View metadata, citation and similar papers at core.ac.uk

brought to you by CORE

provided by Bucknell University

Bucknell University
Bucknell Digital Commons

Spring 2018

Social Relationships and Self-Directed Behavior in Hamadryas Baboons (Papio hamadryas hamadryas)

Melissa C. Painter
Bucknell University, mcp024@bucknell.edu

Follow this and additional works at: https://digitalcommons.bucknell.edu/masters_theses

Part of the Animal Studies Commons, and the Comparative Psychology Commons

Recommended Citation

Painter, Melissa C., "Social Relationships and Self-Directed Behavior in Hamadryas Baboons (Papio hamadryas hamadryas)" (2018). *Master's Theses*. 200.
https://digitalcommons.bucknell.edu/masters_theses/200

This Masters Thesis is brought to you for free and open access by the Student Theses at Bucknell Digital Commons. It has been accepted for inclusion in Master's Theses by an authorized administrator of Bucknell Digital Commons. For more information, please contact dcadmin@bucknell.edu.

I, Melissa Painter, do grant permission for my thesis to be copied.

SOCIAL RELATIONSHIPS AND SELF-DIRECTED BEHAVIOR IN HAMADRYAS BABOONS (*PAPIO HAMADRYAS HAMADRYAS*)

by

Melissa C. Painter

A Thesis

Presented to the Faculty of
Bucknell University
In Partial Fulfillment of the Requirements for the Degree of
Master of Science in Animal Behavior

Approved: Peter Judge
Adviser

Peter Judge
Program Director

4/24/18
Date

Acknowledgments

I would like to thank my committee members, Dr. Z Morgan Benowitz-Fredericks and Dr. Regina Gazes, for their time, advice and support throughout the planning and execution of this project. I would also like to thank Meredith Lutz and Corinne Leard, both recent B.S. graduates from the Animal Behavior Program, for their assistance in navigating R to standardize my data and calculate the baboons' dominance hierarchy. Thank you also to the caretakers at Bucknell's Animal Behavior Laboratory, Mary Gavitt, Amber Hackenberg and Gretchen Long, for taking such great care of my study group and for being so accommodating when I asked to spend hours of undisturbed time with the baboons. Of course, I must also thank my fellow graduate students for enduring my multiple proposal and defense presentation rehearsals.

Beyond Bucknell University, I must first thank my good friend Ankush Khullar for writing original R code to help transform my thousands of lines of behavioral data into my numerous study variables. Without his help, I might still be calculating self-directed behavior rates and relationship insecurity scores by hand. I would also like to thank Dr. Charlotte Hemelrijk at The University of Groningen for inventing the TauKr test and for sharing her original software with me so that I could easily test my hypothesis. Similarly, I would like to thank Dr. Marina Cords at Columbia University for taking the time to discuss her thoughts on self-directed behavior and relationship security with me, and for sharing her ideas regarding future directions for this work.

Finally, a sincere thank you to my adviser, Dr. Peter Judge, for his countless contributions to this project and to my professional development. Thank you, Peter, for

taking a chance on this second-career student, for sparking my interest in primate relationships and self-directed behavior, for giving in to my petition for you to teach an advanced statistics course, and for all of your help and support as I went out on a limb with this somewhat risky thesis project. I am without a doubt a stronger student and a better researcher for my time spent under your guidance.

Table of Contents

List of Tables

List of Figures

Abstract

Self-directed behavior, such as self-scratching and self-grooming, is a behavioral indicator of anxiety in nonhuman primates. Patterns of self-directed behavior are used to identify social and environmental factors related to primate anxiety. This study explored the social context in which individuals in a captive group of hamadryas baboons (*Papio hamadryas hamadryas*) exhibited self-directed behavior. Self-directed behavior in a partner's presence was predicted to increase with relationship insecurity. More than 130 hours of behavioral observations were conducted on 12 baboons. Self-directed and social behavior were recorded with focal sampling to determine each animal's self-directed behavior rate in the presence of each other group member. These data were also used to calculate variation in response to approach over time, a newly proposed measure of relationship insecurity. Aggressive and submissive behavior were recorded *ad libitum* to construct a dominance hierarchy. High-ranking animals were found to exhibit significantly higher rates of self-directed behavior than low-ranking animals. Adults also exhibited higher rates of self-directed behavior than juveniles. Self-directed behavior rate increased with the relative dominance rank of the social partner in close proximity. Self-directed behavior rate also increased with the overall amount of aggression the social partner exhibited over the course of the study. No relationship was found between self-directed behavior rate in a partner's presence and relationship insecurity. Results suggest that baboons in this group experienced anxiety related to their own dominance rank and that of their social partners. Captivity and the steeply linear nature of the group's dominance hierarchy may have prevented any possible relationship insecurity effects from emerging. Variation in response to approach over time did not positively correlate with other relationship variables, suggesting it may serve as an independent and viable measure of relationship security.

Introduction

Group living is thought to confer a number of benefits on gregarious primates, such as reduced predation risk and increased ability to defend food resources from other groups (van Schaik, 1983; Wrangham, 1980). These benefits come with costs, however, including food competition and increased aggression within groups (Janson & Goldsmith, 1995; Mason & Mendoza, 1993). Sociality can also have subtler physiological and emotional costs in the form of stress and anxiety (Cheney & Seyfarth, 2009; Aureli, Preston, & de Waal, 1999). While a physiological stress response is adaptive in that it enables the body to deal with short-term challenges, such as a predation attempt or a food shortage, chronic stress can increase the risk of disease and suppress reproduction (Sapolsky, 2002). Similarly, anxiety is adaptive in that it increases alertness and allows animals to anticipate and respond to threats, but because it disrupts normal activities, excessive anxiety can be costly (Gray, 1987; Coleman & Pierre, 2014). Understanding these costs as they relate to social status and social interactions has been a focus of primatological research for decades.

Physiological stress in nonhuman primates, often measured by glucocorticoid (GC) hormone levels, has been found to be related to various social factors (reviewed in Cheney & Seyfarth, 2009). Traumatic social change has a particularly strong relationship with stress. The immigration of potentially infanticidal males, for example, is associated with increased GC levels in females of several species (mantled howler monkeys, *Alouatta palliata*: Cristobal-Azkarate, Chavira, Boeck, Rodriguez-Luna, & Vea, 2008; chacma baboons, *Papio hamadryas ursinus*: Beehner, Bergman, Cheney, Seyfarth, &

Whitten, 2005). In female chacma baboons, the death of a close relative also coincided with an increase in GC levels (Engh et al., 2006).

Beyond such notable events, patterns of everyday social interactions can also influence stress levels in primates. In pregnant and cycling chacma baboons, GC levels were positively correlated with the rate of receiving aggression (Crockford, Witting, Whitten, Seyfarth, & Cheney, 2008). Females' GC levels were also higher in months when they groomed with a broad network of individuals versus months when their grooming activities were concentrated on a few individuals. Crockford et al. (2008) suggest a lack of ability to control and predict the nature of social interactions may drive these increases in stress levels. Aggression patterns also predicted elevated stress hormones in female chimpanzees (*Pan troglodytes schweinfurthii*) and male Assamese macaques (*Macaca assamensis*; Emery Thompson, Muller, Kahlenberg, & Wrangham, 2010; Ostner, Heistermann, & Schulke, 2008).

The relationship between dominance rank and stress hormone levels is not consistent across primate species or even across time within groups. Sapolsky (2005) suggests the relationship between stress and rank may be mediated by more specific costs of being dominant or subordinate that depend on a species' social structure and a group's social stability. Evidence from cercopithecine primates supports this hypothesis. Within a single chacma baboon group, subordinate males exhibited higher GC levels than dominants during periods of hierarchy stability, whereas dominant males exhibited higher relative GC levels during periods of significant rank change (Bergman, Beehner, Cheney, Seyfarth, & Whitten, 2005). Differences in the coping mechanisms available to animals of different dominance ranks may also influence stress levels across species and sexes. A meta-analysis of stress hormone levels across primate species found that subordinates were more likely to have higher cortisol levels when they were of the dispersing sex, lacking close kin in the group, and when subordinates had disproportionately less opportunity for social support (*e.g.*, social grooming) than did dominants (Abbott et al., 2003).

Stress hormone levels, as products of the endocrine system, can reflect cumulative effects of social and environmental stressors. As such, studies like those described above can contribute to a better understanding of longer-term physiological costs of sociality. They do not, however, allow for identification of individual social interactions that may cause more immediate emotional or psychological costs, often referred to as anxiety (Higham, MacLarnon, Heistermann, Ross, & Semple, 2009). Measuring nonhuman primates' anxiety levels can help us to understand what influences uncertainty and perception of risk in social relationships and social contexts (Castles, Whiten, & Aureli, 1999). Other physiological aspects of the stress response, such as increased heart rate, can provide concurrent indicators of anxiety in social situations (Aureli et al., 1999; Smucny, Price, & Byrne, 1997). However, such responses are difficult to measure non-invasively, creating a need for simpler behavioral indicators of anxiety. In nonhuman primates, displacement activities can provide such a measurement.

Displacement Activities

Displacement activities are behavioral responses that are unrelated to the context in which the animal finds itself, and they are commonly exhibited when an animal has been thwarted in achieving a goal or is experiencing conflicting motivations (Tinbergen, 1952). For example, male great tits (*Parsus major*) engaged in a territorial dispute, presumably experiencing simultaneous and conflicting motivations to flee and to continue to aggress, may intermittently peck at the tree or at food (Hinde, 1952). The most commonly reported displacement activities for nonhuman primates are forms of self-directed behavior (SDB), such as self-scratching, self-touching and self-grooming (Maestripieri, Schino, Aureli, & Troisi, 1992).

Several models have been proposed to explain the proximate mechanisms causing displacement behavior to occur (reviewed in Anselme, 2008). Tinbergen (1952) proposed that thwarted activity or conflicting motivations can create an excess of energy that releases in the form of an irrelevant displacement behavior. Alternatively, van Iersel & Bol (1958) suggested that inhibition of two conflicting motivations can disinhibit a third motivation, allowing a displacement behavior to occur. More recent evidence that displacement activities frequently occur around behavioral transitions supports the idea that these responses may be driven by changes in attentional state (McFarland, 1966; Anselme, 2008). Regardless of the causal mechanism, an array of physiological and circumstantial evidence strongly suggests that displacement behavior can indicate anxiety and related emotional and psychological states (*e.g.*, uncertainty) in primates (Maestripieri et al., 1992).

Displacement in Primates

Primates often exhibit displacement activities, most often SDB, in contexts assumed to trigger anxiety (Maestripieri et al., 1992). For example, a mother being separated from her infant presumably causes her anxiety, as her infant is at greater risk of harassment and harm without her protection (Maestripieri, 1993). This maternal anxiety should decrease as the infant grows older and is better able to fend for itself. In line with this prediction, Maestripieri (1993) found that rhesus macaque (*Macaca mulatta*) mothers self-scratched significantly more often when away from their infants, and that scratching rates in this context subsequently decreased from birth to 12 weeks. Similarly, receiving aggression is presumed to increase anxiety, especially as victims face the risk of renewed aggression (Aureli & van Schaik, 1991). A friendly interaction with the former aggressor should decrease a victim's anxiety, as the risk of further attacks also commonly decreases after such reconciliation (Castles & Whiten, 1998). Aureli and van Schaik (1991) found that long-tailed macaques (*Macaca fascicularis*) increased rates of scratching, self-grooming and body shaking after receiving aggression, and that reconciliation decreased the rate of these responses sooner than when no reconciliation occurred. This predictable variation in SDB around anxiety-inducing events provides circumstantial evidence that SDB is related to the animal's experiencing anxiety. However, it is also possible that motivational conflict, aside from any emotional response, could drive these responses. A mother could scratch more when separated from her infant as a result of a motivational conflict between staying where she is and moving toward her infant. A victim could exhibit more SDB after a fight due to a motivational conflict between avoiding an aggressive individual and reconciling with that individual. Physiological evidence, however, has shown that SDB is related specifically to anxiety.

Certain brain regions are known to regulate anxiety, while certain pharmaceutical drugs are known to either induce or relieve anxiety. Stimulating the locus coeruleus, a brainstem region known to play a role in human fear and anxiety, produces scratching and yawning in stump-tailed macaques (*Macaca arctoides*: Redmond & Huang, 1979). Administering lorazepam, an anxiolytic drug used to relieve anxiety in humans, to long-tailed macaques decreased rates of scratching without affecting rates of other behavior, including locomotion, social grooming and aggression (Schino, Troisi, Perretta, & Monaco, 1991). A follow-up study found that lorazepam decreased rates of self-grooming and body shaking in addition to scratching, without affecting rates of locomotion, aggression or social grooming (Schino, Perretta, Taglioni, Monaco, & Troisi, 1996). Administering FG 7142, which is known to increase anxiety in humans, increased rates of these same activities in long-tailed macaques without influencing rates of social grooming. The effects of both the anxiolytic and anxiogenic drugs were dose-dependent, suggesting amount of anxiety experienced increased along with the rate of SDB exhibited. Combined with the previously reviewed circumstantial evidence, this physiological evidence soundly establishes SDB, including scratching, self-grooming, yawning and body shaking, as an indicator of anxiety in primates.

In contrast, a relationship between SDB rates and glucocorticoid levels has not been found, supporting the notion that these measures assess different aspects of the stress response. In wild female olive baboons, daily changes in SDB rates were not associated with daily changes in fecal cortisol levels (Higham et al., 2009). Similarly, SDB rates did not increase with crowding in a captive hamadryas baboon (*Papio* *hamadryas hamadryas*) group, though salivary cortisol levels were significantly elevated (Pearson, Reeder, & Judge, 2015). These findings demonstrate that anxiety and SDB may be examined separately from physiological stress.

It is important to note that the evidence reviewed thus far draws exclusively from Old World monkeys. Experimental studies with New World monkeys, specifically marmosets, have had less success establishing a relationship between SDB and anxiety. When treated with the anxiogenic drug FG 7142, common marmosets' (*Callitrhix jacchus*) scratching rates were no different than their baseline rates (Kato et al., 2014). Nor did they scratch at higher rates when socially isolated in a novel environment or when shown photographs of predators, both of which were experimental conditions intended to induce anxiety. Neal and Caine (2016) found that common marmosets scratched significantly less during manipulations intended to produce negative arousal (*e.g.*, social isolation, increased food competition, simulated predation threat) and therefore caution against using scratching and other SDB as a blanket indicator of anxiety in any primate. SDB does seem to be a reliable indicator of anxiety in Old World monkeys, however, and continues to be used for this purpose.

