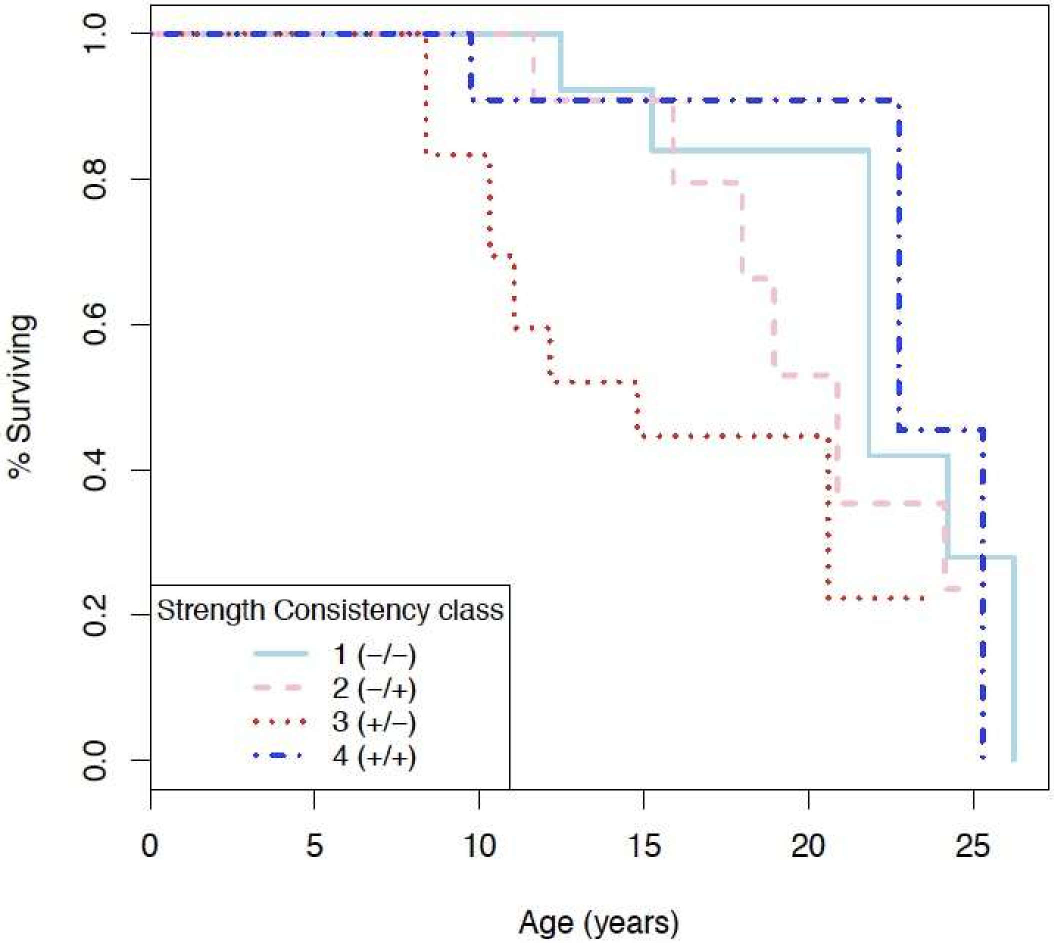

Figure S2. Survival curve of subjects falling into a given annual bond strength – partner consistency (with top 3 partners) class. Class 1) below average bond strength and below average partner consistency (light blue, solid line). Class 2) below average bond strength and above average consistency (pink, dashed line). Class 3) above average bond strength and below average consistency (red, small dotted line). Class 4) above average strength and above average consistency (dark blue, dashed and dotted line). Females in class 3 (+/-) have significantly lower mortality than females in class 4 (+/+)

Table S2.12. Time dependent covariate Cox model including annual classes of strength-consistency (st-cons) with top 3 partners, dominance rank, and number adult female groupmates. N = 354 subject-yrs. (Significant effects in bold)

A) Base class 3 (+st/-cons)

predictor	coef	hazard.ratio	CI
st-cons3 (1 -/-)	-1.4	0.25	[-2.82,0.03]
st-cons3 (2 -/+)	-0.76	0.47	[-2.01,0.48]
st-cons3 (4 +/+)	**-1.52**	**0.22**	**[-3.03,-0.01]**
Rank	0.16	1.17	[-0.32,0.64]
af.groupmates	-0.13	0.88	[-0.6,0.34]

B) Base class 4 (+st/+cons)

predictor	coef	hazard.ratio	CI
st-cons3 (1 -/-)	0.12	1.13	[-1.44,1.69]
st-cons3 (2 -/+)	0.76	2.13	[-0.69,2.2]
st-cons3 (3 +/-)	**1.52**	**4.57**	**[0.01,3.03]**
Rank	0.16	1.17	[-0.32,0.64]
af.groupmates	-0.13	0.88	[-0.6,0.34]

C) Base class 1 (-st/-cons)

predictor	coef	hazard.ratio	CI
st-cons3 (2 -/+)	0.63	1.88	[-0.73,1.99]
st-cons3 (3 +/-)	1.4	4.04	[-0.03,2.82]
st-cons3 (4 +/+)	-0.12	0.88	[-1.69,1.44]
rank	0.16	1.17	[-0.32,0.64]
af.groupmates	-0.13	0.88	[-0.6,0.34]

Annual strength-consistency class with top 6 partners results:

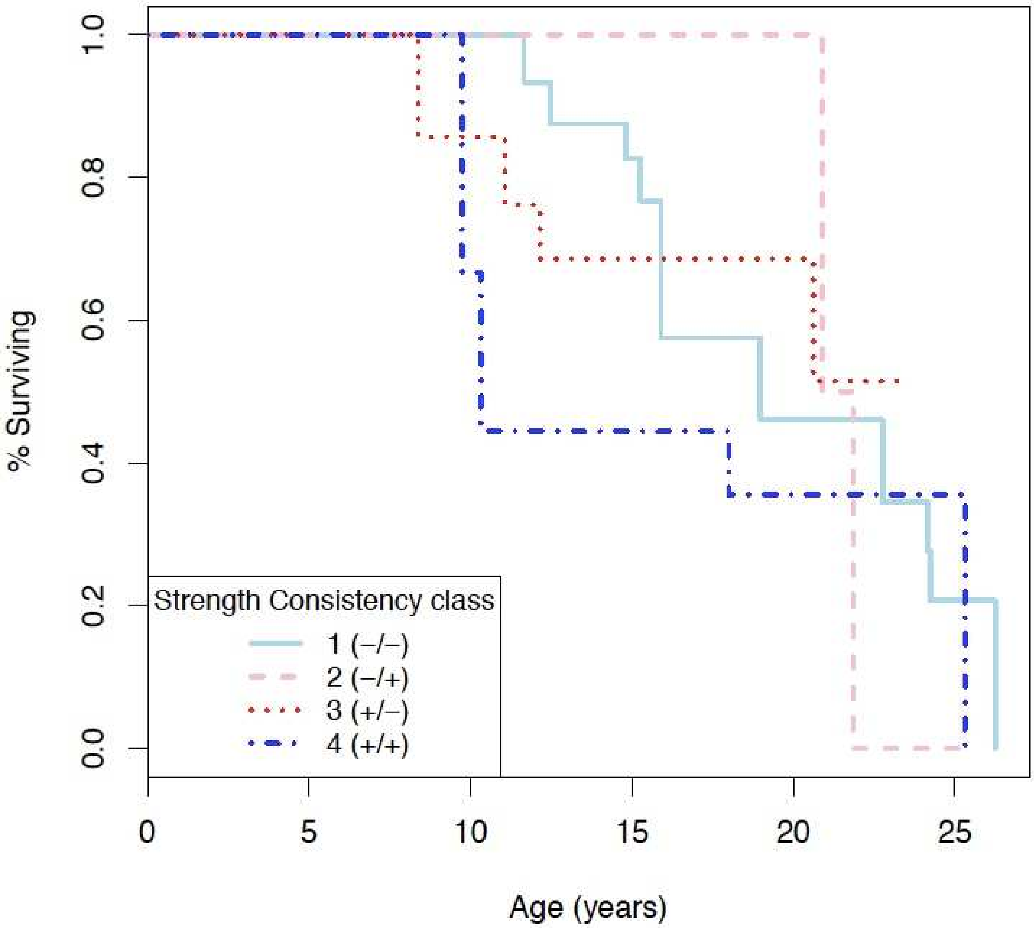

Figure S2.3. Survival curve of subjects falling into a given annual bond strength – partner consistency (with top 6 partners) class. Class 1) below average bond strength and below average partner consistency (light blue, solid line). Class 2) below average bond strength and above average consistency (pink, dashed line). Class 3) above average bond strength and below average consistency (red, small dotted line). Class 4) above average strength and above average consistency (dark blue, dashed and dotted line). Female survival did not vary by class.

Table S2.13. Time dependent covariate Cox model including annual classes of strength-consistency (st-cons) with top 6 partners, dominance rank, and number adult female groupmates. N = 354 subject-yrs

A) Base class 3 (+st/-cons)

predictor	coef	hazard.ratio	CI
st-cons6 (1 -/-)	0.04	1.04	[-1.19,1.27]
st-cons6 (2 -/+)	-0.58	0.56	[-2.42,1.26]
st-cons6 (4 +/+)	-0.02	0.98	[-1.55,1.52]
rank	0.1	1.1	[-0.39,0.58]
af.groupmates	-0.29	0.75	[-0.78,0.21]

B) Base class 4 (+st/+cons)

predictor	coef	hazard.ratio	CI
st-cons6 (1 -/-)	0.05	1.06	[-1.31,1.42]
st-cons6 (2 -/+)	-0.56	0.57	[-2.32,1.19]
st-cons6 (3 +/-)	0.02	1.02	[-1.52,1.55]
rank	0.1	1.1	[-0.39,0.58]
af.groupmates	-0.29	0.75	[-0.78,0.21]

C) Base class 1 (-st/-cons)

predictor	coef	hazard.ratio	CI
st-cons6 (2 -/+)	-0.62	0.54	[-2.32,1.09]
st-cons6 (3 +/-)	-0.04	0.96	[-1.27,1.19]
st-cons6 (4 +/+)	-0.05	0.95	[-1.42,1.31]
rank	0.1	1.1	[-0.39,0.58]
af.groupmates	-0.29	0.75	[-0.78,0.21]

Chapter 3: Socio-ecological drivers of social behavior during development in blue monkeys.

Introduction

In group-living animals, social behavior has evolved to cope with regular intrinsic and extrinsic challenges, including those associated with different life stages and social and physical environments. Juvenility, when individuals are no longer dependent on parental care for survival but not yet reproductively mature, can be a particularly challenging life stage because juveniles are physically small and relatively inexperienced. They often experience higher rates of predation and physical aggression and their growing bodies and brains are prone to suffer nutritional deficiencies (Altmann, 1991; Baker & Thompson, 2007; Caughley, 1966; Clutton-Brock, Major, Albon, & Guinness, 1987; Derocher & Stirling, 1996; Douhard et al., 2014; Kuzawa et al., 2014; Pereira, 2003). Alongside locomotor and neuroanatomical development, particular experiences, or behavioral inputs, during immaturity can be critical to establish adult level competence in behavioral and physiological responses to challenges such as mothering, mounting immune responses, and navigating social competition (Champagne, 2010; Gluckman, Hanson, & Beedle, 2007; Pellis & Pellis, 2007; Sachser et al., 2013; Taborsky, Arnold, Junker, & Tschopp, 2012). Such competence may be integral to fitness, as adverse conditions during this life stage can lead to shorter lifespans and decreased reproductive success (Altmann, 1991; Metcalfe & Monaghan, 2001; Tung, Archie, Altmann, & Alberts, 2016).

To understand the adaptive value of social behavior, one must understand the conditions under which it occurs and with which it co-varies (Duboscq et al., 2017; Silk, Altmann, et al., 2006; Silk et al., 2010a). Despite the unique challenges of the juvenile period, and its important consequences for fitness, juvenile behavior is often overlooked in research on animal behavior (Pereira & Fairbanks, 2003). In primates, the juvenile period is longer relative to mammals of similar body sizes, which has led some to suggest that experiences during development help individuals gain competence in navigating particularly complex adult social environments (Blumstein & Armitage, 1998; Pagel & Harvey, 2003). In part because sex differences that align with adult-typical behavior of a given species tend to become more apparent with age, patterns of juvenile behavior across birds and mammals are often characterized as optimizing current survival (e.g. avoiding competition and predation) while simultaneously “practicing” for the future (Cords, Sheehan, & Ekernas, 2010; Fairbanks, 2003; Heinsohn, Packer, & Pusey, 1996; Kulik, Amici, Langos, & Widdig, 2015; Maestripieri & Ross, 2004; O'Brien & Robinson, 2003; Paukner & Suomi, 2008; Raleigh, Flannery, & Ervin, 1979; Rodrigues, 2014; Rothstein & Griswold, 1991; Rowell & Chism, 1986; Strier, 2003; Templeton et al., 2012; van Noordwijk, Emelrijk, Herremans, & Sterck, 2003). For example, in several female-philopatric primates, juvenile females often spend more time than males grooming adult females (Fairbanks, 2003; Nakamichi, 1989; Rowell & Chism, 1986). Such behavior may be advantageous for the present in pacifying adult females that often disproportionately aggress juveniles that will be their future competitors (Pereira, 1988a), and for the future because those same adults may be life-long partners, and grooming is a large part of adult female social life (Fairbanks, 2003; O'Brien & Robinson, 2003; Pereira, 1988a). Sex differences in behavior typically become more pronounced leading up to sexual maturity, particularly as sex steroids become more abundant and differentiated, provoking adult-like behavior (Gesquiere et al., 2005; Pusey, 1990), further indicating that such behavior is preparatory or transitional.

Several aspects of sociality may constitute a strategy that is adaptive for one's particular current (e.g. age, body size, environment) and future state (e.g. species-specific reproductive roles). Such aspects include amount of time engaged in particular types of social behavior and one's diversity of social partners. Indeed, each of these measures may have important fitness consequences, such as enhanced reproductive success or survival. For example, higher general levels of individual affiliation can increase reproductive success and survival among females in species with strong feeding competition and potential male sexual harassment, such as feral horses and baboons (Archie et al., 2014; Cameron et al., 2009). Integration within a social unit via one's number of direct or indirect social ties can also increase survival, as seen in horses and dolphins, where immature animals receive more physical harassment from competitors than adults (Nuñez et al., 2015; Stanton, Gibson, & Mann, 2011). Although not strategic in terms of choice, number of preferred social partners, such as maternal kin, may also have important consequences for fitness and social strategies themselves. For example, adult female rhesus macaques with more maternal kin in their social group have longer lifespans (Brent et al., 2017) and adult female baboons establish their strongest and most enduring relationships with maternal kin (Silk, Alberts, et al., 2006).

Preferences for particular social partners are indeed another central aspect to social strategies. Choice of partners is often considered strategic, in that individuals invest time associating and affiliating with partners that are "valuable" (Aureli, Cords, & van Schaik, 2002; Kummer, 1978). In several species, individuals preferentially associate and affiliate with kin, which are often more familiar and tolerant (Elizabeth A Archie et al., 2006; Carter, Seddon, Frère, Carter, & Goldizen, 2013; Chapais, 2001; Cords & Nikitopoulos, 2015; Wey & Blumstein, 2010). Kin are also likely allies in competitive aggression, particularly for young animals navigating a relatively new competitive environment (Chapais, 1995; Engh et al., 2000). Age-mates may also be preferred partners for particular kinds of interactions, like play (Cameron, Linklater, Stafford, & Minot, 2008; Thompson, 1996). Juveniles may prefer to play with like-aged partners because they are similar in body size, physical ability, and experience and so may serve as a type of mirror for assessing one's own physical ability (Graham & Burghardt, 2010; Thompson, 1996). Conversely, some studies have found that juveniles prefer to associate with older individuals, possibly because they are *more* experienced, are likely future allies, and/or can serve as a type of role model (Fairbanks, 2003; Sherrow, 2008; Wittemyer, Douglas-Hamilton, & Getz, 2005). There is also evidence to suggest that juveniles could adopt strategies to associate with partners that are either similarly or differently ranked within a dominance hierarchy. Similarly-ranked individuals, apart from perhaps being closely related, are possibly safer and pose less of a risk of physical aggression (Duboscq et al., 2017). Alternatively, individuals may prefer to associate or affiliate with higher-ranking partners because they are potentially powerful allies in aggressive conflicts or their tolerance is beneficial (Schino, 2001). There is very little evidence, however, that individuals regularly trade affiliative behavior for active support in aggressive conflicts (Duboscq et al., 2017; Hemelrijk & Ek, 1991; Kern & Radford, 2016; Schino, 2007).

When examining social behavior to understand its adaptive nature, it is important to control for environmental influences. Seasonal changes in habitat and the distribution of foods can alter individual association patterns, such that fluctuations in space use may influence the amount time individuals spend interacting and the number of partners they have (Henzi et al., 2009; Holekamp, Smith, Strelioff, Van Horn, & Watts, 2012). For example, in South African baboons, adult females associated more intensely when food was scarce, possibly because available food was highly clumped (Henzi et al., 2009). Also, if competition for food and space is strong within groups, dominance rank may influence patterns of spatial association, and thus also interaction patterns (King et al., 2011).

Although some social behavior varies by season, individuals may possess social tendencies in which between-individual differences in behavior persist over time (Bell, Hankison, & Laskowski, 2009). Repeatable differences could indicate a genetically based trait upon which selection may act, and thus are key to understanding the adaptive value and any mode of their inheritance of social tendencies (Dingemanse et al., 2004; Hayes & Jenkins, 1997; Visscher, Hill, & Wray, 2008). Assessing repeatable differences is also important for understanding the occurrence and extent of early-life behavioral programming (Careau, Buttemer, & Buchanan, 2014; Grindstaff, 2016) and perhaps predicting how individuals will behave in the future (Sih & Bell, 2008).

Blue monkeys have a particularly prolonged juvenile period even among slow-developing primates (Cords & Chowdhury, 2010), making them an interesting candidate for understanding the adaptive value of social strategies during the juvenile period and the evolution of its prolongation. Adult male and female blue monkeys are also highly dimorphic in both social behavior and body size, such that females reside in their natal group for life and males disperse at maturity to lead either or both of two lifestyles:

solitary bachelor or in-group resident male (Leigh & Shea, 1995; Roberts & Cords, 2015; Roberts, Nikitopoulos, & Cords, 2014). Such extreme sexual dimorphism in adult social behavior suggests that juveniles of different sexes should also differ strongly in their behavior (Cords et al. 2010).

In this study, I pursue two aims. First, I assess how juvenile blue monkeys' social activities vary with intrinsic and extrinsic variables. Specifically, I examine how time spent playing, grooming, and resting in proximity or in contact with partners, and number of partners in each behavior type, vary according to age, sex, maternal dominance rank, number of maternal kin, and ecological variables, including fruit availability and rainfall. To further understand variation in individual social behavior, I assess whether between-individual differences in social tendencies are consistent over time. Second, I examine what kinds of partners juveniles prefer for each of the above types of social interaction, according to their relatedness, difference in age, and rank. This study differs from a previous study on social behavior in juvenile blue monkeys (Cords et al., 2010) in that I assess variation in behavior (including play) according to ecological variables, more extensively test drivers of partner preferences, and evaluate the consistency in between-individual differences over time. This dataset also allowed us to monitor within-individual longitudinal trends more closely.

Because of strong sexual dimorphism in adult behavior and juvenile sex differences known from previous studies of this species, I expected males to be generally more involved in play and less involved with grooming than females, and for differences to increase with age (Cords et al., 2010). I also predicted that seasonal fruit availability and maternal dominance rank would not strongly influence juvenile social behavior, because blue monkeys are generalist feeders in which dominance rank has rare effects on reproduction and physiology (Foerster et al., 2011; Pazol & Cords, 2005; Roberts & Cords, 2013). I did, however, expect juveniles of higher maternal dominance rank to give more and receive less agonism (Klass & Cords, 2015).

Because adult females bias grooming and association time towards maternal kin (Cords & Nikitopoulos, 2015), I predicted that juveniles would do the same, favoring kin as partners and increasing time affiliating with kin when more were available. I also expected juveniles to prefer to groom with older individuals that were more experienced and could possibly be more effective allies. In contrast, I expected juveniles to prefer playing with like-aged partners that were similar in physical ability and experience. Again, because dominance rank is not related to affiliative behavior among adult females (Cords, 2000), I did not expect juveniles to prefer partners based on relative rank. Finally, as adult females demonstrate repeatable inter-individual differences in several aspects of social behavior, I expected juveniles to do the same. Alternatively, juveniles might not socialize in a repeatable way because they are still developing stable social tendencies.

Methods

Study site and species

The study population inhabits the Isecheno area of Kakamega Forest in western Kenya (0˚19′ N, 34˚52′ E; elevation 1580 m, mean annual rainfall 1997–2011 1942 mm; (Mitchell, 2009). From Aug 2015 – March 2016 (8 months), four observers (including NAT) collected data on 41 juvenile subjects (22 males, 19 females, mean age 4.4 ± 1.7 yrs) from 3 groups that ranged in size from an average of 37 – 65 individuals, including a resident adult male, adult females, and 16 – 31 juvenile offspring. Subjects were individually distinguishable, with ages and maternal kin relations known from precise, long-term demographic records (Cords, 2012).

Behavioral data collection

I conducted 20 min focal follows, recording focal subjects' activity (e.g. resting, grooming, playing, feeding) at 1 min intervals (point samples). "Playing" exclusively refers to social, rough-and-tumble play, or play fighting. Observers also recorded identities of grooming and play partners, and of neighbors resting within 1 m or in contact with (but not grooming) the subject. Observers also recorded all agonistic encounters (threats, lunges, aggressive contact, and approach-retreat). Follows occurred between 07:30 and 17:00, and I prioritized focal subjects to maintain even numbers of follows per subject across each week and across times of day (morning, midday, afternoon). I collected a total of 1591 hours of behavioral data, averaging 39 ± 3.1 hrs per subject.

Data analysis

I collated data into four 2-month periods (e.g. Aug 1st – Sept. 31st), for which I calculated all social and ecological variables. Two-month periods captured seasonal variation in the availability of ripe fruits and rainfall (Fig. S3.1a-b). Two months of behavioral observation (mean: 9.8 ± 1.2 hrs/subject) also conservatively represented characteristic numbers of social partners, as grooming and play partner numbers did not plateau for all subjects before 4 hours of observation.

I calculated individual activity budgets from point sample data, extracting the proportion of time (points) observed in focal follows that subjects spent in social play, resting within 1 m or in contact with at least one partner (both measures excluding grooming; henceforth "sitting close"), and giving or receiving grooming. I calculated the number of partners in each activity type using point sample data pooled among subjects, and standardized partner numbers for each subject by dividing observed numbers by average "shared" observation time with each possible partner. For example, the time subject A could have been observed to interact with a non-subject was simply the time subject A was observed as a focal, but the time subjects A and B could have been observed to interact was the sum of A and B's focal observation time. For agonistic behavior, I expressed frequencies of agonism (each event ≥ 5 min after the last) given and received as rates per hour of a subject's average shared observation time. To measure affiliation within dyads, I calculated the proportions of shared observation time (points) that a dyad spent playing, sitting close, and grooming one another.

I counted maternal kin and estimated relatedness coefficients of known kin relations for use in analyses, with maternal aunts and nieces/nephews ($r = 0.125$) as the most distantly related dyads included. As blue monkey offspring appear to inherit their mothers' rank as adults (Klass & Cords, 2015), I used mothers' rank to represent juvenile dominance relations. To calculate maternal ranks, I used records of adult female agonism collected as part of long-term population monitoring (Cords 2012), collating winner-loser interactions using the I&SI method in DomiCalc (Schmid & de Vries, 2013). I collated data over the entire study for mothers still alive, or otherwise (for 2 subjects) over the mother's last year of life (≤ 5 yrs before study). Dominance rank represented the proportion of co-resident adult females that a mother outranked (range 0 –1). I expressed subjects' ages in each 2-mo period according to its mid-date.

I calculated average daily rainfall per period using rainfall data collected daily by local Kenya Forest Service staff. We calculated a fruit availability index (FAI) by combining data from monthly plant phenology surveys of 36 major food species and data on these species' abundance from vegetation transects. To assess fruiting phenology, ca. 10 focal trees per species were monitored each month, and if they had fruits, an observer estimated the number of fruits (at least twice, to ensure consistency) on a modified log scale (e.g. 100-399, 400-699, 700-1000; Leighton, 1993) and also estimated percentage of ripe fruit (0, 25, 50, 75, 100%). Because not all fruiting focal trees received a fruit count, I averaged number of ripe fruits (midpoints of the above intervals) among trees that received counts and assigned that average to all fruiting trees of a given species, then calculated the average number of ripe fruits among all focal trees of that species (whether fruiting or not). To assess tree abundance, assistants measured basal areas of the 36 tree species in group-specific 10m x 100m transects (N = 13, 6, and 9 for groups 1, 2 and 3 respectively), which represented approximately 10% of each group's home range area. To calculate group-specific FAI, I multiplied the average number of ripe fruits for a given tree species by its average basal area per transect, and summed these products across the 36 species (Foerster, Cords, & Monfort, 2012).

Statistical analysis

I assessed the influence of life history (age, sex, and an age-sex interaction), socio-demographic (number of maternal kin in group, maternal dominance rank), and ecological variables (available ripe fruit, total rainfall) on juvenile social affiliation variables using generalized additive models (GAMs, package "gamlss" in R) (Stasinopoulos & Rigby, 2007). Generalized additive models are a useful alternative to generalized linear models because they allow one to evaluate non-linear relationships between predictors and response variables. The "gamlss" package also easily implements zero-inflated non-parametric error distributions for mixed effects models. To determine the error distributions of each response variable I used Cullen Frey graphs, created with the "descdist" function of "fitdistr" package (Delignette-Muller & Dutang, 2015), and assessed model residuals for normality with Q-Q plots. In all GAMs, predictors were standardized (Schielzeth, 2010) with group and subject ID as a random effects.

I modeled activity budgets (proportions of individual observation time in particular activities) using a zero-inflated beta error distribution. For number of social partners and rates of agonism given and received, I modeled errors using a Poisson distribution (zero-inflated for play partners) and offset response variables by the log of exposure, or the subject's average shared observation time with partners. I considered a predictor variable to have a significant influence on the response if the 95% confidence interval of its parameter estimate did not include zero (Nakagawa & Cuthill, 2007). Because data for number of social partners and rates of agonism were pooled among subjects, their observations were not independent of one another. Therefore, for these response variables, I further assessed the significance of subject-level life history and socio-demographic predictors (i.e. age, sex, maternal rank, number of maternal kin, and the interaction between age and sex) by comparing the estimated parameter of each against a null distribution of parameters estimated from 1000 random node permutations of the underlying interaction matrices (Farine & Whitehead, 2015).

To assess non-linear effects in GAMs, I first fit all continuous predictor variables with a cubic spline smoothing function and visualized the fitted values of the response according to the partial variation of the response explained by a given predictor variable ("term.plot" function, Larsen, 2015). If a predictor variable was significant according to its 95% CI and had a visibly non-linear relationship with the response variable, I compared AIC scores between linear vs. non-linear models and chose the model whose score was lower by at least 2 criteria points. In all instances of significant non-linear effects, the model with the non-linear term was better according to AIC than the model with a linear term.

To explore the relationship between juvenile affiliative interactions within a dyad (i.e. grooming, playing, sitting close), and partner attributes (i.e. kinship, age difference, rank difference) I used generalized linear mixed models (R package “lme4,” function “glmer” (Bates, Maechler, Bolker, & Walker, 2014). Because many within-group dyads never interacted in a given period, the dyadic dataset was extremely zero-inflated (shown in N’s of Tables S3.3–4 vs. S3.5–6). For this reason, I created two types of models to analyze patterns of dyadic interaction. First, I used kinship (estimated r values), age difference, and rank difference to predict the occurrence (0,1) of a given type of interaction. Second, including only dyads that interacted in a given period, I used the same dyadic attributes to predict the proportion of shared observation time that a dyad spent in a given type of interaction.

