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Patterning and Quality of Male-Male Interactions in Hamadryas Baboons (Papio hamadryas)

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PATTERNING AND QUALITY OF MALE-MALE INTERACTIONS

IN HAMADRYAS BABOONS

(*PAPIO HAMADRYAS*)

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A Thesis

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Master of Science

Primate Behavior

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by

John Prescott "J.P." Calcitrai

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ABSTRACT

PATTERNING AND QUALITY OF MALE-MALE INTERACTIONS

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The social structure of a primate group is defined as the content, quality, and patterning of interactions and relationships among the members of the social group. Ecological variables, stress physiology, and phylogenetic inertia play a role in regulating measures of interactions and relationships between non-human primates. To examine social dynamics among male hamadryas baboons, video recordings of focal follows of this species were coded for three behavioral categories: *self-directed behaviors (SDB), socio-positive behaviors,* and *agonistic behaviors.* The analysis of self-directed behaviors revealed no differences in SDB across males of differing sex classes (i.e., *Leader Male*, *Follower Male*, or *Solitary Male*), yet correlations reveal the composite measure of SDB used to be a valid measure of relational anxiety. Descriptive statistics used to interpret the patterns of *socio-positive* and *agonistic* data reveal trends that suggest social dynamics in this species are unique among other despotic primate societies.

ACKNOWLEDGEMENTS

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CHAPTER I

INTRODUCTION AND BACKGROUND

Theoretical Framework

The study of social structures of animal societies is of interest to

ethologists and behavioral ecologists coming from a variety of backgrounds

including biology, anthropology, psychology, and cognitive science.

Primatologists, specifically those who study the social structure of primate

species, will usually incorporate both ethological and behavioral

ecological methodologies and approaches in their work.

The unifying approach employed by researchers from all these

backgrounds comes from Hal Whitehead's (2008) book *Analyzing Animal*

Societies: Quantitative Methods for Vertebrate Social Analysis where

he synthesizes ethological and behavioral ecological methodological approaches

for the study of animal social organization. The first technical line of investigation

comes from Hinde (1976) where he outlines a conceptual framework for the

modeling of relationships and social structure. In this framework, Hinde

highlights three levels: interactions, relationships, and surface structure. This

framework's primary purpose is to offer a unified methodological approach to

constructing research methodologies adequate for the collection of social data in

primates.

Before this framework was developed the paradigms employed for the study of

primate social systems caused:

. . . facts to accumulate in part along well-worn paths, such as the study of

social dominance, from which strait-jacket primatologists have only

recently begun to escape; and in part at random, with no direction or

cohesiveness. (Hinde, 1976, p. 1)

Hinde's approach allows for researchers to continue to use fundamentalist

methods for the study of animal social structure, such as dominance, while

incorporating new perspectives and techniques to better facilitate models of

sociality that capture the essence of primate social systems with more

accuracy.

The first level of Hinde's framework, termed "interactions", are seen as the

basic elements of social structure. Descriptions of interactions require

specification of what the individuals are doing together (i.e., its content) and how

they do it (i.e., quality). The second level, known as "relationships", involves

iterated interactions between two individuals over time. Describing relationships

need specification not only on the content and quality of the iterated interactions;

but also on the patterning of these interactions regarding directionality of the

interaction and time. The third level, called "surface structure", characterizes a

complex social system through empirical data derived from that group. This level

is best described by the nature, quality, and patterning of relationships. It is also

important to note that the distinctions between the three levels of this conceptual

framework carry no implications about the direction of causal relationships.

Interactions influence, and are influenced by, relationships and thus by social structure (Hinde & Simpson 1975, Hinde 1976).

In parallel to Hinde's approach, E. O. Wilson, the founder of the discipline now known as behavioral ecology, has contributed to the study of animal sociality with a top-down approach. Behavioral ecologists tend to focus on functional questions and evolutionary explanations for understanding animal behavior (Krebs & Davies, 2009). This is done through measurement of what Wilson calls "qualities of sociality". These qualities are as follows: group size, demographic distribution, cohesiveness, amount and pattern of connectedness in communication, permeability, compartmentalization or modularity, differentiation of roles, integration of behavior, rate of information flow, and fraction of time devoted to social behavior (Wilson, 1975).