Dominance Rank and SDB

Dominance hierarchies are a core aspect of sociality in many primate species, determining group members' relative access to a variety of resources (Allee, 1952). Low-ranking individuals may experience a variety of anxiety-inducing circumstances, similar to those causing longer-term stress, including limited access to food and mates, higher rates of receiving aggression, and fewer opportunities for social support. High-ranking animals may also experience anxiety-inducing circumstances, particularly those related to giving and receiving aggression and vying for and maintaining rank. Differences in SDB rates across ranks can reveal the relative costs of holding a certain position in a given dominance hierarchy (Ellis, MacLarnon, Heistermann, & Semple, 2011). The influence of rank on SDB rate has been studied in a variety of species with different social structures both in captivity and in the wild.

Several studies have found that low-ranking animals exhibit higher rates of SDB than high-ranking animals. In a captive long-tailed macaque group, scratching rates increased as rank decreased (Pavani, Maestripieri, Schino, Turillazzi, & Scucchi, 1991). Low-ranking female Japanese macaques (*Macaca fuscata*) also groomed themselves more often than did high-ranking females in a provisioned free-ranging group (Duboscq, Romanco, Sueur, & MacIntosh, 2016). In a wild group of Barbary macaques (*Macaca sylvanus*), subordinate females scratched themselves more often than did dominant females (Kaburu, MacLarnon, Majolo, Qarro, & Semple, 2012). In this same group, more aggressive females scratched at higher rates than less aggressive females, and females receiving more aggression from males scratched at higher rates than females receiving less aggression from males, demonstrating the anxiogenic effects of aggression. However, even after controlling for amount of aggression and grooming, subordinates still scratched more often than dominants, suggesting something beyond aggression was a source of anxiety for these females.

Other studies have found that dominant individuals exhibit higher SDB rates. High-ranking captive male anubis baboons (*Papio anubis*) scratched more than low-ranking males (Easley, Coelho, & Taylor, 1987). These high-ranking animals also showed higher rates of yawning and self-touching. Similarly, in a captive mandrill (*Mandrillus sphinx*) group, dominant adults scratched more than subordinate adults (Peignot, Jankowsky, & Anderson, 2004).

Still other studies found no difference in SDB rates across rank. No relationship between rank and scratching and/or self-grooming was found in wild white-faced capuchins (*Cebus capucinus*), nor between rank and scratching in wild tufted capuchins (*Cebus apella*; Manson & Perry, 2000; Polizzi di Sorrentino, Schino, Tiddi, & Aureli, 2012). No relationship between rank and scratching was found for wild ring-tailed lemurs (*Lemur catta*) during the mating season (Sclafani, Norscia, Antonacci, & Palagi, 2012). In a semi-free ranging group of rhesus macaques, the relationship between rank and scratching was only revealed when feeding competition was increased (Diezinger & Anderson, 1986). When food was placed in a single pile in the enclosure, mid-ranking individuals scratched significantly more than either high-ranking or low-ranking individuals. The authors concluded that mid-rankers experienced more anxiety during these tests because their success in obtaining food was more variable than that of high- or low-rankers, and mid-rankers were involved in more aggression than the other rank classes. Similarly, subordinate male chimpanzees scratched more than dominant males in a wild group, but only when in the presence of at least one other individual (Kutsukake, 2003).

The relationship between rank and SDB appears to be just as complex as that between rank and stress hormone levels. Species factors such as tolerance and group factors such as dominance linearity, steepness and stability may influence the anxiety experienced by individuals of different ranks and, therefore, SDB rates (Polizzi di Sorrentino et al., 2012; Sclafani et al., 2012). Experimental evidence supports the hypothesis that rank uncertainty increases SDB rates. Schino, Maestripieri, Scucchi, & Turillazzi (1990) paired captive, group-living female long-tailed macaques with either a familiar unrelated female or an unfamiliar unrelated female. SDB (scratching, self-grooming, yawning and body shaking) was significantly more frequent in unfamiliar pairs that did not immediately establish dominance relationships compared to unfamiliar pairs that immediately established dominance and compared to familiar pairs, leading the authors to conclude that clear dominance relationships can keep anxiety levels lower. In Kaburu et al.'s (2016) Barbary macaque group, the dominance hierarchy was perfectly linear and nearly maximally steep, meaning dominance ranks were firmly established and distinct and individuals differed greatly in the number of dominance encounters they won, which could have increased rank certainty and mitigated anxiety among high-ranking animals. In the opposite direction, hierarchy changes throughout the breeding season in Sclafani et al.'s (2012) ring-tailed lemur group could account for the lack of relationship between rank and scratching. Similarly, capuchin monkeys are relatively tolerant species with shallow hierarchies, meaning behavior going against the hierarchy is more common and individuals vary less in the number of dominance encounters they win, which could contribute to the lack of relationship between rank and SDB rates in these species (Polizzi di Sorrentino et al., 2012). No previous research has examined SDB rates across dominance classes in species organized in one-male units, such as hamadryas baboons, which are also thought to have less pronounced dominance hierarchies (Swedell, 2016).

Rank differences in SDB rates emerging only in certain situations suggests there is more to learn about the sources of primate social anxiety by studying SDB rates in specific contexts (Diezinger & Anderson, 1986; Kutsukake, 2003). For example, the social situations in which subordinate Barbary macaques find themselves could explain why they scratch more than dominants even after controlling for aggression and grooming. Kaburu et al. (2012) propose that subordinates scratch more than dominants because, by nature of their low rank, they are more often near a higher-ranking animal, which can cause anxiety due to increased risk of aggression. Such anxiogenic effects of proximity to certain conspecifics is another line of research exploring social anxiety in primates.

Conspecific Proximity and SDB

Higher rates of SDB around stressful events (*e.g.*, being involved in or witnessing an aggressive conflict) have been well documented in primates (Aureli & Smucny, 2000). On a smaller scale, simply being in the presence of certain individuals may cause anxiety and an increase in SDB rates. One hypothesized source of social anxiety for nonhuman primates is aggression risk (Maestripieri et al., 1992). If risk of aggression is a strong source of anxiety, then primates should exhibit more SDB in the presence of animals from whom they are more likely to receive aggression.

In many primate societies, aggression is directed down the hierarchy, from higher-ranking animals to lower-ranking animals (Silk, 1993). As such, being in close proximity to a higher-ranking animal may represent a greater risk of receiving aggression and therefore cause more anxiety and SDB than would proximity to a lower-ranking animal. Evidence from several species suggests that being near higher-ranking animals, or animals of a generally more aggressive class, may be anxiety provoking. In a captive group of long-tailed macaques, time spent within 1 m of, but not touching, the adult male positively correlated with females' self-grooming rates (Troisi & Schino, 1987). This effect did not apply to time spent in physical contact with the male, leading the authors to conclude that being in contact with the male was a goal situation, but being near him was risky as it could lead to either an aggressive or affiliative interaction. However, this study only assessed the relationship between total time spent self-grooming and total time spent with the potentially aggressive male, rather than examining whether females specifically self-groomed more when in the male's presence than when alone or with other females. A later study with captive long-tailed macaques found that females did scratch at higher rates when within .5 m of a male than when alone or when in contact with the male, providing more direct evidence for the previous interpretation (Pavani et al., 1991). These effects are not limited to proximity to alpha males. Physiological and behavioral evidence suggest rhesus macaques experience more anxiety when in proximity to higher-ranking animals of both sexes. Captive female rhesus macaques experienced increased heart rate when dominant individuals of either sex approached them within 1 m, but not when kin members or subordinate individuals approached (Aureli et al., 1999). In another captive rhesus macaque population, mothers in contact with their young infants scratched more often when within 60 cm of the adult male or a higher-ranking female than they did when alone with their infants (Maestripieri, 1993). Because these mothers were in contact with their infants, this should control for maternal anxiety, and the increase in scratching should reflect social anxiety likely related to the risk of receiving aggression from nearby dominant individuals.

Some studies with wild primates have also shown an effect of a neighbor's dominance rank on an individual's SDB rate. Wild female olive baboons exhibited significantly more SDB (scratch, self-groom, self-touch, body shake and yawn analyzed cumulatively) when their nearest neighbor was a dominant individual than when their nearest neighbor was a subordinate individual (Castles et al., 1999). Wild tufted capuchins scratched more when within 3 m of a dominant animal than when within 3 m of a subordinate animal (Polizzi di Sorrentino et al., 2012). The capuchins also scratched more when in proximity to females compared to males. Aggression data from this group supported the assumption that animals receive more aggression from dominants than from subordinates. In this group, animals also received more aggression from females than from males. Higher scratching rates when in proximity to these more aggressive classes of individuals supports the hypothesis that aggression risk is related to anxiety and SDB in a group member's presence.

Both Castles et al. (1999) and Polizzi di Sorrentino et al. (2012), however, conclude that aggression risk is likely insufficient for predicting SDB in another animal's presence. For a given female olive baboon, SDB rates varied substantially depending on the specific dominant individual in proximity (Castles et al., 1999). It might be expected that an individual would exhibit the most SDB when in proximity to the highest-ranking animals and less when in proximity to dominant animals closer to themselves in rank, but SDB rates did not positively correlate with the neighbor’s rank. Based on this variation, Castles et al. (1999) concluded that another aspect of the dyadic relationship, in addition to relative dominance rank, must also contribute to social anxiety in the presence of a conspecific. While proximity to aggressive classes of animals predicted scratching in tufted capuchins, the direct relationship between how much aggression an animal received from a given group member and how much an animal scratched in that group member’s presence was not significant (Polizzi di Sorrentino et al., 2012). Also, the capuchins scratched more often when near non-kin than when near kin, but rates of aggression received from kin compared to non-kin did not differ significantly.

Castles et al. (1999) propose that an animal’s SDB rate in proximity to another individual can reflect the animal’s perception of the security of that relationship. Cords & Aureli (2000) define relationship security as “the perceived probability that the relationship with the partner will change, which relates to the consistency of the partner’s behavioral responses.” Uncertainty or unpredictability in a relationship is likely to be a source of anxiety (Cords & Aureli, 1993). If relationship insecurity is a strong source of anxiety, then primates should exhibit more SDB in the presence of animals with whom they have less predictable relationships and less SDB in the presence of animals with whom they have more predictable relationships. Kin relationships are likely to be secure, resilient relationships (Cords & Aureli, 1993). As such, tufted capuchins’ lower scratching rates near kin may reflect secure kin relationships (Polizzi di Sorrentino et al., 2012). Castles et al. (1999) also propose that relationship security may explain female olive baboons' variation in SDB rates near dominants, suggesting that low SDB rates in a dominant animal's presence reflects a more secure relationship with that dominant animal. While this study did not present data to explore this possibility, other studies have since attempted to quantify relationship security and examine its relationship with SDB rates.

Several studies have examined the relationship between time spent in proximity to a group member and SDB rates in the presence of that group member. The more time an animal spends near a conspecific, the better it may be able to predict that conspecific's behavior (Kutsukake, 2003). If this prediction is supported, animals should experience less uncertainty and exhibit lower SDB rates near group members with whom they spend more time. After a study of a captive group of vervet monkeys (*Chlorocebus pygerythrus*) found no relationship between a neighbor's rank and an individual's SDB rate (Daniel, dos Santos, & Vicente, 2008), McDougall (2011) examined how the interaction between a neighbor's rank and the pair's association level might relate to SDB rate in wild vervets. For each individual, other group members were classified as either "dominant associate," "dominant non-associate," or "subordinate associate" based on relative dominance rank and amount of time spent within 5 m of one another. Vervets exhibited higher SDB rates when their neighbors were all "dominant non-associates" compared to when they were all "dominant associates." SDB rates in the presence of "dominant associates" and "subordinate associates" did not differ significantly, demonstrating that association level was more predictive of SDB rates than was relative dominance. However, this may be attributable to aggression risk rather than relationship predictability, as individuals in this group received more aggression from non-associates than from associates. While vervets are considered a resident-nepotistic species, characterized by low tolerance of behavior incongruous with the dominance hierarchy, this group's hierarchy was not very steep compared to other vervet groups, suggesting higher tolerance. McDougall (2011) suggests that this could explain why a neighbor's dominance rank was less predictive of SDB rates. Unfortunately, the dynamics of this vervet group did not allow McDougall (2011) to compare SDB rates in proximity to "subordinate associates" versus "subordinate non-associates" to further explore the possible effect of familiarity with a partner while controlling for aggression risk.

When a neighbor's dominance rank does not predict SDB rates, the relationship between association levels and SDB rates becomes easier to examine. In a wild chimpanzee group, neighbor rank did not affect scratching rates for adult males or adult females (Kutsukake, 2003). Rather, females scratched more when all neighbors within 3 m were "non-affiliative" than when all neighbors were "affiliative." Immediate maternal kin and unrelated group members in the top quartile of scores measuring time spent in proximity were classified as "affiliative." Unrelated group members in the bottom quartile of proximity scores were classified as "non-affiliative." Kutsukake (2003) suggests the lack of relationship between neighbor rank and scratching rates could be due to chimpanzees, like capuchin monkeys, being a highly tolerant species, meaning a neighbor's rank may not be strongly related to aggression risk. However, the study did not directly assess which classes or individuals were more aggressive in this group, as McDougall (2011) did for the vervet group and Polizzi di Sorrentino et al. (2012) did for the tufted capuchin group. Kutsukake (2003) also noted that, as chimpanzees live in a fission-fusion society, they may spend little to no time with certain group members, making the behavior of those group members particularly difficult to predict and therefore warranting more anxiety in their presence.

Interestingly, wild female white-faced capuchins exhibited less SDB when within one body length of the alpha male than when within one body length of subordinates (Manson & Perry, 2000). They also exhibited higher rates of SDB when their neighbors were closer in rank to themselves, which happened to be the females with whom they spent more time in proximity. At first glance, it may seem that these data do not support either hypothesized source of social anxiety (aggression risk or relationship insecurity). However, considering these patterns in light of the group's social dynamics suggests relationship insecurity may be a driver. Manson & Perry (2000) conclude that aggression risk is not likely to contribute to SDB rates in this group, as females were most likely to receive aggression from the alpha male but had low rates of SDB in his presence. Rather, they suggest that because dominance challenges in white-faced capuchins often occur between animals of similar rank, and because coalitionary alliances are relatively short-lived, higher SDB rates in proximity to close-ranking affiliates may reflect insecure female-female relationships.

Manson & Perry's (2000) findings suggest that time spent in proximity cannot always be used as a proxy measure for relationship security. Also, spending more time with a partner may not increase the predictability of the partner's behavior if the partner's responses to being in proximity to an individual vary substantially. Also, if a relationship is valuable (*e.g.*, the partner provides coalitionary support), an animal may spend more time with that partner regardless of the security of the relationship. Using an appropriate measure of relationship security is critical to studying its potential association with anxiety and SDB in nonhuman primates.