I used six modifications of the dyadic dataset when modeling patterns of dyadic affiliation. The first included all unique within-group dyads that included a juvenile subject. The second dataset included dyads with at least one male subject as a member (a “male focused” dataset) and the third, at least one female subject (a “female focused” dataset). Lastly, to control for the influence of mother-offspring interactions on patterns of dyadic affiliation, I ran models on datasets that included vs. excluded mother-offspring dyads. In total, I ran 36 mixed models to examine dyadic affiliation: 2 sets analyzing presence/absence and magnitude of interaction; on 3 response variables (playing, grooming, and sitting close); using 6 modified datasets (all dyads, male subjects and partners, female subjects and partners; each including vs. excluding mother-offspring dyads).

I modeled the occurrence of dyadic affiliation in each period using a binomial error structure with a logit link. Because shared time spent affiliating was positively skewed across dyads, I modeled these responses using either gamma or log-normal error distributions, as best allowed parameters to be estimated (described in Tables S3.5–6). In each model, I included three random effects: dyad ID and each dyad member assigned randomly as partner 1 or 2 (as in e.g. Gomes et al., 2009). I repeated random partner assignments in each dataset 1000 times, and then averaged the coefficients and standard errors of each predictor among the 1000 results. I assessed collinearity in all models with the variance inflation factor of each variable, using a function modified to assess VIFs for mixed effects models (Frank, 2014). For both generalized additive and generalized linear models, I assessed goodness of fit by calculating the change in AIC between models with vs. without fixed effects (Nakagawa & Schielzeth, 2013).

Lastly, I assessed the adjusted repeatability, or consistency in inter-individual differences apart from confounding factors, in juvenile social variables using a generalized linear mixed effects model to calculate R, the intra-class coefficient ("rptR" package in R (Nakagawa & Schielzeth, 2010). Linear mixed models assess what proportion of behavioral variation among individuals occurs between individuals, while controlling for factors, such as life history, demographic, and ecological variables, that might account for behavioral variation apart from clustered observations (e.g. by individual ID). In each model, I included variables that significantly influenced behavioral outcomes in GAM models as fixed effects. Among error distributions available in "rptR", I chose to model all behavioral responses using Poisson errors, offsetting number of minutes observed in a given behavior by the log of total minutes observed, and number of social partners and frequencies of agonism by the log of individuals' average shared time observed. Models included group and subject ID as random effects. I assessed significance in repeatability statistics using 1000 randomizations of behavioral matrices (subject x period observations) and confidence intervals of repeatabilities using 1000 parametric bootstraps, without replacement.

Results

Social activity budgets, partner number, and agonism

Overall, juvenile blue monkeys averaged only 2.3 ± 3.1% (N = 162 subject-periods) of observation time playing, 5.2 ± 3.1% sitting close to partners, and 4.3 ± 3.6% grooming (Table S3.1, Fig. S3.2). Subjects averaged 4.3 ± 4.1 play partners, 13.7 ± 5.9 sitting partners, and 4.9 ± 3.1 grooming partners per 2-month period. Juveniles gave agonism at a rate of 0.16 ± 0.17 events/hour, and received agonism at 0.3 ± 0.3 events/hour.

Age and sex had strong effects on almost all behavioral variables. Males spent more time playing than females, but less time sitting close or grooming (Fig. 3.1a–c, Table S3.2a–c). Males also had more play partners, but fewer sitting and grooming partners than females (Fig. 3.2a–c, Table S3.2d–f). There was a weak sex difference in agonism given, whereby males gave agonism slightly more often than females, however any difference between males and females in rates of agonism *received* did not reach significance (Fig. 3.3a–b, Table S3.2g–h).

Although age had some universal effects on behavior, its effect frequently varied by sex. Both sexes increased the amount of time they spent sitting close to partners as they aged (Fig. 3.1b, Table S3.2b). Females spent more time grooming as they grew older, whereas males appeared to spend less time grooming (Fig. 3.4a, Table S3.2c). Surprisingly, play time did not decrease with age among male or female juveniles (Fig. 3.1a, Table S3.2a); however, the number of play partners did decrease with age, and more sharply for females than males (Fig. 3.2a, Fig. 3.4b, Table S3.2d). Similarly, females increased the number of grooming partners as they grew older more than males did (Fig. 3.4c, Table S3.2c). Both males and females participated more in agonism with age, giving and receiving agonism at higher rates (Fig. 3.3, Table S3.2g–h).

Maternal rank and number of maternal kin had few effects on juvenile social behavior. Juveniles with higher-ranking mothers sat close to more partners than juveniles of lower-ranking mothers (Fig. 3.2b, Table S3.2e). As predicted, rates of agonism given and received did vary by maternal rank, such that juveniles with higher-ranking mothers gave more and received less agonism than juveniles with lower-ranking mothers (Fig. 3.3, Table S3.2g–h). Juveniles with more maternal kin also received less agonism (Fig. 3b, Table S3.2h), however number of maternal kin did not influence any other behavior or number of partners.

Several behavioral variables varied seasonally in relation to the availability of ripe fruit (FAI) and rainfall. Time sitting close, number of grooming partners, and rates of agonism given and received all varied in a non-linear manner in relation to FAI, decreasing as ripe fruit became more available, but then increasing when ripe fruit was most abundant (Fig. 3.1b, 3.2c, 3.3, Table S3.2b, f, g, h). FAI had a simple linear relationship with number of play partners and number of sitting partners, such that juveniles played with more partners and rested with fewer partners as ripe fruit became more available (Fig. 3.2a–b, Table S3.2d–e). Rainfall generally decreased play and sitting close: juveniles spent less time playing and sitting close to partners (Fig. 3.1a–b, Table S3.2b–c), and similarly played and sat close to fewer partners, as rainfall increased (Fig. 3.2a–b, Table S3.2d–e). Because rainfall and fruit abundance did not co-vary exactly (Fig. S3.2) and were both included in the same GAMs, each likely had its own independent influence on number of play and sitting partners.

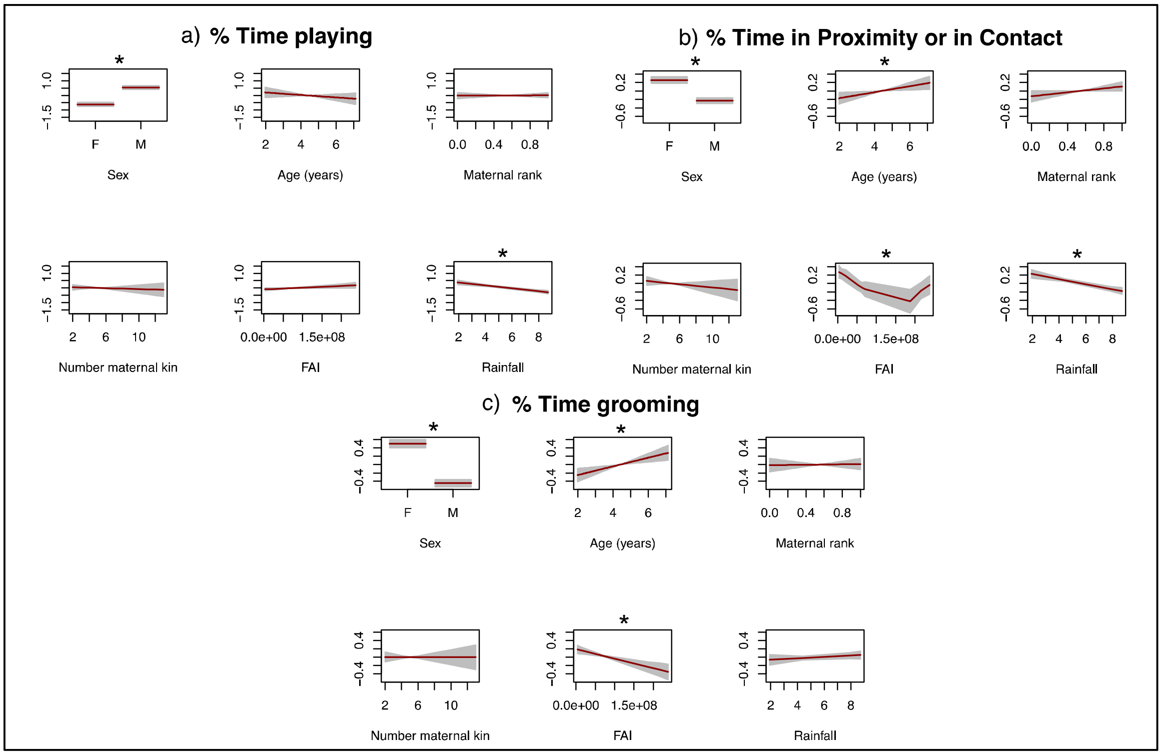

Figure 3.1. Variation in juvenile social activity budget according to life history, socio-demographic, and ecological factors using generalized additive models. Trend lines are the fitted value of the partial variation of the response a) %Time playing, b) %Time in 1 m proximity or in contact, and c) % Time grooming, explained by a given predictor variable (sex, age, maternal rank, etc.) and shaded regions are standard errors. * Indicates significant effect. N = 162 subject – periods.

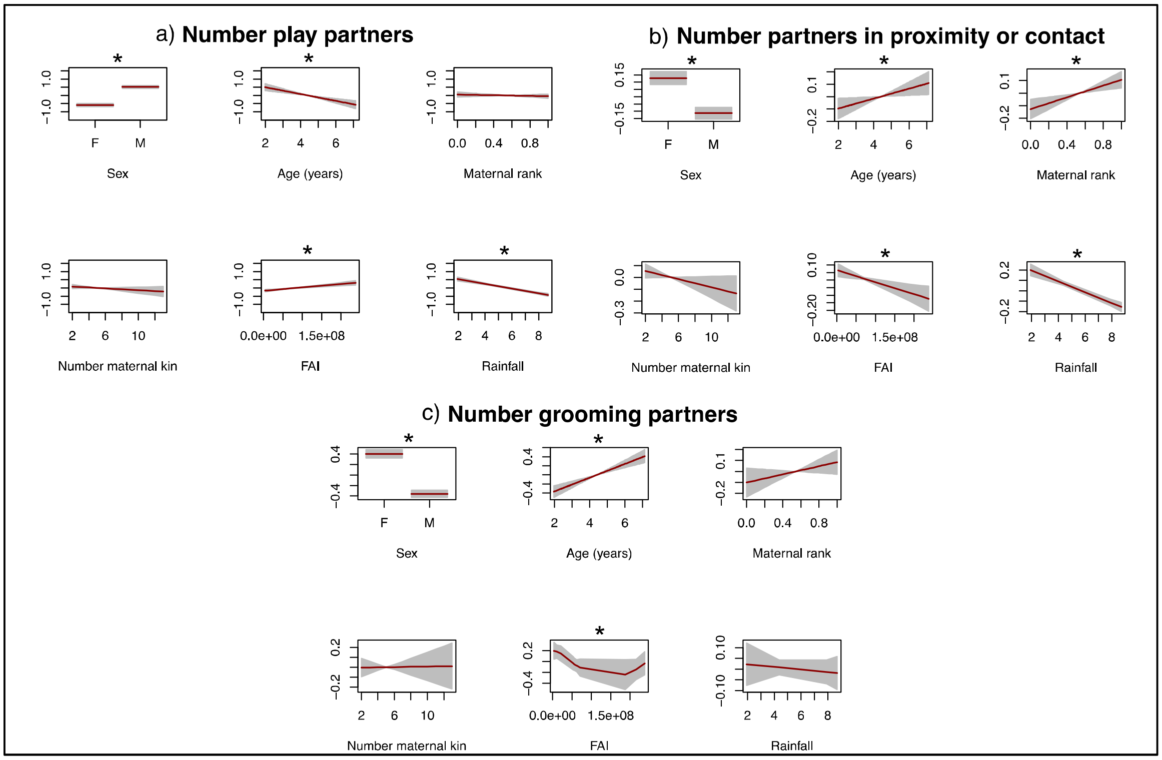

Figure 3.2. Variation in juvenile social partner numbers according to life history, socio-demographic, and ecological factors. Trend lines are the fitted value of the partial variation of the response a) Number play partners, b) Number partners in 1 m proximity or in contact, and c) Number grooming partners, explained by a given predictor variable (sex, age, maternal rank, etc.) and shaded regions are standard errors. * Indicates significant effect. N = 162 subject – periods.

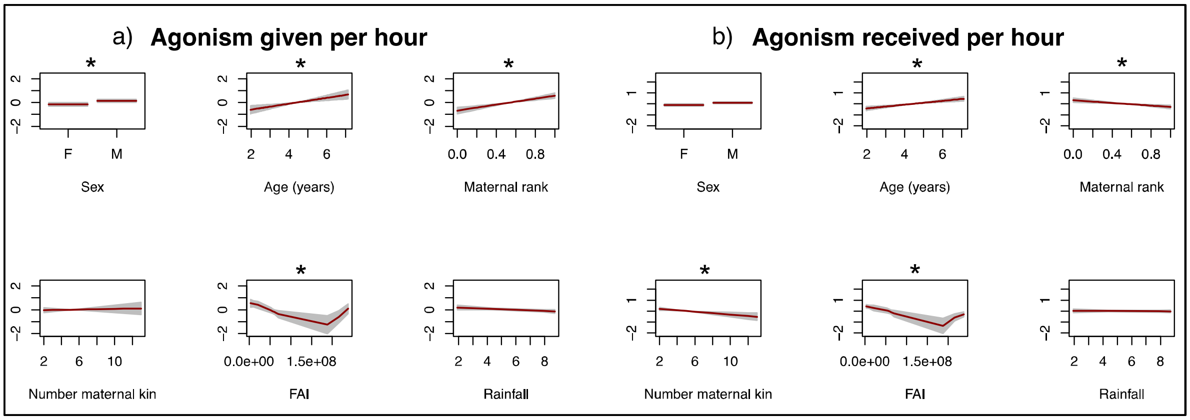

Figure 3.3. Variation in juvenile rates of agonism according to life history, socio-demographic, and ecological factors. using generalized additive models. Trend lines are the fitted value of the partial variation of the response a) rate of aggression given per hour and b) rate of aggression received per hour, explained by a given predictor variable (sex, age, maternal rank, etc.) and shaded regions are standard errors. * Indicates significant effect. N = 162 subject – periods.

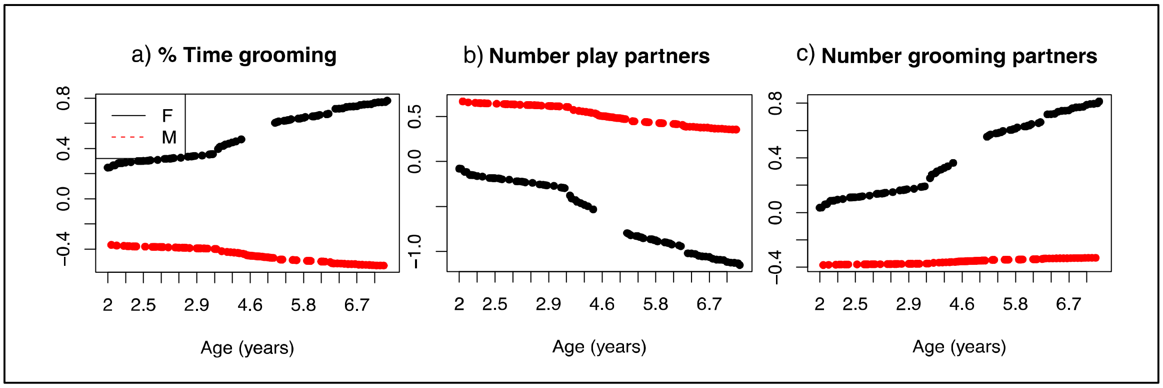

Figure 3.4. Age influence on juvenile social activity and partner number by sex. Mean values of the partial variation of the responses (a-c) fitted by Generalized Additive Models. Only significant relationships shown.

Partner preferences in dyadic interactions

Kinship, age difference, and rank difference had several effects on the occurrence of affiliation within dyads (Fig. 3.5, Tables S3.3–4), and among partners that did affiliate, the amount of time doing so (Fig. 3.6, Tables S3.5–6)**.** Few results differed when datasets included vs. excluded mother-offspring pairs. To more generally represent juvenile social tendencies with non-mothers, I provide figures from models excluding mother-offspring dyads, though all results are available in supplementary tables (Tables S3.3–6). Further, while Fig. 3.5 represents the influence of all dyadic attributes on the occurrence of affiliation, Fig. 3.6 shows only the significant relationships (in either male- or female-focused datasets) between amount of time that partners spent affiliating and partners' relative attributes.

Kinship increased the odds of play only among males and their partners, and only when excluding mother-offspring dyads (Fig. 3.5a, Table S3.3-4). For both male and female-focused datasets, the odds of play occurring between a juvenile and its partner were lower as their age gap increased (Fig. 3.5a, Tables S3.3-4). Rank difference between partners decreased the odds of play more weakly than difference in age. When I considered male- vs. female-focused data sets, rank difference lowered the odds of play only for female-focused dyads. Unlike occurrence models, no dyadic attributes influenced the amount of time partners spent playing with one another (Tables S3.5-6).

Juvenile subjects were more likely to sit close to partners that were more closely related or were more similar to themselves in either age or rank (Fig. 3.5b, Tables S3.3-4). These patterns were consistent whether mother-offspring dyads were included or not (Tables S3.3-4). Similarly, juveniles spent more *time* sitting close to partners who were more closely related (Fig. 3.6b, Tables S3.5-6). Despite having higher odds of sitting close with like-aged partners, juveniles that did sit with partners spent more time sitting with differently-aged partners (Fig. 3.6a-b, Tables S3.5-6). Female-focused dyads followed these same patterns, but among male-focused dyads (including mother-offspring dyads), the effect of age difference on time sitting close was not significant (Table S3.5). Also, while rank difference decreased the *occurrence* of sitting close, differences in rank did not influence time spent sitting close (Tables S3.5-6).

Similar to sitting close, the odds of juveniles grooming with partners increased if they were close in age and relatedness (Fig. 3.5c, Tables S3.3-4, whether including or excluding mother-offspring dyads). These overall results masked some differences between the sexes. Relatedness and a larger age gap were associated with more grooming time for juvenile females and their partners, both when including and excluding mother-offspring dyads (Fig. 3.6c–d, Tables S3.5-6). For dyads including a juvenile male, however, relatedness increased grooming time only if mothers were included as partners (Table S3.5), and age difference had no effect (Tables S3.5-6). Rank differences decreased the odds of grooming, but this effect disappeared for male juveniles if mother-offspring dyads were excluded (Fig. 3.5c, Tables S3.3-4). Among dyads that did groom, rank difference did not influence the amount of time spent grooming, whether including mothers or not (Tables S3.3-4). The maximum VIF in all models, using either male- or female-focused datasets or datasets including or excluding mothers, was 1.75.

Repeatability

The only behavioral variables that demonstrated significant inter-individual differences across periods were rates of agonism given and received, although number of grooming partners was near significantly repeatable (Table S3.7). The rarity of repeatable social behavior occurred despite controls for life history, socio-demographic and ecological variables that explained variation in behavior in general additive models.

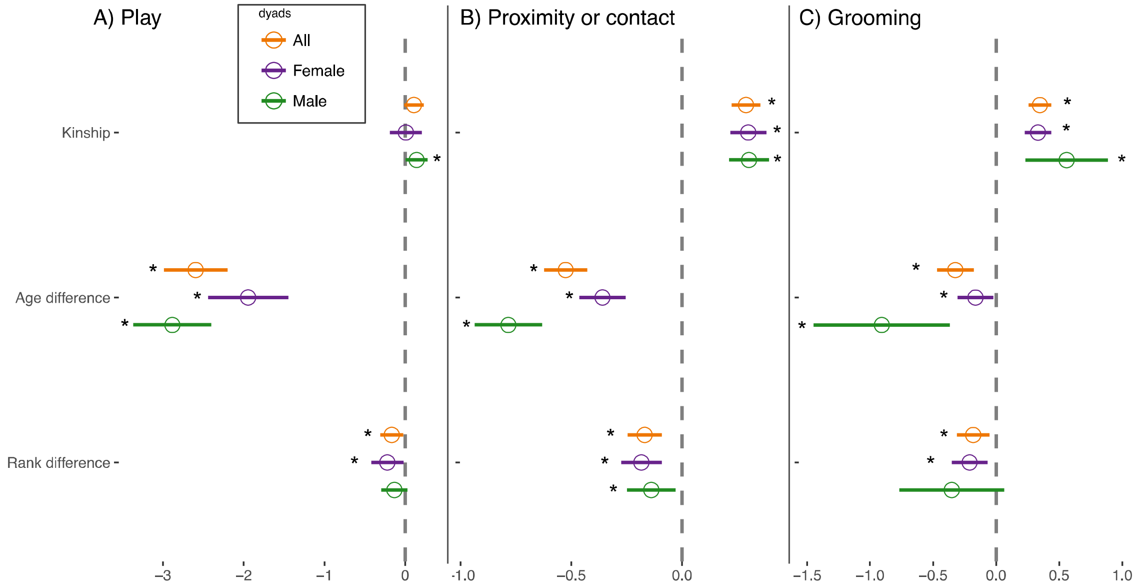

Figure 3.5. Coefficient plot of the influence of kinship, age difference, and rank difference on odds of a dyadic interaction: A) playing B) sitting close and C) grooming. Circles represent maximum-likelihood estimated parameters of predictor variable and horizontal lines indicate 95% CIs. Parameters estimated for data sets including all dyads (orange), female juveniles and their partners (purple), and male juveniles and their partners (green). * indicates significant effect.

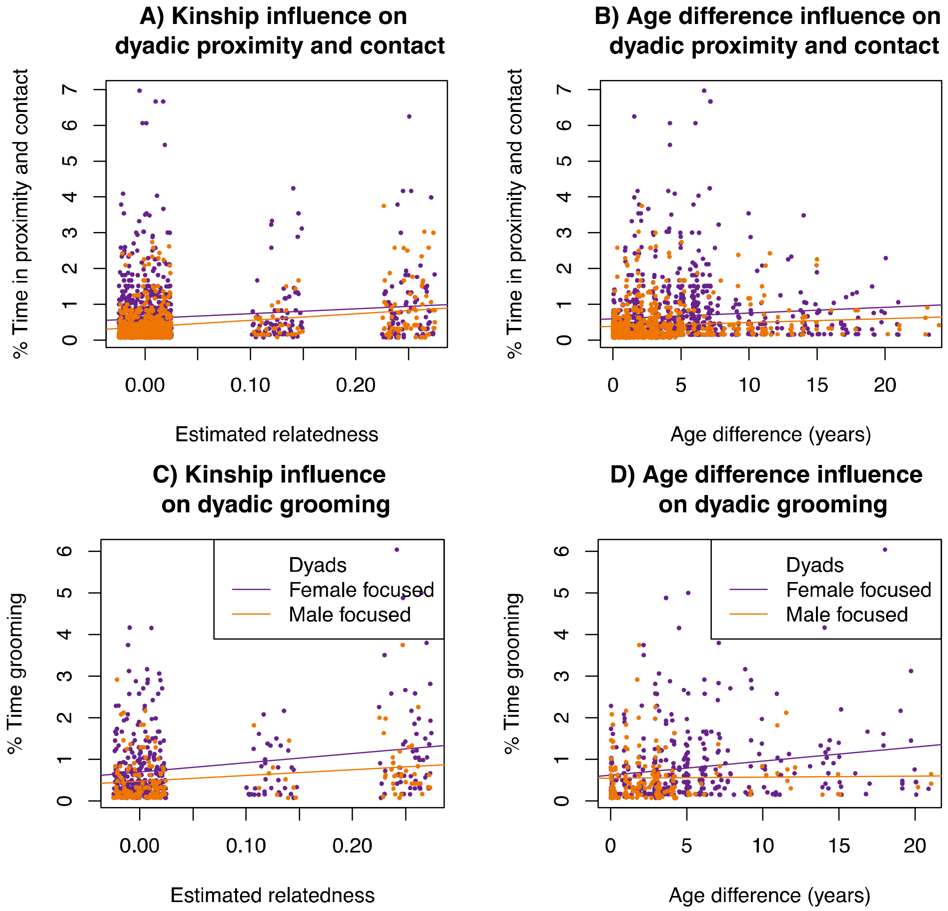

Figure 3.6. Relationships between relative attributes and percentage of observation time a dyad spent in a given behavior, *excluding* mother-offspring dyads. Trend lines created with simple linear regression, unlike statistical models using GLMM. Male juveniles and partners plotted in orange, females and partners plotted in purple, and points jittered along estimated relatedness axes. Only significant relationships shown, except C & D) kinship and age difference influence dyadic grooming only among female-focused dyads.

Discussion

Playing

i. Time playing, play partner diversity

Male juveniles spent more time playing and played with more partners than females did, as is often seen among social mammals where males disperse and compete physically for reproductive access to females (Fagen, 2003; Maestripieri & Ross, 2004; Paukner & Suomi, 2008; Power 1999; for exceptions see Graham & Burghardt, 2010; Rowell & Chism, 1986). Male-biased play supports the hypothesis that play is preparation for novel social interactions, motor development, and future physical aggression (Spinka et al., 2001), which adult male blue monkeys regularly engage in when competing for access to mates and/or the reproductively dominant position of resident male once they have dispersed (Cords, 2004; Roberts & Cords, 2015). While there is some evidence that "winning" play bouts during immaturity corresponds with higher dominance status in adulthood (e.g. yellow-bellied marmots, Blumstein et al., 2013), a higher frequency of play does not necessarily translate into obtaining social positions with higher reproductive success (e.g. meerkats, Sharpe, 2005a). On a proximate level, sex-differences in play may be driven by differential levels of sex-steroid hormones such as testosterone, which is strongly associated with aggressive behavior, social dominance, and often corresponds with greater rough and tumble play within each sex (Graham & Burghardt, 2010; Pedersen, Glickman, Frank, & Beach, 1990). These proximate and ultimate drivers of male-biased play may also contribute to the pattern in which male juveniles gave (but did not receive) more aggression than females. That males give more aggression than females perhaps foreshadows males' social dominance over females in adulthood.

Surprisingly, neither males nor females appeared to reduce play time with age, unlike other species (Pusey, 1990; Rowell & Chism, 1986; van Noordwijk et al., 2003). Nevertheless, both sexes decreased their number of play partners, demonstrating some shift in priorities away from social play as individuals approached sexual maturity. As rates of aggression given increased with age, older juveniles may be transitioning from practice in play to application in competition (Barale, Rubenstein, & Beehner, 2015). The number of partners with whom females played declined at a faster rate than males as subjects grew older, again demonstrating females' overall muted interest in play relative to males, perhaps because it does not prepare females as well for adult life. Females' more rapid decline in play partners with age is somewhat similar to patterns in female geladas, who stopped playing at a younger age than males (Barale et al., 2015).

ii. Play partner preferences

Juvenile males and females were more likely to play with individuals closer in age to themselves, similar to other primates (Barale et al., 2015; Fairbanks, 2003; Palagi, Antonacci, & Cordoni, 2007) and non-primate species (Byers, 1980; Nunes et al., 2004; Rothstein & Griswold, 1991; Thompson, 1996). While attraction to peers may simply indicate that adults rarely play, it could also support the hypothesis that play functions, in part, for individuals to assess their own physical ability (Thompson, 1998). However, because no relative attributes increased the amount of time that juveniles played with partners, self-assessment is perhaps neither the exclusive nor the predominant function of play in juvenile blue monkeys.