Wilson and Hinde's frameworks for measuring aspects of social structure and organization can be seen as a dichotomy, two sides of the same coin. Wilson presents measurable qualities of the social group at large, while Hinde begins at the lowest possible level of social analysis, individual interactions, and builds up from there. Wilson takes the behavioral ecology approach while Hinde employs an ethology approach.

These two approaches to the study of animal behavior have been synthesized for practical analysis of primate sociality by Whitehead, leading to extraordinary advances in our understanding of primate social organization. The framework underlying the methodological and analytical interpretations in this

thesis are inspired by the framework for analyzing animal societies Whitehead presents. The primary goal of this project is to examine the patterning and structure of male-male relationships, as well as the impact of the differentiation of roles among male sex-classes, in hamadryas baboons using Whitehead's synthesis of Wilson and Hinde's methods to the extent allowed under the circumstances of data collection.

By observing the differences in dimensions of social behavior among different sex-classes of adult male hamadryas baboon, I aim to provide descriptions of social dynamics among males in this species while also exploring the socioecological variables that drive these behavioral patterns that are necessary for our understanding of hamadryas male social structure.

Primate Sociality at Large

Sociality and group living in non-human primates has been proposed as an evolved function of many gregarious primate species and has been shown to confer benefits on individuals within a social system in ways such as: an increased ability to defend resources from other groups (Wrangham, 1980), increased predator protection through the selfish-herd effect (Crook & Gartlan, 1966), additional vigilance from other group members that may help individuals avoid potential dangers (Seyfarth et al.,1980), and increased access to "inalienable resources" such as partners for allogrooming or coalitionary endeavors (Barrett et al., 1999; Lewis, 2002). There are costs stemming from sociality however, which can include increased food competition and aggression

at the intergroup level (Janson & Goldsmith, 1995). Additionally, the specific

social dynamics that emerge from a social structure can inflict physiological tolls

on individuals (Cohen & Manuck, 1995), including increased anxiety and stress

hormone levels. The relationship between specific social dynamics of a social

group and which individuals will be physiologically affected, either positively or

negatively, is complex and not always conspicuous (see

section: **The Stress Response and Self-Directed Behavior**), making the

collection of data on patterns of social relationships and self-directed behavior of

particular interest to researchers interested in the physiological consequences of

sociality.

The primate order displays a plethora of complex social system dynamics

and structures. Even among populations within a species, we can see arrays of

differentiated social systems and structures resulting from phenomenon that are

dynamically significant to local patterns of sociality. These can include

differences in ecological variables between populations of a species (Chapman

& Rothman, 2009) or sociocultural differences between populations (Hobaiter et

al., 2017).

More broadly, phylogenetic inertia and higher-level ecosystem pressures account

for the intricately evolved differences in sociality between entire species or even

genus of primates (Chapman & Rothman, 2009; Kappeler & van Schaik, 2002). A

carefully designed, long term and systematic approach to researching primate

sociality must be taken to properly understand what measures of social structure

and relationships are needed to answer questions pertaining to the differences in

the primate social structures we observe at any level. Wilson's suggested

measures of "quality of sociality" are the standard for researchers interested in

questions relating to ultimate-level evolutionary phenomenon and high-

level socio-ecological interactions, while Hinde's framework captures the

essence of sociocultural selection pressures. Whitehead (2008) points out that

even with these invaluable approaches, "we are still missing the holy grail of

social analysis: a measure of social complexity that can be employed across

species" (p.20). Until such a measure is found however, it is compelling to use

Wilson and Hinde's quantitative approaches in conjunction with detailed

descriptive accounts and observations of primate social systems to study social

system dynamics.

Some of the most common and foundational approaches to studying

primate social systems are heavily qualitative and descriptive in nature. Wilson

and Hinde published their systems for quantitative social analysis in the 1970s,

however primatology was an active research discipline in the United States and

Europe for at least a decade before these approaches were published. The

genesis of the discipline of primatology has an even longer history in Japan,

stretching back almost three decades before quantitative methods of social

analysis began to become mainstream (Itani, 1977). This means that for at least

a decade globally, and three decades regionally, the study of primate sociality

and behavior was a majority descriptive endeavor, a tradition that continues to

have importance today. Descriptive studies may lose some depth, precision, and

analytical rigor that are considered the major strength of properly conducted quantitative analysis, but descriptions of important yet observable social and behavioral tendencies are still powerful and informative ways to understand a primate's social system. These descriptions are also easier for non-experts to understand and continue to act as foundational premises for advances in quantitative and theoretical research.