Measuring Relationship Security

Whereas aggression risk can be simply approximated based on observed aggressive interactions between individuals, measuring relationship security poses a greater challenge. Several studies have used principal component analysis (PCA) to parse out the different measurable aspects of relationships that may indicate relationship security. PCA consolidates any correlated variables into distinct components, which are not correlated with one another (Fraser, Schino, & Aureli, 2008). This method has been used to analyze relationship quality in species including chimpanzees, Japanese macaques, spider monkeys (*Ateles geoffroyi*), Barbary macaques, and ravens (*Corvus corax;* Fraser et al., 2008; Majolo, Ventura, & Schino, 2010; Rebecchini, Schaffner, & Aureli, 2011; McFarland & Majolo, 2011; Bugnyar & Fraser, 2010). Some of these studies have suggested that one of the distinct components identified aligns with Cords & Aureli's (2000) definition of relationship security. A study of captive chimpanzees identified "grooming asymmetry" and "consistency of affiliation over time" as a single component of dyadic relationships and labeled this "security" (Fraser et al., 2008). The authors note that "consistency of affiliation over time," defined as variation in time spent in proximity or grooming over time, is more in line with Cords & Aureli's (2000) definition of security than is grooming asymmetry. However, a drawback to the "consistency of affiliation over time" measure is that it is one score for the dyadic relationship, which does not account for the fact that individuals may perceive the security of the relationship differently. A measure that captures an individual's experience related to the probability that a relationship will change will be a more useful measure of relationship security (Castles et al., 1999). A later study with ravens found a relationship component consisting only of "variation in response to approach over time," which was labeled "security" (Bugnyar & Fraser, 2010). For a single dyadic relationship, this measure had two scores, one from the perspective of each partner, and therefore accounted for possible asymmetry in perception of relationship security.

A PCA run on wild Japanese macaque relationship variables identified "grooming variability over time" and "frequency of aggression" as a single component, which the authors labeled "security" (Majolo et al., 2010). Analysis of wild Barbary macaque relationships also identified "grooming asymmetry" as a stand-alone component (McFarland & Majolo, 2011). The authors labeled this "security" as well, as they assert this captures the variability of a relationship. A PCA run on wild spider monkey relationships did not label any components as "security" but found that "aggression rates" contribute to a single component, which they labeled "risk" (Rebecchini et al., 2011).

These other relationship variables do not seem to capture Cords & Aureli's (2000) definition of relationship security as well as "variation in response to approach over time." Grooming asymmetry, for example, may simply reflect asymmetries in individuals' investment in the relationship, which is to be expected if partners offer different value to one another. Another challenge associated with this measure is that not all dyads may engage in grooming. Similarly, aggression rates are not necessarily related to unpredictability. If an animal is frequently aggressive, for example, a partner should be able to predict that aggressive behavior as easily as the affiliative behavior of a frequently affiliative animal. The variable "variation in response to approach over time" seems to best capture the nature of relationship predictability and security. This is essentially a measure of the consistency of a partner's behavioral responses, which Cords & Aureli (2000) note should be related to an individual's perception of the likelihood that the relationship will change. In fact, Cords & Aureli (2000) propose that a measure of relationship security might consider "what proportion of approaches are acknowledged by a neutral or friendly response, and what proportion are ignored… or even rebuffed." This aligns well with the variation in response to approach over time measure.

Present Study

This study aimed to test whether relationship security predicted an individual's anxiety levels in the presence of a conspecific in hamadryas baboons. Castles et al. (1999) and Cords & Aureli (2000) proposed that animals will experience greater anxiety/uncertainty in proximity to partners with whom they have a less predictable and therefore less secure relationship. In this study, variation in response to approach over time was used as a measure of relationship security, and SDB rates were used as a measure of anxiety. Therefore, I predicted animals would exhibit higher rates of SDB when in proximity to individuals whose responses to their approach vary more over time.

To date, variables used to predict SDB rates in proximity to conspecifics have not done so cleanly across species and contexts. Previously tested relationship variables, such as a neighbor's dominance rank, classify animals broadly and fail to capture differences in how rank affects individual relationships across species, social structures and levels of social stability. However, more direct measures of the risk of receiving aggression from an individual (*i.e.*, observed rate of aggression received from a conspecific) have also failed to correlate with SDB rates (Polizzi di Sorrentino et al., 2012; Manson & Perry, 2000). While relationship insecurity has been hypothesized to drive social anxiety, only association level has been used as a proxy measure for this relationship variable in studies examining this relationship. As SDB patterns in white-faced capuchins demonstrate, association level may not properly capture an animal's perception of the probability that a relationship will change (Manson & Perry, 2000). Drawing from the relationship quality literature, this study examined the link between relationship security and social anxiety in hamadryas baboons using an improved measure for security: variation in response to approach over time. To provide a comprehensive exploration of potential social predictors of anxiety, this study also tested the relationship between SDB rate in a partner's presence and variables such as a partner's relative dominance rank, amount of aggression received from a partner and time spent in proximity to a partner. This study also explored the association between this new relationship security measure and other measures previously used to predict partner-specific SDB rates, including those listed above, to perhaps establish variation in response to approach over time as an independent measure of an aspect of relationship quality.

SDB rates and proximity to conspecifics have not yet been studied in species organized in harems or one-male units, such as hamadryas baboons. However, the post-conflict behavior of hamadryas baboons has been well-studied, providing a solid understanding of the species' common SDB responses to social events (Judge & Mullen, 2005; Judge & Bachmann, 2013; Romero, Colmenares, & Aureli, 2009). This project capitalized on this knowledge to explore the relationship between social context and anxiety in hamadryas baboons. Hamadryas baboons provide an interesting social structure in which to explore these questions, as female dominance relationships are thought to be less well-defined by aggressive and submissive interaction patterns than in other baboon species (Swedell, 2016). As seen with chimpanzees and capuchins, I anticipated that muted dominance relationships might have allowed any association between SDB and individual relationship variables, as opposed to rank relationships, to become more apparent.

In the process of answering the specific question regarding relationship security and SDB rates, this study also analyzed non-conflict related SDB patterns across age, sex, rank and aggression patterns in hamadryas baboons. As SDB rates, like stress hormone levels, may depend on social structure and hierarchy variables, it was difficult to predict how SDB patterns will vary with these factors. Therefore, I refrained from making any predictions related to these variables, and these initial analyses were exploratory.

Methods

Subjects and Housing

Behavioral observations were conducted on a group of 15 hamadryas baboons housed at Bucknell University's Animal Behavior Laboratory in Lewisburg, Pennsylvania. This group consisted of one adult male, five adult females, four juvenile males, two juvenile females, two infant females and one infant male (Table 1). With the exception of the adult male (Jd) and one adult female (Hn), all adult females were born and raised in the group, which was first established at Bucknell University in 1968. Jd and Hn were acquired in April, 2014, and introduced to the group. Since the time of the introduction, the colony has consisted of the adult male, the five adult females and their offspring.

The baboons' enclosure included indoor and outdoor areas constructed of concrete, cinderblock and chain-link fencing. When temperatures were above 40 F°, the group was confined to their outdoor quarters, which measured 9 x 11 x 4.5 m and had a gravel substrate. When temperatures were below 40 F°, baboons were confined to their indoor quarters, which measured 9 x 6 x 2.25 m. The outdoor enclosure included climbing structures and perches, and enrichment objects were continuously available. Commercial monkey chow and water were available *ad libitum*. This diet was supplemented daily with an assortment of fruits, vegetables, seeds and nuts.

Data Collection

Focal sampling. Behavioral observations were conducted from late April through early November, 2017, for a total of 130.5 hours of focal observations. Focal samples were conducted on all adults and juveniles (12 animals) to record the focal animal's social interactions and SDB continuously (Martin & Bateson, 2007). The ethogram used during focal follows is detailed in Table 2. Focal follows lasted 10 min and were conducted on individuals in a randomized order. Individuals were not sampled more than once per day. At least 65 focal samples were conducted on each individual, equaling 10 hours and 50 minutes. Data from focal samples were used to determine individuals' overall SDB rates, SDB rates in the presence of other group members, and variation in response to approach over time, as detailed in the data analysis section to follow.

Scan sampling. Group scans were conducted to record the social activities and partners of each of the 15 individuals instantaneously (Martin & Bateson, 2007). Scans were conducted at the beginning and end of each observation session and between focals, approximately every 10 min. The ethogram used during group scans is detailed in Table 3. These data were used to determine association scores for each dyad.

Behavior sampling. Behavior sampling was used to record any aggressive or submissive behavior occurring in the group during a focal sample but not involving the current focal individual (Martin & Bateson, 2007). The "aggressive behavior" and "submissive behavior" sections of the ethogram detailed in Table 2 were used to capture these interactions. These data were used to construct a dominance hierarchy for the group and to capture patterns of aggressive interactions.

Observation protocol. The following protocol was used to conduct behavioral observations. All observations were conducted between 08:00 and 16:00 when the baboon group was confined to the outdoor enclosure. Observations were not conducted when it was raining, as the baboons tended to congregate under overhangs where they were more difficult to observe, and because wet hair may have affected scratching or self-grooming rates. Observation sessions began at least 30 min after the group was fed. I used a Sony ICD-BX112 digital flash voice recorder to record all observations, later transcribing them onto a computer. Because I used a voice recorder, I did not need to look away from the group to record data during observation sessions.

At the start of an observation session, I recorded the date, time, temperature and identity of any females showing a sexual swelling. I then conducted a group scan, noting the social activities and partners of each individual according to the ethogram in Table 3, starting with individuals at the left side of the enclosure and moving to the right. At the start of each group scan, I recorded the time of day. Following the first group scan, I used the ethogram in Table 2 to conduct a 10-min focal follow on the first awake animal (defined as having its eyes open) on a randomized list of the 12 focal individuals. Initiating focal samples on awake animals increased the likelihood of recording behavior of interest, including SDB and social behavior. At the start of each focal follow, I noted the time of day and started a stopwatch from 0 s. For each behavior recorded, I noted the time on the stopwatch. When the stopwatch read 10 min, the focal was ended, and the next group scan was conducted. After the last focal follow of the observation session, a final group scan was conducted.

Instances of aggressive and submissive behavior not involving the focal individual were recorded throughout the observation session. For each aggressive interaction, only one behavior was recorded to prevent inflation of aggression frequency counts. If the aggressive behavior was witnessed, I recorded the identity of the aggressor, the aggressive behavior, the identity of the victim, and the time of the event. Any submissive behavior following the aggressive behavior was not recorded. If only submissive behavior was observed, I recorded the identity of the submissive individual, the submissive behavior, the recipient of the submissive behavior and the time of the event.

Data Analyses

All analyses were restricted to the 12 focal individuals, unless otherwise stated.

Dominance hierarchy. A dominance hierarchy was constructed to order individuals according to their overall outcomes in aggressive and submissive interactions within the group. To construct the hierarchy, aggressive and submissive interactions recorded via behavior sampling were first organized in a dominance interaction matrix. Aggressive behavior exhibited was counted as a win for the actor over the recipient, and submissive behavior exhibited was counted as a win for the recipient over the actor. Each animal's wins against each other group member were organized in a square matrix, with winners along rows and losers along columns. If multiple aggressive or submissive interactions occurred between the same dyad within 30 s, with the actor and recipient roles remaining the same, only the first interaction was included in the dominance interaction matrix. If another interaction occurred more than 30 s after the first, that interaction was included in the matrix as a new event. This procedure reduced the weight of extended aggressive or submissive interactions in the construction of the hierarchy (Polizzi di Sorrentino et al., 2012).

The David’s score method was then used to determine the dominance hierarchy for the group based on the dominance interaction matrix (David, 1987). This method calculates an individual’s dominance based on the proportion of wins against opponents, as well as the relative strength of opponents (Gammell, de Vries, Jennings, Carlin & Hayden, 2003). David’s score is preferred to the similar Clutton-Brock, Albon, Gibson, & Guinness (1979) index because it is less sensitive to minor deviations from the general direction of aggressive interactions within a dyad (Gammell et al., 2003). The ‘Elo Rating’ package for R software was used to calculate each animal’s David’s score and normalized David’s score (Neumann & Kulik, 2014). Normalized scores are David’s scores converted to scale of 0 to N-1 (de Vries, Stevens, & Vervaecke, 2006). These scores were important for analysis of dominance hierarchy steepness. Animals were assigned dominance ranks according to their David’s score, with 1 being the highest-ranking animal with the highest David’s score and 12 being the lowest-ranking animal with the lowest David’s score.

Partner’s relative dominance rank was one of the relationship variables examined in this study. This variable was based on the number of dominance ranks between the partner animal’s rank and the subject animal’s rank, as well as the direction. If the partner animal was dominant to the subject animal, the partner’s relative dominance rank was positive. If the partner animal was subordinate to the subject animal, the partner’s relative dominance rank was negative. For example, if the lowest-ranking animal was the subject and the highest-ranking animal was the partner, the partner’s relative dominance rank was 11. There were 11 ranks between the two animals, and the partner was higher ranking than the subject, so the value was positive. If the highest-ranking animal were the subject and the lowest-ranking animal were the partner, the value would be -11. This measure was intended to quantify how much higher or lower ranking a partner was compared to the subject on an ordinal scale.

In order to draw any conclusions about the relationship between SDB and dominance rank, it must first be shown that the dominance hierarchy is linear. For a dominance hierarchy to be considered perfectly linear, each dyad within the group must consist of one dominant individual and one subordinate individual (*i.e.*, there are no neutral relationships or tied dominance ranks), and all dominance relationships must be transitive rather than circular (de Vries, 1995). It has been shown that dominance hierarchies determined from David's scores are consistently linear (Balasubramaniam et al., 2013). A modified form of Landau's linearity index *h*, known as *h'*, was used to determine the linearity of the baboon group's dominance hierarchy (de Vries, 1995). This testing procedure used the dominance interaction matrix to determine the degree to which dominance relationships within a hierarchy conformed to the rules of linearity described above. An *h'* value of 0.9 or greater indicates a strongly linear hierarchy, and de Vries's (1995) randomization procedure was used to determine the statistical significance of *h'*. The *h'* statistic and its statistical significance were calculated using the 'compete' package for R software (Curley, 2016).

While linearity measures the extent to which dominance relationships are transitive, steepness measures the differences in dominance success between adjacently ranked individuals (de Vries et al., 2006). If, for example, the top ranking animal won 20 dominance interactions in total and the second ranking animal won only 5 dominance interactions in total, this would reflect a large difference in dominance success between ranks, and this hierarchy's steepness measure would likely be high. Steepness can be calculated from David's scores, as they measure the overall dominance success of individuals (de Vries et al., 2006). To characterize the baboon dominance hierarchy in this way, individuals' normalized David's scores were plotted against their dominance ranks, and the absolute slope of the line of best fit was taken as the steepness measure (*s*), per de Vries et al. (2006). The steepness measure can be interpreted like a standard slope, with a maximum value of 1. A randomization procedure was used to determine the statistical significance of the steepness score, both of which were calculated using the 'steepness' package for R software (Leiva & de Vries, 2014).