While all juveniles preferred to play with similarly aged partners, only males and their play partners were more likely to be closely related. Preferences for closer kin may highlight a balance that males seek between novelty vs. familiarity during play. Closer kin are likely to be more predictable partners and possibly more tolerant if play fighting goes awry. Therefore, unpredictable play sequences would occur under relatively safe circumstances. If closer kin are also more similar in physical ability, a preference for playing with kin may also support play as a form of self-assessment (Thompson, 1998). A preference for kin as play partners contrasted with patterns seen in juvenile geladas and vervet monkeys (Barale et al., 2015; Fairbanks, 2003), but was similar to several other primate species where juveniles play preferentially with kin (Cheney, 1978; Glick, Eaton, Johnson, & Worlein, 1986; Kulik et al., 2015).

That female juveniles were more likely to play with partners of similar rank was curious. While rank similarity could correspond with relatedness, this was not the case, as relatedness was statistically controlled for and only male juveniles were more likely to play with closer kin. Attraction to similarly ranked partners among dyads involving females could indicate either of two scenarios. First, females may choose partners whose mothers are more similar in power to their own because they are more risk-averse than males during play – as play may go awry and escalate into true aggression. Alternatively, *males* may avoid the possibility of a relatively more powerful mother intervening on her daughter's behalf, and engage females that are more similarly ranked. Because aggressive interventions are so rare in blue monkeys, I do not know whether adult females favor male vs. female offspring in aggressive conflicts. Other more fine-scale data on initiations and retreats in play bouts could also reveal whether preference for similarly ranked play partners is driven by males or females.

iii. Seasonality in time playing and play partners

Time spent playing and number of play partners also varied seasonally. Decreases in play time and partner number during rainier periods probably resulted from rainfall's influence on access to preferred play substrates. Juveniles often played on or near the ground, particularly in dry areas (pers. obs.). Further, during the hot and dry season, individuals occupied lower, cooler levels of the canopy, making the ground more easily accessible. Juveniles played with more partners when local fruit availability was higher, likely because fruit availability translates into higher energy balance among juveniles (Chap. 4). Food availability, and corresponding energy balance, has a well-established influence on rates of social play, with individuals often decreasing play when energy is limited (Krachun, Rushen, & de Passillé, 2010; Loy, 1970; Muller-Schwarze, Stagge, & Muller-Schwarze, 1982) and increasing it when in more positive energetic states (Sharpe et al., 2002). These results both agree and contrast with findings in geladas, where juveniles spend more time playing when rainfall is higher, probably because rainfall corresponded directly with higher food availability (Barrett, Dunbar, & Dunbar, 1992).

Spatial association and grooming

i. Time sitting close, grooming and diversity of partners

Female juveniles spent more time sitting close with more neighbors, and more time grooming with more partners than males did. These patterns are similar to those reported in other female-bonded primates, such as vervets, geladas, sooty mangabeys, and baboons (Barale et al., 2015; Fairbanks, 2003; Nakamichi, 1989; Pereira, 1988b; Raleigh et al., 1979; Range, 2006; Rowell & Chism, 1986; van Noordwijk et al., 2003). These findings confirm an earlier report by Cords *et al*. (2010) on this population, though Cords *et al*. found no sex differences in number of association partners. As this study's records of association were based on closer association, i.e. either within 1 m or in bodily contact vs. within 3 m with no contact, this contrast suggests that females associate intimately with more partners than males but are perhaps not more integrated at a slightly larger spatial scale. Juvenile female patterns of association and grooming support the hypothesis that individuals of the philopatric sex make social choices both to practice the overtly affiliative behavior that constitutes a large part of adult social life and invest in relationships with potentially life-long social partners (Cords et al., 2010; Fairbanks, 2003; O'Brien & Robinson, 2003; Strier, 2003). Whether females are practicing social interaction vs. investing in enduring relationships would require a longitudinal study to see if 1) females that interacted more as juveniles were more competent socially as adults, or 2) the strength of females' ties with preferred partners persisted into adulthood, as seen in vervet and capuchin monkeys (Fairbanks, 2003; O'Brien & Robinson, 2003). Nevertheless, practice and investment are likely not to be mutually exclusive functions of affiliation for juvenile females. These sex differences in spatial association and grooming behavior were also consistent with a previous study on juvenile blue monkey social behavior, where behavioral sampling was limited to certain seasons of the year (Cords et al., 2010).

While, females spent more time with more neighbors and grooming partners, both sexes increased their social time and the number of partners with age. This increase may reflect juveniles growing more familiar and comfortable with diverse group members or vice versa. Still, this pattern contrasted to that seen in juvenile long-tailed macaques, where individuals appeared to aggregate in a "main party" when traveling and foraging, and younger juveniles were more likely to be present in this main party (van Noordwijk et al., 2003). The number of partners with whom female blue monkeys groomed varied with age in an opposite but similar pattern to their number of play partners: while both sexes increased grooming partners with age, females increased more steeply than males, adding more grooming partners with each year of age. As novel grooming, but not play, partners are likely to prepare females for adult life, these patterns again demonstrated the different priorities and life trajectories of males and females (Cords et al., 2010).

ii. Preferences for sitting and grooming partners

In general, juveniles appeared more likely to sit close and groom with partners that were similar to them. Kinship and age similarity were important in predicting juvenile spatial and grooming partners, for both males and females. Rank similarity, while increasing the odds of spatial association in both sexes, increased only the occurrence (but not the duration) of grooming between females and their partners. This trend for juveniles to prefer affiliative partners similar to themselves suggests that homophily serves not only to allow self-assessment during play, but is more generally important for juveniles. Homophily based on age and kinship strongly structures group-wide affiliative networks in yellow-bellied marmots, and may be a source of stability and predictability among group members (Wey & Blumstein, 2010). Associating with similar partners can also increase reciprocity between partners, in grooming or other forms of cooperation (de Waal & Luttrell, 1988), as in bats and chimpanzees (reviewed in Massen et al., 2010). For juveniles, similarly aged and ranked partners may also be more tolerant of one another's presence or provide mutual practice in grooming behavior. I further discuss the adaptive benefits of associating with kin below.

While juveniles were more likely to sit close and groom with like-aged partners, both males and females *spent more time* associating with, and females spent more time grooming with, older partners. These patterns were not driven by preferences to sit close and groom with mothers. As older partners were primarily adult females, juveniles may be more interested in associating spatially with established and core members of their social group, who are potentially important sources of social and ecological knowledge (Galef & Laland, 2005; McComb et al., 2011; Sherrow, 2008). In terms of grooming, males spent more time grooming older partners only when mothers were included, indicating that while juvenile females groom with non-mother adult females, juvenile males do not. These grooming patterns generally concur with those of Cords *et al*. (2010), who found that males preferentially groomed peers while females avoided them. Females are perhaps more interested than males in partners that are more experienced at grooming and with whom they may spend all their lives interacting. Males, in contrast, focus their grooming on the individuals that best prepare them for their adult life, i.e. their highly tolerant mothers and the peers with whom they play.

Juvenile females' preference, and males' lack of preference, for similarly ranked grooming partners may reflect the particularly large divergence in adult sex-typical social behavior in this species. In sooty mangabeys, which form multi-male/multi-female groups, both male and female juveniles preferred to sit close with similarly ranked adult females, although male preferences were weaker relative to females' and males showed no rank preferences when associating with peers (Range, 2006). Generally in female philopatric species, relative rank may be a less salient feature in determining male patterns of overt affiliation because males will eventually disperse, losing their natal group relationships (e.g. Kulik et al., 2015). In blue monkeys, adult males rarely need to behave subordinately, spending most of their time either as the dominant individual of a social group or largely solitary as a bachelor. Adult male social roles may make relative rank less consequential to their preferences for affiliative partners during development, relative to male juveniles of other species. By contrast, female juveniles in female-philopatric species will maintain their relative ranks for a much longer period than males, if not for life, and in multi-female groups, they will perpetually interact with potential competitors. The tendency for female juveniles to groom more similarly-ranked partners was consistent with the finding of Cords *et al.* (2010), where female juveniles disproportionately groomed adult females from the middle of the dominance hierarchy, such that females with high-maternal rank groomed down the hierarchy and females with low-maternal rank groomed up.

Kinship was the only dyadic attribute that simultaneously increased both the odds and the amount of time that juveniles sat close or groomed with a partner (except for, notably, not increasing the amount of time males groomed with non-mother partners). Preferences for kin as sitting and grooming partners were generally evident when excluding mother-offspring interactions, indicating that even more distantly related kin (siblings, aunts, grandmothers) are important social partners for both male and female juveniles. The strong positive influence of kinship on juveniles' sitting and grooming with partners concurs with trends among adult females in this population, who prefer to sit close and groom with maternal kin (Cords & Nikitopoulos, 2015). Kin-biased association is widespread in social mammals (Silk, 2007), as familiarity among kin may increase tolerance, cooperation, and reciprocity in affiliative behavior (Chapais, 2001;

Cords & Nikitopoulos, 2015; Smith, 2014). Immature individuals, who are smaller and less experienced physically and socially, may benefit particularly from such tolerant and positive associations and so preferentially interact with kin in many ways (e.g. grooming and playing, Glick et al., 1986; Kulik et al., 2015). Still, despite favoring kin in association and affiliation, the presence of more maternal kin in a social group did not influence either the amount of time or the number of individuals with whom juveniles sat close or groomed, suggesting perhaps that juveniles seek a target amount of positive social interaction from kin, that even few relatives can fulfill.

Influence of maternal rank and presence of kin on social activity budget

Subjects' own maternal dominance rank influenced social behavior less pervasively than their maternal rank relative to social partners'. Specifically, individual maternal rank influenced only the number of partners with whom juveniles sat close and individual rates of aggression given and received, whereas relative ranks influenced preference for sitting partners in both sexes, and preference of play and grooming partners in females. That juveniles with higher maternal rank gave more and received less aggression was expected, as adult dominance ranks are themselves characterized by aggressive and submissive behavior, and dominance relations among juveniles in this and other gregarious species regularly follow those of their mothers (Cheney, 1977; Engh et al., 2000; Horrocks & Hunte, 1983; Klass & Cords, 2015). Juveniles of higher-ranking mothers may "get away" with intimidating others because their mothers are more likely able to dominate their victims. As aggression occurs primarily over fruit, an energy rich resource, there is incentive for juveniles to take advantage of their mother's social position and aggress others (Klass & Cords, 2015; Pazol & Cords, 2005). Given that juveniles of low-ranking mothers receive agonism at higher rates, they are perhaps motivated to avoid more social partners than juveniles of high-ranking mothers, leading them to sit close to fewer partners than juveniles of high-ranking mothers. Although blue monkeys do not appear to form central aggregations of group members, rank-related patterns of juvenile association may resemble those seen in adult female long-tailed macaques, where low-ranking females are also more likely to forage on the periphery of a main party (van Schaik & Van Noordwijk, 1986).

Seasonality changes in affiliation and aggression

Several results together suggested that affiliation and aggression were closely related aspects of juvenile sociality. Juvenile blue monkeys' number of neighbors, grooming partners, and rates of aggression given and received all varied in the same non-linear pattern with FAI, such that social interactions and partners were fewer when the availability of ripe fruit was intermediate, but were highest when ripe fruit was at its minimum or at its peak. Both scarce and highly abundant fruit may be clumped in the environment such that it attracts individuals to the same area, leading to opportunities for both friendly and aggressive interactions over food and space. For example, clumped resources during low food abundance increased aggregations in adult female Sumatran orang-utans (Sugardjito, te Boekhorst, & van Hooff, 1987) and social ties increased in intensity during food scarcity in adult female baboons (Henzi et al., 2009). However, adult female blue monkeys appeared to spread out while foraging and feeding, though not groom less, when fruit availability was lowest (Pazol & Cords, 2005). The trees of the species that contributed most strongly to peak fruit in all social groups' home ranges, *Harungana madagascariensis*, were not rare or highly clustered in the environment, however they did frequently occur on the edge of the forest in highly exposed areas where individuals often engaged in long bouts of resting, feeding, and grooming (pers. obs.). The microhabitat offered by this tree species therefore may increase social partner exposure and visibility, and consequently both positive and negative social interactions among juveniles and groupmates. Interestingly, rates of aggression among adult female blue monkeys did not vary with food availability (Pazol & Cords, 2005). This contrast with juvenile rates of aggression concurs with previous findings that juvenile blue monkeys appear to experience feeding competition more intensely than adults (Cords *et al.* 2010).

General absence of consistent inter-individual differences

Published analyses of repeatable between-individual differences in affiliative behavior are rare, and even fewer have explored repeatable differences in juveniles (Barale et al., 2015; Bell et al., 2009; Vander Wal et al., 2014). Unlike geladas, where juveniles ranked similarly among peers in the amounts of time playing and grooming over a two-year period (Barale et al., 2015), juvenile blue monkeys did not demonstrate repeatable differences in any affiliative behavior. These results may contrast with the study on geladas because of different statistical techniques, namely Barale *et al.* (2015) tested a simple rank correlation between individual observations made over time, not looking at actual *between vs. within* individual variation nor controlling for factors that can make inter-individual differences in social behavior more pronounced, such as sex. In Kakamega blue monkeys, adult females demonstrated repeatable differences in the intensity of their close annual ties, their time grooming with groupmates, and time associating with other adult females over several years (2–8) (Chap. 2 and 5). Their contrast with juveniles could suggest that repeatability emerges when data for observations are collated over longer periods and when individuals have more observations. Additionally, this contrast could suggest that different aspects of affiliation are more repeatable than others (e.g. intensity of close ties vs. number of ties), *or* that juveniles become more stable in their behavioral phenotypes with age. Aside from affiliation, juvenile blue monkeys did show repeatable differences in the amount of aggression they gave and received, even when controlling for other stable social factors such as maternal dominance rank and social group. Repeatable rates of aggression suggest that aggression is a regular and stable part of social life in juvenile blue monkeys.

Summary and Future Directions

Overall, as expected, juvenile social behavior varied strongly by age and sex. Nevertheless, there were several commonalities that drove both male and female preferences for social partners, such as similarity in kinship, age, and, though less pervasively, dominance rank. Patterns of social preferences were largely consistent whether including or excluding mothers as potential partners. Interestingly, time spent in a given social activity and number of partners engaged in that activity did not always follow the same patterns in relation to life history, demographic, or ecological variables. For example, time playing did not decrease sharply with age, but number of play partners did. This suggests that the time one spends socializing and one's diversity of social partners may be distinctly different aspects of sociability. Similarly, the influence of kinship, age, and relative dominance rank did not always influence the amount of time juveniles spent interacting with a given partner as strongly or even in the same direction as it did the odds of a juvenile and its partner interacting. For example, juveniles as a whole were more likely to sit close with similarly aged partners, but those that did sit close spent more time associating with partners that were older than themselves.

Measures of juvenile sociality demonstrated a large degree of within individual variation over time. Juveniles varied in their social behavior according to the availability of ripe fruit, rainfall, or both. Further, even when controlling for such external seasonal factors, individuals differed repeatably only in their rates of aggression given and received. Covariation of affiliative and aggressive behavior with available fruit suggested that juveniles might experience affiliation and aggression as two sides of a single social coin, with both closely related to feeding competition. As expected, evidence suggested that juvenile blue monkeys experience feeding competition more strongly than adults.

The results of this study confirm previous studies that juveniles indeed behave in ways that appear preparatory for species and sex-typical roles in adulthood, and further demonstrate that juvenile social behavior can fluctuate dramatically according to seasonal changes in the environment. Future studies may look to explore the development of individual stability (repeatability) in different types of social behavior. As primates' particularly slow pace of life perpetually hinders longitudinal studies of social development, investigators running long-term field sites may consider adding juvenile subjects to their data collection protocols to pursue this aim. Comparative analyses could also explore variation in developmental timing and degree of differentiation in social behavior between the sexes in relation to degree of sexual dimorphism in adult-typical behavior. Sex differences in overt affiliative behavior, such as grooming, may emerge earlier in species where, for example, adult males are largely asocial vs. species where adult males affiliate with coalitionary allies. Also, differences in maternal rank may drive grooming interactions only in the sex that regularly navigates stable dominance relationships as adults, e.g. males and females in sooty mangabeys but only females in blue monkeys. Of course, such meta-analyses should seek to standardize the degree of intimacy of various proximity measures, given that association distances varying in intimacy could differentially vary by sex even within a species.

Supplemental Information

Table S3.1. Mean and standard deviation of juvenile behavioral variables calculated across each subject's focal follows collated per period: All = all subjects, M = males, and F = females. N = 40–41 subjects per period, 21–22 males, 19 females.

Period	Sex	Time Playing		Time sitting close		Time grooming		Number play partners		Number prox partners		Number groom partners		Rate ago given		Rate ago received	
		mean	sd	mean	sd	mean	sd	mean	sd	mean	sd	mean	sd	mean	sd	mean	sd
p1	All	1.14	1.87	5.82	3.41	5.52	4.40	1.65	2.07	11.70	3.72	4.67	2.72	0.21	0.21	0.39	0.34
p1	F	0.15	0.39	7.43	3.55	8.25	4.57	0.26	0.56	12.58	3.96	6.21	2.97	0.16	0.19	0.33	0.23
p1	M	2.03	2.23	4.36	2.58	3.05	2.33	2.90	2.14	10.90	3.39	3.29	1.49	0.25	0.22	0.45	0.41
p2	All	1.69	3.16	3.87	1.66	4.43	3.48	2.76	2.62	11.10	3.88	4.68	2.32	0.09	0.11	0.22	0.18
p2	F	0.17	0.35	4.45	1.94	6.76	3.67	0.68	1.11	11.47	4.48	6.21	2.12	0.07	0.09	0.16	0.15
p2	M	3.00	3.88	3.37	1.20	2.43	1.56	4.55	2.20	10.77	3.37	3.36	1.56	0.11	0.12	0.27	0.18
p3	All	3.04	3.21	4.73	2.75	3.13	2.97	6.12	4.09	13.41	4.77	4.44	2.94	0.12	0.15	0.18	0.29
p3	F	0.92	1.18	5.66	3.02	4.94	3.26	3.53	2.93	15.11	4.95	6.84	2.39	0.13	0.13	0.16	0.25
p3	M	4.88	3.30	3.92	2.25	1.56	1.45	8.36	3.62	11.95	4.18	2.36	1.36	0.11	0.16	0.19	0.33
p4	All	3.38	3.32	6.57	3.70	4.18	3.05	6.85	4.63	18.52	7.37	5.95	4.19	0.21	0.19	0.31	0.20
p4	F	1.22	1.18	8.95	3.78	6.27	2.96	4.16	3.37	23.00	7.74	8.79	4.30	0.19	0.21	0.29	0.22
p4	M	5.34	3.43	4.42	1.90	2.28	1.52	9.29	4.29	14.48	3.96	3.38	1.75	0.22	0.17	0.32	0.18
All period mean:		**2.31**	**3.07**	**5.24**	**3.12**	**4.31**	**3.59**	**4.35**	**4.11**	**13.67**	**5.87**	**4.93**	**3.14**	**0.16**	**0.17**	**0.27**	**0.27**

Table S3.2. Influence of life history, socio-demographic, and ecological variables on juvenile social behavior. General additive models, group and subject as random effects. N = 162 subject-periods.

Response	Predictor	Beta	se	CI	P(Beta>null)*	P(Beta<null)
a) Time playing ΔAIC = -24	**Sex (Male)**	**1.15****	0.14	**[0.87, 1.43]**		
	Age	-0.14	0.12	[-0.38, 0.09]		
	Maternal rank	0.01	0.06	[-0.11, 0.12]		
	Number maternal kin	-0.04	0.07	[-0.18, 0.1]		
	FAI	0.09	0.05	[-0.01, 0.19]		
	Rainfall	**-0.27**	0.06	**[-0.39, -0.16]**		
	Age:Sex	0.14	0.15	[-0.15, 0.43]		
b) Time sitting close ΔAIC = -42	**Sex (Male)**	**-0.48**	0.07	**[-0.63, -0.34]**		
	Age	**0.12**	0.05	**[0.02, 0.22]**		
	Maternal rank	0.07	0.04	[0, 0.15]		
	Number maternal kin	-0.05	0.04	[-0.13, 0.03]		
	cs(FAI)	**-0.13†**	0.04	**[-0.21, -0.06]**		
	Rainfall	**-0.16**	0.04	**[-0.24, -0.09]**		
	Age:Sex	-0.13	0.08	[-0.29, 0.03]		
c) Time grooming with ΔAIC = -29	**Sex (Male)**	**-0.94**	0.1	**[-1.13, -0.76]**		
	Age	**0.18**	0.06	**[0.07, 0.28]**		
	Maternal rank	0.01	0.05	[-0.08, 0.1]		
	Number maternal kin	0	0.05	[-0.09, 0.09]		
	FAI	**-0.19**	0.05	**[-0.29, -0.09]**		
	Rainfall	0.05	0.04	[-0.04, 0.13]		
	Age:Sex	**-0.23**	0.1	**[-0.44, -0.03]**		
d) Number partners play ΔAIC = -105	**Sex (Male)**	**1.11**	0.1	**[0.92, 1.29]**	0	1
	Age	**-0.35**	0.08	**[-0.52, -0.19]**	1	0
	Maternal rank	-0.03	0.04	[-0.11, 0.05]	0.732	0.268
	Number maternal kin	-0.07	0.05	[-0.16, 0.03]	0.749	0.251
	FAI	**0.17**	0.04	**[0.1, 0.24]**		
	Rainfall	**-0.39**	0.04	**[-0.48, -0.31]**		
	Age:Sex	**0.25**	0.1	**[0.04, 0.45]**	0.026	0.974
e) Number partners sitting close ΔAIC = -72	**Sex (Male)**	**-0.24**	0.04	**[-0.33, -0.16]**	1	0
	Age	**0.07**	0.03	**[0.01, 0.13]**	0.028	0.972
	Maternal rank	**0.07**	0.02	**[0.03, 0.12]**	0	1
	Number maternal kin	-0.04	0.02	[-0.09, 0]	0.91	0.09
	FAI	**-0.07**	0.02	**[-0.11, -0.02]**		
	Rainfall	**-0.14**	0.02	**[-0.19, -0.1]**		
	Age:Sex	-0.09	0.05	[-0.19, 0]	0.952	0.048
f) Number partners grooming ΔAIC = -19	**Sex (Male)**	**-0.76**	0.08	**[-0.91, -0.61]**	1	0
	Age	**0.26**	0.05	**[0.17, 0.35]**	0.001	0.999
	Maternal rank	0.06	0.04	[-0.02, 0.13]	0.094	0.906
	Number maternal kin	0	0.04	[-0.07, 0.07]	0.658	0.342
	cs(FAI)	**-0.1†**	0.04	**[-0.17, -0.02]**		
	Rainfall	-0.02	0.04	[-0.09, 0.05]		
	Age:Sex	**-0.24**	0.08	**[-0.4, -0.08]**	0.98	0.02
g) Rate agonism given ΔAIC = -34	**Sex (Male)**	**0.31**	0.15	**[0.01, 0.6]**	0.062	0.938
	Age	**0.42**	0.12	**[0.19, 0.66]**	0	1
	Maternal rank	**0.39**	0.08	**[0.24, 0.55]**	0	1
	Number maternal kin	0.03	0.08	[-0.13, 0.2]	0.429	0.571
	cs(FAI)	**-0.24†**	0.08	**[-0.4, -0.08]**		
	Rainfall	-0.13	0.07	[-0.27, 0]		
	Age:Sex	0.06	0.17	[-0.28, 0.39]	0.332	0.668
h) Rate agonism	Sex (Male)	0.21	0.11	[0, 0.42]	0.084	0.916
	Age	**0.29**	0.07	**[0.16, 0.42]**	0.005	0.995

received ∆AIC = -46	**Maternal rank**	**-0.19**	0.06	**[-0.31, -0.07]**	0.994	0.006
	Number maternal kin	**-0.16**	0.05	**[-0.27, -0.05]**	0.981	0.019
	cs(FAI)	**-0.29†**	0.05	**[-0.39, -0.2]**		
	Rainfall	-0.02	0.06	[-0.14, 0.11]		
	Age:Sex	-0.2	0.1	[-0.41, 0]	0.907	0.093

* Null distribution of betas for partner numbers and rates of agonism based on 1000 node permutations of dyadic matrices.

** Predictor variables with significant effects in bold.

† Fruit availability modeled non-linearly with a cubic spline (cs).

Table S3.3. Influence of relative partner attributes on *occurrence* of dyadic affiliation, *excluding* mother-offspring dyads. Binomial regression with logit link, N = 7269 all dyads, N = 3698 female-focused dyads, N = 4132 male-focused dyads.

Dyadic behavior	Predictor	Dyads	Beta*	SE	Odds Ratio	95% CI
Playing ∆AIC = -259	Kinship	all	0.11	0.06	1.11	[-0.01, 0.23]
		female	0.01	0.1	1.01	[-0.19, 0.21]
		male	**0.14****	0.07	1.15	**[0.01, 0.28]**
	Age difference	all	**-2.59**	0.2	0.07	**[-2.99, -2.2]**
		female	**-1.94**	0.25	0.14	**[-2.44, -1.45]**
		male	**-2.88**	0.25	0.06	**[-3.36, -2.4]**
	Rank difference	all	**-0.17**	0.07	0.85	**[-0.31, -0.02]**
		female	**-0.22**	0.1	0.8	**[-0.42, -0.02]**
		male	-0.13	0.08	0.88	[-0.29, 0.03]
Sitting close ∆AIC = -236	Kinship	all	**0.29**	0.03	1.33	**[0.22, 0.35]**
		female	**0.3**	0.04	1.35	**[0.22, 0.38]**
		male	**0.3**	0.05	1.35	**[0.21, 0.39]**
	Age difference	all	**-0.53**	0.05	0.59	**[-0.62, -0.43]**
		female	**-0.36**	0.05	0.7	**[-0.46, -0.25]**
		male	**-0.78**	0.08	0.46	**[-0.94, -0.63]**
	Rank difference	all	**-0.17**	0.04	0.84	**[-0.25, -0.09]**
		female	**-0.18**	0.05	0.83	**[-0.28, -0.09]**
		male	**-0.14**	0.06	0.87	**[-0.25, -0.03]**
Grooming with ∆AIC = -116	Kinship	all	**0.35**	0.05	1.42	**[0.26, 0.44]**
		female	**0.33**	0.05	1.39	**[0.23, 0.44]**
		male	**0.56**	0.17	1.75	**[0.23, 0.89]**
	Age difference	all	**-0.32**	0.07	0.72	**[-0.47, -0.18]**
		female	**-0.16**	0.07	0.85	**[-0.31, -0.02]**
		male	**-0.91**	0.28	0.4	**[-1.45, -0.37]**
	Rank difference	all	**-0.18**	0.07	0.83	**[-0.31, -0.05]**
		female	**-0.21**	0.07	0.81	**[-0.35, -0.07]**
		male	-0.35	0.21	0.7	[-0.77, 0.06]

*Betas, SE, and 95% confidence interval values averaged over 1000 random assignments of partner IDs to random effects.

**Betas and 95% CIs in bold when effect significant.

Table S3.4. Influence of relative partner attributes on <u>*occurrence*</u> of dyadic affiliation, <u>*including*</u> mother-offspring dyads. Binomial regression, N = 7419 dyads, N = 3768 female-focused dyads, N = 4212 male-focused dyads.