Across the primate order, descriptions of important social dynamics act as the primary entry point to building a systematic understanding of the literature. Some of the important descriptive characteristics used to help classify and understand primate social system dynamics include their mating system, the dispersing sex, and system of tolerance.

Mating systems among primates vary wildly but can be sub-grouped into three primary categories. Monogamous species, uni-multi species, and multi-male multi-female species. Monogamous mating systems can be just sexually monogamous, meaning individuals pair bond to one other individual but socialize with other individuals apart from their mated partner, or socially monogamous, where the entirety of an individual's socio-positive or affiliative interactions (i.e., sexual or otherwise) occur only between an individual and their monogamous partner (Palombit, 1996). An example of a monogamous primate species is the white-handed gibbon (*Hylobates lar*). Uni-multi species involve a mating system where a single male mates with multiple females, known as polygyny or a uni-male multi female mating system. Examples include

Hanuman's langur (*Semnopithecus entellus)* as well as the one-male

unit (OMU) level of hamadryas baboons. Uni-female multi-male mating systems,

known as polyandrous social systems are rare amongst primates but do exist

within the family *Callitrichidae* (Díaz-Muñoz, 2011)*.*

The dispersing sex of a species is important to note because it has wide

ranging effects on social dynamics of the population. Generally, either males or

females who are born into a population will disperse from their natal group at

sexual maturity and go off searching for another population to join as an adult.

Evidence suggests this is an evolved response to inbreeding depression (Smith,

1992) as populations where neither males nor females emigrate would result in

highly related adult breeding populations. This is significant for the study of social

systems mainly because of the benefits gained by the non-dispersing sex (i.e.,

the philopatric sex). The sex that does not disperse will stay in their natal group

into adulthood, allowing for social dynamics to evolve within that species sex that

are contingent upon kin selection (Axelrod & Hamilton, 1981). A relevant

example of this can be illustrated by comparing the kin-based social dynamics of

the common chimpanzee (*Pan troglodytes*) and the olive baboon

(*Papio hamadryas anubis*). Both species exist within a multi-male multi-female

social system, although in chimpanzee populations females are the dispersing

sex (Stumpf et al., 2009) while in olive baboon populations males are the

dispersing sex (Smith, 1992). This distinction leads to differing higher level social

dynamics among males of these species, as chimpanzee males must navigate a

social hierarchy in which males who are related to them can be relied upon for social or coalitionary support in times of conflict or upheaval while adult male olive baboons are much less likely to have other related adult males in their social group that they can rely on. This in turn feeds back from higher level socio-familial demographics into the behavioral patterns of individuals, as male chimpanzees are known to spend an inordinate amount of time tending to social relations of kin (Mitani et al., 2000; Nishida et al., 1992) while male olive baboons have been observed to spend a significant amount of time facilitating other social relationships such as male-female "friendships" (Lemasson et al., 2008) and male-male coalitions among non-kin (Bercovitch, 1988).

Primate social systems have varying degrees of tolerance between individuals within a population. It is described akin to a spectrum, with egalitarian falling on one extreme and despotic falling on the other. A purely egalitarian species would have a high tolerance between individuals with very little to no directed agonism and the complete absence of a dominance hierarchy. A purely despotic species on the other hand would exhibit almost no tolerance for other individuals; particularly individuals who may be competitors over a resource, would exhibit a high frequency of directed agonism, and would exhibit a strict linear dominance hierarchy (Matsumura, 1999). Insights into where a species or population would fall on this spectrum can allude to important characteristics influencing why the system is structured the way it is. An egalitarian species is more likely to have a dispersed and plentiful set of resources, while despotic

species would suggest clumped, easily monopolizable, and infrequent resources (Vehrencamp, 1983).

Hamadryas Baboons

Hamadryas baboons are a cercopithecine primate belonging to the genus *Papio*. They share this genus with four other species of baboons: the olive baboon, chacma baboon, yellow baboon, and guinea baboon. Of these species, the hamadryas baboon has the most distinct social organization, patterning of relationships, and ecological homerange which makes this species unique and particularly useful for the study of sociality in nonhuman-primates. It has been suggested by Swedell and Plummer (2012) that hamadryas baboon social organization is highly reminiscent of early-human social systems, specifically because hamadryas baboons are the only non-human primate to exhibit male-kin bonding, female-kin bonding, and cross sex bonding that we see in human societies, making them a prime analogue for the understanding of the evolution of human social behavior.