Groups with strongly linear, steep dominance hierarchies can be described as despotic, while groups with weakly linear, shallow hierarchies can be described as more egalitarian (van Schaik, 1989). The nature of the dominance hierarchy may help to explain differences in how social anxiety, and therefore SDB, manifests in a group (Polizzi di Sorrentino et al., 2012).

Association scores. Association scores were calculated by summing the number of group scans in which an individual had another specific individual as a social partner. For these purposes, a scan in which individuals were grooming was weighted the same as a scan in which the individuals were simply sitting in proximity. Each individual had an association score for each other individual in the group. These scores served as an indicator of how much time an individual spent with a partner relative to other group members.

Overall SDB rates. For each individual, focal data were used to calculate an overall rate of SDB events exhibited per hour. Being involved in or witnessing an aggressive conflict is known to co-occur with an increase in SDB in hamadryas baboons (Judge & Bachmann, 2013; Judge & Mullen, 2005). As such, post-conflict times were removed from the focal data before any SDB rates were calculated. If the focal individual was involved in an aggressive interaction as either the aggressor or the victim, the 3 min of focal data following the aggressive interaction were excluded from analyses. Similarly, if a strong or intense aggressive interaction (*i.e.*, a chase or a bite) occurred between two other individuals during a focal, the 3 min of focal data following the aggressive interaction were also excluded from analyses. These exclusions were intended to reduce the confounding influence of being involved in or witnessing an aggressive interaction on an animal's SDB rate.

After excluding post-conflict time, each animal's overall SDB rate was calculated as follows:

$$= \frac{total\ number\ of\ SDB\ events}{(total\ focal\ time\ in\ hours - total\ "out\ of\ sight"\ focal\ time\ in\ hours)}$$

Partner-specific SDB rates. Testing the hypothesis that hamadryas baboons exhibit higher rates of SDB in the presence of low-security partners required using focal data to calculate each animal's SDB rate in the presence of each other animal. These rates are referred to hereafter as "partner-specific SDB rates" (Polizzi di Sorrentino et al., 2012). Post-conflict times were excluded from these analyses in the same manner that they were excluded from overall SDB rate calculations. Analyses were also restricted to times when the focal animal was in the presence of exactly one other group member to control for the possible confounding effect of multiple neighbors on SDB rate (Polizzi di Sorrentino et al., 2012). As an exception to this rule, when a mother was with her young infant and one other individual, the young infant's presence was ignored so that any SDB exhibited in this context was counted as occurring in the other partner's presence. This adjustment ensured that there were sufficient data for mothers of young infants, as they were rarely separated from their infants. These mother infant pairs included Ac and Ig, Hn and Hl, and Al and Ln.

After excluding post-conflict times and adjusting for infant presence, Animal X's partner-specific SDB rate for another Anima Y was calculated as follows:

$$= \frac{number\ of\ SDB\ events\ X\ exhibited\ while\ associating\ exclusively\ with\ Y}{total\ X\ focal\ time\ spent\ associating\ exclusively\ with\ Y\ in\ hours}$$

For these calculations, all time spent in proximity, contact, or grooming was summed and counted as total time "associating." Any SDB event occurring during any level of association (proximity, grooming or contact) was captured in the numerator for this rate. A partner-specific SDB rate could not be calculated if an animal did not spend any focal time associating exclusively with a certain partner.

Relationship insecurity scores. For each of the 12 focal animals, variation in response to approach over time was calculated for each other group member. It has been proposed that variance in the result of Animal X approaching Animal Y will influence Animal X's perception of the relationship's security, and vice versa. Calculating two scores for each dyad, one considering the result of Animal X approaching Animal Y and the other considering the result of Animal Y approaching Animal X, accounted for possible asymmetry in perception of relationship security. This concept, and the classifications and calculations that follow, were based on those from Bugnyar & Fraser (2010) and Majolo et al. (2010).

For each dyad, focal data from both individuals were combined to examine responses to approach and classify them as positive or negative. An approach was defined as one animal initiating an association (proximity, contact or grooming) with another animal. A response to approach was considered positive if: 1) proximity lasted for 20 s or more, *or* a more intimate affiliation (contact, grooming or play) began within 20 s of the approach; and 2) no aggressive or submissive interaction occurred between the individuals for the duration of the association. For these purposes, back-to-back bouts of proximity, grooming or contact were considered one association. For example, if Animal X initiated proximity with Animal Y, then the pair came into contact without a break in proximity, then the pair broke contact and immediately moved out of proximity, the total time from start of proximity to end of contact would be considered one association. A response to approach was considered negative if: 1) proximity lasted for less than 20 s *and* a more intimate affiliation (contact, grooming or play) did not occur; or 2) an aggressive or submissive interaction occurred between the individuals at any time during the association. An estrous female presenting to a male was not counted as a submissive behavior for these purposes. Response to approach was not scored if a dyad was already in proximity, contact or grooming at the start of a focal or immediately after the focal animal returned from being out of sight, as the individual initiating the interaction could not be identified in these circumstances. Similarly, response to approach was not scored if a focal ended or the focal individual moved out of sight before an associating dyad had been in proximity for 20 s, so that these interactions were not presumed to be negative.

Focal data were divided into four seven-week time periods. For each of these time periods, Animal X's proportion of negative responses to approach for Animal Y was calculated as follows:

$$= \frac{number\ of\ \ negative\ responses\ to\ Animal\ X\ approaching\ Animal\ Y}{\begin{pmatrix} number\ of\ negative\ responses\ to\ Animal\ X\ approaching\ Animal\ Y\ + \\ number\ of\ positive\ responses\ to\ Animal\ X\ approaching\ Animal\ Y \end{pmatrix}}$$

If an animal never approached a certain partner during a seven-week time period, the proportion of negative responses to approach could not be calculated for that time period. To measure variation in response to approach over time, the coefficient of variation (CV) was calculated as follows:

$$= \left(\frac{standard\ deviation}{\begin{matrix} mean\ proportion\ of\ negative\ responses\ to\ Animal\ X \\ approaching\ Animal\ Y\ over\ the\ time\ periods \end{matrix}} \right) * 100\%$$

If an animal did not have a proportion of negative responses to approach score for a certain partner for all four time periods, the CV was calculated using the two or three scores available. If an animal only had a proportion of negative responses to approach score for a certain partner for one of the four time periods, the CV could not be calculated. As long as an animal approached a partner once in each of two time periods, a CV could be calculated for that partner. This is true regardless of whether additional animals were also in proximity during approaches. Because partner-specific SDB rates could only be calculated if animals were associating in the absence of other group members, it is possible that an animal could have a CV for a partner but lack a partner-specific SDB rate for that same partner.

The coefficient of variation is a measure of relative variation that has been used in relationship quality studies to calculate relationship variables such as grooming variability and consistency in affiliation (Fraser et al., 2008; Majolo et al., 2010). Higher CV percentages indicate greater variation in response to approach over time. Because more variation in response to approach indicates less predictability for Animal X when approaching Animal Y, a higher CV indicates that Animal X has a less secure relationship with Animal Y. Because higher scores indicate greater insecurity, these CVs are referred to as “relationship insecurity scores.”

Comparing SDB rate across age, sex, rank and aggression received. Several statistical analyses were conducted to explore which individual and social factors were associated with higher overall SDB rates. Mean overall SDB rates were compared across sex (male versus female) and age class (adult versus juvenile) with independent samples t-tests. Mean general SDB rates were also compared across rank classes (the four highest-ranking animals versus the four mid-ranking animals versus the four lowest-ranking animals) with a one-way ANOVA. A Pearson’s correlation was used to test whether overall SDB rate varied with the total number of aggressive acts received by the subject during the study. The correlation included aggressive acts directed toward the subject from all 15 animals in the group (focal animals as well as the three infants). A two-tailed alpha level of .05 was used for all tests of statistical significance.

Predicting partner-specific SDB rates. Data for partner-specific SDB rates, relationship insecurity scores, association scores, aggressive acts received from each partner, total aggressive acts exhibited by each partner, and partner's relative dominance rank were organized in square matrices. Each cell included the subject animal's score for a specific partner. Subjects were represented along rows, and partners were represented along columns. Any missing values were replaced by the average of the scores in that row. Hemelrijk (1990) recommended handling missing values in this way when they accounted for less than 10 percent of all data.

The data in each of these datasets were based on interactions between two individuals, and each group member contributed to multiple data points within each dataset. This means that these data were not independent and required analysis with nonparametric tests. Therefore, Tau Kr matrix correlations – nonparametric tests that also account for individual differences among subjects – were used to analyze the relationships within different pairs of matrices. Hemelrijk's (1990) Tau Kr test adapts Kendall's Tau, a nonparametric test using ranks rather than values to determine correlation, for use with matrices. This test first determines the direction of change (positive or negative) between each possible pair of cells within each row (*i.e.*, each possible pair of one subject's scores) in Matrix X and notes whether the direction is the same as that between the corresponding pair of cells in Matrix Y. For each row, the number of corresponding pairs that do not match in direction of change are subtracted from the number of corresponding pairs that are matched in direction of change. These values are then summed across rows and divided by the total number of within-row pairs in a matrix. The resulting statistic will be between 0 and 1 and should be interpreted like any other correlation. Replacing missing values with row means does not influence a matrix's association with other variables because the number of values in the row that are greater than the mean will equal the number of values in the row that are less than the mean. Further details and examples are available in Hemelrijk (1990).

By only comparing scores within rows/subjects and using ranks rather than values, the Tau Kr test controls for individual differences and reduces the influence of outliers (Hemelrijk, 1990). A permutation procedure, which randomly varied the placement of scores within rows for one matrix while holding the other matrix constant, provided a measure of statistical significance. All Tau Kr statistics were calculated using the MatrixTester 3.0.1 add-on for Microsoft Excel (Hemelrijk, 2017).

Tau Kr matrix correlations were calculated between partner-specific SDB rates and each of the following predictor variables: relationship insecurity scores, association scores, aggressive acts received from the partner, total aggressive acts exhibited by the partner, and partner's relative dominance rank. Total aggressive acts exhibited by the partner was measured as the total number of aggressive acts exhibited by the partner individual throughout the study, regardless of recipient. This included aggressive acts directed toward the 12 focal animals as well as the three infants. As this measure was not influenced by the relationship between the subject and the partner, a partner animal's score was the same regardless of the subject's identity. This measure was used to assess whether subjects exhibited more SDB in the presence of animals who were generally more aggressive.

Testing independence of the relationship insecurity measure. To my knowledge, only one study has looked for the specific variable “variation in response to approach over time” in a PCA of relationship quality (Bugnyar & Fraser, 2010). The results of this PCA found that this variable did not correlate with time spent in proximity or dyadic aggression rates in ravens. However, this has not been explicitly tested in primates. To test whether response to approach over time is independent of other relationship variables previously used to predict SDB rate, Tau Kr correlations were conducted between relationship insecurity scores and association scores, aggressive acts received from the partner, and partner’s relative dominance rank.

Results

Dominance Hierarchy and Aggression Patterns

Table 4 details each animal's raw David's score, normalized David's score, and resulting dominance rank. According to de Vries's (1995) modification of Landau's linearity index, this dominance hierarchy was highly linear, $h' = .95$, $p <.001$, 10,000 permutations. A test of hierarchy steepness, based on the slope of the normalized David's scores graphed in Figure 1, showed that the hierarchy was also steep, $s= .90$, $p <.001$, 10,000 permutations. In the analyses to follow, 1 represented the highest dominance rank, and 12 represented the lowest dominance rank. Therefore, if a variable was negatively correlated with rank, that variable was said to increase with rank.

Dominance ranks were based on aggressive behavior as well as submissive behavior. Analyzing aggressive behavior patterns separately revealed that adults exhibited significantly more aggressive acts ($M = 55.17$, $SD = 50.31$) than did juveniles ($M = 8.17$, $SD = 7.25$), $t(10) = 2.27$, $p = .047$. There were no differences in number of aggressive acts exhibited across dominance rank classes, $F(2, 9) = 1.87$, $p = .209$. However, when compared directly, low-ranking individuals were the recipients of significantly more aggressive acts ($M = 38.25$, $SD = 10.81$) than were high-ranking individuals ($M = 14.25$, $SD = 5.41$) $t(6) = -3.00$, $p = .024$.

SDB Rates Across Age, Sex, Rank and Aggression Received

Across all individuals, the average SDB rate was 41.18 events per hour. Individual SDB rates ranged from 20.87 events per hour for the lowest-ranking, youngest individual to 51.73 events per hour for the highest-ranking individual, the adult male.

Adults exhibited SDB at significantly higher rates (*M* = 51.92, *SD* = 8.82) than juveniles (*M* = 30.45, *SD* = 5.69), *t*(10) = 5.01, *p* = .001, 95% CI [11.92, 31.01], *d* = 1.18 (Figure 2). SDB rates were also significantly different across rank classes, *F*(2, 9) = 7.26, *p* = .013, $\eta^2 = .62$ (Figure 3). A post-hoc Fisher's LSD test found that high-rankers (*M* = 52.73, *SD* = 10.28) exhibited significantly higher SDB rates than low-rankers (*M* = 28.40, *SD* = 5.59), *p* = .004. SDB rates of mid-rankers (*M* = 42.43, *SD* = 10.27) did not differ significantly from those of high-rankers (*p* = .14), nor those of low-rankers (*p* =.06). Age (in months at the end of the study) and rank were strongly correlated in this group, *r* = -.87, *p* < .001, $r^2 = .75$. This made it difficult to test these variables' separate influence on SDB rate. There were no significant differences in SDB rate between males (*M* = 33.77, *SD* = 11.61) and females (*M* = 46.48, *SD* = 12.41), *t*(10) = -1.79, *p* = .10. Total number of aggressive acts directed toward the subject did not predict SDB rates, *r* = -.37, *p* = .24.

Predictors of Partner-specific SDB Rates

A total of 129 partner-specific SDB rates were calculated (Table 5). The three missing values reflect dyads that did not spend any focal time associating exclusively and therefore had a zero in the denominator for the rate equation. A total of 130 relationship insecurity scores were calculated (Table 6). The two missing scores reflect dyads that did not have any approaches during the study. All missing values were replaced with the average score for the row.

Partner-specific SDB rate did not vary with relationship insecurity scores, $\tau_{Kr} = -.11$, *p* = .10, 10,000 permutations, or with total aggression received from the partner

(Table 7), $\tau_{Kr} = -.08$, $p = .26$, 10,000 permutations. Association scores (Table 8) did not predict partner-specific SDB rates either, $\tau_{Kr} = -.11$, $p = .13$, 10,000 permutations.