Dyadic behavior	Predictor	Dyads	Beta*	SE	Odds Ratio	95% CI
Playing	Kinship	all	0.14	0.09	1.15	[-0.04, 0.32]
ΔAIC = -265		female	-0.02	0.15	0.98	[-0.31, 0.27]
		male	0.19	0.11	1.22	[-0.01, 0.4]
	Age difference	all	**-2.66****	0.2	0.07	**[-3.06, -2.26]**
		female	**-1.99**	0.26	0.14	**[-2.49, -1.48]**
		male	**-2.96**	0.25	0.05	**[-3.45, -2.47]**
	Rank difference	all	**-0.17**	0.07	0.84	**[-0.32, -0.03]**
		female	**-0.23**	0.1	0.8	**[-0.43, -0.02]**
		male	-0.14	0.08	0.87	[-0.3, 0.02]
Sitting close	Kinship	all	**0.44**	0.03	1.56	**[0.38, 0.51]**
ΔAIC = -333		female	**0.37**	0.04	1.44	**[0.28, 0.45]**
		male	**0.54**	0.05	1.72	**[0.45, 0.64]**
	Age difference	all	**-0.53**	0.05	0.59	**[-0.62, -0.43]**
		female	**-0.35**	0.05	0.7	**[-0.46, -0.25]**
		male	**-0.79**	0.08	0.45	**[-0.94, -0.64]**
	Rank difference	all	**-0.17**	0.04	0.84	**[-0.25, -0.09]**
		female	**-0.2**	0.05	0.82	**[-0.29, -0.1]**
		male	**-0.13**	0.06	0.88	**[-0.24, -0.02]**
Grooming with	Kinship	all	**0.61**	0.04	1.84	**[0.52, 0.7]**
		female	**0.5**	0.06	1.64	**[0.39, 0.6]**
ΔAIC = -302		male	**0.77**	0.08	2.16	**[0.62, 0.92]**
	Age difference	all	**-0.29**	0.07	0.75	**[-0.43, -0.16]**
		female	**-0.14**	0.07	0.87	**[-0.28, -0.01]**
		male	**-0.7**	0.14	0.5	**[-0.97, -0.43]**
	Rank difference	all	**-0.17**	0.06	0.84	**[-0.3, -0.04]**
		female	**-0.22**	0.07	0.81	**[-0.36, -0.08]**
		male	**-0.24**	0.12	0.79	**[-0.47, -0.01]**

*Betas, SE, and 95% confidence interval values averaged over 1000 random assignments of partner IDs to random effects.

**Betas and 95% CIs in bold when effect significant.

Table S3.5. Influence of relative partner attributes on *magnitude* of dyadic affiliation, *excluding* mother-offspring dyads.

Dyadic behavior	Predictor	Dyads	Beta*	SE	95% CI
Playing ΔAIC = 3	Kinship	all	-0.17	0.13	[-0.43, 0.08]
		female	-0.04	0.07	[-0.18, 0.11]
		male	-0.27	0.14	[-0.54, 0]
	Age difference	all	0.12	0.12	[-0.12, 0.36]
		female	0.03	0.08	[-0.12, 0.18]
		male	0.13	0.13	[-0.12, 0.39]
	Rank difference	all	-0.06	0.14	[-0.33, 0.2]
		female	-0.06	0.07	[-0.2, 0.08]
		male	-0.24	0.15	[-0.53, 0.05]
N = 447 all play dyads, Gamma distributed errors with inverse link; N = 144 female-focused dyads, Gamma errors with log link; N = 354 male-focused dyads, Gamma errors with inverse link.					
Sitting close ΔAIC = -17	Kinship	all	**0.13****	0.03	**[0.06, 0.19]**
		female	**0.1**	0.04	**[0.01, 0.18]**
		male	**-0.39†**	0.14	**[-0.67, -0.11]**
	Age difference	all	**0.08**	0.03	**[0.01, 0.14]**
		female	**0.09**	0.04	**[0.01, 0.17]**
		male	**-0.23†**	0.11	**[-0.44, -0.02]**
	Rank difference	all	-0.03	0.04	[-0.1, 0.04]
		female	-0.03	0.04	[-0.12, 0.06]
		male	0.14	0.13	[-0.11, 0.39]
N = 1563 all proximity dyads, Gaussian distributed errors with log link; N = 997 female-focused dyads, Gaussian errors with log link; N = 761 male-focused dyads, Gamma errors with inverse link.					
Grooming with ΔAIC = -16	Kinship	all	**0.19**	0.06	**[0.08, 0.31]**
		female	**0.15**	0.07	**[0.02, 0.28]**
		male	0.19	0.1	[0, 0.38]
	Age difference	all	**0.18**	0.05	**[0.08, 0.28]**
		female	**0.21**	0.06	**[0.1, 0.32]**
		male	0.03	0.08	[-0.13, 0.18]
	Rank difference	all	-0.03	0.05	[-0.13, 0.08]
		female	-0.06	0.06	[-0.18, 0.06]
		male	0	0.1	[-0.19, 0.2]
N = 517 all grooming dyads, Gamma distributed errors with log link; N = 404 female-focused dyads, Gamma errors with log link; N = 174 male-focused dyads, Gaussian errors with log link.					

*Betas, SE, and 95% confidence interval values averaged over 1000 random assignments of partner IDs to random effects.

**Betas and 95% CIs in bold when effect significant.

†Parameter estimated with an inverse link function, i.e. negative estimates indicate a positive relationship between the predictor on the response.

Table S3.6. Influence of relative partner attributes on *magnitude* of dyadic affiliation, *including* mother-offspring dyads.

Dyadic behavior	Predictor	Dyads	Beta*	SE	95% CI
Playing ΔAIC = 3	Kinship	all	-0.17	0.13	[-0.43, 0.08]
		female	-0.02	0.07	[-0.16, 0.13]
		male	-0.27	0.14	[-0.54, 0]
	Age difference	all	0.12	0.12	[-0.12, 0.36]
		female	0.03	0.08	[-0.13, 0.18]
		male	0.13	0.13	[-0.12, 0.39]
	Rank difference	all	-0.06	0.14	[-0.33, 0.2]
		female	-0.06	0.07	[-0.2, 0.09]
		male	-0.24	0.15	[-0.53, 0.05]
N = 447 all play dyads, Gamma distributed errors with inverse link; N = 144 female-focused dyads, Gamma errors with log link; N = 354 male-focused dyads, Gamma errors with inverse link.***					
Sitting close ΔAIC = -29	Kinship	all	**0.14****	0.04	**[0.07, 0.21]**
		female	**0.11**	0.04	**[0.02, 0.2]**
		male	**-0.45†**	0.15	**[-0.74, -0.16]**
	Age difference	all	**0.08**	0.04	**[0.01, 0.15]**
		female	**0.09**	0.04	**[0.01, 0.18]**
		male	-0.22	0.11	[-0.43, 0]
	Rank difference	all	-0.05	0.04	[-0.12, 0.02]
		female	-0.03	0.04	[-0.12, 0.05]
		male	0.17	0.12	[-0.07, 0.41]
N = 1656 all proximity dyads, Gaussian distributed errors with log link; N = 1039 female-focused dyads, Gaussian errors with log link; N = 812 male-focused dyads, Gamma errors with inverse link.					
Grooming with ΔAIC = -68	Kinship	all	**0.39**	0.06	**[0.26, 0.51]**
		female	**0.31**	0.07	**[0.16, 0.45]**
		male	**0.49**	0.11	**[0.27, 0.71]**
	Age difference	all	**0.18**	0.05	**[0.07, 0.29]**
		female	**0.21**	0.06	**[0.09, 0.32]**
		male	0	0.09	[-0.18, 0.18]
	Rank difference	all	-0.03	0.05	[-0.14, 0.07]
		female	-0.05	0.06	[-0.17, 0.06]
		male	0.02	0.1	[-0.17, 0.21]
N = 610 all grooming dyads, Gamma distributed errors with log link; N = 449 female-focused dyads, Gamma errors with log link; N = 222 male-focused dyads, Gaussian errors with log link					

*Betas, SE, and 95% confidence interval values averaged over 1000 random assignments of partner IDs to random effects.

**Betas and 95% CIs in bold when effect significant.

*** Type of link function chosen to allow parameter estimates to converge.

†Parameters estimated with an inverse link function, i.e. negative estimates indicate a positive effect of the predictor on the response.

Table S3.7. Repeatabilities (intra-class correlations, R) of inter-individual differences in juvenile social behavior. N = 162 observations, 41 subjects, 3 social groups. Group and subject included as random effects.

Behavior	R	se	CI*	P(R > null)**
% Time playing	0.05	0.05	[0,0.17]	0.3
% Time in proximity or	0	0.03	[0,0.11]	0.57
% Time grooming	0.04	0.05	[0,0.15]	0.28
Number partners play	0.06	0.07	[0,0.22]	0.1
Number partners in	0	0.03	[0,0.11]	0.39
Number grooming	0.07	0.05	[0,0.16]	0.04
Rate agonism given	**0.25**	0.1	**[0.02,0.43]**	0
Rate agonism received	**0.23**	0.1	**[0.03,0.41]**	0

*95% CI based on 1000 bootstraps without replacement
** null R distribution based on 1000 permutations of observation matrix.

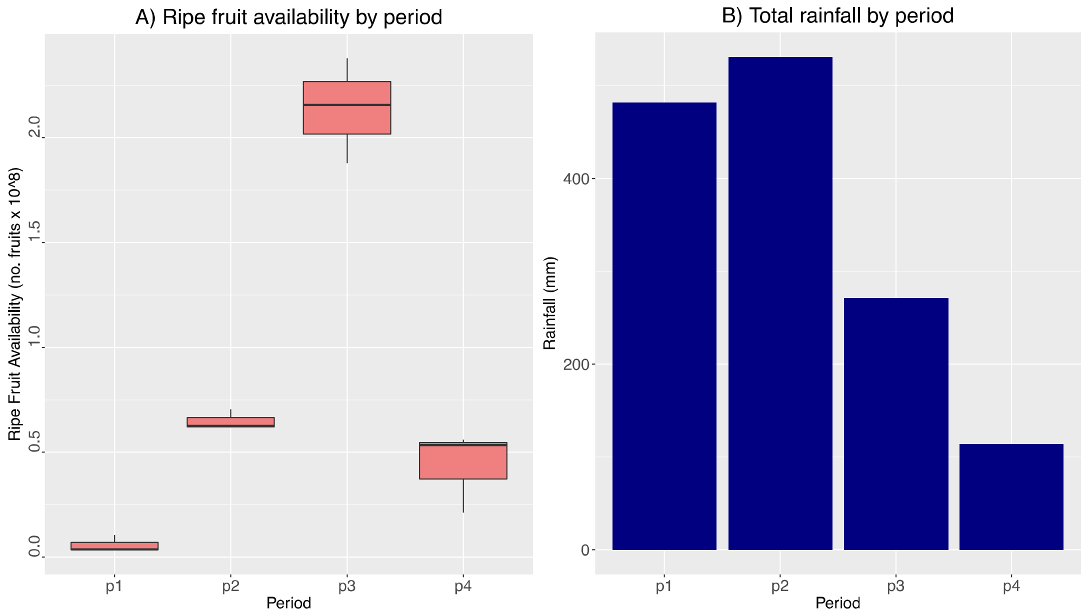

Figure S3.1. Seasonal variation in A) group homerange-specific availability of ripe fruit and B) total rainfall by observation period.

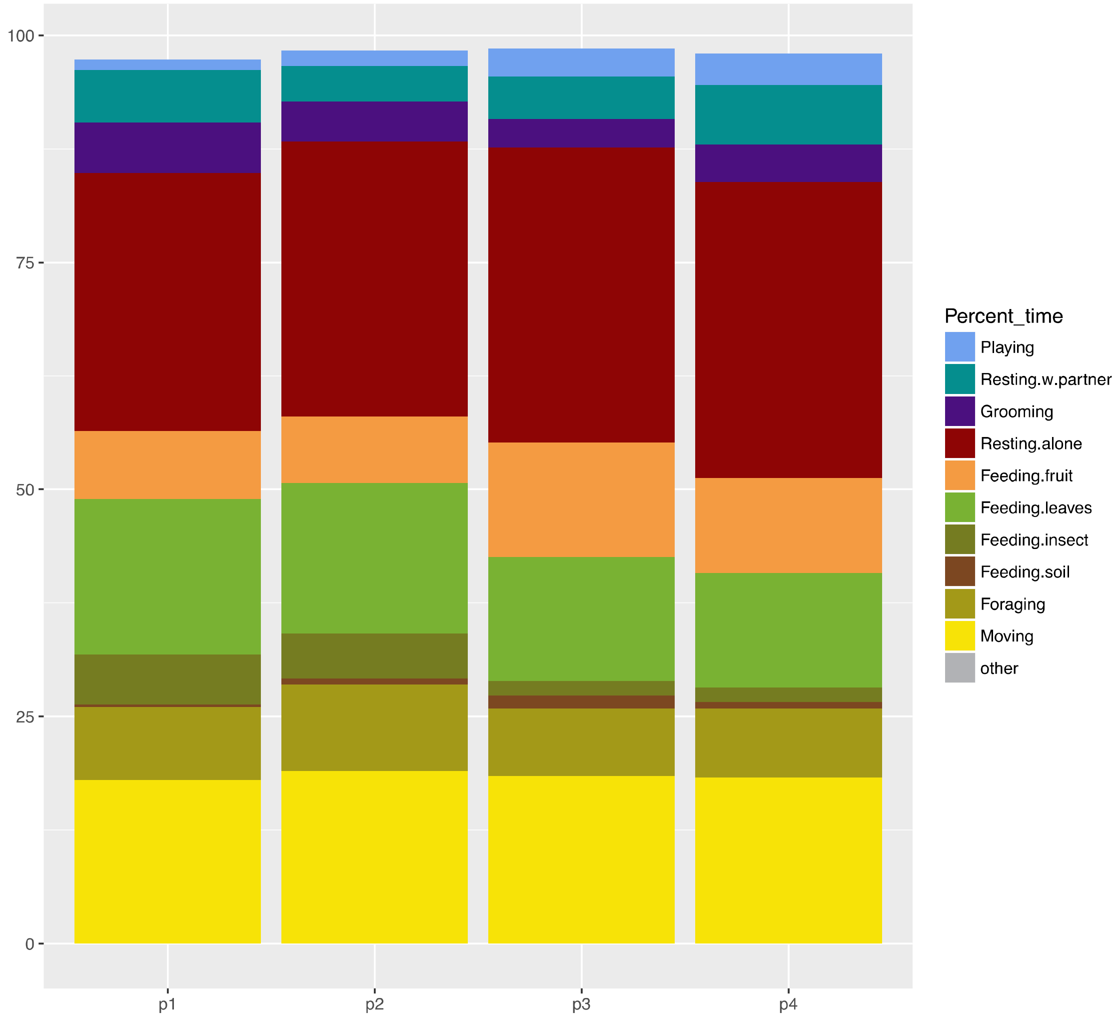

Figure S3.2. Juveniles' time spent in a given activity per observation period, averaged over N = 40-41 subjects per period.

Chapter 4: Socio-ecological correlates of allostatic load during development in an Old World monkey.

Introduction

Overt affiliation, such as social grooming and play, evolved among group-living animals for several reasons, including navigating competition and accessing resources (Cords & Thompson, 2017; Chap. 1). Once the tendency to form social ties then evolved, ties became able to decrease individual allostatic load, or the cost of maintaining homeostasis through predictable and unpredictable environmental change (Romero et al., 2009). Mediators of homeostasis, including hormones and behavior, vary in circadian and seasonal rhythms and according to life history state, however additional challenges related to food availability, temperature, exposure to predators, and social environment can alter levels of allostatic mediators in a "stress response" (Reeder & Kramer, 2005; Romero, 2002). While challenges to homeostasis can vary by life stage, most studies of allostasis (and its behavioral mediators) in wild populations have focused on adults, with effects of age explored primarily during infancy or senescence (Reeder & Kramer, 2005). Juvenile individuals, which are neither dependent on parental care nor yet reproductively active (Pereira & Fairbanks, 2003), have been largely overlooked, leaving a deficit in our understanding of the links between socioecology and allostatic load during this important life stage.

Juveniles are particularly vulnerable to social competition from older and larger individuals (Pereira & Fairbanks, 2003; Stanton et al., 2011). Simultaneously, because they dedicate energy to physical growth and development, they are more vulnerable to the negative effects of food shortage (Douhard et al., 2014). Catch-up growth to compensate for nutritional deficiencies during episodes of food scarcity can increase individuals' exposure to predators during foraging, disrupt cell function, and advance the deterioration of telomeres (Metcalfe & Monaghan, 2001). In baboons, for example, females have shorter lifespans if they experience a combination of poor social and nutritional conditions during development, such as early maternal loss, competing siblings, and drought during the first year of life (Altmann, 1991; Tung et al., 2016).

A commonly measured mediator of allostatic load is circulating levels of glucocorticoids (GCs, Romero et al., 2009), which are released into the bloodstream to mobilize energy and inhibit bodily maintenance that is not immediately essential for survival (Sapolsky et al., 2000).

Because of their metabolic function, elevated GC levels can indicate energetic challenges, or stressors, in the environment. If individuals sustain GC levels higher than those within their "reactive scope," their physiological systems can succumb to "wear and tear" (Romero et al., 2009), with effects on cardiovascular health, fertility, and memory (Sapolsky et al. 2000). Whether such "chronic" elevations of GCs *directly* reduce fitness, or even regularly occur in wild-living animals, is not clear (Beehner & Bergman, 2017; Boonstra, 2013), however elevated GCs in tandem with food shortages may signal that individuals are vulnerable to disease or death (Bonier et al., 2009; Pride, 2005; Wilkening & Ray, 2016).

Food shortages can lead individuals into negative energy balance and, in several vertebrates, cause increased glucocorticoid secretion to mobilize energy for foraging and bodily maintenance (Bonier *et al.* 2009). A food shortage associated with an El Niño event caused iguanas in the Galapagos to lose body mass, which after crossing a certain threshold, led to large spikes in GCs (Romero & Wikelski, 2001). Iguanas with the highest GCs were most likely to die during the year. Food shortage during periods of great energetic demand, such as reproduction, can lead to pronounced energetic deficiencies. In wild kittiwakes, a decrease in fish abundance corresponded with an increase in GCs (Kitaysky, Piatt, & Wingfield, 2007), and reproductive females with higher GCs had lower annual reproductive success and a higher probability of disappearing. In blue monkeys, females undergoing the energetically costly process of lactating had higher GCs if they were lower ranking, indicating their energetic deficiency (Foerster et al., 2011). Although dominance rank does not influence female blue monkeys ability to conceive (Roberts & Cords, 2013), it is possible that higher energetic stress during lactation affects fitness by influencing the life history trajectory of offspring (Berghänel, Heistermann, Schülke, & Ostner, 2016; Douhard et al., 2014).

Energy balance is defined by the rate of energy intake minus the rate of energy expenditure (Hall et al., 2012). It is difficult to calculate precisely for wild animals. Specifically, measuring expenditure requires administering doubly labeled water and measuring intake requires records of all items consumed and their caloric content. Biomarkers such as insulin can often adequately represent energy balance, as insulin secretion may correspond with changes in body mass (Deschner, Kratzsch, & Hohmann, 2008; Girard-Buttoz et al., 2011) and signals energy balance to the brain (Emery Thompson, 2016). C-peptide of insulin (hereafter, CP) is produced on an equimolar basis to insulin after the cleavage of pro-insulin (Norman & Litwack, 1997). Because CP is excreted in urine, its levels can be quantified relatively easily (and non-invasively) in wild animals (Emery Thompson & Knott, 2008; Emery Thompson, Muller, Kahlenberg,

& Wrangham, 2010; Emery Thompson, Muller, Wrangham, Lwanga, & Potts, 2009; Higham, Heistermann, & Maestripieri, 2011). It is therefore a useful biomarker to assess whether allostatic load derives from negative energy balance.

While the physical environment presents several challenges, such as food shortages, social relationships can help individuals avoid or cope with them. For example, grooming may increase tolerance while co-feeding in adult female baboons (King et al., 2011) and in adult Barbary macaques and vervets, the number of affiliative ties may shelter individuals from cold temperatures (Lehmann et al., 2016; McFarland et al., 2015). Social ties can also moderate challenges presented by the social environment itself, such as competition for food or mates. For instance, adult females that affiliate with other females more frequently (e.g. horses) or maintain strong bonds with the opposite sex (e.g. Assamese macaques) may avoid sexual harassment from males (Cameron et al., 2009; Haunhorst et al., 2017).

Social ties can not only prevent the experience of stressors such as harassment and cold, but also correspond with, and modify, GC levels when ties contribute to stability in the social environment (Gunnar, 2017; Hennessy, Kaiser, & Sachser, 2009). In several primates, GC levels are higher in low-ranking adult animals when low-rank corresponds with fewer opportunities for grooming, social contact, alliances, and unpredictable receipt of aggression (Abbott et al., 2003). Close affiliates may buffer the experience of stressors because they are more consistently available for socio-positive contact (female baboons Silk, Alberts, et al., 2006), which may stimulate the release of oxytocin, an anxiolytic that likely inhibits HPA axis reactivity (Heinrichs, Baumgartner, Kirschbaum, & Ehlert, 2003). For example, among adult male Barbary macaques that frequently experienced aggression, those that affiliated more intensely with their closest partners had lower baseline GC levels than males with weaker bonds to top partners (Young, Majolo, Heistermann, Schülke, & Ostner, 2014). In blue monkeys, grooming behavior moderates adult females' GC levels, which are likely energetically driven (Foerster et al., 2011). GCs can also be elevated among individuals that experience a relative lack of social contact, such as in baboons where both males and females experience higher GC levels when socially isolated (Sapolsky et al., 1997; Seyfarth, Silk, & Cheney, 2012).

Very few studies have examined the influence of the social environment on the GC levels of juvenile non-human animals (Gust, Gordon, Brodie, & McClure, 1996; Hennessy et al., 2009; Mustoe et al., 2014; Stoewe et al., 2008). To my knowledge, only Seabloom, Iverson, and Turner (1978) conducted such a study in wild animals (meadow voles), and even so, the influence of social environment was assessed only indirectly as a part of seasonal variation. Captive studies suggest that juveniles can maintain lower GC levels if they have even a single familiar social partner during stressful events (i.e. experimental transfer to a new social group, rhesus macaques, Gust et al., 1996), or by engaging in social play (marmosets, Mustoe et al., 2014). In contrast, post-fledgling ravens had higher GC levels the more time they spent associating and allopreening with partners (Stoewe et al., 2008). Social styles or strategies, more broadly measured by several pro- and anti-social behavioral variables, can also relate to GC levels. Anestis (2005) examined the relationship between juvenile chimpanzees' social style and baseline GCs. Contrary to predictions, she found that "smart" juveniles (i.e. those that received grooming, had play partners, and used coalitions) and "aggressive" juveniles (i.e. those that frequently initiated aggression and had several coalition partners) both had higher

GC levels than less “smart” or “aggressive” juveniles. Her results suggest that juveniles may actually bear some physiological cost when actively navigating the adult social environment.

I explore the links between socioecology and allostatic load in juvenile blue monkeys. Blue monkeys are gregarious, group-living primates that live in a habitat with seasonal fluctuations in both fruit availability and rainfall (Mitchell, 2009; Pazol & Cords, 2005), which are known to correspond with variation in glucocorticoid levels among adult females (Foerster et al., 2011, 2012). Juvenile blue monkeys also face challenges that are likely representative of those faced by developing individuals more broadly. Juveniles receive more agonism than do adult females (Cords et al., 2010; Chap. 3) and have a wider range of annual mortalities, which are possibly related to variation in food availability and predation (Cords & Chowdhury, 2010). Further, blue monkeys have particularly long developmental periods, which permits a broader exploration of how homeostatic challenges and social behavior can co-vary during development. To my knowledge, this is the first study of the homeostatic challenges and possible coping strategies of juveniles in a wild primate.

The goals of this study were twofold. I first aimed to understand how juveniles’ energy balance varied according to their life history status (i.e. their age, sex, and maternal dominance rank) and their physical environment (local fruit availability and rainfall). I predicted that the availability of ripe fruit would be the strongest driver of energy balance among juveniles. I also predicted that maternal dominance rank would have a weak or negligible influence on energy balance, as it only affected adult females’ energetic stress in rare situations (Foerster et al., 2011). Second, I wished to understand how life history variables, energy balance, and social strategy influenced GC levels, or allostatic load. As a part of this aim, I characterized juvenile social strategies according to an exploratory principle components analysis and examined the life history, demographic, and seasonal correlates of such strategies. I predicted that energy balance would decrease GC levels, as seen in adult females of this species (Foerster et al., 2011, 2012). I also predicted that social strategies involving positive social contact, such as social play or grooming, would lower GC levels and have a buffering effect in helping juveniles overcome ecological challenges such as variable energy balance.

Methods

Study site and population

The wild study population inhabits the Isecheno area of Kakamega Forest in western Kenya (0˚19´ N, 34˚52´ E; elevation 1580 m, mean annual rainfall 1997–2011 1942 mm; (Mitchell, 2009). We collected data on 41 juveniles (22 males, 19 females, mean age 4.4 ± 1.7 yrs) for 8 months (August 2015 – March 2016). Subjects lived in 3 social groups that neighbored one another (average group size: 37 – 65 individuals; average juveniles per group: 16 – 31), and male juveniles of neighboring groups often interacted with one another. Subjects were individually identifiable by their natural, physical variation. Subjects' ages were known from precise, long-term demographic records of the study population (Cords, 2012). A team of 4 observers, including author NAT, collected all behavioral and biomarker samples after a 2-month training period to ensure inter-observer agreement in behavioral coding.

Fecal and urine sample collection and fecal glucocorticoid (fGC) and urinary C-peptide (uCP) analysis

We collected fecal and urine samples *ad libitum* between 07:30 and 17:00, immediately after observing excretion from identified subjects. For fecal samples, we homogenized the whole sample and placed ca. 1 g of feces, uncontaminated with dirt, urine or other feces, with a stick and stored it in 1.5 to 15 ml plastic tubes. We pipetted urine from leaves or other substrates that were uncontaminated with dirt, feces, or urine from other animals, and stored samples in 1.5 ml polypropylene tubes. Urine and fecal samples were immediately placed in field thermoses with ice packs until they were returned to a -20ºC freezer < 4 hours later. Samples remained frozen and in the dark until they were shipped to the USA on ice and transferred to a -20ºC freezer at New York University, where they remained frozen until further processing. In total, we collected 627 fecal and 612 urine samples, averaging 15.3 ± 2.1 fecal and 15.0 ± 2.4 urine samples per subject.

I extracted glucocorticoid metabolites from feces following the protocol of Heistermann et al. (1995) and Palme, Touma, Arias, Dominchin, and Lepschy (2013) at the Anthropology Department of New York University. I lyophilized and pulverized samples and extracted an aliquot of ca. 0.05 – 0.1 grams (exact weights recorded) of fecal powder into 3 ml of 80% methanol in water by vortexing for 15 min. Following centrifugation (2000 g, 20 min) of the fecal suspension, I removed 1 ml of the resulting supernatant and stored it at -20ºC until hormone analysis.

I assayed fecal extracts for concentrations of cortisol metabolites at the German

Primate Center using an enzyme immunoassay (EIA) for immunoreactive 11ß-hydroxyetiocholanolone, a group-specific assay for the measurement of 5-reduced 3α,11ß-dihydroxylated cortisol metabolites which represent a major and quantitatively abundant portion of metabolites of cortisol in the feces of primates and other mammals (e.g. Heistermann et al. 2006; Ostner et al. 2008; Shutt et al., 2012; Ganswindt et al., 2003; Braga Goncalves et al. 2016). This assay has previously been validated and shown to reliably track changes in glucocorticoid output in several mammal species (e.g. Palme and Möstl, 1997; Braga Goncalves et al. 2016; Ganswindt et al., 2003), including numerous primate species of all major taxa (i.e. lemurs, South American primates, Old World monkeys and great apes; Heistermann et al. 2006; Fichtel et al. 2007; Hämälainen et al., 2014; Heistermann et al., 2004; Ostner et al. 2008; Pirovino et al., 2013; Weingrill et al., 2011; Shutt et al., 2012; Wheeler et al., 2013; Rimbach et al., 2013; Kalbitzer et al., 2015), indicating its outstanding versatility for assessing adrenocortical activity across the primate order. The 11ß-hydroxyetiocholanolone EIA has also been shown to generally present enhanced biological sensitivity when compared to more specific fGC assays designed to measure cortisol or corticosterone, making this assay generally superior over most other fGC assays for assessing glucocorticoid output from fecal samples (e.g. Shutt et al., 2012; Heistermann et al.; 2006; Fichtel et al., 2007; Weingrill et al., 2011; Hämälainen et al., 2014; Braga Goncalves et al, 2016; but see Wheeler et al., 2013).