Cercopithecine primates are mainly dietary generalists, giving them the flexibility to flourish in a wide variety of habitats. The home range of hamadryas baboons spans the north-eastern portion of the African continent, with some extension to the southern tip of Arabia. According to Kummer (1968), their home range consists mainly of environments that can be categorized as arid brushland. This range starts in eastern Sudan and extends to the lowlands of Ethiopia and Somalia. The southern-western boundary of its distribution runs

from Port Sudan to the lower course of the Webi Shebli River (Winney et al., 2004). Separated from this main area by the Red Sea, this species is also found in south-west Arabia (Kummer, 1968). The typical hamadryas habitat displays a scarcity of tall trees that are more typical to the habitats of other *Papio* species. Hamadryas baboons spend their nights on vertical rock-faces found on cliffs that are scattered around the species home range (Kummer, 1968).

This species' endemic range consists of primarily semi-arid desert habitats (Al-Safadi, 1994) that consist of widely dispersed distributions of important food resources. The most universally recognized primary food source for hamadryas baboons are fruits from *Acacia* tree species. They also are known to consume insects, flowers, seeds, grasses, fruits of other plants, and small invertebrate species (Oates, 2008; Swedell et al., 2008). Like all the other species in the *Papio* genus, hamadryas baboons are adapted to be able to subsist on a low-quality diet for extended periods of time (Oates, 2008).

Hamadryas baboons display a pronounced level of sexual dimorphism, with males growing to at least twice the size of females (Phillips-Conroy & Jolly, 1981). Males also develop several other secondary sexual characteristics that other baboon species display, which include voluminous mantles of hair and large, sharp canines (Stammbach, 2008). They also have a distinct coloration that changes from population to population, with females appearing dark brown while males are usually lighter in coloration, especially when looking at a male's mantle hair which is silver-white (Shefferly, [n.d.]).

Social organization is one of the most distinct and defining aspects of this species. In hamadryas society, social organization hinges on a fission-fusion multi-level social system as opposed to a multi-male multi-female grouping that other baboon species exhibit (Abegglen, 1984). The distinction between the multi-level fission fusion system seen in hamadryas baboons and the traditional fission-fusion dynamics displayed by, for example, chimpanzee or spider monkey societies stems from static versus dynamic demographics of individuals within fissioned groups. The fissioning of larger level social structures in a multi-level fission-fusion society occurs along consistent and predictable lines (i.e., Troop -> Band -> Clan -> OMU), while in standard fission-fusion societies the higher-level social structures break apart on more arbitrary lines that are dynamic. A male chimpanzee can fission with two other individuals one week and the next week he could fission with a completely different group of individuals.

There are four primary levels to this societal organization as depicted in Figure 1, and they are as follows: The troop, the band, the clan, and the OMU. Starting from the largest level, the troop consists of several different bands. There is little social interaction at this level as most interactions between individuals occurs at the band level or lower. The primary function of this level of organization is predator protection since the troop level of organization is only relevant to the baboons when it comes to deciding where to spend the night and which direction the group will move to forage. Once the troop leaves the sleeping

rock for the daily forage, the troop breaks up into several bands (Kummer, 1968;

Schreier & Swedell, 2009).
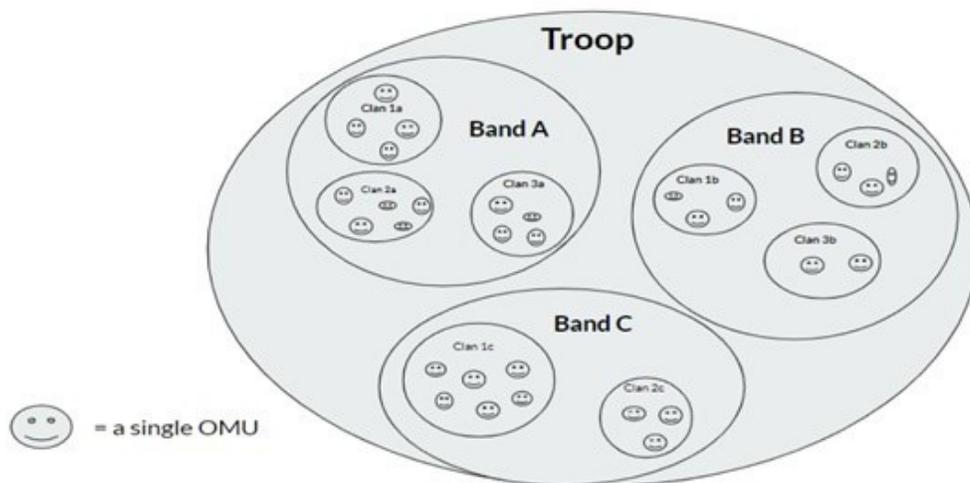
Figure 1. Hamadryas social structure. A diagram showing the multi-level structuring
of hamadryas baboon social systems.