A slight positive correlation was found between partner-specific SDB rate and a partner's relative rank, $\tau_{Kr} = .12$, $p = .040$, 10,000 permutations (Figure 4). The higher ranking the partner was relative to the subject, the more SDB the subject exhibited in that partner's presence. Squaring the Tau Kr correlation statistic estimates that relative rank accounted for 1.4 percent of the variance in partner-specific SDB rate.

Partner-specific SDB rate was also slightly positively correlated with the total number of aggressive acts exhibited by the partner, $\tau_{Kr} = .14$, $p = .014$, 10,000 permutations (Figure 5). This variable accounted for an estimated 2.1 percent of the variance in partner-specific SDB rate.

Partner's relative rank and partner's total aggressive acts were strongly positively correlated, $\tau_{Kr} = .69$, $p < .002$, $\tau_{Kr}^2 = .47$, 10,000 permutations. Neither of these variables' relationship with partner-specific SDB rate remained significant when the other variable was controlled for, *i.e.* partialed out of the predictor and predicted variables.

Independence of Relationship Insecurity Measure

Relationship insecurity scores were slightly negatively correlated with association scores, $\tau_{Kr} = -.16$, $p < .026$, $\tau_{Kr}^2 = .03$, 10,000 permutations. As relationship insecurity scores increased, association scores decreased. Relationship insecurity scores were not significantly correlated with aggressive acts received from the partner ($p = .09$), nor with partner's relative dominance rank ($p = .37$).

Discussion

Age and Rank Effects for Overall SDB Rate

In this captive hamadryas baboon group, high-ranking animals exhibited significantly higher rates of SDB than did low-ranking animals. The animals' rank order from highest to lowest was nearly identical to their age order from oldest to youngest. As a result, the four animals classified as high-ranking were all adults, and the four animals classified as low-ranking were all juveniles. Therefore, it is difficult to separate rank and age effects for SDB rate in this group. I will consider several possible explanations for these observed differences, starting with those related to age.

Previous studies have found a positive relationship between amount of aggressive/threatening behavior exhibited and SDB rate (Kaburu et al., 2012; Easley et al., 1987). In the current study group, adults were significantly more aggressive than juveniles. Though post-conflict times were excluded from SDB rate calculations in this study, it is possible that more aggressive animals experienced more anxiety generally, resulting in higher overall SDB rates for adults.

Maternal anxiety could also contribute to the higher observed SDB rates in adults. Mothers are known to exhibit SDB related to the activities of their young offspring (Maestripieri, 1993). Three of the five adult females in this group had young infants during the course of the study, ranging in age from two to six months at the start of behavioral observations. These mothers may have experienced more anxiety and exhibited higher rates of SDB while caring for their young infants, which may have contributed to higher adult SDB rates.

Alternatively, adult primates may simply have a more sophisticated sense of risk than juveniles, leading to more anxiety and SDB. Studies of post-conflict SDB do not seem to support this interpretation, however. No differences in SDB rate after conflicts with kin were found between adult and juvenile Japanese macaques, suggesting they experience post-conflict anxiety similarly (Kutsukake & Castles, 2001). Juvenile hamadryas baboons are also known to exhibit higher rates of SDB after witnessing conflicts, demonstrating that even social interactions not directly involving them can cause juveniles anxiety (Judge & Bachmann, 2013). This evidence suggests any age class differences in the cognitive abilities required to experience social anxiety were likely to be small.

There were several possible explanations for higher SDB rates in high-ranking animals as well. High-ranking baboons have been shown to have higher GC levels than low-ranking baboons during times of social instability (Sapolsky, 1993). Dominance hierarchy instability may show a similar pattern for SDB rates (Polizzi di Sorrentino, 2012). It was possible that hierarchy instability could contribute to the high SDB rates of high-ranking baboons in the present study. Unfortunately, long-term data on the group's dominance relationships were lacking, so hierarchy stability could not be analyzed. Relatedly, rank uncertainty has been shown to increase SDB rate (Schino et al., 1990). While the baboon group's dominance hierarchy was steep and linear overall, suggesting rank clarity, the three high-ranking females had similar normalized David's scores, ranging from 8.06 to 8.40. These females may have experienced some rank uncertainty and related anxiety, increasing the high-ranking animals' SDB rate. The dominance hierarchy among low-ranking animals was much steeper, with David’s scores ranging from .067 to 3.38.

While low-ranking animals received more aggression than did high-ranking animals, other costs associated with being a low-ranking animal in this group were minimal. Regular, dispersed feedings in a captive environment limit the effects of food competition. As low-ranking animals were all juveniles in this group, they did not experience any mate competition. This could have kept low-ranking animals’ anxiety related to these factors relatively low.

Partner-specific SDB Rate Predictors

This study failed to reject the null hypothesis that relationship security and anxiety in a group member’s presence are unrelated. Relationship insecurity scores did not correlate with partner-specific SDB rates, nor did association scores or aggression received from a partner. Partner’s relative dominance rank was the only relationship variable predicting SDB rate in a partner’s presence. Total amount of aggression exhibited by a partner also predicted partner-specific SDB rates and was positively correlated with partner’s relative dominance rank. The result suggests aggression risk was a source of anxiety in this group, while relationship insecurity was not.

There are two possible explanations for failing to reject the null hypothesis. Either this study failed to detect an association between relationship security and anxiety that did exist, or these variables were, in fact, unrelated. Discussion explored the possibility that the association existed but failed to be observed in this baboon group using the current study’s methods.

The nature of this group's dominance hierarchy may have masked any possible association between relationship insecurity and anxiety in a group member's presence. This group had a remarkably steep, linear dominance hierarchy, contrary to the prediction that dominance relationships below the alpha male would be muted in this species (Swedell, 2016). Because dominance rank was such a strong organizing principle in this group, it follows logically that anxiety in a group member's presence would be linked to dominance relations. In the opposite direction, studies with more tolerant species and groups with flatter dominance hierarchies did not find a strong relationship between a neighbor's rank and SDB rates in a neighbor's presence (Kutsukake, 2003; McDougall, 2011). Instead, time spent associating was a stronger predictor SDB rate in these studies. When dominance relationships are muted, other aspects of the relationship may predict social anxiety.

Conditions in captivity could also account for the lack of relationship between anxiety and relationship insecurity or association score. Unpredictability in relationships is hypothesized to increase social anxiety (Cords & Aureli, 1993). Cords & Aureli (2000) argue that the predictability of a partner's behavioral responses is at the core of relationship security, and a partner's behavior may become more predictable as the animals spend more time together (Kutsukake, 2003). In this captive study group, all animals were housed together at all times, and the nature of the outdoor enclosure allowed all individuals to be visible to one another. This constant exposure to all other group mates may have inherently increased the predictability of social partners, dampening any differences in anxiety related to individual social relationships.

Association scores captured how often animals were within 1 m of one another, but if anxiety is related to predictability and predictability is related to more general exposure to a partner's behavior, anxiety would not be expected to vary with time spent in close proximity in this group. Previous studies finding a relationship between SDB rate and time spent in proximity were conducted with wild populations in which individuals varied more in their exposure to one another.

While SDB rate in a partner's presence did increase with a partner's relative dominance rank, this correlation was weak. Partner's relative dominance rank predicted less than two percent of the variation in partner-specific SDB rate. Study limitations and the influence of variables not measured in this study could have prevented detection of strong relationships between the tested variables and partner-specific SDB rate.

This behavioral study was conducted over 130.5 hours. While some comparable studies were conducted with a similar amount of data (*e.g.*, Daniel et al., 2008), many studies evaluating the social context of SDB were conducted over at least twice as many hours. This study's data set may have been too small for strong correlations to emerge, especially as analyses were limited to times when two animals were associating exclusively. This restriction was necessary, however, to reduce the influence of possible confounding variables.

Previous studies have demonstrated that SDB is frequently exhibited during transitions into or out of association with others (white-faced capuchins: Manson & Perry, 2000; rhesus macaques, Diezinger & Anderson, 1986; ring-tailed lemurs, Buckley & Semple, 2012). Some of these transitions may be more anxiogenic than others, depending on the context and partner (Buckley & Semple, 2012). Because a focal animal was only counted as associating with another group member when the animals were within 1 m, SDB events during transitions were not fully captured in this study. For example, any SDB exhibited while a group member approached a focal animal from farther than 1 m away was counted as SDB exhibited while alone. If SDB during transitions varied with any relationship variables, this study design would not allow results to reflect this.

It was also possible that anxiety in this group would be better predicted by factors not analyzed in this study than by any of the tested relationship variables. Maternal anxiety, for example, may have been a significant source of anxiety for females with young offspring. When a mother was with her infant and another individual, any SDB exhibited in this context contributed to the mother's partner-specific SDB rate for the non-infant neighbor. This would be the case even if the infant, or the infant's interaction with the other individual, was in fact the source of the mother's anxiety in this context. This illustrates that this study was not designed to assess maternal anxiety, but with subjects including three mothers of young infants and one mother of a yearling, this may have been a source of anxiety in this group.

Finally, anxiety may simply be more strongly associated with specific events than with the status of social relationships in this group. The evidence that SDB increases in Old World monkeys after anxiety provoking events, such as aggressive interactions, is extensive (Aureli & Smucny, 2000). This applies not only to aggressors and victims, but also to bystanders (Judge & Mullen, 2005). The current study removed post-conflict time before calculating SDB rates in an attempt to assess non-conflict-related predictors of anxiety. Including post-conflict times may have allowed previous studies to find stronger relationships between SDB in a neighbor’s presence and various relationship variables, particularly neighbor’s dominance rank. Castles et al. (1990) and McDougall (2011) did not control for post-conflict time, and both studies found higher SDB rates in the presence of dominant group members. As aggression tends to be directed down the dominance hierarchy, these findings may have been driven by high subordinate SDB rates while in proximity to dominants from whom they had just received aggression. In contrast, Kutsukake (2003) and Daniel et al. (2008) controlled for post-conflict time and found no relationship between SDB rate and a neighbor’s rank. These studies were all conducted with Old World primates.

Other subtler events may also cause anxiety and trigger self-directed behavior in nonhuman primates. For example, this study examined patterns of negative responses to approach as a measure of relationship security, but a negative response to an approach could be anxiety provoking on its own. Regardless of a dyad’s history, an approaching animal’s attempt at social interaction is rebuffed if the partner walks away upon approach. This experience may be anxiety provoking, and self-directed behavior may follow. If SDB is linked to immediate circumstances, patterns between SDB and relationship characteristics such as security may not emerge.

Relationship Insecurity Measure

Though variation in response to approach over time did not predict SDB patterns in this group, this variable may still be a viable measure of relationship security. These relationship insecurity scores were not positively correlated with any other relationship variable measured in this study, suggesting that the variable measures a different aspect of relationship quality. Interestingly, association scores did decrease slightly as relationship insecurity increased. If this measure is a valid estimate of relationship security, this finding suggests animals spend less time affiliating with less secure, less predictable partners.

The variation in response to approach measure was originally used to measure relationship quality in ravens (Bugnyar & Fraser, 2010). Adapting this measure for use with primates required adjusting the definitions of positive and negative responses to approach. For example, Bugnyar & Fraser (2010) counted the response to approach as positive if the two ravens handled the same object during their association. Primates rarely handle objects jointly, so I did not include this in my classifications. Similarly, Bugnyar & Fraser (2010) did not note how much time two animals had to remain in proximity for the interaction to be counted as positive. Therefore, my choice of 20 s for this baboon group was somewhat arbitrary. Future studies may want to adjust the classifications of positive and negative responses to approach to attempt to accommodate the species under study.

In this study, the individual initiating an approach was recorded, and an approach was classified as negative or positive based on the general outcome of the interaction. This study did not distinguish between interactions ended by the approacher and interactions ended by the approachee. Classifying interactions more strictly based on the approachee’s behavior may be a conceptual improvement upon the current study’s measure, as an animal's perception of relationship security is hypothesized to be related to consistency in the partner's behavior (Cords & Aureli, 2000). Variation in response to approach over time is a new measure, and any adjustments based on relationship quality theory that may bring the measure closer to accurately estimating relationship security are encouraged.

My relationship security measure was based on change in the outcome of interactions over time. If the time periods used were not far enough apart to detect change, or if animals did not interact in each time period, the validity of this measure might have been weakened. In the current study, 27 of 132 dyads had at least one seven-week time period in which no approaches were recorded. For these dyads (excluding the two that interacted in only one time period), change over time had to be calculated using two or three time periods rather than four. This may have reduced this measure's ability to estimate relationship security. Future studies should plan to conduct focal sampling over substantially more hours (previous SDB studies have analyzed more than 1,000 focal hours), and potentially over a longer period of time, to most accurately measure variation in response to approach over time.

Future Directions and Conclusion

This study provided the first analysis of non-conflict-related SDB patterns across age, sex and rank classes in a species organized in one-male units. In this hamadryas baboon group with a steep, linear dominance hierarchy, SDB rates were related to age, rank and aggression, suggesting aggression risk was a greater predictor of anxiety than was relationship security. While hamadryas baboons were chosen for this study for their hypothesized flat dominance structure, other aspects of their sociality may also influence how they experience anxiety. Specifically, future work should examine how the adult male's aggressive herding influences anxiety experienced by adult females. Studying a larger colony or wild population of hamadryas baboons would also allow exploration of adult male anxiety related to mating competition in the presence of bachelor males or other one-male units.

This study was also the first to use a PCA-identified component of relationship quality to test for the association between SDB and relationship security originally proposed by Cords & Aureli (2000).Though variation in response to approach over time did not predict partner-specific SDB rates in this group, future studies should look for this relationship in a wild primate group with a flatter, less linear dominance hierarchy. As relationship insecurity scores did not increase with other relationship variables used to predict SDB, they may be used in future studies as an independent measure of an aspect of relationship quality. I also plan to use the present study's dataset to explore patterns in the sequence of events preceding SDB. There is much more work to be done to understand the social context of nonhuman primate anxiety.

References

Abbott, D. H., Keverne, E. B., Bercovitch, F. B., Shively, C. A., Mendoza, S. P., Saltzman, W., …& Sapolsky, R. M. (2003). Are subordinates always stressed? A comparative analysis of rank differences in cortisol levels among primates. *Hormones and Behavior, 43*, 67-82.

Allee, W. C. (1952). Dominance and hierarchy in societies of vertebrates. *Colloques Internationaux du CNRS, 34*, 157-181.

Anselme, P. (2008). Abnormal patterns of displacement activities: A review and reinterpretation. *Behavioural Processes, 79*, 48-58.