The assay was carried out as described in detail by Heistermann et al. (2004). Prior to assay, samples were diluted at 1: 80 or 1:800 (depending on concentration) in assay buffer (0.04 M PBS, pH 7.2) to bring hormone concentrations into the working range of the assay. Sensitivity of the assay at 90% binding was 0.6 pg. Serial dilutions of fecal extracts from samples of different animals gave displacement curves that were parallel to the 11ß-hydroxyetiocholanolone standard curve. Inter-assay coefficients of variation (CV), assessed by replicate determinations of high- and low-value quality controls run in each assay, were 8.9% (high, N = 42 wells) and 11.9% (low, N = 42) and intra-assay CVs were 3.9% (high; N = 20 plates) and 6.0% (low, N = 20). All hormone concentrations are expressed as mass hormone per fecal dry mass.

I assayed urinary C-peptide of insulin (uCP) by radioimmunoassay (RIA) using a Merck Millipore™ RIA kit for human C-Peptide in the Anthropology Department at Rutgers University. The C-peptide molecule is extremely well conserved among mammals (Peterson, Nehrlich, Oyer, & Steiner, 1972) and C-peptide in blue monkey samples dilutes in parallel when using Merck Millipore kits™ (Michelle Brown, personal communication). Prior to assay, samples were diluted at 1:2 or 1:20, depending on concentration. Inter-assay coefficients of variation of high- and low-value quality controls were 5.1 (high) and 7.3 (low, N = 9 batches), and average intra-assay coefficient of variation was 4.4% (N = 666 CVs including samples, standards, and controls). I standardized uCP concentrations by samples' specific gravity, measured by an Atago™ handheld refractometer, following Miller et al. (2004). To control for variable water content of urine samples, the uCPs in a given sample were multiplied by the average specific gravity of all samples divided by the specific gravity of the given sample (Miller et al., 2004).

Concentrations of fGCs per sample did not vary by hour of collection during the day, however uCP concentrations did decrease with time of day (linear mixed effects regression on log uCP levels, subject ID as random effect, N = 612, ß = -0.1, p = 0.007; Fig. S4.1). I did not include group as a random effect when modeling time-effects on uCP levels because it decreased model fit according to a ΔAIC > 2. I therefore calculated uCP baselines by averaging the residuals of log uCP levels vs. time of day (Emery Thompson et al., 2010). To focus on variation in fGCs driven by socio-ecological factors rather than inter-individual differences in baseline levels, I expressed each sample concentration in terms of its deviation from the subject's 8-month baseline and then averaged individuals' deviations from baseline for each 2-month observation period (see Behavioral data collection and analysis). As 3 pairs of fecal and 2 pairs of urine samples were collected from the same subject on the same day, I averaged the fGCs and uCP residuals for each pair, yielding a total of N = 623 fGC and N = 610 uCP values, and overall N = 160 subject-period average deviations in fGCs and N = 156 subject-period average uCP residuals.

Behavioral data collection and analysis

My team conducted 20-min focal follows in which we recorded a focal subject's activity (e.g. resting, grooming, playing, feeding, moving) at 1 min intervals (i.e. point samples) and recorded the identities of social partners and of neighbors resting within 1 m of and in contact (but not grooming) with the subject and food item if feeding (e.g. fruit, leaves, insects). We recorded whether a subject self-scratched or self-groomed during a given minute as a 0-1 occurrence. During a follow, we continuously recorded the occurrence of affiliative approaches (an individual arriving and remaining within 1 m) and agonistic behavior (aggressive threats, lunges, growls, contact, and approach-retreat interactions), and social partners in either scenario. Focal follows occurred between 07:30 and 17:00, and we chose focal subjects throughout the day to maintain even numbers of follows each week per subject, and per day-period (i.e. morning, midday and afternoon). We collected a total of 1591 hours of behavioral data, averaging 39 ± 3.1 hrs per subject.

I divided the study into four 2-month periods (e.g. Aug 1st – Sept. 31st), for which I calculated all social variables and baseline (average) biomarker concentrations. Two months of observation (mean: 9.8 ± 1.2 hrs/subject) were conservatively representative of regular numbers of social partners, as preliminary data revealed that grooming and play partner numbers do not plateau for all subjects before 4 hours of observation. Further, 2 months allowed us to collect enough fecal and urine samples per subject to establish minimally sufficient average biomarker concentrations (mean 3.9 ± 0.9 fecal and 4.0 ± 1.0 urine samples/subject/period).

From point samples, I calculated the proportion of each subject's observation time per period that was spent in a given activity (e.g. grooming, playing, resting). I pooled focal data to calculate each subject's number of affiliative partners (i.e. neighbors during resting, groomers and groomees, and play partners) and standardized them relative to the average amount of observation time it shared with other members of the study population. I calculated subjects' tie or bond strength using a dyadic sociality index (DSI as in Silk et al., 2013). The DSI included dyadic time spent grooming, resting within 1 m without grooming one another, sitting in contact without grooming, and their hourly rate of approaches. I included these types of behavior in a DSI because they were positively correlated among dyads within groups for each period (QAP matrix correlation with double Dekker semi-partialling technique, using function "netlm" in R package "sna",

Table S4.1; Dekker et al., 2007) . The only type of affiliative behavior that did not consistently correlate positively with other types of affiliation was play (Table S4.1), therefore, I calculated a separate measure of the amount of play with closest partners. To calculate affiliative tie strength, I averaged DSIs over each subject's closest 3 partners, excluding its mother, as ties with mothers are disproportionately strong relative to non-mothers among all juveniles (Cords et al., 2010). For play tie strength, I similarly averaged dyadic time spent playing among a subject's top 3 partners. I calculated subjects' rates of agonism given and received per hour of shared observation time from continuously recorded events during focal follows, pooled among subjects. Lastly, I calculated the proportion of minutes observed in which a subject self-scratched or self-groomed.

To characterize juveniles' social strategies concisely, I entered behavioral variables in a principal components analysis (function "princomp" in R "base" package). I tested for sampling adequacy of all variables using a Kaiser-Meyer-Olkin test and for adequate correlations between variables using Bartlett's test (Budaev, 2010). I chose the number of components to retain (3) based on Kaiser's rule, a scree test, and parallel analysis with 1000 iterations using the function "paran" in the R "paran" package (Dinno & Dinno, 2010; Zwick & Velicer, 1986). I chose not to rotate components after retaining them because rotation did not increase components' interpretability (Jolliffe, 2002).

For each 2-month period (e.g. Aug – Sep, Oct – Nov), I calculated subjects' ages using the mid-date of the period. I used mothers' dominance rank to represent juvenile dominance relations because offspring appear to inherit mothers' rankings in blue monkeys (Klass & Cords, 2015). Maternal dominance rank was calculated based on decided winner-loser interactions either from data collated over the study period if mothers were still alive, or over the mother's last year of life, using the I&SI method in DomiCalc (Schmid & de Vries, 2013). Dominance rank ranged from 0 –1 representing the proportion of co-resident adult females that a mother outranked. I counted subjects' maternal kin present in the social group based on known pedigrees, where maternal aunts and nieces ($r = 0.125$) were the most distant relations included.

Fruit availability

I calculated a fruit availability index (FAI) using data from monthly plant phenological surveys of 36 major food species (consistently constituting > 0.05% of annual adult feeding time) and their basal areas in 44 group-specific transects (N = 13 10m x 100 m transects, group 1; N = 6 transects, group 2; N = 9 transects, group 3), which represented approximately 10% of each group's home range area. A field assistant collected data on ca. 10 focal trees of each food species, recording each as fruiting or non-fruiting, and for fruiting trees, counting number of fruits (twice, to check for accuracy) on a log scale (e.g. 100–399, 400–699, 700–1000) and estimated percentage of ripe fruit to the nearest 25%. Not all focal trees designated as "fruiting" received a fruit count, therefore I averaged number of ripe fruits among trees that received counts and assigned that average to all fruiting trees. I then calculated the average number of ripe fruits across all focal trees of a given species (fruiting or not fruiting). To calculate group-specific FAIs, I summed the products of the average mid-point estimate of number of ripe fruits per fruit-tree species and each species' average basal area among group-specific transects. I calculated average daily rainfall per period using daily rainfall data collected by local Kenya Forest Service staff.

Statistical analysis

I first examined how ecological (fruit availability, rainfall) and life history variables (age, sex, maternal dominance rank) influenced energy balance as measured by uCP. Because of an unexpected sex difference in uCP levels, I ran a follow-up model to assess potential sex differences in percentage time feeding on fruit (blue monkeys' main source of calories, Takahashi in prep.). I also assessed how life history and ecological variables predicted scores on PCs 1 – 3. For both analyses I used linear mixed effects regressions using the "lmer" function in the R package "lme4" (Bates et al., 2014). I included only subject as a random effect in modeling uCP levels, as including social group as a random effect decreased model fit (ΔAIC > 2). For models of PC scores, I nested subject in group as random effects, as including group generally increased models' fit (PC1 ΔAIC = 1.46; PC2 ΔAIC = 9.86; PC3 ΔAIC = 12.12). To then understand social, life history, and ecological influences on fGC levels, I again used a linear mixed effects model that included the three retained principal components, age, sex, maternal dominance rank, and uCP levels as fixed effects. I included social group alone as a random effect, because the random effect of "subject" no longer improved model fit when fGCs were expressed as deviations from individual baseline (AIC model with RE subject = 472, AICc model without RE subject = 470).

I standardized predictors according to their mean and standard deviation for interpretability and standardized response variables to adjust for their scales (Schielzeth, 2010). I assessed collinearity of fixed effects via their variance inflation factors, using the "vif.mer" function in R (Frank, 2014) and confirmed normality of model residuals using

Q-Q plots. I considered a predictor's influence on an outcome variable to be significant if the 95% confidence interval of its parameter estimate did not include zero (Nakagawa & Cuthill, 2007). Because scores on the first principal component of behavioral variables significantly influenced fGCs, I created two post-hoc models to test how percentage of time grooming and playing (i.e. the two variables that loaded most strongly yet in opposite directions on PC1) corresponded to fGC levels. I then used these two variables to further assess whether social ties buffer the effect of energy balance on fGC levels, testing the interaction between energy balance and percentage of time grooming or playing. Because percentage time grooming moderated the effect of energy balance on fGCs in an unexpected way, I further hypothesized that individuals spending the most time grooming could be grooming with riskier social partners. To compare whether time spent grooming kin vs. non-kin differed for juveniles according to how much grooming they participated in, I used a linear mixed effects model, where the response was subjects' percentage of time spent grooming (separately for kin and non-kin partners) per period. I then predicted percentage time spent grooming according to the categorical variable of grooming quartile and kin or non-kin groom partner (e.g. groom quartile 4 – non-kin, see Fig. 4.3C), resetting the reference class to compare time grooming with kin vs. non-kin within each quartile. Subject ID nested in group ID were random effects.

Results

Influences on energy balance measured by uCP

Energy balance as measured by uCP levels was less positive in males than females (linear mixed model, ß = - 0.15, 95% CI = - 0.28 – - 0.02, N =156,) and was very nearly higher as subjects grew older (ß = 0.06, 95% CI = - 0.01 – 0.12; Fig. 4.1A,B, Table S4.2). Juveniles entered into a more positive energy balance as ripe fruit became more available in their home range (ß = 0.15, 95% CI = 0.08 – 0.22, Fig. 4.1A,C) and a less positive energy balance with higher average daily rainfall (ß = - 0.1, 95% CI = - 0.17 – - 0.04, Fig. 4.1A,D). Although ripe fruit availability roughly corresponded with less rainfall across the four periods, these variables did not mirror one another (Chap. 3, Fig. S3.1), and including them in a single model did not introduce problems of collinearity (maximum VIF in model was 1.08). Fruit availability and rainfall therefore likely contributed independent effects to individual uCP levels. Although male uCP levels were lower than those in females, males did not spend significantly less time feeding on fruit than females did (linear mixed model of % Time feeding on fruit, subject as random effect, ß sex (male) = 0.09, 95% CI -1.4 –1.58). uCP levels were not related to maternal dominance rank.

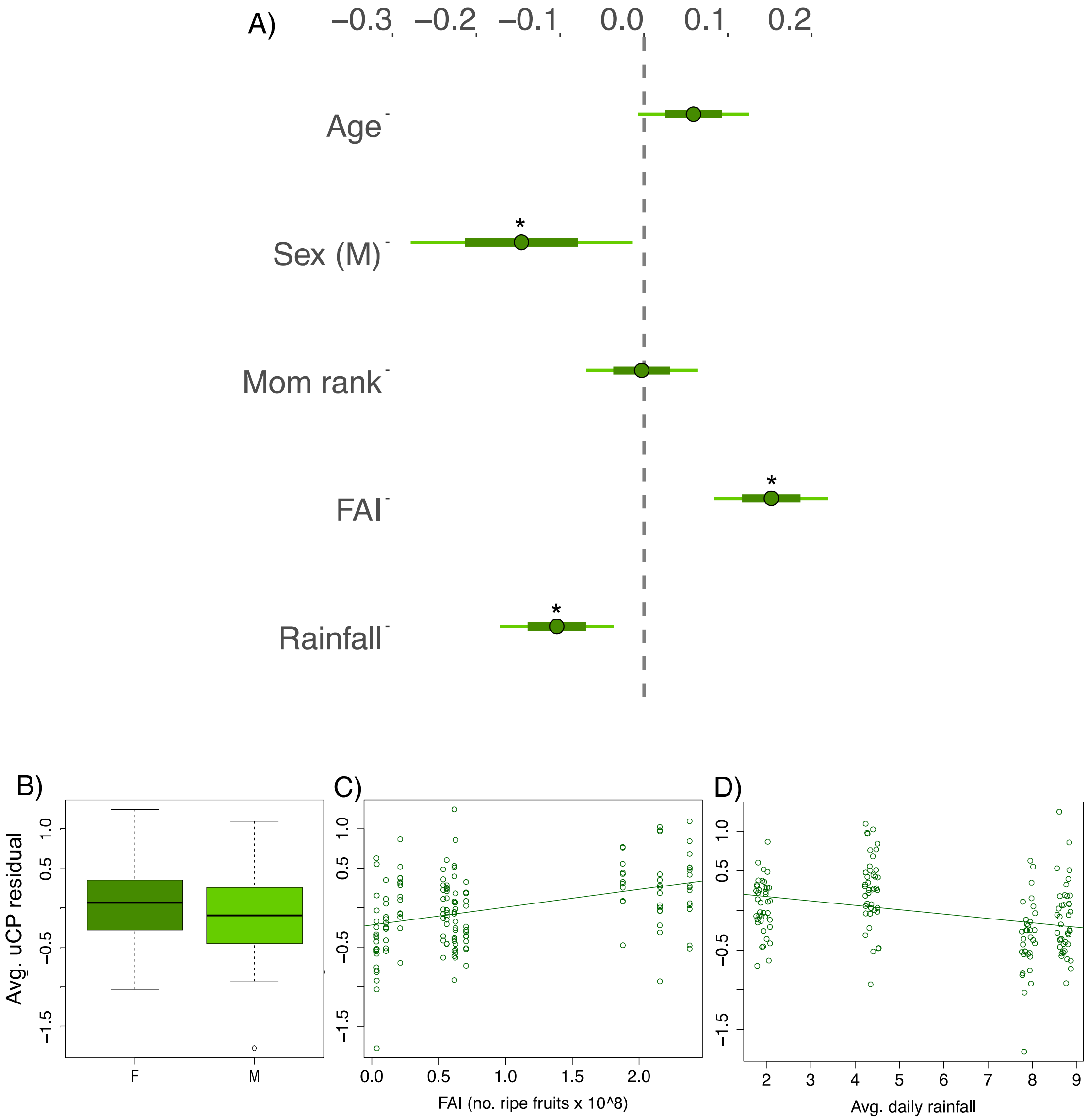

Figure 4.1. Influences on juvenile uCP levels. A) Effects of standardized predictors on subject uCP levels in linear mixed model. Point is restricted maximum likelihood estimated coefficient. Thick and thin lines represent 50 and 95% confidence intervals, respectively. Dashed vertical line indicates a parameter estimate of zero. * 95% CI does not include zero. Variation in average uCP residuals by B) sex, C) fruit availability index, D) average daily rainfall. Trend lines added with simple linear regression.

Social strategies: Behavioral variables and principal components

All variables had appropriate sampling adequacy for PCA (Kaiser-Meyer-Olkin test, min measure of sampling adequacy (MSA) = 0.57, overall MSA = 0.72; Dziuban & Shirky, 1974). Correlations between variables were also appropriately strong for PCA (Bartlett's test, $\chi^2(45)=601.64$ $p < 0.0001$). Both Kaiser's rule and parallel analysis indicated that retaining the top 3 PCs was appropriate and these collectively explained 65% of variance in behavioral measures (Table 4.1.).

I characterized each component according to the patterns by which variables loaded on it. Grooming and play measures both loaded strongly on PC1, however in opposite directions (Table 4.1). This led us to characterize PC1 as the groomer vs. player component. Number of play partners, number of neighbors while resting, and both agonism given and received loaded strongly on PC2. Variables loading weakly or in the opposite direction of tie number and involvement in agonism included time spent grooming and rates of self-directed behavior, which either do not require a diversity of partners (time grooming) or are largely done solitarily (self-directed behavior). Indeed, 89% of self-directed behavior occurred when subjects were resting and not within 1 m or in contact with neighbors. Given this pattern of loadings, I characterized PC2 as social vs. solitary. Of the several variables that loaded strongly on PC3, only agonism given loaded positively. Variables that loaded negatively were socio-positive (e.g. play and affiliative bonds) or solitary (self-directed behavior), leading us to characterize PC3 as aggressive vs. peaceful.

Table 4.1. Loadings of behavioral variables on top 3 principal components (A) and coefficients of life history and ecological variables predicting scores on components (B). Component loadings |x| > 0.40 shaded grey. Significant predictors of PC scores in bold. N = 162 subject-periods.

A)

Behavioral variable	PC1 Groomer vs. Player	PC2 Social vs. Solitary	PC3 Aggressive vs. Peaceful
Variation explained by component	35%	17%	13%
% Time playing	-0.41	0.23	-0.3
# Play partners[1]	-0.37	0.38	-0.09
Mean top play bond	-0.34	0.17	-0.35
% Time grooming	0.43	-0.04	-0.3
# Groom partners[1]	0.43	0.25	-0.22
Mean top affiliative bond	0.35	0.13	-0.44
# Neighbors$_a$	0.21	0.56	-0.05
Agonism received[2]	0	0.43	0.13
Agonism given[2]	0.04	0.44	0.43
Rate of self-directed behavior	-0.2	-0.09	-0.49

B)

Predictor of PC score	ß	95% CI	ß	95% CI	ß	95% CI
Sex (M)	**-2.65**	**[-3.09, -2.2]**	0.28	[-0.13, 0.69]	0.34	[-0.02, 0.7]
Age	**0.38**	**[0.16, 0.61]**	**0.24**	**[0.03, 0.46]**	0.00	[-0.18, 0.2]
Number maternal kin	0.11	[-0.13, 0.40]	-0.13	[-0.35, 0.12]	-0.04	[-0.25, 0.17]
Maternal rank	0.09	[-0.15, 0.31]	0.12	[-0.10, 0.33]	0.16	[-0.02, 0.35]
FAI	**-0.25**	**[-0.41, -0.10]**	**-0.22**	**[-0.38, -0.05]**	-0.07	[-0.22, 0.08]
Rainfall	**0.28**	**[0.12, 0.44]**	**-0.42**	**[-0.58, -0.25]**	0.06	[-0.09, 0.21]

[1] # partners (relative to shared observation time) per subject-period; [2] rates per hour of shared observation time

Juvenile scores on PCs 1 and 2 varied according to different life history and ecological variables (Table 4.1). Scores on PC1 were lower in males relative to females, indicating that males were generally less involved in grooming and non-play affiliation and relatively more involved in play than females. Older individuals were more likely to have higher scores on PC1, and thereby were more involved in grooming-related affiliation and less involved in play. Scores on PC1 decreased (less grooming, more play) when ripe fruit was less available and increased with greater rainfall. Juveniles had higher scores on PC2 as they aged, indicating that older juveniles had a higher number of social partners and higher involvement in agonism. Scores on PC2 decreased (fewer social partners, less agonism) with both fruit availability and rainfall. Scores on PC3, related to giving agonism vs. engaging in peaceful social or asocial activities, did not vary according to life history or ecological variables. The maximum VIF in all models was 1.13.

Influences on allostatic load

Subjects' average deviation in fGC concentrations varied according to their scores on the grooming vs. playing component (PC1) and their energy balance. fGCs increased among subjects that groomed more and played less (i.e. higher score on PC1, ß = 0.15, 95% CI 0.03 – 0.28, N = 155; Fig. 4.2A, B, Table S4.3) and decreased when subjects had a more positive energy balance (ß = - 0.17, 95% CI -0.33 – -0.013; Fig. 4.2A,C). Subjects' scores on social vs. solitary (PC2) and aggressive vs. peaceful (PC3) components did not relate to fGCs, nor did their age, sex, or maternal rank. All VIFs were < 2.5, with highest values of 2.37 (PC1) and 2.40 (sex), demonstrating a relationship between grooming-related affiliation, play, and sex. FGC concentrations did not vary significantly by group, when group ID was tested as a fixed effect (linear model, CIs of all between-group contrasts contain 0).

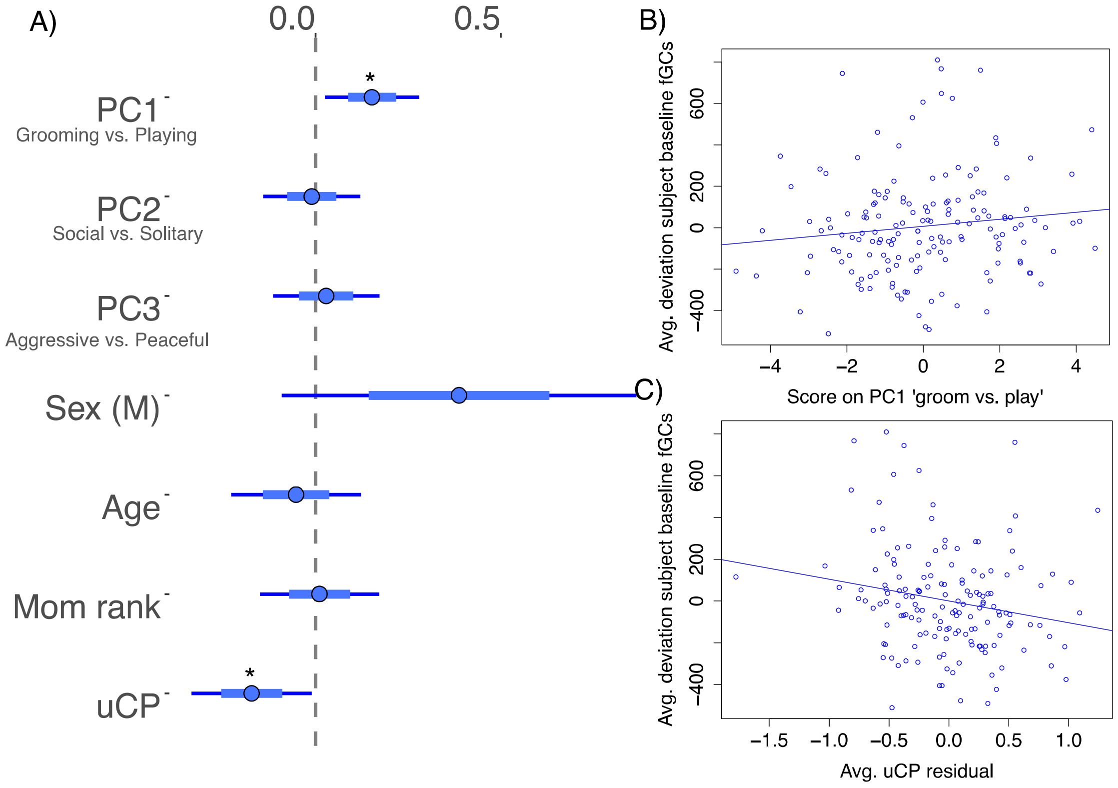

Figure 4.2. Influence on juvenile fGC levels. A) Effects of standardized predictors on subject fGC levels. Point is restricted maximum likelihood estimated coefficient. Thick and thin lines represent 50 and 95% confidence intervals, respectively. Dashed vertical line indicates a parameter estimate of zero. *95% CI does not include zero. Variation in fGCs by B) scores on PC1, C) average uCP residual. Trend lines added with simple linear regression.

Although PCAs conducted separately on male- and female-only datasets also revealed first principal components in which time spent grooming and time spent playing loaded most strongly and in opposite directions, the effect of sex-specific PC1 (and any sex-specific PC) on fGCs did not reach significance in models separated by sex (linear mixed model, Male PC1 95% CI -0.01 – 0.25, Female PC1 95% CI -0.24 – 0.01). Nevertheless, the influence of scores on the sex-specific PC1s on fGC levels were in the same direction as the first PC that included both sexes, with time playing loading positively and grooming loading negatively on the female-specific PC1 (Female PC1 ß = - 0.11), and time grooming loading positively and time playing loading negative on male-specific PC1 (Male PC1 ß = 0.12). Sampling adequacy according to a KMO test reached criteria for females (min MSA = 0.64, overall MSA = 0.72), but was weak for males (min MSA = 0.47, overall MSA = 0.57), suggesting that the lack of a significant effect of PC1 on fGCs within each sex may have resulted from limited statistical power.

The influence of PC1 on fGCs was driven by both the positive influence of percentage time grooming on fGCs and the negative influence of percentage time playing on fGCs (Table 4.2). Play behavior did not moderate the negative relationship of energy balance on fGCs, but grooming behavior did. Surprisingly, energy balance had an increasingly *positive* influence on fGCs as time spent grooming increased (Table 4.2). Biologically, increasing energy balance should not increase HPA activity (Sapolsky et al., 2000). Therefore one might best express this interaction as the more positive a juvenile's energy balance, the more strongly its grooming positively corresponded with fGCs (Fig. 4.3A). Indeed, it appeared that juveniles that spent the greatest amount of time giving and receiving grooming were those that were mostly likely to have a positive relationship between energy balance and fGCs (Fig. 4.3B). I found that individuals in the top grooming quartile spent significantly more time grooming non-kin vs. kin, though there were no differences in grooming non-kin vs. kin among subjects in other quartiles (Fig. 4.3C, Table S4.4).

Table 4.2. Effects on fGCs of % time grooming and % time playing, the variables loading most strongly on PC1, and their interactions with energy balance in linear mixed effect models. Significant effects in bold. N = 155 subject-periods.