The band level of social organization is analogous to what primatologists

who study other species would refer to as the troop (Schreier & Swedell, 2009).

A majority of social interaction occurs at the band level or lower in this species,

with the main social interactions at the band level consisting of intergroup

competition (Pines & Swedell, 2011).

The third level of social organization, which is consumed by the band

level, is the clan level. The clan level of organization was first described

by Abegglen as distinct subgroupings that "rested and travelled together within a

band" (1984, p. 165). He also was the first to suggest that males at the clan level

are probably related, basing his reasoning on phenotypic similarities he observed

between males within clans. More recent studies support this, such as a study on

captive hamadryas preferences for forming clans with related males

(Colmenares, 1992) and a study on the genetic assessment of male Y-linked and

autosomal microsatellite loci that found that males are generally philopatric at the

clan level with females dispersing among OMU's within clans (Städele et al.,

2015).

The smallest level of organization, which is the principal social unit that

builds the foundation for the rest of the multi-level social structure observed, is

the OMU. The OMU consists primarily of an adult leader male, his females, and

their dependent offspring. Occasionally follower males, who are generally sub-

adult males that do not have enough life experience to create their own OMU yet,

will join an OMU for extended periods of time. Research has shown the function

of this relationship between a leader male and his follower to be an adaptive one,

as leader males who have a follower male in their OMU are able to maintain

tenure lengths as an OMU leader for up to twice as long as leader males without

a follower male. Follower males, while they generally still do not have sexual

access to the females of their leader's OMU, benefit from this arrangement by

having increased chances of acquiring some of his leader's females once the

leader becomes too old to continue to control his OMU or is injured in a duel to

the degree that he cannot keep the integrity of his OMU together (Chowdhury et

al., 2015).

Male Hamadryas Baboon Social Life History

Virtually all hamadryas baboon males go through multiple "life phases" that constitute all of the positions a male will hold throughout their lifetime. Some non-human primates have differentiated life phases, and not all males will experience the same positions/statuses throughout their lifetime. An example of this would be in orangutans (genus *Pongo*), where some males will become "flanged" at a certain point in their life while other males never develop flanges. Female orangutans prefer flanged male mates that have a significant increase in body size, the development of a disk-shaped structure (i.e., flange) around their head, and a bulbous throat sac that allows them to produce booming long-calls that attract females and alert other males to their presence (Mitani et al., 1996). Males that never flange maintain a body type quite like the females', apart from their male reproductive anatomy, and employ a different reproductive strategy of forced copulations as opposed to their flanged male counterparts (Knott, 1999). Hamadryas baboons, however, will generally all experience a similar progression though life phases, although the fitness outcomes of different individual males will vary (Swedell & Leigh, 2006). The mating system that male hamadryas baboons must navigate to fulfill their biological imperative to reproduce involves adult male individuals aggressively herding and protecting their females from other males within their band as well as from males from outside their band. The OMU structure is sometimes referred to as a harem,

although functionally the OMU is a principal unit of the larger multi-level social structure that is not a harem.