Aureli, F., Preston, S. D., & de Waal, F. B. M. (1999). Heart rate responses to social interactions in free-moving rhesus macaques (*Macaca mulatta*): A pilot study. *Journal of Comparative Psychology, 113*, 59-65.

Aureli, F., & Smucny, D. (2000). The role of emotion in conflict and conflict resolution. In F. Aureli, & F.B.M. de Waal (Eds.), *Natural conflict resolution* (199-224). Los Angeles, CA: University of California Press.

Aureli, F., & van Schaik, C. P. (1991). Post-conflict behaviour in long-tailed macaques (*Macaca fascicularis*): Coping with the uncertainty. *Ethology, 89*, 101-114.

Balasubramaniam, K. N., Berman, C. M., De Marco, A., Dittmar, K., Majolo, B., Ogawa, H., Thierry, B., & de Vries, H. (2013). Consistency of dominance rank order: A comparison of David's scores with I&SI and Bayesian methods in macaques. *American Journal of Primatology, 75*, 959-971.

Beehner, J. C., Bergman, T. J., Cheney, D. L., Seyfarth, R. M., & Whitten, P. L. (2005). The effect of new alpha males on female stress in free-ranging baboons. *Animal Behaviour, 69*, 1211-1221.

Bergman, T. J., Beehner, J. C., Cheney, D. L., Seyfarth, R. M., & Whitten, P. L. (2005). Correlates of stress in free-ranging male chacma baboons, *Papio hamadryas ursinus*. *Animal Behaviour, 70*, 703-713.

Buckley, V., & Semple, S. (2012). Evidence that displacement activities facilitate behavioural transitions in ring-tailed lemurs. *Behavioural Processes, 90*, 433-435.

Bugnyar, T., & Fraser, O. N. (2010). The quality of social relationships in ravens. *Animal Behaviour, 79*, 927-933.

Castles, D. L., & Whiten, A. (1998). Post-conflict behaviour of wild olive baboons: Stress and self-directed behaviour. *Ethology, 104*, 148-160.

Castles, D. L., Whiten, A., & Aureli, F. (1999). Social anxiety, relationships and self-directed behavior among wild female olive baboons. *Animal Behaviour, 58*, 1207-1215.

Cheney, D. L., & Seyfarth, R. M. (2009). Stress and coping mechanisms in female primates. *Advances in the Study of Behavior, 39*, 1-44.

Clutton-Brock, T. H., Albon, S. D., Gibson, R. M., & Guinness, F. E. (1979). The logical stag: adaptive aspects of fighting in red deer (*Cervus elaphus L.*). *Animal Behaviour, 27*, 211–225.

Coleman, K., & Pierre, P. J. (2014). Assessing anxiety in nonhuman primates. *ILAR Journal, 55*, 333-346.

Cords, M. & Aureli, F. (1993). Patterns of reconciliation among juvenile long-tailed macaques. In M. E. Pereira, & L. A. Fairbanks (Eds.), *Juvenile primates: Life history, development and behavior* (271–284). New York, NY: Oxford University Press.

Cords, M., & Aureli, F. (2000). Reconciliation and relationship qualities. In F. Aureli, & F.B.M. de Waal (Eds.), *Natural conflict resolution* (177-198). Los Angeles, CA: University of California Press.

Cristobal-Azkarate, J., Chavira, R., Boeck, L., Rodriguez-Luna, E., & Vea, J. J. (2008). Glucocorticoid levels in free ranging resident mantled howlers: A study of coping strategies. *American Journal of Primatology, 69*, 866-876.

Crockford, C., Wittig, R. M., Whitten, P. L., Seyfarth, R. M., & Cheney, D. L. (2008). Social stressors and coping mechanisms in wild female baboons (*Papio hamadryas ursinus*). *Hormones and Behavior, 53*, 254-265.

Curley, J. P. (2016). compete: Analyzing Social Hierarchies (R package version 0.1) [Software]. Available from https://CRAN.R-project.org/package=compete

Daniel, J. R., dos Santos, A. J., & Vicente, L. (2008). Correlates of self-directed behaviors in captive *Cercopithecus aethiops*. *International Journal of Primatology, 29*, 1219-1226.

David, H. A. (1987). Ranking from unbalanced paired-comparison data. *Biometrika, 74*, 432-436.

de Vries, H. (1995). An improved test of linearity in dominance hierarchies containing unknown or tied relationships. *Animal Behavior, 50*, 1375-1389.

de Vries, H., Stevens, J. M. G., & Vervaecke, H. (2006). Measuring and testing the steepness of dominance hierarchies. *Animal Behaviour, 71*, 585-592.

Diezinger, F., & Anderson, J. R. (1986). Starting from scratch: A first look at a "displacement behavior" in group-living rhesus macaques. *American Journal of Primatology, 11*, 117-124.

Duboscq, J., Romanco, V., Sueur, C., & MacIntosh, A. J. J. (2016). Scratch that itch: revisiting links between self-directed behavior and parasitological, social and environmental factors in a free-ranging primate. *Royal Society Open Science, 3*, 160571.

Easley, S. P., Coelho, A. M., & Taylor, L. L. (1987). Scratching, dominance, tension, and displacement in male baboons. *American Journal of Primatology, 13*, 397-411.

Ellis, J. J., MacLarnon, A. M., Heistermann, M., & Semple, S. (2011). The social correlates of self-directed behavior and faecal glucocorticoid levels among adult male olive baboons (*Papio hamadryas anubis*) in Gashaka-Gumti National Park, Nigeria. *African Zoology, 46*, 302-308.

Emery Thompson, M., Muller, M. N., Kahlenberg, S. M., & Wrangham, R. W. (2010). Dynamics of social and energetic stress in female chimpanzees. *Hormones and Behavior, 58*, 440-449.

Engh, A. L., Beehner, J. C., Bergman, T. J., Whitten, P. L., Hoffmeier, R. R., Seyfarth, R. M., & Cheney, D. L. (2006). Behavioural and hormonal responses to predation in female chacma baboons (*Papio hamadryas ursinus*). *Proceedings of the Royal Society B: Biological Sciences, 273*, 707-712.

Fraser, O. N., Schino, G., & Aureli, F. (2008). Components of relationship quality in chimpanzees. *Ethology, 114*, 834-843.

Gammell, M., de Vries, H., Jennings, D. J., & Hayden, T. J. (2003). David's score: A more appropriate dominance ranking method than Clutton-Brock et al.'s index. *Animal Behaviour, 66*, 601-605.

Gray, J. A. (1987). Perspectives on anxiety and impulsivity: A commentary. *Journal of Research in Personality, 21*, 493-509.

Hemelrijk, C. K. (1990). A matrix partial correlation test used in investigations of reciprocity and other social interaction patterns at group level. Journal of Theoretical Biology, 143, 405-420.

Hemelrijk, C. K. (2017). MatrixTester (Excel add-on version 3.0.1) [Software]. Available from C. K. Hemelrijk: c.k.hemelrijk@rug.nl

Higham, J. P., MacLarnon, A. M., Heistermann, M., Ross, C., & Semple, S. (2009). Rates of self-directed behaviour and faecal glucocorticoid levels are not correlated in female wild olive baboons (*Papio hamadryas anubis*). *Stress, 12*, 526-532.

Hinde, R. A., (1952). The behavior of the great tit (*Parus major*) and some other related species. *Behaviour, 2*, 1–201.

Janson, C. H., & Goldsmith, M. L. (1995). Predicting group size in primates: foraging costs and predation risks. *Behavioral Ecology, 6*, 326–336.

Judge, P. G., & Bachmann, K. A. (2013). Witnessing reconciliation reduces arousal of bystanders in a baboon group (*Papio hamadryas hamadryas*). *Animal Behaviour, 85*, 881-889.

Judge, P. G., & Mullen, S. H. (2005). Quadratic postconflict affiliation among bystanders in a hamadryas baboon group. *Animal Behaviour, 69*, 1345-1355.

Kaburu, S. S. K., McLarnon, A., Majolo, B., Qarro, M., & Semple, S. (2012). Dominance rank and self-scratching among wild female Barbary macaques (*Macaca sylvanus*). *African Zoology, 47*, 74-79.

Kato, Y., Gokan, H., Oh-Nishi, A., Suhara, T., Watanabe, S., & Minamimoto, T. (2014). Vocalizations associated with anxiety and fear in the common marmoset (*Callithrix jacchus*). *Behavioral Brain Research, 275*, 43-52.

Kutsukake, N. (2003). Assessing relationship quality and social anxiety among wild chimpanzees using self-directed behaviour. *Behaviour, 14*, 1153-1171.

Kutsukake, N., & Castles, D. L. (2001). Reconciliation and variation post-conflict stress in Japanese macaques (*Macaca fuscata fuscata*): Testing the integrated hypothesis. *Animal Cognition, 4*, 259-268.

Leiva, D., & de Vries, H. (2014). steepness: Testing Steepness of Dominance Hierarchies (R package version 0.2-2) [Software]. Available from https://CRAN.R-project.org/package=steepness

Maestripieri, D. (1993). Maternal anxiety in rhesus macaques: measurement of anxiety and identification of anxiety-eliciting situations. *Ethology, 95*, 19-31.

Maestripieri, D., Schino, G., Aureli, F., & Troisi, A. (1992). A modest proposal: Displacement activities as an indicator of emotions in primates. *Animal Behaviour, 44*, 967-979.

Majolo, B., Ventura, R., & Schino, G. (2010). Asymmetry and dimensions of relationship quality in the Japanese macaque (*Macaca fuscata yakui*). *International Journal of Primatology, 31*, 736-750.

Manson, J. H., & Perry, S. (2000). Correlates of self-directed behavior in wild white-faced capuchins. *Ethology, 106*, 301-317.

Martin, P., & Bateson, P. (2007). *Measuring behaviour: An introductory guide* (3rd ed.). Cambridge, UK: Cambridge University Press.

Mason, W. A., & Mendoza, S. P. (1993). Primate social conflict: An overview of sources, forms, and consequences. In W. A. Mason & S. P. Mendoza (Eds.), *Primate social conflict* (1-11). Albany, NY: State University of New York Press.

McDougall, P. (2011). Scratching our heads: Social anxiety in vervets (*Chlorocebus aethiops*). *International Journal of Primatology, 32*, 335-345.

McFarland, D. J. (1966). On the causal and functional significance of displacement activities. *Ethology, 23*, 217-235.

McFarland, R., & Majolo, B. (2011). Exploring the components, asymmetry and distribution of relationship quality in wild Barbary macaques. *PloSOne, 6*, e28826.

Neal, S. J., & Caine, N. G. (2016). Scratching under positive and negative arousal in common marmosets (*Callithrix jacchus*). *American Journal of Primatology, 78*, 216-226.

Neumann, C., & Kulik, L. (2014). EloRating: Animal Dominance Hierarchies by Elo Rating (R package version 0.43) [Software]. Available from https://CRAN.R-project.org/package=EloRating

Ostner, J., Heistermann, M., & Schulke, O. (2008). Dominance, aggression and physiological stress in wild male Assamese macaques (*Macaca assamensis*). *Hormones and Behavior, 54*, 613-619.

Pavani, S., Maestripieri, D., Schino, G., Turillazzi, P. G., & Scucchi, S. (1991). Factors influencing scratching behavior in long-tailed macaques (*Macaca fascicularis*). *Folio Primatologica, 57*, 34-38.

Pearson, B. L., Reeder, D. M., & Judge, P. G. (2015). Crowding increases salivary cortisol but not self-directed behavior in captive baboons. *American Journal of Primatology, 77*, 462-467.

Peignot, P., Jankowski, F., & Anderson, J. R. (2004). On self-scratching in captive mandrills (*Mandrillus sphinx*). *Folio Primatologica, 75*, 160-164.

Polizzi di Sorrentino, E., Schino, G., Tiddi, B., & Aureli, F. (2012). Scratching as a window into the emotional responses of wild tufted capuchin monkeys. *Ethology, 118*, 1072-1084.

Rebecchini, L., Schaffner, C., & Aureli, F. (2011). Risk is a component of social relationships in spider monkeys. *Ethology, 117*, 691-699.

Redmond, D. E., & Huang, Y. H. (1979). New evidence for a locus coeruleus-norepinephrine connection with anxiety. *Life Sciences, 25*, 2149-2162.

Romero, T., Colmenares, F., & Aureli, F. (2009). Testing the function of reconciliation and third party affiliation for aggressors in hamadryas baboons (*Papio hamadryas hamadryas*). *American Journal of Primatology, 71*, 60-69.

Sapolsky, R. M. (1993). The physiology of dominance in stable versus unstable social hierarchies. In W. A. Mason & S. P. Mendoza (Eds.), *Primate social conflict* (171-204). Albany, NY: State University of New York Press.

Sapolsky, R. M. (2002). Endocrinology of the stress-response. In J. B. Becker, S. M. Breedlove, D. Crews & M. M. McCarthy (Eds.), *Behavioral Endocrinology* (409-450). Cambridge, MA: MIT Press.

Sapolsky, R. M. (2005). The influence of social hierarchy on primate health. *Science, 308*, 648-652.

Schino, G., Maestripieri, D., Scucchi, S., & Turillazzi, P. G. (1990). Social tension in familiar and unfamiliar pairs of long-tailed macaques. *Behaviour, 113*, 264-272.

Schino, G., Troisi, A., Perretta, G., & Monaco, V. (1991). Measuring anxiety in nonhuman primates: Effect of lorazepam on macaque scratching. *Pharmacology Biochemistry & Behavior, 38*, 889-891.

Schino, G., Perretta, G., Taglioni, A.M., Monaco, V., & Troisi, A. (1996). Primate displacement activities as an ethopharmacological model of anxiety. *Anxiety, 2*, 186-191.

Sclafani, V., Norscia, I., Antonacci, D., & Palagi, E. (2012). Scratching around mating: Factors affecting anxiety in wild *Lemur catta*. *Primates, 53*, 247-254.

Silk, J. B. (1993). The evolution of social conflict among female primates. In W. A. Mason & S. P. Mendoza (Eds.), *Primate social conflict* (49-83). Albany, NY: State University of New York Press.

Smucny, D. A., Price, C. S., & Byrne, E. A. (1997). Postconflict affiliation and stress reduction in captive rhesus macaques. *Advances in Ethology, 32*, 157.

Swedell, L. (2016). *Strategies of sex and survival in hamadryas baboons: Through a female lens* (2nd ed.). New York, NY: Routledge.

Tinbergen, N. (1952). "Derived" activities: Their causation, biological significance, origin, and emancipation during evolution. *The Quarterly Review of Biology, 27*, 1-32.