Response variable	Predictor variables	ß	95% CI
fGCs	**% Time grooming**	**0.23**	**0.035, 0.43**
	Sex (M)	0.26	-0.13, 0.64
	Age	-0.03	-0.18, 0.13
	Maternal rank	0.03	-0.12, 0.19
	Energy balance	**-0.18**	**-0.34, -0.02**
fGCs	**% Time grooming**	**0.27**	**0.07, 0.46**
	Sex (M)	0.29	-0.09, 0.67
	Age	-0.05	-0.20, 0.11
	Maternal rank	0.05	-0.10, 0.20
	Energy balance	**-0.19**	**-0.34, -0.03**
	% Time grooming *Energy balance	**0.19**	**0.05, 0.33**
fGCs	**% Time playing**	**-0.21**	**-0.39, -0.03**
	Sex (M)	0.20	-0.16, 0.56
	Age	-0.001	-0.16, 0.15
	Maternal rank	0.022	-0.13, 0.18
	Energy balance	**-0.18**	**-0.34, -0.02**
fGCs	**% Time playing**	**-0.22**	**-0.40, -0.04**
	Sex (M)	0.21	-0.15, 0.57
	Age	-0.003	-0.16, 0.15
	Maternal rank	0.03	-0.13, 0.18
	Energy balance	**-0.19**	**-0.35, -0.03**
	% Time playing *Energy balance	-0.05	-0.22, 0.12

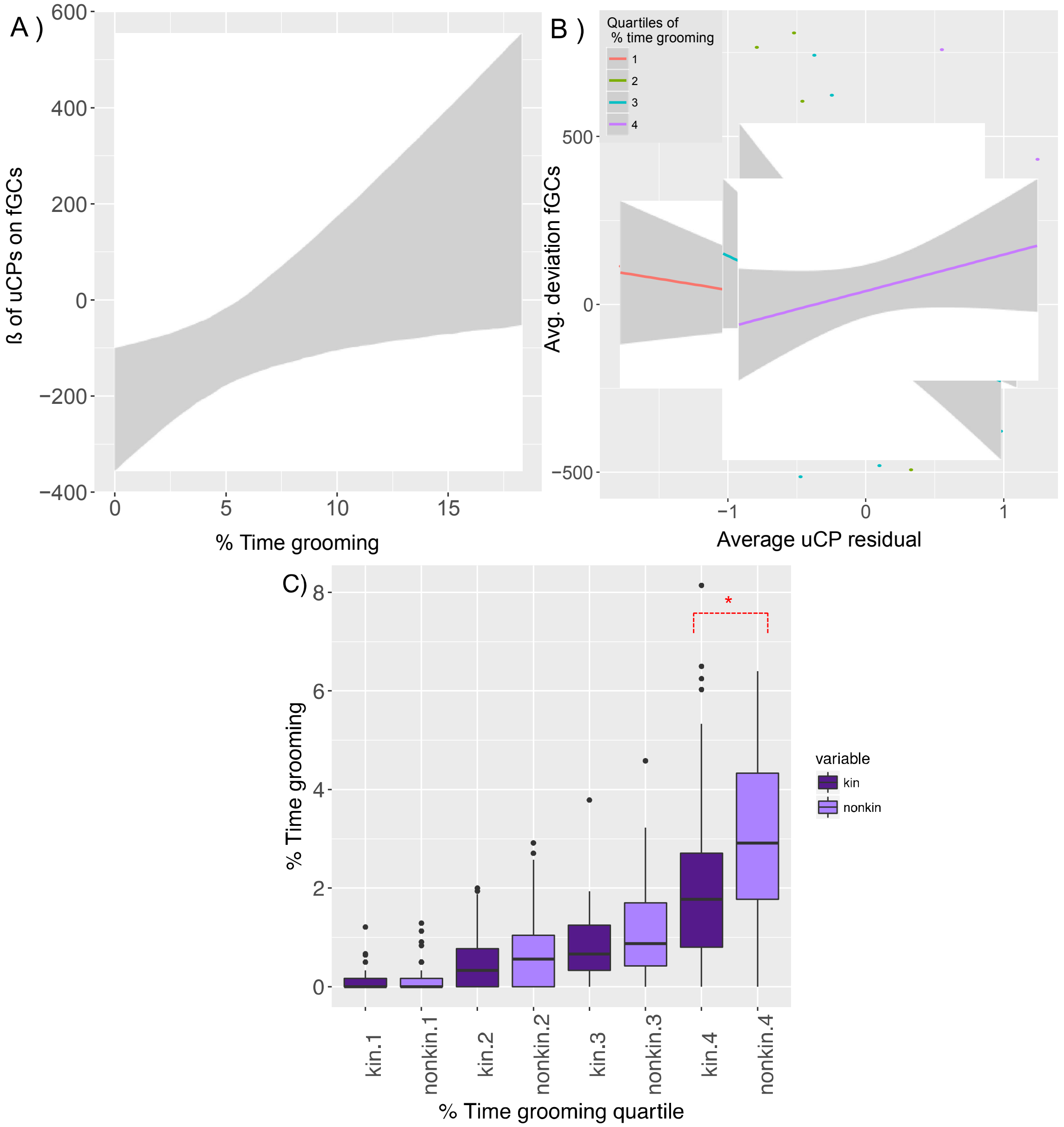

Figure 4.3. Exploring effects of time grooming. A) Conditional coefficient of uCP levels on fGCs as % time grooming varies. Predictors unstandardized. B) fGC levels on uCP levels by quartiles of % time grooming. C) % Time grooming kin vs. non-kin among subjects in each grooming quartile (significant difference for top quartile).

Discussion

In juvenile blue monkeys, both ecological and social variables appear to contribute to allostatic load, as measured by fecal glucocorticoid metabolites. Juvenile energy balance varied according to fruit availability, rainfall, and sex, and as energy balance became more positive, individual baseline fGC levels decreased. The first principal component characterizing social behavior, "groomer vs. player," also predicted baseline fGC levels: when sex was controlled for, juveniles that groomed more and played less had higher baseline fGCs. I did not find evidence that maternal dominance rank or involvement in agonism corresponded with fGCs. Neither grooming behavior nor playing appeared to buffer juveniles' experiences of energetic stressors. In fact, fGCs surprisingly increased with energy balance among juveniles that groomed the most. Time playing had no such moderating effect on energy balance and fGCs. It is possible that juveniles that groomed most were engaging riskier partners, as only they groomed more with non-kin than kin.

Variation in energy balance during development

Juvenile energy balance, as measured by urinary C-peptide levels, increased with the availability of ripe fruit in juveniles' home range, as known for wild chimpanzees and orangutans (Emery Thompson & Knott, 2008; Emery Thompson et al., 2009). Thus, as in other primate species (e.g. Deschner et al., 2008; Girard-Buttoz et al., 2011; Grueter, Deschner, Behringer, Fawcett, & Robbins, 2014; Harris, Chapman, & Monfort, 2010; Higham, Girard-Buttoz, Engelhardt, & Heistermann, 2011), uCP is also a valid measure of energy balance in wild, juvenile blue monkeys, confirming the general usefulness of this biomarker for investigating the association of environmental, social and life history variables with energetic condition of wild-living primates. Females were in a more positive energy balance than males, though they did not spend a larger percentage of their observation time feeding on fruit than males. Future studies of feeding and nutritional strategies might explore whether males and females select for different qualities of food during development. It is possible that males were more often in a less positive energy balance than females were because they spent more time playing, which is energetically costly (Held & Špinka, 2011). Additionally, older juvenile males could be in a less positive energy balance than similarly-aged females because they are entering or undergoing a growth spurt. Male growth rates appear to accelerate in blue monkeys at approximately 5 years old (Leigh, 1992), and 7 male subjects were older than this throughout the study. Unlike sex, maternal rank did not predict juvenile energy balance, although adult females form linear dominance hierarchies in which higher-ranking individuals have been observed to spend more time feeding on fruits than low-ranking females (Foerster et al., 2011). Also, probably because rainfall coincided somewhat with low availability of ripe fruit, individuals had lower energy balance during rainy periods.

Social strategies and their drivers during development

PCA revealed that playing and grooming accounted for the greatest variation in juvenile behavioral patterns (PC1), and were driven by differences in age, sex, fruit availability, and rainfall. Sex differences in playing and grooming in this species are pronounced, and higher scores on PC1 among older individuals likely derive from females increasing their time spent grooming with age (Cords et al 2010, Chap. 3). Fruit availability may have lowered scores on PC1 primarily through its influence on grooming, rather than play, as both time spent grooming and number of grooming partners decreased when more fruit was available, but number of play partners increased (Chap. 3). Higher fruit availability may influence group spatial dynamics such that individuals are more spread out and have fewer opportunities to groom. Nevertheless, males may have been more willing to overcome distant spacing to play, a behavior that could potentially be more vital to males than grooming is to females in terms of developing adult-typical behavioral competence in this species. More highly abundant fruit could also provide larger energy stores, which either motivate or allow males to play more (Sharpe et al., 2002). Peaks in fruit availability also corresponded with relatively low rainfall and higher daytime temperatures (Mitchell, 2009). On hot days individuals rest on or nearer the ground, which particularly while dry, is an attractive substrate for play (pers. obs.).

The second most important behavioral dimension (PC2), characterized as social vs. solitary, revealed that interacting with more affiliative partners frequently corresponded with giving and receiving agonism from them. Sexes did not differ in their scores on PC2 and, with age, both sexes appeared to expand their social networks and, concomitantly, their involvement in agonism. Interestingly, both fruit availability and rainfall decreased juveniles' number of social partners and their involvement in agonism. Again, juveniles are possibly more dispersed in the forest when foraging for widely available fruit and they may interact with fewer partners when huddling during heavy rain (Chap. 3).

Roles of social strategies and energy balance in juvenile allostatic load

As expected, given the major metabolic role that glucocorticoids play for mobilizing energy during unfavorable energetic conditions (Sapolsky et al., 2000), juveniles in a more positive energy balance had lower fGCs. This finding concurs with a previous study of adult female blue monkeys, which suggested that females increase circulating GCs to mobilize energy when energy balance is relatively low or insufficient (Foerster et al., 2011, 2012). Unlike adult females, *all* juveniles appeared prone to experience energetic stressors. Surprisingly, juveniles had higher fGC levels if they spent more time grooming (opposite to what was reported for adult females; Foerster et al., 2011) and were more intensely bonded to close affiliative partners, and if they spent less time playing and were less bonded to close play partners (i.e. had higher scores on PC1). These patterns appear to result from both a positive influence of time grooming on fGCs and a negative influence of time playing on fGCs. Although the negative relationship between play and fGCs was expected, the positive relationship between grooming and fGCs was not.

Two processes possibly underlie the relationships between playing, grooming, and fGCs. First, fruit availability and rainfall could be third variables corresponding to both social behavior and fGCs. Fruit availability and rainfall influence energy balance, correspond with temperature, and potentially alter habitat-use (e.g. more fruit leads to less associating and grooming; less rain leads to individuals closer to the ground and more play). Therefore, the relationship of social behavior and fGCs may be primarily driven by the effect of energetic status on fGCs, i.e. a more positive energetic state leads to lower GCs, and corresponds with more playing and less grooming. An alternative set of explanations, given that the influence of energy balance on fGCs was analytically controlled for in models, is that social behavior and fGCs have a relationship independent of energy balance. Within this set of explanations, GC levels may be a cause or a consequence of affiliative behavior.

The study by Anestis (2005), in which juvenile chimpanzees had higher GC levels if they were socially "smart" (i.e. if they received grooming, engaged in social play, and used coalitions), suggested that metabolic state was somehow associated with or caused social behavior. Because the study population of juvenile chimpanzees was captive, there was less opportunity than in the present study for variation in energy balance to simultaneously influence behavior and GC levels. Similarly, among ravens, post-fledgling individuals were thought to seek spatial associates and affiliative contact as a result of social stressors, leading to a positive relationship between GC levels and affiliative behavior (Stoewe et al., 2008). Nevertheless, Stoewe *et al.* (2008) did not directly examine whether rates of agonism *per se* corresponded with GC levels. A similar relationship between GCs and sociality may exist in juvenile blue monkeys, in which energy mobilized by GCs could motivate affiliative behavior.

Alternatively, navigating social groups may in itself be a (psychological) stressor to individuals, in which grooming interactions lead to elevations in GC levels. Although involvement in agonism (i.e. high scores on PC2) did not correspond with higher fGCs in the juvenile study subjects, affiliative interactions like grooming could be risky or uncertain because they increase opportunities for agonism. For example, in Japanese macaques, individuals that groom partners are more likely to subsequently receive agonism from groomees, although over time groomees reduced agonism and seemed to increase tolerance of groomers (Schino & Alessandrini, 2015). I found that juvenile blue monkeys that spent the most time grooming spent more time grooming with non-kin vs. kin. Unrelated partners may be riskier because they are less familiar and often more likely to aggress juveniles, such as in savannah baboons (Pereira, 1988a). Among chimpanzees, adults consistently have higher urinary cortisol after bouts of grooming non-bond partners than after bouts of grooming bond partners, with whom they are more familiar (Wittig et al., 2016). If blue monkey juveniles often groom with non-kin in feeding contexts, this might lead to the observed positive relationship between energy balance and fGCs among individuals that groomed the most.

Neither play nor grooming acted as a buffer of energy balance on fGC levels. In fact, the relationship between energy balance and fGCs was increasingly positive as time spent grooming increased, a reverse of the main effect of energy balance decreasing fGC levels. This suggests that, indeed, grooming with partners acts as some kind of stressor to juveniles, particularly when fruit availability is high.

Despite strong sex differences in grooming vs. play behavior (Chap. 3) and the influence of grooming vs. play on fGCs, sex did not predict further variation in fGC levels. This is likely because, while females groomed more and played less than males, thereby increasing fGCs, they also typically had higher energy balance than males, thereby lowering fGCs. This pattern may account for the large confidence interval of the estimated effect of sex on fGCs (Fig. 4.2). Stressors that juveniles experience did not appear to vary considerably with age. Similarly, maternal dominance relations do not confer any kind of advantage in terms of allostatic load in their offspring. The absence of dominance rank's influence on fGCs concurs with other studies in blue monkeys that demonstrate limited consequences of female dominance relations (Cords, 2000; Foerster et al., 2011; Pazol & Cords, 2005; Roberts & Cords, 2013).

Conclusions and Future Directions

Challenges to homeostasis during development stem from both ecological and social environments in blue monkeys. Notably, social strategies do not appear to help individuals cope with ecological challenges, but they do appear to exert other challenges of their own. Affiliative behavior, particularly when juveniles engage unfamiliar adults, may be may be inherently risky or uncertain for individuals that are relatively inexperienced or in a young life stage.

It is possible that the stress-inducing or energetic cost of grooming with non-kin is a worthwhile investment for juveniles, particularly among females that will spend the remaining years of their life potentially cooperating and competing with these non-kin partners. As other research on adult female blue monkeys shows (Chap. 2), if females are able to develop strong affiliative relationships with social partners that are consistent over years, this investment might pay off in greater survival. This study contributes to our understanding of short-term, proximate mechanisms by which social behavior potentially influences individual fitness.

Supplemental Information

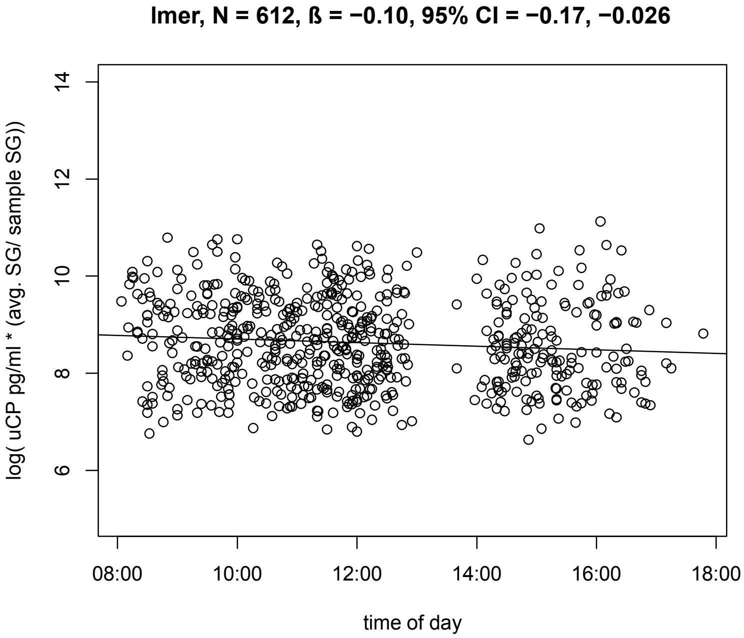

Figure S4.1. Log uCP value vs. time at collection.Term line is fitted from simple linear regression, unlike linear mixed model used for statistical analysis. N = 612 urine samples.

Table S4.1. QAP matrix correlations of DSI components: proportions of observation time that dyads engaged in grooming, approaching within 1 m, sitting in contact, resting in 1 m, and playing. N = 120 group-periods.

		Group 1 : GN		Group 2 : TWN		Group 3 : TWS	
period	Paired behavior	R	P (R) > null *	R	P (R) > null *	R	P (R) > null *
p1	grooming & approaches	2.81	0	1.4	0	1.46	0
p2		2.21	0	1.21	0	2.2	0
p3		0.86	0	1.43	0	0.53	0
p4		1	0	1.64	0	0.28	0
p1	contact & approaches	1.22	0	0.98	0	0.84	0
p2		0.8	0	0.64	0	0.36	0
p3		0.33	0	0.61	0	0.24	0
p4		0.34	0	0.94	0	1.36	0
p1	grooming & contact	1.08	0	0.46	0	0.35	0
p2		1.37	0	1.58	0	1.96	0
p3		2.03	0	1.87	0	0.3	0.001
p4		0.49	0	0.99	0	0.09	0.003
p1	grooming & playing	**-0.07†**	**0.719**	**0.03**	**0.149**	**0.03**	**0.169**
p2		0.57	0	**-0.01**	**0.385**	**0.01**	**0.193**
p3		0.09	0.03	**0.07**	**0.061**	**0.03**	**0.05**
p4		0.08	0.013	**-0.01**	**0.43**	**0.02**	**0.157**
p1	grooming & resting in 1 m	0.67	0	0.2	0.002	0.35	0
p2		0.39	0	0.23	0.003	0.29	0.002
p3		0.26	0	0.16	0.033	0.26	0
p4		0.17	0	0.37	0	0.07	0.003
p1	play & approaches	0.07	0.001	1.36	0	0.22	0
p2		0.67	0	2.85	0	0.45	0
p3		0.93	0	1.99	0	1.02	0
p4		1.35	0	1.76	0	0.5	0
p1	play & contact	0.01	0.008	**0.04**	**0.092**	**0**	**0.109**
p2		0.1	0.001	0.22	0.021	0.07	0.014
p3		0.29	0	0.37	0.003	0.11	0.034
p4		0.12	0.01	**0.05**	**0.063**	0.02	0.034
p1	play & resting in 1 m	0.01	0.018	**0.02**	**0.062**	0.04	0.004
p2		0.09	0	0.19	0.006	0.05	0.003
p3		0.1	0	0.24	0.006	0.14	0
p4		0.1	0	0.13	0.005	0.04	0.004
p1	resting in 1 m & approaches	1.56	0	1.22	0	1.42	0
p2		1.62	0	1.33	0	1.49	0
p3		1.77	0	0.6	0	1.34	0
p4		2.04	0	1.38	0	1.81	0
p1	resting in 1 m & contact	0.41	0	0.81	0	0.4	0
p2		0.62	0	0.37	0.006	0.74	0
p3		0.78	0	0.2	0.002	0.72	0
p4		0.88	0	0.3	0	0.62	0

* null distribution of correlation coefficients calculated using 1000 random permutations of social matrices.

† *Non*-significant correlations of behavior types in bold. Play did not correlate with other affiliative behavior in 13 of 120 comparisons.

Table S4.2. Influence of standardized predictors on energy balance as measured by average residual of log urinary C-Peptide (pg/ml urine) vs. time of day. Linear mixed effects regression, N = 156 subject-periods.

Predictor	Beta	SE	95% CI
Age	0.06	0.03	[-0.01, 0.12]
Sex (M)	**-0.15**	0.07	**[-0.28, - 0.02]**
Maternal rank	0	0.03	[-0.07, 0.06]
FAI	**0.15**	0.03	**[0.08, 0.22]**
Rainfall	**-0.1**	0.03	**[-0.17, -0.04]**

* 95% CI does not cross zero.

Table S4.3. Influence of standardized predictors on subjects' average deviation from baseline fGC levels (ng/g feces). Linear mixed effects regression, N = 155 subject-periods.

Predictor	Beta	SE	95% CI
PC1	**0.15**	0.07	**[0.03, 0.28]**
PC2	-0.01	0.07	[-0.14, 0.12]
PC3	0.03	0.07	[-0.11, 0.17]
Age	0.39	0.24	[-0.08, 0.86]
Sex (M)	-0.05	0.09	[-0.22, 0.12]
Maternal rank	0.01	0.08	[-0.15, 0.17]
uCP	**-0.17**	0.08	**[-0.33, -0.01]**

*95% CI does not cross zero.

Table S4.4. Linear mixed effects model comparing subjects' % time grooming kin vs. non-kin, subjects grouped by % time grooming quartile (1-4). N = 324 observations of groom time w kin and nonkin per subject-period.

comparison	ß	se	95% CI
nonkin.1-kin.1	0.05	0.25	[-0.44, 0.54]
nonkin.2-kin.2	0.24	0.25	[-0.25, 0.73]
nonkin.3-kin.3	0.32	0.25	[-0.17, 0.81]
nonkin.4-kin.4	0.9	0.25	**[0.41, 1.39]**

* significant difference in % time grooming kin vs. non-kin

Chapter 5: Mothers' role in shaping offspring social tendencies in a gregarious primate.

Introduction

In group-living animals, individuals often vary in the nature and degree to which they engage socially. Examining the causes of such variation is an important part of understanding the adaptive function of social behavior. Mothers are an important source of variation in social behavior, particularly in mammals, where mothers are critical social partners both early on and potentially throughout an offspring's lifetime. Indeed, in several animals, interactions with mothers early in life shape individual's social behavior throughout life (Champagne, 2010; Cushing & Kramer, 2005). In mammals, this effect occurs in part because neuroendocrinological mechanisms that maintain mammalian mother-offspring bonds underlie affiliative ties with all other social partners, phylogenetically and ontogenetically (Curley & Keverne, 2005; Keverne et al., 1989). The maternal genome also strongly affects the development of areas of the brain that are most involved in complex decision-making and social behavior, and which have undergone relative expansion in primates (Isles, Davies, & Wilkinson, 2006; Keverne, Martel, & Nevison, 1996). For these reasons, individuals often appear to inherit their mothers' social tendencies, socializing in ways that either resemble or are profoundly shaped by their mothers' behavior (e.g. Berman, 1990; Boehnke, 2015; Champagne, 2010; Maestripieri, 2003; Stevenson-Hinde & Simpson, 1981; Sullivan, Mendoza, & Capitanio, 2011).

Individuals can inherit their mothers' behavior in several ways. Inheritance can be primarily genetic, as assessed by either quantitative genetics (Wehner, Radcliffe, & Bowers, 2001) or cross-fostering experiments (Maestripieri, 2003; Møller, 2002), or epigenetic, via environmentally induced modifications of histone structure or methylation of gene promoter regions (Champagne, 2008). Behavior can also be transmitted via observation and learning, as when chimpanzees gain expertise in termite fishing by observing their mothers (Lonsdorf, 2006). Maternal effects are one class of particularly important phenomena in which an individual's behavior is shaped by its mother's, either epigenetically or by learning (Mousseau & Fox, 1998). Maternal effects typically refer to how an offspring's direct interaction with either its mother or the socio-ecological niche she creates changes its phenotype. Maternal effects are widespread: mothers influence offspring phenotypes and fitness even in animals with minimal parental care, such as in some herbivorous insects where the location in which mothers choose to lay their eggs influences offspring phenotype (Mousseau & Fox, 1998). One powerful example of maternal effects on behavior via epigenetic pathways comes from rats, where a mother's licking and grooming behavior determines the development of the same behavior in her daughters (Champagne, 2008)

Unlike strict genetic inheritance, epigenetic/learned inheritance often involves critical periods in which experience is especially likely to modify behavior. Early-life is one such critical window (Fawcett & Frankenhuis, 2015). During early-life development, aspects of individual physiology develop according to present experiences, in part because these serve as cues of the individual's future states, thus leading to what are called predictive adaptive responses (Bateson et al., 2014; English, Fawcett, Higginson, Trimmer, & Uller, 2016; Fawcett & Frankenhuis, 2015). In Assamese macaques for example, a mother's prenatal glucocorticoids increase with food scarcity and this in turn corresponds with her offspring's accelerated physical growth, a likely sign of early maturation that suggests an overall emphasis on reproduction over survival (Berghänel et al., 2016). Within early life, infancy, when individuals depend on parental care for survival, is often seen to be a critical window during which mother-offspring interactions and the mother's social niche influence later offspring behavior (Champagne, 2010; Fairbanks, 1996; Maestripieri, 2005; Maestripieri, Lindell, & Higley, 2007). For example, studies of laboratory rodents, humans, and non-human primates have revealed that infants with more secure attachments to mothers have greater emotional well-being later in life (lower anxiety, depression, and fearfulness) and lower sensitivity to external stressors (reviewed in Champagne, 2010).

The kinds of behavior subject to maternal effects, or in which mother-offspring similarities occur, are variable and include both social and non-social realms. In some birds, individuals may resemble mothers in their tendency to disperse (Doligez, Gustafsson, & Pärt, 2009) or their propensity to explore novel environments (Dingemanse, Both, Drent, Van Oers, & Van Noordwijk, 2002). In terms of broad social preferences, parents and offspring in some swallows prefer joining colonies of similar size post dispersal (Brown & Brown, 2000; Møller, 2002). In primates, individuals and their mothers display similar rates of affiliative social contact and aggression (Maestripieri, 2003), general social temperament or personality (Boehnke, 2015; Stevenson-Hinde & Simpson, 1981; Sullivan et al., 2011), and maternal style (Berman, 1990; Champagne, 2008; Fairbanks, 1996). Seyfarth et al. (2012), however, found no similarities between the social personalities of mothers and their adult daughters in baboons.

Similarities in the behavior of individuals and their mothers may be particular to sex. Sex-specific reproductive strategies select for different behavioral tendencies, the underlying neuroendocrinological mechanisms of which may cause each sex to respond differently to the same environmental or hormonal stimuli (Cushing & Kramer, 2005). For example, centrally administered oxytocin decreases sexual behavior in male prairie voles, but does not influence sexual behavior in females, potentially because of the mediating effects of differential levels of estrogen or expression of estrogen-receptors each sex (in Cushing & Kramer, 2005). Such neuroendocrinological differences could result in sex-differentiated responses to the same maternally-induced environment. Rhesus macaque mothers and daughters, but not sons, resemble one another in their “confidence” (lack of hesitation) and “excitability” (reactiveness to novelty) as assessed from observer surveys, whereas mothers’ “excitability” is inversely related to the “confidence” of their sons (Stevenson-Hinde & Simpson, 1981). Similarly, in a study that assessed rhesus mother’s and offspring’s temperaments during infancy, mothers that responded to novel challenges “confidently” had sons, but not daughters, that approached novel challenges in a “gentle” (calm, curious) and less vigilant way (Sullivan et al., 2011). Sullivan *et al.* (2011) argued that this sex-dependent relationship between mother-offspring behavior results from sex differences in sensitivity to early maternal behavior, such that sons are more responsive than daughters to maternal signals because they will eventually separate from mothers when they disperse.

Behavior that is similar between individuals and their mothers can be specific to interactions with particular partners. For example, similarities in maternal style are (by definition) relevant only to mothers' interactions with offspring. Peers, i.e., individuals within the same life stage, could be one such subset of partners with whom interactions follow a particular pattern or strategy, as peers are possibly both competitors and allies. For example, individuals often prefer to play with partners that are similar in age, presumably because they are also similar in size and experience and therefore facilitate individuals' self-assessment and motor development (Thompson, 1998). Because self-assessment could be a function particular to play with peers, patterns of play with peers could differ substantially from patterns of any play that occurs with non-peers. As another example, grooming between un-related adults could function to build alliances (Hemelrijk & Ek, 1991), whereas a mother grooming her infant functions as maternal investment and to improve offspring hygiene (Blanchard, Pays, & Fritz, 2017). Therefore, an adult female's pattern of grooming with adult peers likely differs from her pattern of grooming with her offspring.