Upon reaching reproductive sub-adult age (i.e., three to six years of age), males are separated into three sex-classes (i.e., leader male, follower male, or solitary male). At this stage hamadryas males will leave their mother's OMU and attempt to start their own OMU. This process is a difficult one, as leader males will violently defend their females and employ both aggressive threats to young males and violent sexual coercion towards their females to prevent interactions between females and males not within the OMU (Swedell & Schreier, 2009). Until a male forms his own OMU or joins a leader male's OMU as a follower male, the sub-adult male will maintain the position of solitary male. It is important to note that some males never become followers and jump from solitary straight to leader male. Solitary males are males that do not belong to or have their own OMU, but they continue to stay in proximity to a given band. These males will follow the band during the daily march from the sleeping site to the daily foraging area, and they will overnight at the same sleeping site as the band they are following (Schreier & Swedell, 2008). Being a solitary male is a position that is filled by both newly sub-adult males, as well as by old males who have lost their OMU due to age/injury but continue to live in the band. For many hamadryas males, this solitary position is how they will start and end their lives.

Many males will attain the position of follower male, which is claimed by sub-adult or newly reproductive adult males that successfully join an OMU as a

follower. The leader of the OMU will tolerate their presence but does not allow the follower to engage in sexual activity with the OMU's females. The leader-follower male relationship has been shown to have an adaptive significance (Chowdhury et al., 2015) although for the follower to be able to reap the benefits of this "arrangement", the dynamic between leader and follower must shift eventually. For a male to become a leader male, he must obtain his own female and start his own OMU. There are four primary strategies employed by pre-reproductive males that allow them to move into the leader male position. They are as follows: the initial unit (IU) strategy, the challenge strategy, the opportunistic strategy, and the inheritance strategy (Pines et al., 2011).

In the IU strategy, followers or solitary males will consistently interact with an adult female's juvenile offspring, forming a relationship. This relationship can slowly change to the point where the juvenile female spends less time with her mother and more time with the male employing this strategy, until she reaches sexual maturity and joins the male's OMU as his first female. This strategy has been hypothesized as a driver allowing the follower male position to exist (Pines et al., 2011; Schreier & Swedell, 2009; Swedell & Leigh, 2006), as followers gain social access to females and their offspring without the threat of leader male aggression. Follower males have been found to employ the IU strategy for 43.75% of observed female acquisitions, while solitary males employed this strategy 46% of the time (Pines et al., 2011). This was found to be the most common strategy for development of leader males.

The second strategy, called the challenge strategy, is employed by males when a male directly challenges a leader male to aggressive competition over one of the leader's females. This strategy has been reported to occur in captive populations between leader males (Colmenares, 1992), although it has never been reported between leader males in the wild. Research on wild populations suggests that in the wild, only non-leader males will employ this strategy to try and obtain a female from an OMU leader (Abegglen, 1984; Kummer, 1968; Swedell, 2000). Out of the 16-follower male OMU formations observed in Pines et al. (2011), 12.5% of these were done using the challenge strategy. Among the 26 solitary male OMU formations observed, 27% of these were formed using the challenge strategy.

The third strategy employed by males to obtain females is the inheritance strategy, in which a follower male associates with the females of an OMU and builds an affiliative relationship with the OMU's females. Eventually, this male can extricate the female(s) and add them to his own OMU without violence. This usually occurs when a leader male is leaving his prime age and is becoming too old to continue to effectively defend all the females in his OMU. According to Pines et al. (2011), follower males employed this strategy for 18.75% of observed OMU formations, while solitary males never used the inheritance strategy.

The final strategy employed is the opportunistic strategy, which is used by both leader males to increase their OMU size and follower/solitary males looking to start their OMU. The opportunistic strategy involves a male taking over a

female who has been separated from her OMU leader. The reason for separation can include: her leader male has incurred debilitating injuries, the male has fallen ill or is too old and weak to defend her, he has died or disappeared altogether, or he lost her in a bout of inter-band conflict. This strategy is similar to the inheritance strategy as the female is taken from her previous OMU without a direct challenge occurring between males, although it relies more upon chance rather than the cultivation of relationships between the acquiring male and the females of an OMU. Twelve and a half percent of follower male OMU formations used this strategy, as opposed to among the solitary male sex-class where it was used 27% of the time (Pines et al., 2011).

Based on these results the IU strategy is the most preferred strategy for female acquisition, while the inheritance strategy is limited to follower males only. The exclusivity of this strategy to followers only may help explain why solitary males are more likely to employ the challenge strategy.