Troisi, A., & Schino, G. (1987). Environmental and social influences on autogrooming behavior in a captive group of Java monkeys. *Behaviour, 100*, 292-302.

van Iersel, J. J., & Bol, A. C. A. (1958). Preening of two terns: A study on displacement activities. *Behaviour, 13*, 1-88.

van Schaik, C. P. (1983). Why are diurnal primates living in groups? *Behaviour, 87*, 120-144.

van Schaik, C. P. (1989). The ecology of social relationships amongst female primates. In V. Standon & R. Foley (Eds.), *Comparative socioecology of mammals and man* (195-218). Oxford, UK: Blackwell Scientific.

Wrangham, R. W. (1980). An ecological model of female-bonded primate groups. *Behaviour, 75*, 262-300.

Table 1

Group members

Name (ID)	Sex	Age Class	Date of Birth	Mother (if in group)	Focal sampling? (Y/N)
Judge (Jd)	Male	Adult	08/16/2007	n/a	Y
Kelso (Ks)	Female	Adult	11/23/1999	n/a	Y
Ali (Al)	Female	Adult	04/13/2000	n/a	Y
Acacia (Ac)	Female	Adult	07/15/2004	Al	Y
Honey (Hn)	Female	Adult	09/17/2008	n/a	Y
Azalea (Az)	Female	Adult	10/12/2011	Ac	Y
Anakin (Ak)	Male	Juvenile	01/05/2015	Al	Y
Arthur (Ar)	Male	Juvenile	01/07/2015	Ac	Y
Hans (Hs)	Male	Juvenile	10/08/2015	Hn	Y
Lily (Ly)	Female	Juvenile	12/27/2015	Al	Y
Ivy (Iv)	Female	Juvenile	01/17/2016	Ac	Y
Zed (Zd)	Male	Juvenile	06/03/2016	Az	Y
Holly (Hl)	Female	Infant	11/03/2016	Hn	N
Luna (Ln)	Female	Infant	12/22/2016	Al	N
Iggy (Ig)	Male	Infant	02/28/2017	Ac	N

Table 2

Ethogram for focal sampling

Behavior	Definition	Onset	Offset	Duration recorded? (Y/N)
	Self-directed behavior (SDB)			
Body shake	A quick side-to-side shaking movement of the head and upper body.	n/a	n/a	N
Gravel dig[1]	Pushing through gravel with hands. Often accompanied by animal extracting items from gravel and placing items in mouth.	2 strokes	5 s	Y
Throw dig	Quickly pushing through gravel, often in a sideways motion. Recorded as "gravel dig" if individual brings anything to its mouth at any point.	2 strokes	5 s	Y
Self-groom	Manipulating, brushing or licking of hair of oneself.	3 s	3 s	Y
Self-scratch	Movement of the hand or foot during which the fingers/fingernails and/or toes/toenails are drawn across the hair or skin. A new bout is counted if a different body part is scratched or a different limb is used to scratch.	2 strokes	3 s	N
Self-touch	Making directed contact with one's own body with the hands, feet, or mouth that does not qualify as self-grooming or self-scratching.	n/a	3 s	N

---

[1] Gravel dig was not counted as a SDB. It was included in the ethogram to distinguish the throw dig behavior.

Swipe	Dragging hand across non-gravel substrate in a sweeping/digging motion.	2 strokes	5 s	Y
Yawn	Slowly opening the mouth wide with a downward thrust of the lower mandible. Most often includes narrowing the eyes and exposing the teeth.	n/a	n/a	N
Affiliative behavior*				
Proximity	Approaching to within 1 m of another animal. Not scored during more intimate affiliative states (contact, groom).	3 s	5 s	Y
Contact	Touching another individual. Bouts end if partners move more than 1m away before 5 s pass. Not scored during grooming.	3 s	5 s	Y
Groom	Manipulating, brushing or licking of hair of another individual. Bouts end if partners move more than 1m away before 5 s pass.	3 s	5 s	Y
Play	Social interactions characterized by apparent low tension, usually accompanied by a “play face” (mouth is open and facial features are relatively relaxed). May include: grunting, wresting, sham-biting, jumping on or over, chasing, fleeing, hiding. Proximity/contact also scored during play.	3 s	10 s	Y

	Aggressive behavior*			
Rough behavior	Mild agonistic interaction involving slight physical contact, usually no facial signal. May include: nipping, grabbing, kicking, pulling, pushing, poking, slapping, pulling hair, butting, shoving.	n/a	5 s	N
Threat	Moderate agonistic interaction containing any of the following components: Head thrust – Jabbing head toward another individual, often accompanied by raised eyebrows and staring at an individual. Open-mouth threat – Opening mouth wide quickly, usually accompanied by thrusting of the head toward target and staring at an individual. Raised eyebrows – Glare with display of white portion of skin around eyes. Teeth gnashing – Conspicuous, exaggerated grinding of teeth. Lunge – Charging toward another animal that does not exceed the recipient's location at the time the action begins. Pin – Holding another animal down.	n/a	5 s	N
Chase	Strong agonistic interaction involving pursuit past the location the recipient maintained at the start of the interaction.	n/a	5 s	N
Bite	Intense agonistic interaction during which the skin/limb of another animal is grasped with the teeth. Does not include "nips" which consists of a brief pinch of the skin with the incisors (classified as "rough behavior").	n/a	5 s	N

	Submissive behavior*			
Avoid	Moving more than one step from another animal upon its approach.	3 s	n/a	N
Bare-teeth	Pulling back the face muscles to display the teeth.	n/a	n/a	N
Bark	Emitting a high-pitched yapping vocalization (usually repeated) during which the mouth may remain open and in which no component noises are longer than 1 s.	n/a	5 s	N
Flee	Rapid withdrawal from another animal, usually occurring in response to aggressive behavior or an approach.	n/a	n/a	N
Present	Orientating the hindquarters toward another animal, usually accompanied by lowering of the forelimbs, lifting of the tail, or looking back over the shoulder.	n/a	n/a	N
Scream	Emitting a loud high-pitched vocalization occurring in a defensive or retreating context in which one of the component noises is sustained for longer than 1 s.	n/a	5 s	N
	Other behavior			
Out of sight	Animal is out of the observer's view	n/a	n/a	Y

Note. A behavior must persist for the amount of time noted in the onset column before it is recorded. After a behavior ceases, the amount of time in the offset column must pass before the end of the behavior duration is recorded.

*Social partner and the direction of the behavior were recorded for these categories.

Table 3

Ethogram for scan sampling

State	Definition
Alone	No other animals within 1 m.
In proximity	Within 1 m of another animal without touching.
In contact	Touching another animal without grooming.
Grooming	Manipulating, brushing or licking of hair of another individual.
Receiving grooming	Being the subject of grooming, as defined above.

Note. For each state (other than alone), all social partners were recorded.

Table 4

David's scores

ID	Raw David's Score	Normalized David's Score	Dominance Rank
Jd	64	10.833	1
Al	34.789	8.399	2
Ks	33.75	8.313	3
Ac	30.708	8.059	4
Hn	27.728	7.811	5
Az	4.246	5.854	6
Ak	-4.429	5.131	7
Ar	-11.286	4.560	8
Hs	-25.471	3.377	9
Ly	-40.632	2.114	10
Iv	-55.404	0.883	11
Zd	-58	0.667	12

Table 5

Partner-specific SDB rates (SDB events/hour)

	Jd	Al	Ks	Ac	Hn	Az	Ak	Ar	Hs	Ly	Iv	Zd
Jd	-	70.55	43.59	44.94	44.66	36	**49.23**	0	**49.23**	42.13	161.19	0
Al	30.70	-	59.12	76.39	40.91	65.69	50.70	160.27	47.37	49.09	12.93	29.51
Ks	52.41	67.99	-	77.94	400.00	27.91	56.25	59.34	40.19	189.47	46.75	0
Ac	51.03	19.95	58.38	-	30.54	55.83	46.84	52.52	33.88	49.57	55.60	54.55
Hn	58.76	83.31	0	89.92	-	112.50	49.05	124.86	91.92	251.75	231.08	269.60
Az	43.37	28.95	**42.58**	61.93	104.85	-	18.93	75.85	34.32	0	12.31	45.31
Ak	211.77	64.00	16.81	33.52	26.88	66.31	-	32.98	30.06	17.93	44.00	40.45
Ar	0	41.10	40.74	24.94	61.21	48.89	21.80	-	12.68	37.88	23.53	32.41
Hs	0	39.39	31.46	91.53	48.18	49.76	23.38	11.09	-	19.65	38.00	32.42
Ly	38.16	49.09	189.47	28.57	75.99	0	35.07	14.09	33.06	-	50.11	26.19
Iv	81.82	14.96	100.94	67.18	18.81	66.06	40.88	37.27	26.23	53.85	-	13.46
Zd	48.65	30.72	28.13	13.90	144.00	10.09	18.63	14.52	17.06	13.48	6.78	-

Note. Bolded scores are row means included to replace missing values. Subjects are along rows; partners are along columns.

Table 6

Relationship insecurity scores (percentages)

	Jd	Al	Ks	Ac	Hn	Az	Ak	Ar	Hs	Ly	Iv	Zd
Jd	-	40.70	72.64	33.98	24.71	49.49	141.42	34.64	23.09	40.94	20.41	86.60
Al	49.61	-	94.24	127.66	10.19	44.44	46.58	70.71	81.45	25.80	116.89	76.92
Ks	35.59	59.51	-	42.86	70.71	50.00	74.32	47.24	64.34	91.65	76.59	17.32
Ac	33.42	120.00	115.47	-	70.71	117.80	200.00	84.85	141.42	120.00	118.42	141.42
Hn	37.50	87.18	91.65	62.32	-	100.00	23.70	26.14	13.90	23.52	91.07	43.49
Az	62.09	115.47	**57.23**	46.78	28.28	-	24.25	51.07	59.73	44.54	40.60	99.50
Ak	**40.35**	54.71	43.96	84.18	17.61	40.49	-	31.45	24.63	43.42	15.33	47.69
Ar	86.60	52.07	36.07	100.15	42.93	19.37	25.15	-	37.99	51.01	24.76	24.15
Hs	141.42	25.80	54.98	31.11	19.69	8.944	73.14	20.50	-	53.05	39.08	57.06
Ly	46.99	73.62	70.11	69.90	34.93	60.96	18.00	28.97	21.32	-	42.27	63.62
Iv	29.94	57.16	31.58	38.37	83.40	72.84	40.34	45.11	41.82	40.82	-	47.08
Zd	87.67	40.07	57.46	80.39	21.88	52.22	57.97	39.11	36.19	43.44	30.60	-

Note. Bolded scores are row means included to replace missing values. Subjects are along rows; partners are along columns.

Table 7

Aggressive acts received

	Jd	Al	Ks	Ac	Hn	Az	Ak	Ar	Hs	Ly	Iv	Zd
Jd	-	0	0	0	0	0	0	0	0	0	0	0
Al	9	-	0	0	1	0	0	0	0	0	0	0
Ks	18	1	-	1	0	0	0	0	0	0	0	0
Ac	24	0	1	-	0	0	0	0	2	0	0	0
Hn	7	5	0	1	-	1	0	0	0	0	0	0
Az	25	4	10	13	17	-	2	0	1	0	1	0
Ak	5	0	1	3	4	6	-	0	0	0	0	0
Ar	13	1	1	2	5	11	1	-	0	0	0	0
Hs	7	5	0	6	6	21	3	3	-	0	0	0
Ly	13	0	3	5	1	2	4	9	4	-	0	0
Iv	12	2	1	1	7	5	2	1	2	2	-	0
Zd	3	1	2	2	4	5	2	5	1	0	0	-

Note. Recipients are along rows; aggressors are along columns.

Table 8

Association scores

	Jd	Al	Ks	Ac	Hn	Az	Ak	Ar	Hs	Ly	Iv	Zd
Jd	-	305	235	127	115	24	1	4	4	22	20	1
Al	305	-	160	40	69	33	26	24	26	49	29	23
Ks	239	160	-	60	9	11	30	55	42	18	15	10
Ac	127	39	56	-	35	61	67	48	10	34	60	24
Hn	117	69	10	35	-	8	54	46	64	28	63	21
Az	24	33	11	60	8	-	75	55	62	28	18	210
Ak	1	26	32	67	53	75	-	193	97	69	77	39
Ar	4	24	55	48	46	55	193	-	67	87	77	51
Hs	4	26	42	10	63	61	96	66	-	93	138	126
Ly	23	48	18	34	29	28	70	88	93	-	114	105
Iv	19	29	15	62	66	18	76	76	140	113	-	86
Zd	1	24	10	25	20	209	39	51	125	105	86	-

Note. Subjects are along rows; partners are along columns.

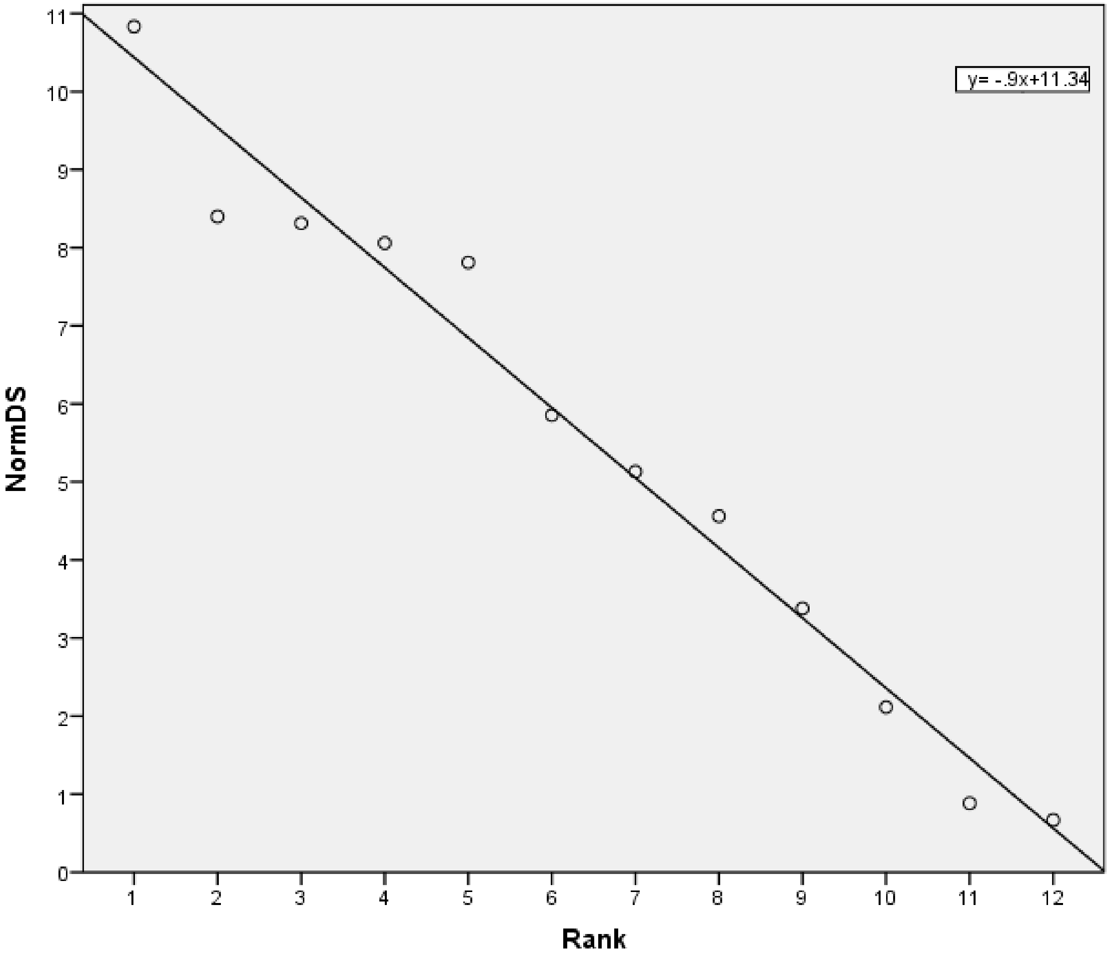

Figure 1. Dominance hierarchy steepness. This graph plots the baboons' normalized David's scores against their dominance ranks and includes the line of best fit. The equation for the line of best fit appears in the upper right hand corner.