In this study, I explore the relationship between the affiliative tendencies of juvenile animals with those of their mothers in wild blue monkeys (*Cercopithecus mitis stuhlmanni)*. Blue monkeys are an interesting species in which to examine the inheritance of social behavior: although adult females spend little time associating closely with one another (< 8% of observation time, Cords, 2002), variation in their affiliation with peers does appear to influence survival (Chap. 2). Specifically, females with strong but inconsistent ties to close partners have a relatively high risk of death. Further, social strategies of juveniles correspond with energetic costs and benefits, such that individuals that play more have lower and those that groom more have higher baseline glucocorticoids (Chap. 4).

I focus on affiliative vs. aggressive behavior because blue monkeys are relatively peaceful primates, exhibiting low rates of aggression (Klass & Cords, 2015). Further, I already know that individuals and their mothers are likely to be similar in their rates of agonism given and received because individuals appear to inherit their mothers' dominance ranks (Klass & Cords, 2015) and maternal dominance rank is a strong predictor of juveniles' agonistic behavior (Chap. 3). To examine similarities in the social behavior of juveniles and their mothers, I combined a long-term dataset on adult female social behavior in the wild study population with an independent dataset on juvenile social behavior from a shorter period. This study was observational and as it focused on long-lived animals, records were too limited to conduct robust quantitative genetic analyses. I assumed that transmission of behavior could occur by any means, including genetic or epigenetic inheritance, or learning. I evaluated maternal effects on juvenile social behavior by characterizing mothers' social niche and mother-offspring interactions during the juvenile subjects' infancy to predict later juvenile behavior. I used a broad-scale social metric (spatial association) to conduct an exploratory analysis aimed to generate hypotheses about inheritance and maternal effects on affiliative social behavior in this and other gregarious species. I also assessed the potential inheritance of strategies specific to association with peers.

Methods

Study site and subjects

The wild study population inhabits the Isecheno area of the Kakamega Forest, Kenya (0˚19´ N, 34˚52´ E; Mitchell, 2009). Study subjects were 41 juveniles (19 males, 22 females, average age = 4.4 ± 1.7 years, range = 2.2 – 6.9) and their 29 mothers (average age = 13.4 ± 4.1 years, range = 8.2 – 22), living in 3 social groups that ranged in size from 35 – 66 individuals, and 16 – 31 juveniles. 12 of 29 mothers were mother to two juvenile subjects, and 7 of the 12 had both a son and a daughter. Group composition and birthdates for juveniles and adult females were known from long-term demographic records (Cords, 2012). All subjects were individually identifiable by natural physical variation. I considered juveniles to be any individual that had not yet dispersed or given birth but was not born in the annual birth cohort (starting Dec 1, 2014) immediately prior to the start of juvenile observation.

Behavioral data collection

A team of observers collected data on mothers' behavior from October 2006 to August 2015, as a part of an ongoing long term study. Mothers' behavioral data spanned an average of 7.3 ± 2.1 yrs (range = 3–9 yrs, N=29 females). Data on juvenile behavior were collected during an 8-month study from August 2015 to March 2016 by a team of observers including author NAT. Observers conducted 30 min focal follows on mothers and 20 min follows on juveniles, recording at 1 minute intervals the subjects' activity (e.g. grooming, resting, moving, feeding, and playing for juveniles) and the IDs of its partners within 1 m, in contact, during grooming and play. When focal subjects were not visible, observers recorded their activity as “out of sight.” Upon relocating the subject, observers continued follows until they completed 20 or 30 min of observation for juveniles and mothers, respectively. If focal subjects were out of sight for 10 (juveniles) or 15 (mothers) consecutive minutes, the follow was terminated and the data discarded. In total, observers collected an average of 38.6 ± 3.0 hrs of behavioral data per juvenile and 553 ± 189 hrs per mother, for an average of 73.3 ± 18 hrs per mother–year.

Data analysis

I used data from focal follows to calculate 3 measures of association for mothers and 4 for juveniles: proportion of time spent (1) giving or receiving allo-grooming, (2) within 1 m or in contact with a partner, without allo-grooming, and (3) in 1 m of a partner whether grooming or not (general proximity). For juveniles, I additionally calculated time spent (4) playing, a behavior that hardly ever occurs among adult females. To better differentiate juveniles’ and mothers’ association measures, I also excluded mothers as partners that would count towards juveniles’ time in proximity or grooming. For mothers, I expressed proportions of time spent in association in two ways: (a) as an average across all years in which she was observed as a focal subject (“average”), and (b) during the first year of life of her offspring who was a juvenile subject. For both mothers and juveniles, I calculated association measures with two sets of partners (i) all groupmates and (ii) peers, i.e., at a given point sample, at least one other adult female was a partner for mothers and one other juvenile for juveniles. Finally, I calculated the time that mothers spent associating (measures 1-3) with her juvenile subject in its first year, and her time in general proximity to her juvenile in each year that she was observed during which the juvenile subject was alive (a proxy for juvenile age).

I expressed juvenile ages relative to the mid-date of their observation period. As controls in repeatability analyses, I calculated the annual number of peers and groupmates that mothers had in each observation year by averaging the daily number of co-resident adult females and other groupmates (including infants, juveniles, and adult males) over an observation year.

Statistical analysis

I modeled the time that juveniles spent associating with partners as a response in generalized additive models (GAMs) using the "gamlss" package in R (Stasinopoulos & Rigby, 2007). Generalized additive models easily implement beta and zero-inflated beta error distributions, which were appropriate for the responses.

We modeled juveniles' time in association as a function of the corresponding association type and partner subset of mothers. For example, mothers' time in general proximity to other adult females was used to predict juveniles' time in general proximity to other juveniles (example in Fig. 5.1). I also modeled juveniles' time in association as a function of the same association type of mother's with their juvenile offspring in its first year. Because play had no directly equivalent behavior among adult females, we used mothers' time in general proximity and time grooming in separate models to predict juveniles' time playing. I used mother's time with her juvenile subject in its first year of life to predict the juvenile's time spent in association with both subsets of partners, i.e. any partner and peers.

In each GAM, I included juveniles' sex and age as analytical control variables and an interaction term of mothers' social variable and juvenile sex, to explore whether relationships between juvenile and mother sociality varied by sex. I included mother and group IDs as random effects. Continuous fixed effects were standardized according to their mean and standard deviation (Schielzeth, 2010). In a two-step process to control for repeated testing, I first selected models in which the 95% confidence intervals of the parameters of interest (i.e. mother's time in association and mother's time in association by sex) did not include zero. After selecting models, I created adjusted confidence intervals of parameters of interest to control for their false coverage rate (FCR) arising from multiple testing (Benjamini & Yekutieli, 2005). Confidence intervals were adjusted according to the 60 hypotheses tested, i.e. 30 models x 2 parameters of interest. I considered predictors to have a significant effect on the response if the adjusted confidence intervals of their parameters did not include zero. I assessed overall model fit by comparing the AIC of the fitted model to a model that did not include any fixed effects (Nakagawa & Schielzeth, 2013). I used qq-plots to assess the normality of residuals in all models.

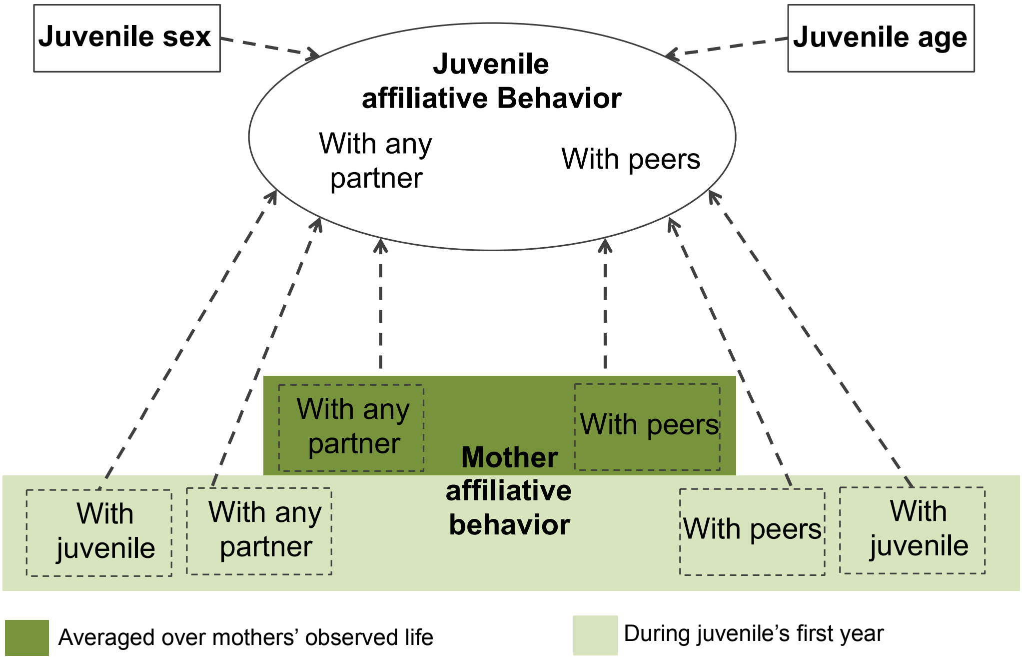

Figure 5.1. Conceptual diagram of modeled hypotheses: juvenile affiliative behavior is shaped by mother's social behavior and juvenile age and sex.

To further assess the possibility that juveniles and mothers were socially similar because their mutual association meant that they shared a social environment, I conducted two additional analyses. First, I examined how the time that mothers spent with their offspring changed over time. Using data on adult females, I constructed a GAM in which mothers' time in association with her juvenile was the response, observation year in which the juvenile was alive as a proxy for juvenile age, sex, and a sex by observation year interaction were fixed effects, with mother and group ID as random effects. Second, I examined whether juveniles' time in general proximity to their mothers (data from juvenile study) predicted their time in general proximity to non-mothers in a GAM with juvenile age, sex, time in general proximity to mother, and an interaction between time with mother and sex as fixed effects, and no random effects.

To assess whether mothers had social personalities, I calculated the consistency of between individual differences, or repeatability, in mothers' annual association time with a linear mixed model approach, using the "rptR" package in R (Nakagawa & Schielzeth, 2010; Stoffel, Nakagawa, & Schielzeth, 2017). This approach calculates the intra-class correlation coefficient (R) by grouping observations according to a random effects term (here, individual ID) and then assessing the variation among observations that is attributable to variation among individuals. The mixed model also allows one to control for confounding factors, e.g. group size or sex, that might otherwise bias an assessment of behavioral variation within or between individuals. Accordingly, mothers' annual association measures with any partner and peers were modeled as responses with either average total group size and number of adult females per year included as fixed effects. I further assessed the repeatability of mothers' annual association time in general proximity to their juveniles, including total group size and observation year with juvenile as fixed effects. I calculated confidence intervals and p values of R estimates by performing 1000 bootstraps without replacement and 1000 random permutations of observations, respectively.

Results

Juveniles spent an average of 9.5 ± 2.8% of time during the 8-month observation period in general proximity to ("near") another partner (excluding mothers), 6.3 ± 2.1% of time near another juvenile (though perhaps not exclusively), and 1.8 ±1.4% near their mothers. Juvenile females on average spent more time near groupmates than males did (females: 10.6 ± 3.2 %, males: 8.5 ± 2.0%, $t_{29.4} = 2.5$, *two-tailed* $p = 0.020$), whereas males spent more time near peers than females did (females: 5.3 ± 1.5 %, males: 7.1 ± 2.2%, $t_{36.6} = -3.0$, *two-tailed* $p = 0.005$). Male and female juveniles spent similar amounts of time near mothers during their 8-month study period (females = 2.0 ± 1.7%, males = 1.6 ± 1.0%, t-test, *two-tailed*, $t_{27.4} = 0.92$, $p = 0.37$). Both males and females spent less time near other partners the more time they spent near their mothers (GAM, response = time in general prox of groupmates, ß of time near mothers = -0.15, 95% CI = -0.26 – -0.03, ß of interaction between time near mothers and sex = 0.18, 95% CI = -0.01 – 0.37).

Over all observation years, mothers spent an average of 20.3 ± 4.9 % of observation time near another partner, and an average of 6.5 ± 2.5% near another adult female, specifically. During the juveniles' first year of life, mothers spent an average of 22.7 ± 5.6% of their observation time near their juveniles, and did not spend different amounts of time near or grooming offspring according to its sex (GAM, sex as fixed and mother as random effect, Sex (M) ß = 0.005, 95% CI = -0.004 – 0.015 for proximity, Sex (M) ß = 0.0004, 95% CI = -0.003 – 0.002 for grooming). Mothers groomed offspring, rather than received grooming from offspring, for an average of 99.2 ± 3% of total mother-infant grooming time. Mothers of male subjects alone spent no more or less of their time near partners (averaged over all observation years, 20.6 ± 5.0%, N=15) than mothers of only female subjects (20.7 ± 4.6%, N = 12; t-test*, two-tailed* $t_{24.5} = 0.077$, $p = 0.94$).

Because I was primarily interested in the relationship between juveniles' and mothers' sociality, I focused my presentation of results on those comparisons in which the relationship was significant. As expected, juvenile sex and age significantly predicted several measures of juveniles' time in association. Detailed analyses of sex differences during development in this species can be found in Cords *et al.* (2010) and Chap. 3.

Juveniles' sociality was related to their mothers' in only one instance, according to adjusted confidence intervals. Namely, the time that a juvenile spent grooming with its mother in its first year of life had a positive relationship with the time that male juveniles spent grooming with peers and a negative relationship with the time that female juveniles spent grooming with peers (Table 5.1, Fig. 5.2a, Fig. S5.1a). The difference in the time that male and female juveniles groomed with peers was largest when the time that they had groomed with mothers as infants was low. For those juveniles that groomed most with mothers during infancy, there was (almost) no sex difference in grooming with peers (Fig. 5.2a, Fig. S5.1a). Juveniles did not appear to groom differently with non-peers according to their grooming with peers, as the two values were unrelated when controlling for juvenile sex, age, and their interaction (GAM, response = time grooming with non-peers, time grooming with peers ß = 0.04, CI = - 0.16 – 0.24).

Other comparisons that were initially selected for 95% CI of interaction parameters, but not significant according to their adjusted CI, revealed similar effects of mother sociality moderated by sex (Table 5.1, Fig. 5.2b-c, Fig. S5.1b-c). A mother's time spent near any partner, either averaged over all observation years or during their juvenile's the first year of life, also had a positive relationship with their sons' and a negative relationship with their daughters' general proximity to any partner. Also as mothers' spent more time near partners (averaged over all years), daughters spent less time playing, whereas the amount of time sons played did not vary (Table 5.1, Fig. 5.2d, Fig. S5.1d).

Notably, the majority of comparisons did not reveal significant relationships between juveniles' and mothers' sociality (Table S5.1). No measure of mothers' association time with any groupmate (excluding mother-offspring association in juveniles' first year) predicted juveniles' association time. Further, mothers' time near peers did not predict their juveniles' time near peers, regardless of the measure of association time (i.e. time grooming, time in proximity without grooming, etc.), and regardless of whether I included mother's average behavior or her behavior during her offspring's first year. Mother-offspring association time in juveniles' first year did not predict juveniles' time in association with any groupmate, and neither mother's time in proximity to (and not grooming) nor time near the juvenile in its first year predicted the time that juveniles spent in the same behavior with their peers.

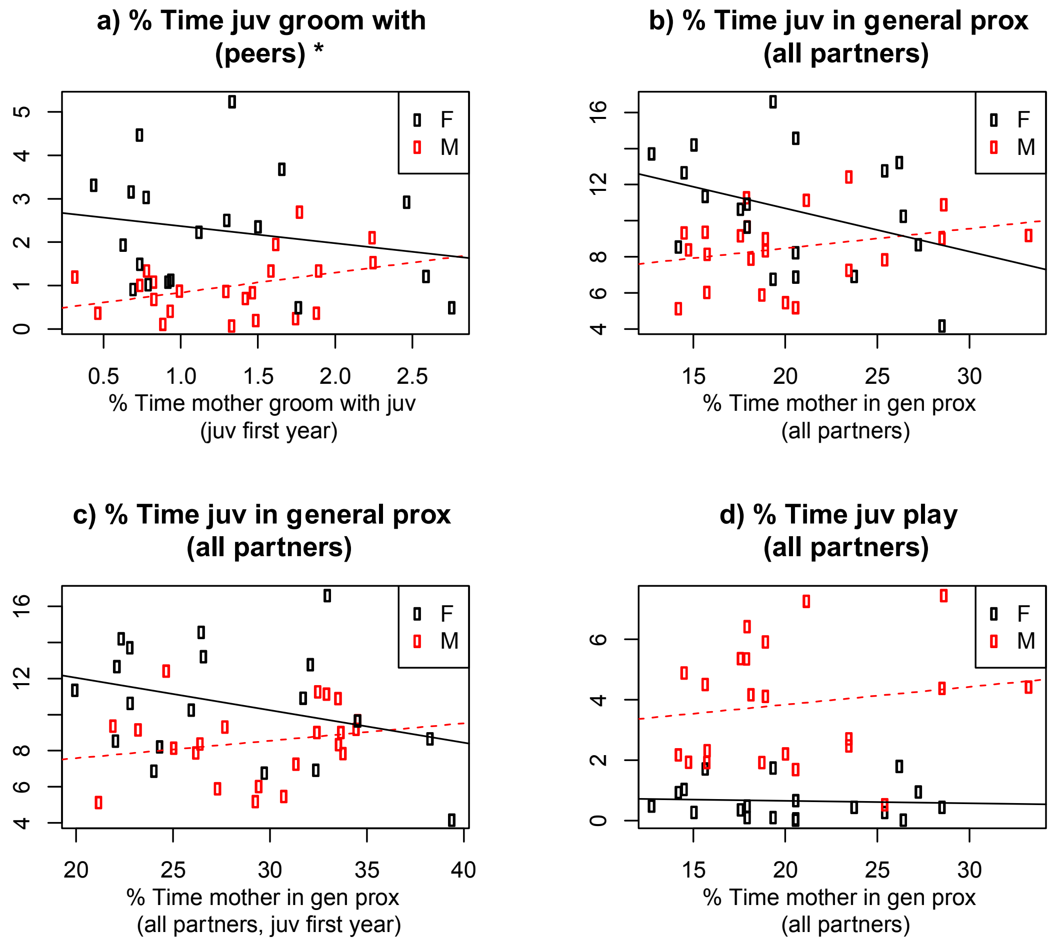

Figure 5.2. Juveniles' time spent in association by mothers' social variables. a) Juveniles' % time grooming peers, b and c) in general proximity of partners, and d) playing according to mothers' time in association with partners (x-axis) by sex (males in red and females in black). Trend line is simple linear regression, unlike GAM models in results. Models selected according to 95% CI of interaction's parameter estimate. * Indicates significant effect according to CI adjusted for false coverage rate.

Table 5.1. Selected and significant relationships between juvenile and mothers' association measures (General additive models, mother and group ID as random effects, N = 41 mother-juvenile pairs). Selected parameters (significant according to unadjusted CI) italicized, significant parameters according to adjusted CI in bold.

Response: % Time juv… (partners)	ΔAIC*	Predictor: % Time mother…, (partners, time period)	ß	se	95% CI	adjusted CI**
Juv groom (peers)	-22.93	Intercept	-3.91	0.07	[-4.044, -3.774]	
		Mother groom with juv (juv first year)	*-0.19*	*0.07*	*[-0.325, -0.057]*	[-0.39, 0.01]
		Juv sex (M)	-0.78	0.12	[-1.015, -0.554]	
		Juv age	0.23	0.05	[0.126, 0.338]	
		Mother groom with juv (fy) : Sex (M)	*0.44*	*0.13*	*[0.186, 0.696]*	**[0.06, 0.82]**
Juv general prox (any partner†)	-11.31	Intercept	-2.15	0.06	[-2.26, -2.041]	
		Mother general prox (any partner, all years)	-0.08	0.06	[-0.199, 0.047]	
		Juv sex (M)	-0.23	0.08	[-0.384, -0.073]	
		Juv age	0.13	0.04	[0.051, 0.219]	
		Mother general prox (ap, ay) : Sex (M)	*0.18*	*0.08*	*[0.023, 0.336]*	[-0.05, 0.41]
Juv general prox (any partner)	-11.55	Intercept	-2.16	0.06	[-2.273, -2.048]	
		Mother general prox (any partner, juv first year)	-0.06	0.05	[-0.165, 0.041]	
		Juv sex (M)	-0.24	0.08	[-0.398, -0.076]	
		Juv age	0.14	0.04	[0.06, 0.23]	
		Mother general prox (ap, fy) : Sex (M)	*0.2*	*0.09*	*[0.03, 0.365]*	[-0.05, 0.45]
Juv play (any partner)	-48.11	Intercept	-5.1	0.15	[-5.391, -4.816]	
		Mother general prox (any partner, all years)	-0.28	0.15	[-0.568, 0.016]	
		Juv sex (M)	1.83	0.16	[1.526, 2.136]	
		Juv age	-0.17	0.06	[-0.28, -0.052]	
		Mother general prox (ap, ay) : Sex (M)	*0.31*	*0.16*	*[0.003, 0.616]*	[-0.15, 0.77]

* ΔAIC = AIC full model - AIC null model (no fixed effects)

** Confidence intervals adjusted to control for false coverage rate (Benjamini & Yekutieli, 2005).

† Mother excluded as potential partner of juvenile.

Mothers showed consistent inter-individual differences in the amount time that they spent grooming with any partner, but the amount of time that they spent in proximity to any partners without grooming or simply near partners was not repeatable over years (Table 5.2). Time that mothers spent in association with other adult females (whether grooming, resting in proximity without grooming, or in general proximity) was repeatable over years. These repeatable differences in mothers' social behavior were evident even as I accounted for their number of potential partners. In contrast to these results for mothers interacting with other group mates, no variant of their association with offspring was repeatable over years (Table 5.2). Further, the time that mothers spent near their offspring declined with each observation year during which the juvenile was alive, similarly for both males and females (Fig. 5.3; GAM, ß observation year = - 0.41, 95% CI = -0.46 – -0.35, ß observation year by sex = -0.02, 95% CI = -0.1 – 0.05, N = 186 mother-offspring observation years).

Table 5.2. Repeatability of % of observation time that mothers spent in association with different partner subsets.

	Association type	R	se	CI	Permuted p	N (mother-years)
Any partners	In general prox	0.03	0.04	[0, 0.12]	0.22	212
	Grooming with	0.59	**0.08**	**[0.42,**	**0***	
	In prox (no grooming)	0	0.03	[0, 0.09]	1	
Peers	**In general prox**	0.81	**0.05**	**[0.69,**	**0**	212
	Grooming with	0.72	**0.06**	**[0.57,**	**0**	
	In prox (no grooming)	0.76	**0.06**	**[0.62, 0.84]**	**0**	
Juvenile offspring	In general prox	0	0.02	[0, 0.08]	0.36	186
	Grooming with	0	0.02	[0, 0.07]	1	
	In prox (no grooming)	0	0.02	[0, 0.07]	1	

*Significantly repeatable behavior in bold.

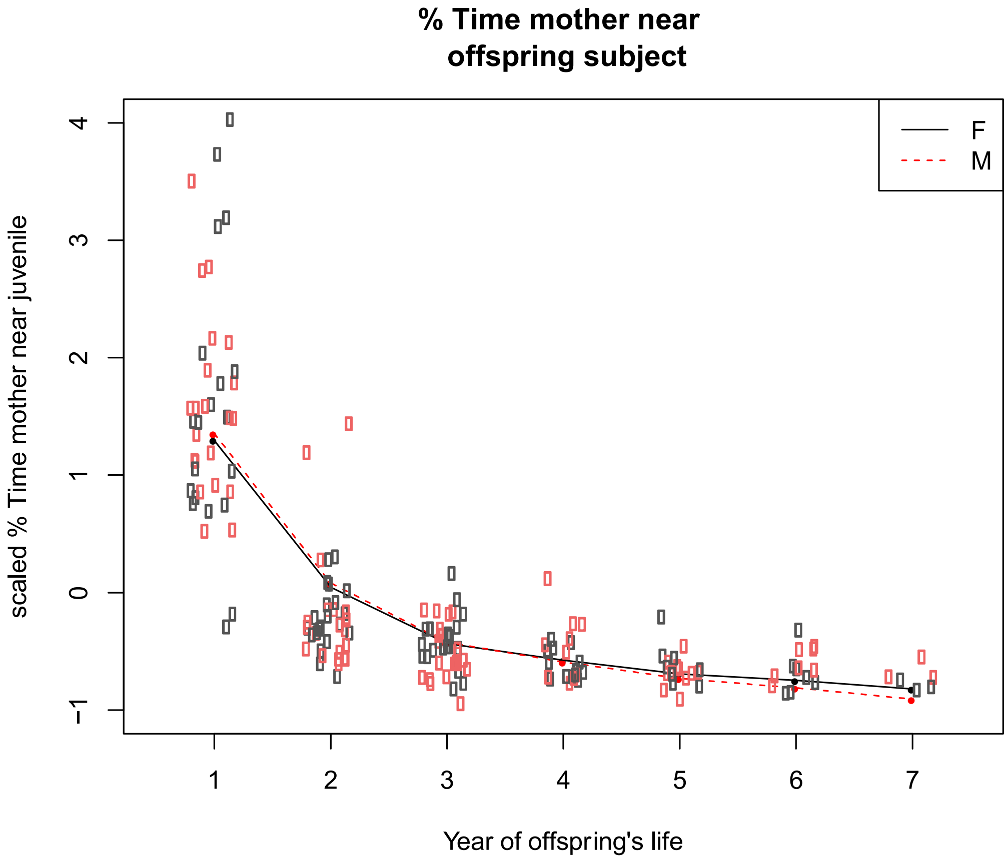

Figure 5.3. Standardized variation in percentage of observation time that mothers spent near their juveniles during each year of offsprings' life. Solid points fitted by a general additive model, hollow data points jittered by observation year, N = 186 mother-offspring observation years. Time with male offspring in red/pink and female offspring in black/grey.

Discussion

Of the several hypotheses tested regarding the relationship between juveniles' and mothers' sociality, only one was strongly supported: the time that an animal spent grooming with its mother in its first year of life predicted the time it spent grooming fellow juveniles later in life. Within this effect, males that groomed more with mothers during infancy spent more time grooming with juvenile peers later in life, whereas females that groomed more with mothers as infants groomed fellow juveniles less. Variation in grooming with peers did not appear to be a part of a larger grooming strategy, as juveniles' time grooming with peers was not related to time grooming non-peers.

I discuss my findings in two parts, treating first the timing of this apparent maternal effect and second the facts that the effect was related to grooming behavior and differed by sex. I acknowledge that my measure of early life grooming, derived from focal sampling adult females, clearly focused attention exclusively on the infant's interactions with its mother alone. A previous study of blue monkey infants found that non-mothers account for more grooming during infancy than mothers do (Förster & Cords, 2005), and therefore the dataset excludes what could be important variation in the amount of time that infants were groomed by non-mothers. I critically discuss both likely and unlikely explanations for the findings.

If patterns of juvenile grooming behavior were caused in part by interactions with mothers, interactions during infancy were the more likely cause than interactions with mothers throughout development for two reasons. First, the time that mothers and their offspring spent together decreased drastically after a juvenile's second year. Second, variation among mothers in the amount of time they spent with their offspring was not consistent from year to year. It is also unlikely that the relationship between mother-infant and juvenile-peer grooming behavior represented the continuation of juveniles' behavioral phenotypes from infancy into juvenility. Nearly all mother-infant grooming time involved mothers as the groomers, and therefore mothers, not infants, were largely responsible for grooming time. Further, variation in nutrition, rather than in maternal behavior, was also unlikely to cause variation in later juvenile behavior, because suckling was considered a form of contact and so was primarily captured by either mothers' time spent in proximity without grooming or general proximity to infants. Although mothers could suckle infants while grooming them, such simultaneous occurrences were rare. Although the influence of nutrition during infancy on later behavior would be interesting to examine, exact rates of suckling are difficult to quantify, as even time observed on the nipple may not equate to feeding.