By employing these strategies male hamadryas baboons move from sub-adult but reproductively capable classes of solitary and follower male to the exalted leader male class. While the strategies employed to obtain females most likely vary from individual to individual, virtually all males in this species will go through a predictable sequence of social life history phases. They start as infants and grow up in their mother's OMU, they then will leave their mother's OMU and attempt to create their own OMU through the positions and strategies listed above. They will then live their prime adult years as a leader male who tries to

expand and defend his current OMU, and as his age peaks and he moves past his adulthood prime, he will lose his females because he has died, or he cannot defend his OMU anymore due to old age. In the latter case, he will become a solitary male who lives out his final days on the periphery of the band he was born into.

We can view the different sex-classes of males as different social roles (Wilson, 1975) which exposes males of different sex-classes to different social and evolutionary pressures. Changes in behavioral patterns, such as increased intolerance to other males' presence by leaders (Sugiyama, 1965) and changes in female acquisition tactics (Pines et al., 2015) are examples of such changes that may occur when a primate male changes sex-class. The optimal strategy for studying this is to observe and record the patterns of behavior among males of different sex-classes.

Patterning of Relationships

Based on the lines of reasoning presented by Hinde (1976), it is reasonable to suggest that for future research focusing on social structure of hamadryas baboons to flourish, an understanding of the patterning of interactions among individuals is necessary. Hamadryas baboons display bonding via social interactions across sexes and between them, much like human societies do but unlike most other primate species (Swedell & Plummer, 2012). This is patterning of interactions has been described as a star-shaped sociogram (Kummer, 1968). Previous research studying the patterning of interactions and relationships

between leader males and the females of their OMU, as well as studies focusing on interactions and relationships between females, has been conducted extensively (Leinfelder et al., 2001; Stammbach, 1978; Swedell, 2002). However, research focusing on male-male relationships in this species has been largely ignored with one of the only studies on male-male interactions coming from a captive colony in Madrid (Romero & Castellanos, 2010).

In contrast to Hinde's approach, Wilson's approach urges us to think about hamadryas baboon socioecology and how it affects male-male relationships. The standard hamadryas ecosystem consists of arid scrub lands with food resources that are generally of lower abundance and patchier in their distribution than the ecosystems of other *Papio* species, with the exception of chacma baboons that live in the desert of Namibia (Schreier, 2010; Schreier & Swedell, 2012). This scarce patterning of food availability is likely a driver of the fissioning that occurs from band to clan to OMU throughout peak foraging times, while in contrast, the presence of potential predators such as the lion (*Panthera leo*), the spotted hyena (*Crocuta crocuta*), predatory birds, and snakes (Swedell & Saunders, 2006; Zinner and Pelaez, 1999; Zinner et al., 2001) would intensify pressures on the multi-level societies of the hamadryas to cluster back together into larger groupings during times where predator activity is high (Clutton-Brock, 1974). These variables can be thought of as the initial parameters that limit what social stratagems can be used and displayed in this

species, and these parameters more clearly define what aspects of social organization should be investigated further.

Operating within these parameters it is evident that the social structure of hamadryas baboons is constrained by resource availability, which means females are likely to cluster in order to obtain the sparsely distributed, high quality resources in the ecosystem (Schreier & Swedell, 2012). This in turn would facilitate males in employing a mating strategy of OMUs, since groups of females would cluster at high value resource patches anyways. The existence of a variety of predators on the other hand forces these OMUs to congregate into the larger facets of the hamadryas social structure that we observe as clans, bands, and troops (Swedell & Saunders, 2006). This interpretation of the dynamical equilibrium between the socioecological pressures causing fissioning dynamics of hamadryas societies is supported as a viable explanation for the drivers of the specific hamadryas baboon social organization we observe (Kummer, 1971; Sigg & Stolba, 1981). Sigg and Stolba (1981) found a positive relationship between average daily path length (i.e., or the average distance an individual travels each day) and the availability of food resources in an individual baboon's habitat. They also found hamadryas baboons to have the longest daily path length of all *Papio* species, which is directly related to the sparse distribution of resources in their habitat (Sigg & Stolba, 1981).

In addition to those two parameters, coercion is also a major factor within this species' social system (Clutton-Brock & Parker, 1995; Swedell et al., 2014).

Females spend the entirety of their lives under the protection of a male, whether that male is the leader of their mother's OMU or any of the leader males whose OMUs she may join throughout her life. Males use violent coercion to herd the females of their OMU regularly, with even a minor infraction such as a female wandering too far from her leader male resulting in a neck bite or other aggressive herding behavior by her leader. This is how leader males block other males from having social/sexual access to their females and may be a viable strategy for males because of the clustering of females that results from their sparse available resources (Swedell & Schreier, 2009).