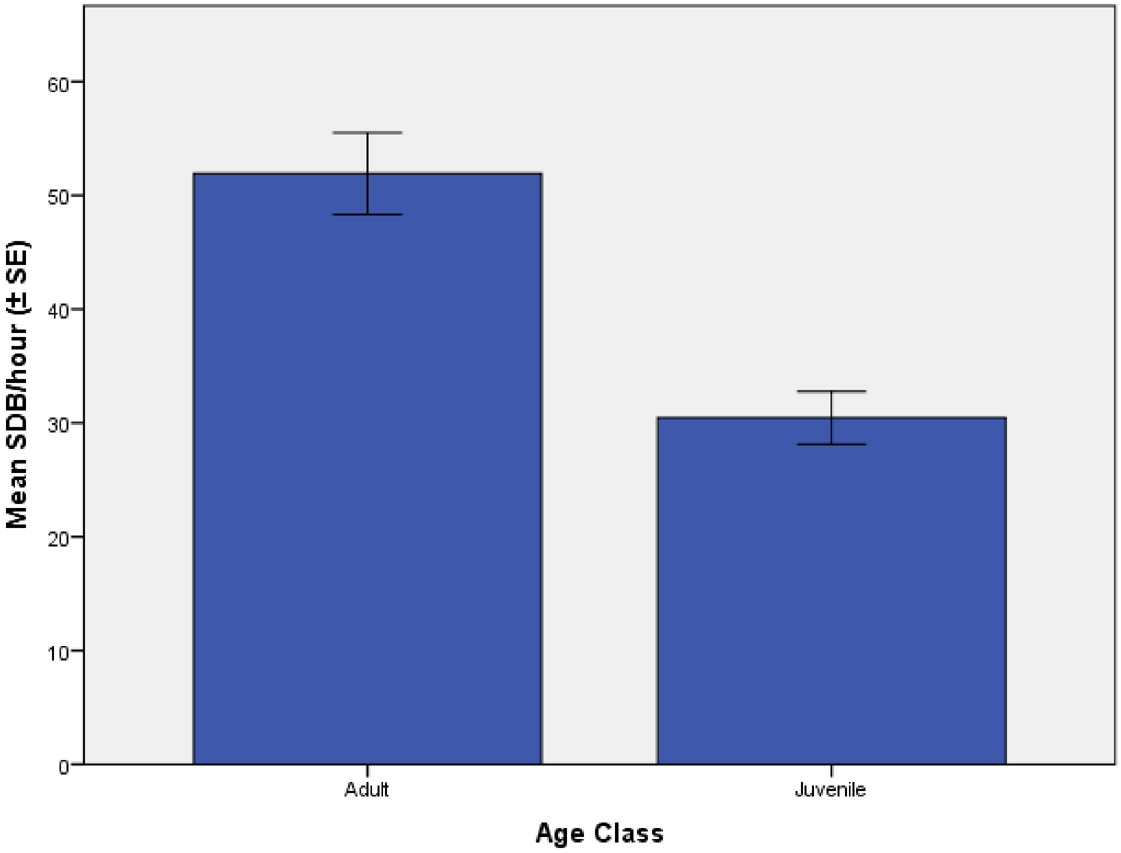

Figure 2. Overall SDB rate by age class. This graph illustrates the mean number of SDB events per hour for adult and juvenile baboons. Mean SDB rate was significantly different between these age classes at a two-tailed alpha-level of .05.

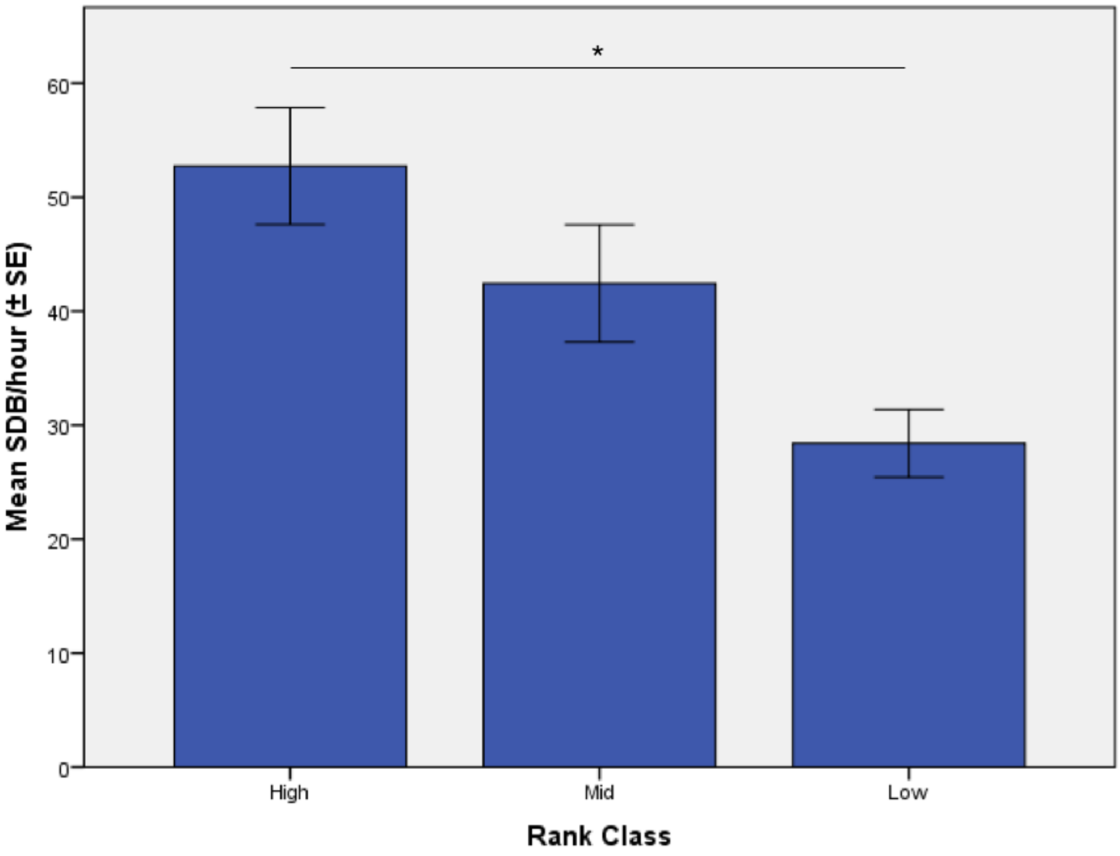

Figure 3. Overall SDB rate by rank class. This graph illustrates the mean number of SDB events per hour for high-, mid-, and low-ranking baboons. * $p < .05$

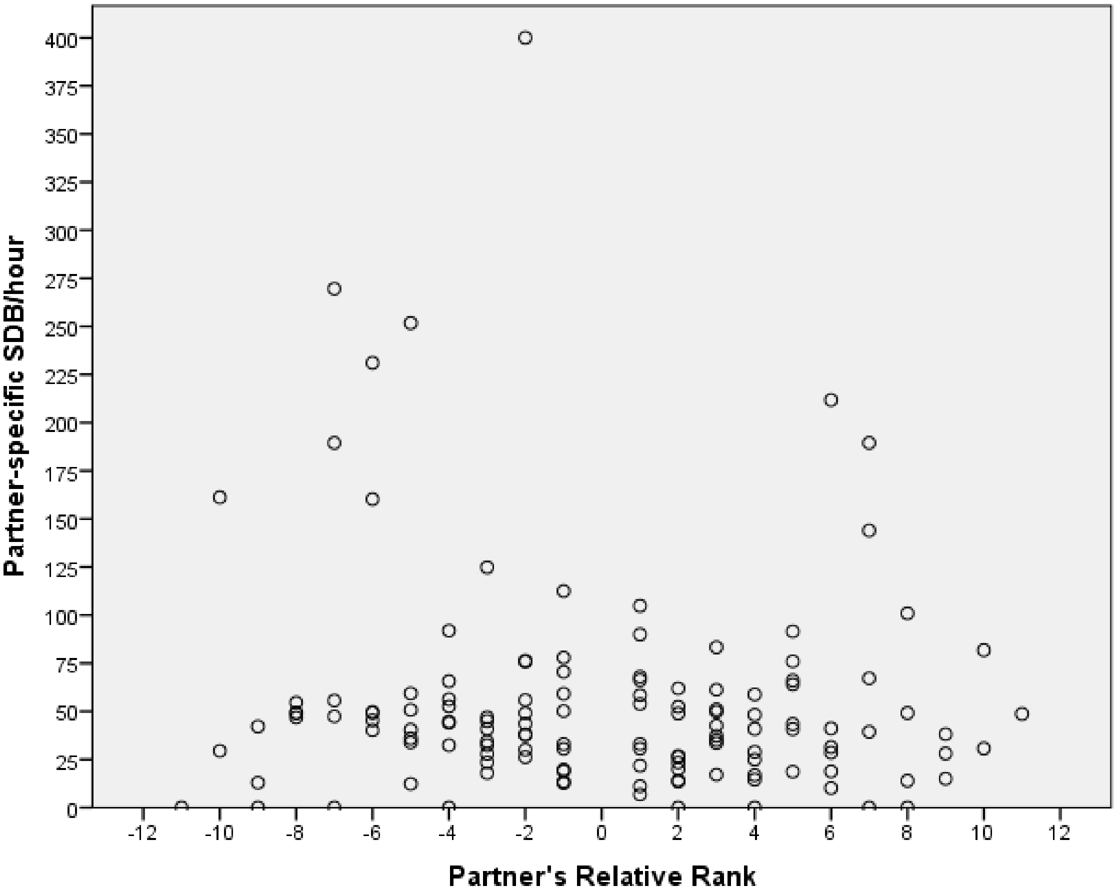

Figure 4. Scatterplot of partner-specific SDB rate and partner's relative rank. This graph plots the values from the partner-specific SDB rate matrix by those from the partner's relative rank matrix.

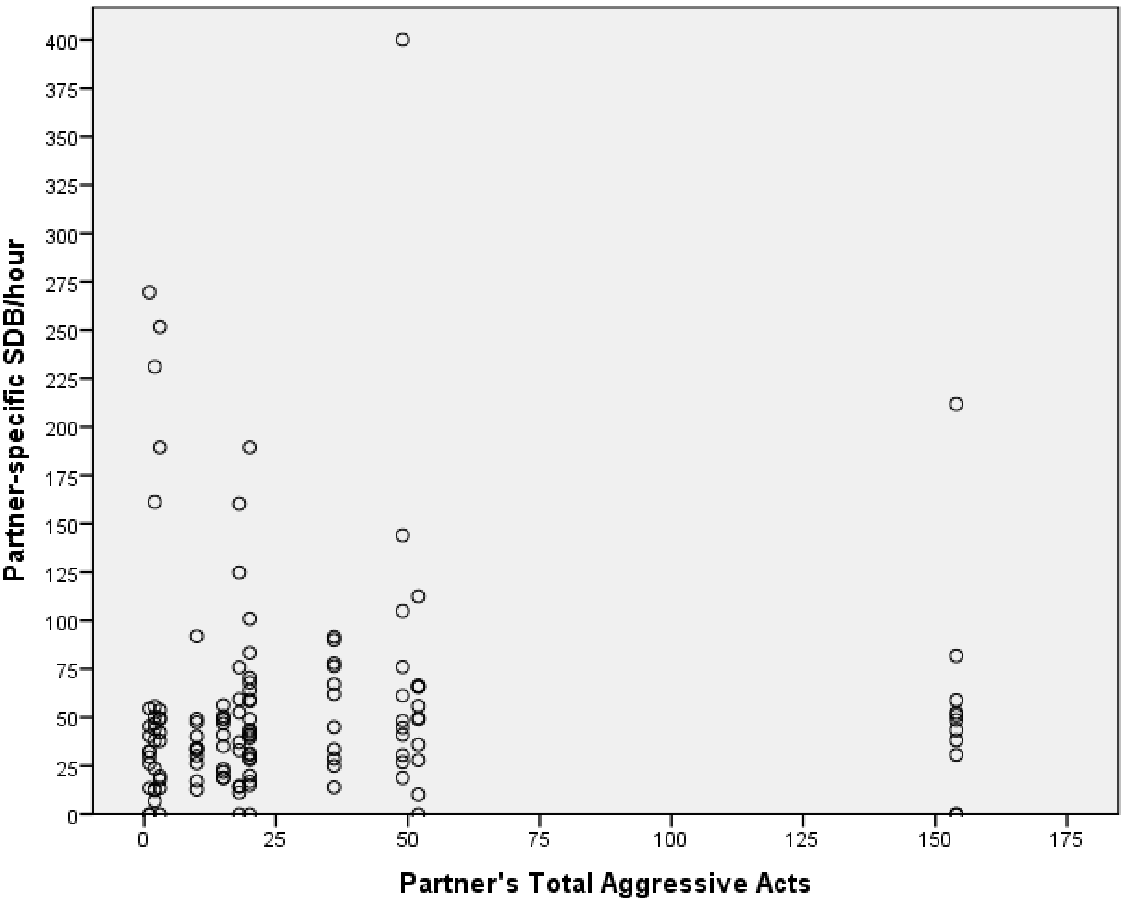

Figure 5. Scatterplot of partner-specific SDB rate and partner's total aggressive acts. This graph plots the values from the partner-specific SDB rate matrix by those from the partner's total aggressive acts matrix.