Differential social experiences with mothers during infancy do not appear to explain sex differences in how a juvenile's grooming with its mother during infancy related to its grooming with peers. Males and females groomed with their mothers for similar amounts of time during infancy and also spent similar amounts of time with mothers during juvenility. Mothers' social environments, in terms of association with other group-mates, also did not differ if their offspring in this study were only male vs. female. Further, previous analyses have shown that non-mothers do not treat infants differently according to their sex (Förster & Cords, 2005). During juvenility, both males and females spent less time near non-mothers as time near their mothers increased, suggesting that neither sex gained different amounts of time associating with other groupmates as a result of associating with their mother.

If grooming behavior towards peers is learned or transmitted epigenetically, it appears that males and females *respond* differently to early-life grooming with their mothers. It is difficult to imagine a scenario in which the transmission of grooming behavior was strictly genetic and behavior simply manifested differently in males vs. females. In general, one might expect a relative deprivation of maternal grooming to decrease grooming behavior in offspring, as seen in rats that were separated from their mothers during infancy for daily 4.5 hr periods (Vivinetto, Suárez, & Rivarola, 2013). While such evidence in rats adds insight to maternal effects on grooming behavior among male juvenile blue monkeys, it does not explain the opposite pattern that occurs in females. Evidence of sex-specific maternal effects on social behavior comes mostly from rodents, particularly relating to play behavior. More maternal licking and grooming decreases rates of social play in male but not female rat pups (reviewed in Auger & Olesen, 2009), although this effect seems not to occur in mice (Franks, Champagne, & Curley, 2015). Maternal contact and grooming in early life may modify the development of important neurotransmitter receptors that differ according to sex, possibly resulting in behavioral outcomes that differ by sex. For example, maternal licking and grooming in rats corresponds with increased oxytocin receptors in the brains of female pups, but not of males, and increased vasopressin receptors in males' but not females' brains (Francis, Young, Meaney, & Insel, 2002).

In blue monkeys, grooming constitutes a large portion of adult female, but not adult male, social life; accordingly, female juveniles on average spend more time grooming than do males (Cords et al., 2010; Chap. 3). As grooming experience may be more important for developing behavioral competence among females than males, juvenile females that received little grooming from their mothers during infancy may have compensated for their lack of experience by spending more time grooming peers as juveniles. Such a compensatory or "rebound" effect following relative social deprivation has been seen in the play behavior of several rodent species (Hole, 1991), although no studies to my knowledge reveal a similar effect in grooming. Maternal grooming in blue monkeys could correspond to one of several "mothering styles," which are often characterized as spanning a spectrum of protective – rejecting, such that female offspring that receive very little grooming from mothers are encouraged to be independent and less neophobic, whereas female offspring that receive lots of grooming from mothers are more wary of novel environments and social partners (as seen in Bardi & Huffman, 2002; Fairbanks & McGuire, 1988; Schino, Speranza, & Troisi, 2001). A related and underlying neurological process of female juvenile grooming patterns could be related to the development of their reward pathways. Low maternal grooming during infancy could result in low dopamine receptor density, causing females to seek out additional rewarding interactions (Peña, Neugut, Calarco, & Champagne, 2014). It could also be possible, as in vervets, that mothers and female offspring are carriers of the dopamine D4 receptor polymorphism, which decreases maternal sensitivity and attentiveness, increases juvenile impulsivity, and results in offspring with a highly impulsive and novelty-seeking phenotype when both offspring and mother are carriers (Fairbanks, Way, Breidenthal, Bailey, & Jorgensen, 2012).

Alternatively, of course, female infants that were groomed less by their mothers could have been groomed more by non-mothers, specifically by large juvenile females and older siblings (Brent, Bramblett, Bard, Bloomsmith, & Blangero, 1997; Förster & Cords, 2005). Female infants could have simply continued to interact with such juveniles as they aged, and so spent more time grooming "peers" than females that received more grooming from mothers as infants. The current dataset is unfortunately limited to records of infant behavior from the perspective of the mother. Nevertheless, if less grooming from mothers equated to more grooming from non-mother groupmates, it would still not explain why male and female grooming behavior with peers would differ according to their time grooming with their mother as infants.

Male juveniles spent more time with peers than females did, probably because juvenile male blue monkeys spend more time playing than females and are more likely to play with partners that are close vs. distant in age to them (Chap. 3), similar to patterns in other species (Templeton et al., 2012; van Noordwijk et al., 2003). Although male juveniles generally spend less time grooming than females (Cords *et al.*, 2010; Chap. 3), it is not uncommon to see male juveniles grooming one another during breaks in play bouts (pers. obs.). It is possible, therefore, that as males received more grooming from their mothers as infants they were more disposed to groom their peer play partners.

Relationships between juveniles' and mothers' social behavior that were selected but did not reach significance according to CIs adjusted for false coverage rate were similar to those between mother-infant and juvenile-peer grooming. Although these patterns did not reach significance, their similarity to the effect of mother-offspring grooming on juvenile-peer grooming behavior – i.e. males' association time increased and females' association time decreased with increased mothers' sociality – suggests that this effect is real. It is possible that mothers' time grooming juveniles' in their first year, and juveniles' time grooming with peers, were large enough contributions to mothers' and juveniles' time near partners that patterns of grooming behavior drove patterns of general proximity. Alternatively, there could be other relationships between mother and offspring social behavior that a study with greater statistical power could uncover. Although mother-infant grooming time and juvenile-peer grooming time do not clearly translate to the behavioral patterns known to correspond with survival and energetics in adult female and juveniles, respectively (Chap. 2, 4), this study takes a first step to understand how potentially adaptive behavior is transmitted from one generation to the next in blue monkeys.

Conclusions

The findings of this preliminary study are meant to encourage the development of hypotheses to be tested in future studies. Although I found no direct links between juveniles' sociality with groupmates and that of their mothers, I did find an apparent maternal effect in which juveniles' grooming with peers varied according to the time their mother had groomed with them during infancy. The results of this study suggest that males and females demonstrated different amounts of affiliative behavior in response to the affiliative experiences they had with their mothers as infants. Although I found evidence for such an early-life maternal effect on juvenile grooming behavior, future studies should focus on the infant and measure the total grooming it receives from non-mothers. One striking implication of the apparent influence of mother-infant grooming on juvenile grooming behavior is that the rather conventional sex difference in juvenile grooming behavior in blue monkeys (at least among peers) arises only when mother-infant grooming time is low. Future experimental studies could modify mother-infant interactions to observe maternal effects on offspring social behavior in a controlled environment, avoiding the cruelty and confound of complete isolation (e.g. Holloway & Suter, 2004).

Supplemental Information

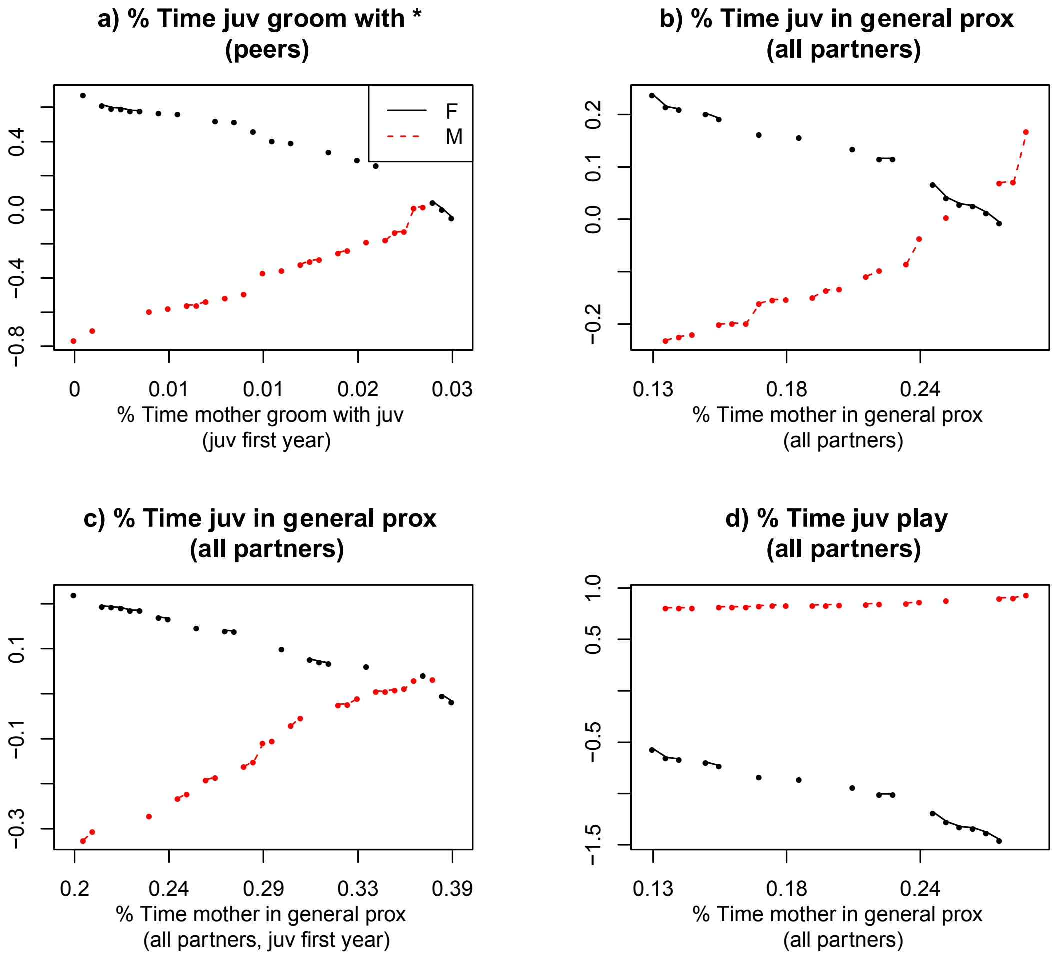

Figure S5.1. Modeled partial variation of juveniles' time spent with partners : a) grooming peers, b and c) in general proximity of partners, and d) playing according to mothers' time in association with partners (x-axis) by sex (males in red and females in black). Models selected according to 95% CI of interaction's parameter estimate. * Indicates significant effect according to CI adjusted for false coverage rate.

Table S5.1. Non-significant relationships between juvenile and mothers' association measures (General additive models, mother and group as random effects, N = 41 mother-juvenile pairs). ΔAIC = AIC full model - AIC null model (no fixed effects).

Response: % Time juv… (partners)	ΔAIC	Predictor: % Time mother…, (partners, time period)	ß	se	95% CI
Juv groom (any partners)	-38.86	Intercept	-3.04	0.09	[-3.211, -2.859]
		Mother groom (any partners, all years)	-0.08	0.08	[-0.23, 0.077]
		Juv sex (M)	-1.29	0.16	[-1.614, -0.973]
		Juv age	0.35	0.07	[0.21, 0.498]
		Mother groom (ap, ay) : Sex (M)	0.21	0.15	[-0.086, 0.504]
Juv groom (any partners)	-39.85	Intercept	-3.04	0.09	[-3.217, -2.861]
		Mother groom (any partners, juv first year)	-0.11	0.11	[-0.325, 0.114]
		Juv sex (M)	-1.26	0.16	[-1.58, -0.938]
		Juv age	0.35	0.09	[0.164, 0.535]
		Mother groom (ap, fy) : Sex (M)	0.26	0.15	[-0.042, 0.565]
Juv groom (any partners)	-41.33	Intercept	-3.04	0.08	[-3.206, -2.875]
		Mother groom with juv (juv first year)	-0.15	0.08	[-0.317, 0.008]
		Juv sex (M)	-1.31	0.16	[-1.621, -1.007]
		Juv age	0.35	0.07	[0.22, 0.486]
		Mother groom with juv (fy) : Sex (M)	0.31	0.17	[-0.015, 0.638]
Juv groom (peers)	-13.49	Intercept	-3.86	0.09	[-4.03, -3.694]
		Mother groom (peers, all years)	0.06	0.1	[-0.132, 0.26]
		Juv sex (M)	-0.77	0.14	[-1.049, -0.499]
		Juv age	0.23	0.07	[0.098, 0.371]
		Mother groom (prs, ay) : Sex (M)	0.05	0.15	[-0.241, 0.334]
Juv groom (peers)	-14.27	Intercept	-3.83	0.09	[-3.999, -3.665]
		Mother groom (peers, juv first year)	-0.1	0.09	[-0.285, 0.082]
		Juv sex (M)	-0.85	0.15	[-1.136, -0.559]
		Juv age	0.18	0.08	[0.035, 0.332]
		Mother groom (prs, fy) : Sex (M)	-0.01	0.15	[-0.317, 0.287]
Juv prox no groom (any partners)	-28.1	Intercept	-2.71	0.05	[-2.805, -2.617]
		Mother prox no groom (any partners, all years)	-0.04	0.06	[-0.149, 0.067]
		Juv sex (M)	-0.56	0.07	[-0.707, -0.415]
		Juv age	0.11	0.04	[0.029, 0.187]
		Mother prox no groom (ap, ay) : Sex (M)	0.13	0.07	[-0.019, 0.271]
Juv prox no groom (any partners)	-25.75	Intercept	-2.71	0.05	[-2.813, -2.612]

		Mother prox no groom (any partners, juv first year)	-0.01	0.05	[-0.107, 0.079]
		Juv sex (M)	-0.57	0.08	[-0.723, -0.41]
		Juv age	0.11	0.04	[0.029, 0.188]
		Mother prox no groom (ap, fy) : Sex (M)	0.06	0.08	[-0.106, 0.222]
Juv prox no groom (any partners)	-25.49	Intercept	-2.71	0.05	[-2.81, -2.606]
		Mother prox no groom with juv (juv first year)	0.03	0.06	[-0.086, 0.141]
		Juv sex (M)	-0.57	0.08	[-0.725, -0.407]
		Juv age	0.11	0.04	[0.033, 0.191]
		Mother prox no groom with juv (fy) : Sex (M)	-0.04	0.09	[-0.214, 0.126]
Juv prox no groom (peers)	3.47	Intercept	-3.53	0.06	[-3.662, -3.407]
		Mother prox no groom (peers, all years)	-0.11	0.07	[-0.246, 0.022]
		Juv sex (M)	-0.08	0.09	[-0.254, 0.098]
		Juv age	-0.07	0.05	[-0.166, 0.017]
		Mother prox no groom (prs, ay) : Sex (M)	0.06	0.09	[-0.125, 0.247]
Juv prox no groom (peers)	1.72	Intercept	-3.52	0.06	[-3.649, -3.398]
		Mother prox no groom (peers, juv first year)	-0.13	0.07	[-0.265, -0.004]
		Juv sex (M)	-0.1	0.09	[-0.281, 0.071]
		Juv age	-0.12	0.05	[-0.231, -0.018]
		Mother prox no groom (prs, fy) : Sex (M)	0.02	0.09	[-0.16, 0.205]
Juv prox no groom (peers)	5.04	Intercept	-3.55	0.07	[-3.685, -3.424]
		Mother prox no groom with juv (juv first year)	-0.07	0.08	[-0.218, 0.077]
		Juv sex (M)	-0.05	0.09	[-0.224, 0.131]
		Juv age	-0.05	0.05	[-0.137, 0.043]
		Mother prox no groom with juv (fy) : Sex (M)	0.01	0.1	[-0.174, 0.202]
Juv play (any partners)	-44.94	Intercept	-5.08	0.17	[-5.407, -4.755]
		Mother general prox (any partners, juv first year)	-0.03	0.14	[-0.309, 0.247]
		Juv sex (M)	1.78	0.18	[1.437, 2.13]
		Juv age	-0.1	0.07	[-0.229, 0.033]
		Mother general prox (ap, fy) : Sex (M)	0.24	0.16	[-0.079, 0.556]
Juv play (any partners)	-43.99	Intercept	-5.07	0.16	[-5.393, -4.753]
		Mother general prox with juv (juv first year)	0.01	0.16	[-0.309, 0.327]
		Juv sex (M)	1.8	0.17	[1.462, 2.142]
		Juv age	-0.14	0.06	[-0.26, -0.014]
		Mother general prox (fy) : Sex (M)	0.11	0.18	[-0.243, 0.464]
Juv play (peers)	-30.66	Intercept	-4.98	0.19	[-5.359, -4.602]
		Mother general prox (peers, all years)	-0.25	0.17	[-0.579, 0.088]
		Juv sex (M)	1.64	0.2	[1.243, 2.041]
		Juv age	-0.07	0.07	[-0.216, 0.072]
		Mother general prox (prs, ay) : Sex (M)	0.27	0.18	[-0.088, 0.637]
Juv play (peers)	-28.87	Intercept	-4.93	0.2	[-5.335, -4.533]
		Mother general prox (peers, juv	-0.24	0.19	[-0.618, 0.137]

		first year)			
		Juv sex (M)	1.6	0.22	[1.176, 2.023]
		Juv age	-0.08	0.1	[-0.275, 0.125]
		Mother general prox (ap, fy) : Sex (M)	0.25	0.2	[-0.132, 0.638]
Juv play (peers)	-28.03	Intercept	-5	0.2	[-5.399, -4.601]
		Mother general prox with juv (juv first year)	0.06	0.2	[-0.328, 0.453]
		Juv sex (M)	1.66	0.21	[1.242, 2.083]
		Juv age	-0.04	0.08	[-0.187, 0.116]
		Mother general prox (fy) : Sex (M)	-0.02	0.22	[-0.455, 0.418]
Juv play (any partners)	-45.24	Intercept	-5.08	0.16	[-5.384, -4.771]
		Mother groom (any partners, all years)	-0.07	0.13	[-0.319, 0.189]
		Juv sex (M)	1.8	0.17	[1.48, 2.13]
		Juv age	-0.13	0.06	[-0.247, -0.009]
		Mother groom (ap, ay) : Sex (M)	0.17	0.15	[-0.115, 0.454]
Juv play (any partners)	-40.84	Intercept	-5.02	0.19	[-5.384, -4.647]
		Mother groom (any partners, juv first year)	0.01	0.18	[-0.347, 0.363]
		Juv sex (M)	1.77	0.2	[1.383, 2.162]
		Juv age	-0.02	0.11	[-0.229, 0.195]
		Mother groom (ap, fy) : Sex (M)	0.13	0.19	[-0.231, 0.497]
Juv play (any partners)	-43.43	Intercept	-5.06	0.17	[-5.4, -4.715]
		Mother groom with juv (juv first year)	-0.02	0.14	[-0.3, 0.257]
		Juv sex (M)	1.8	0.19	[1.439, 2.165]
		Juv age	-0.12	0.07	[-0.249, 0.013]
		Mother groom with juv (fy) : Sex (M)	0.2	0.16	[-0.127, 0.52]
Juv play (peers)	-28.92	Intercept	-4.98	0.2	[-5.376, -4.588]
		Mother groom (peers, all years)	-0.2	0.16	[-0.514, 0.119]
		Juv sex (M)	1.65	0.21	[1.232, 2.061]
		Juv age	-0.06	0.08	[-0.206, 0.094]
		Mother groom (prs, ay) : Sex (M)	0.15	0.18	[-0.202, 0.505]
Juv play (peers)	-30.54	Intercept	-4.94	0.2	[-5.326, -4.553]
		Mother groom (peers, juv first year)	-0.35	0.21	[-0.756, 0.061]
		Juv sex (M)	1.58	0.21	[1.172, 1.991]
		Juv age	-0.13	0.09	[-0.318, 0.05]
		Mother groom (prs, fy) : Sex (M)	0.23	0.21	[-0.193, 0.645]
Juv play (peers)	-28.39	Intercept	-4.99	0.21	[-5.397, -4.579]
		Mother groom with juv (juv first year)	-0.03	0.16	[-0.352, 0.285]
		Juv sex (M)	1.64	0.22	[1.213, 2.076]
		Juv age	-0.04	0.08	[-0.195, 0.122]
		Mother groom with juv (fy) : Sex (M)	0.23	0.19	[-0.145, 0.608]
Juv general prox (any partners)	-6.58	Intercept	-2.15	0.06	[-2.262, -2.03]
		Mother general prox with juv (juv first year)	-0.01	0.06	[-0.138, 0.111]
		Juv sex (M)	-0.23	0.08	[-0.4, -0.068]
		Juv age	0.14	0.04	[0.054, 0.219]
		Mother general prox (fy) : Sex	0.03	0.09	[-0.149, 0.215]

		(M)			
Juv general prox (peers)	-1.26	Intercept	-2.85	0.08	[-3.002, -2.703]
		Mother general prox (peers, all years)	-0.08	0.08	[-0.245, 0.085]
		Juv sex (M)	0.27	0.1	[0.082, 0.466]
		Juv age	0.01	0.05	[-0.082, 0.111]
		Mother general prox (prs, ay) : Sex (M)	0.14	0.1	[-0.063, 0.339]
Juv general prox (peers)	-2.02	Intercept	-2.84	0.08	[-2.991, -2.689]
		Mother general prox (peers, juv first year)	-0.1	0.08	[-0.263, 0.058]
		Juv sex (M)	0.26	0.1	[0.067, 0.461]
		Juv age	0.01	0.06	[-0.113, 0.13]
		Mother general prox (ap, fy) : Sex (M)	0.15	0.1	[-0.04, 0.341]
Juv general prox (peers)	0.11	Intercept	-2.86	0.08	[-3.015, -2.71]
		Mother general prox with juv (juv first year)	-0.06	0.08	[-0.215, 0.105]
		Juv sex (M)	0.28	0.1	[0.085, 0.476]
		Juv age	0.02	0.05	[-0.071, 0.118]
		Mother general prox (fy) : Sex (M)	0.05	0.11	[-0.159, 0.258]

Chapter 6: Summary and Conclusions.

The preceding chapters contribute new information about the potential causes, consequences, and correlates of social behavior over the life cycle in a gregariously social mammal. The chapters integrate long-term behavioral and life history data on adult females with short-term behavioral and physiological data on male and female juveniles, to provide a body of results that are uniquely broad in scope yet integrative across life stages. This final chapter summarizes findings from previous chapters and highlights avenues for future research.

In Chapter 1, I created a framework to understand the pathways by which social ties potentially influence fitness. In it, I also discussed methodological issues important to meaningfully describe ties and individual social tendencies, and their neuroendocrinological and developmental bases. The framework is useful to generate hypotheses for future analyses of the benefits of social ties over the life cycle in an array of social species, as the pathways described therein are relevant to different socio-ecologies and life stages. This chapter served as a framework for later chapters: namely, in understanding 1) the overall connection between adult ties and longevity (Chapter 2); 2) socio-demographic drivers of ties and their function in developing adult behavioral competence (Chapter 3); 3) the ability of ties to help individuals maintain homeostasis (Chapter 4); and 4) the origins of social ties and early life maternal effects on social behavior (Chapter 5).

In Chapter 2, I found that strong bonds do not always increase longevity among adult blue monkey females, as they appear to do in closely related baboons. Maintaining strong bonds with close partners increased survival only when close partners were consistent over time. I also found both a current and cumulative relationship between bond quality and survival, the first finding of its kind among non-human animals. This analysis suggested that strong bonds are perhaps costly to adult females, as maintaining strong bonds with inconsistent partners over multiple years corresponded with lower mortality than maintaining weak bonds with inconsistent partners. Future studies can aim to quantify the costs of social bonds and the pay-offs of maintaining them with consistent partners, who may provide a stable, reciprocal, and long-term alliance. Examining the physiological correlates of relationship quality in adult females can reveal the mechanisms by which social ties are linked to mortality in this species.

In Chapter 3, I found that juvenile gregariousness, or time spent socializing, and aggression varied according to sex and age in ways that supports the hypothesis that sociality during juvenility functions to develop adult sex-typical social competence. Male juveniles spent more time playing with more partners and gave agonism at higher rates than females, whereas females spent more time sitting close to and grooming with more partners. Sex differences in grooming and sitting close to partners increased with age, and while both sexes decreased their number of play partners as they approached maturity, females did so at a higher rate. Juvenile partner preferences also demonstrated a mixed strategy of developing adult competence and avoiding the risk of being dominated by older and larger individuals. In general, both males and females preferred to interact with partners that were more similar to themselves, in relatedness, age, and maternal rank. These results support the hypothesis that juveniles use partners for “self-assessment” (Thompson, 1998). Nevertheless, both males and females increased the time they spent resting near partners the older that partners were, and females spent more time grooming with older partners, suggesting that certain older individuals were either safe havens (e.g. tolerantly providing vigilance), role models that could potentially enhance grooming skills or access to ecological information, or were potential future allies. I also found fruit availability drove individual spacing patterns and that close proximity during peak fruit abundance seemed to provide an opportunity for both positive (affiliative) and negative (agonistic) social experiences for juveniles.

In Chapter 4, I found that juveniles' allostatic load, as measured by fecal glucocorticoid (fGC) metabolites, was related to both social strategy and energy balance. Juvenile sex, age, and maternal dominance rank were unrelated to fGC levels. In general, juvenile fGC levels decreased with more positive energy balance, an expected effect wherein fewer GCs are secreted to mobilize glucose as energy is readily available from the diet. Also in line with predictions, time spent playing corresponded with lower fGC levels; however, time spent grooming had a positive relationship with fGCs. Indeed, among individuals that spent the most time grooming (top quartile) fGCs actually increased with energy balance, suggesting perhaps some perceived or actual risk in feeding contexts among highly social individuals. Juveniles that groomed the most spent more time grooming non-kin than kin, a contrast that was not significant among juveniles in any other grooming quartile. This further suggests that grooming with unrelated and less familiar social partners was associated with a real or perceived risk of harm.

Lastly in Chapter 5, I found that juveniles' social behavior does correspond with their mothers' social behavior. Specifically, the amount of time that mothers groomed with their offspring during its infancy predicted the amount of time that their offspring groomed with their peers later as juveniles. The significant relationship between juveniles' and mothers' behavior was restricted to their direct interactions with one another during the juveniles' first year of life, suggesting that juvenile grooming behavior is subject to maternal effects. The maternal effect then varied according to juvenile sex, such that as females groomed more with their mothers during infancy they groomed their peers less, whereas when males groomed more with their mothers during infancy they groomed their peers more. These results set up a future study to examine the physiological correlates of maternal grooming during infancy, particularly in relation to hormone and neurotransmitter receptor densities (e.g. estrogen, dopamine), or their genetic correlates, that could correspond to sex-specific affiliative behavior later in life.

Although I conducted the analyses of each chapter under the hypothesis that affiliative ties would benefit individuals, whether as mature adults or immature juveniles, results demonstrated that affiliative behavior is often associated with both short and long-term costs. The apparent costs of strong bonds among adult females (lower survival when maintained with inconsistent partners), of juveniles' proximity to partners in a feeding context (agonism received), and of juveniles' grooming with unrelated social partners (higher allostatic load), do not suggest that socializing and social ties are not beneficial. These costs are potentially outweighed by benefits particular to context or time scale. For example, strong bonds with consistent partners could result in reciprocal, long-term alliances and a stable social environment; feeding on desirable foods could result in increased access to energy; and socializing with less familiar individuals could develop adult behavioral competence and future alliances during intergroup competition.

The results of this dissertation research provide a strong outline as to how the fitness benefits of differentiated social ties can be further studied. The true function of sociality during development requires a follow-up examination of how fitness-related performance in the adult social environment corresponds to juvenile social behavior. Simultaneously, the mechanisms by which adult social behavior correlated with fitness outcomes require further elaboration. If grooming with unfamiliar individuals is generally associated with higher allostatic load, as it appears to be in juveniles, adult females could pay the same cost when maintaining strong bonds with new and unfamiliar partners, i.e. close partners that change from year to year. Future studies can focus on quantifying the costs of social behavior relative to its potential pay-offs, both over the short and long term, to understand how social tendencies are maintained and why they have evolved. This work therefore emphasizes the necessity of long-term field studies to understand the evolution of social behavior wild animals.

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