Based on the socioecology of this species, we know that patterning of interactions is limited by the previously mentioned parameters. Females will not frequently interact with males (or other females) outside of their OMU, males will create an OMU by acquiring females that he protects aggressively, although he can only obtain so many before it becomes impossible to maintain the number of females he has, and males will be wary of other males in situations where males not associated with his OMU are nearby. From here, we can further examine the patterning of behaviors to ascertain a clearer picture of male hamadryas baboon social norms.

Males of this species generally interact in the ways described by Kummer (1968):

For troop life, the most important contacts between the units are the short interactions between their leaders. Grooming was never observed among

leaders of mature units. Whereas adult males having no females often

groom each other, the unit leaders do not approach each other at

grooming distance, but ordinarily keep 1.5 meters apart. This spatial

separation appears to be related to the leaders' strong tendency to keep

their units from intermingling. The ordinary distance is only understepped

during two types of interactions. The first type serves to coordinate troop

movement and is cooperative rather than aggressive. The other type of

contact observed between group leaders is aggression. (p.47)

To study the nuances of the quality and patterning of social relationships among

male hamadryas baboons, I chose to focus on the collection of data pertaining to

three primary classes of male behavior. One non-social category (i.e., self-

directed behaviors) and two social categories (i.e., socio-positive and agonistic)

of behavior were measured and used to construct the analysis of male-male

relationships in this species, with a particular emphasis on sex-class of adult

male (i.e., leader, follower, or solitary male) and their subsequent interactions.

The Stress Response and Self-Directed Behavior

It is well known that sociality is intricately related to physiological stress

(reviewed in Cheney & Seyfarth, 2009). While sociality and social position are

known to influence physiological health, the relationship between stress

physiology and social status is not consistent across space or time (Sapolsky,

2005). Sapolsky suggests that physiological indicators of stress and anxiety (e.g.,

increased heart rate, increased circulating glucocorticoid levels, increased

frequency of self-directed behaviors) vary given the relative costs of existing as a dominant or subordinate individual within the context of a social system's structuring. In some situations, dominant individuals may be the most stressed while other situations cause increased stress indicators in subordinate individuals instead. An example of this comes from observations of male olive baboons *(P. hamadryas anubis)*, where in cases where the stability or certainty of dominance rankings was high, indicating a stable hierarchy ordering, low ranking males experienced elevated glucocorticoid levels. When the stability or certainty of dominance ranks was low, meaning a transition in the rank-ordering of individuals was likely, high ranking individuals experienced increased glucocorticoid levels (Sapolsky, 1993). The physiological stress response functions to help individuals deal with short-term challenges to homeostasis (Cabezas et al., 2007), however chronic activation of the stress response can be highly detrimental to an individual's health and fitness (Sapolsky et al., 2000).

It is of interest to explore the relationship between socio-positive, agonistic, and self-directed behaviors (SDB). SDB are behaviors that do not involve a social compatriot. Examples of behaviors that fall under this category include self-grooming, self-scratching, and yawning. These behaviors are indicative of high-anxiety levels in non-human primates. Even when an individual is not directly involved in an agonistic or otherwise stress inducing encounter, the act of witnessing other individuals acting aggressively towards one another has been shown to increase anxiety in the individuals watching the encounter (Aureli

& Smucny, 2000). Common measures of anxiety in non-human primate species
include SDB (Painter, 2018), while indicators of stress include physiological
indicators of stress such as increased heart rate (Aureli et al., 1999), and
analysis of hormones involved in the hypothalamic-pituitary-adrenal axis such as
glucocorticoids (Bergman et al., 2005). Research suggests that while these
measures are all valid indicators of physiological stress and anxiety in primates
(Smucny et al., 1997), there isn't a clear relationship between SDB rates and
glucocorticoid levels, suggesting that measures of SDB and measures of
glucocorticoid levels could be indicative of different aspects of the stress
response (Higham et al., 2009).

  Mechanistically, the occurrence of SDB or an increase in glucocorticoids
have been suggested to have divergent root causes. There are several
hypotheses that suggest varying proximate causes of SDB and are briefly
described below (reviewed in Anselme, 2008). The first primary hypothesis
explaining the occurrence of SDB comes from Tinbergen (1952), which
posited that conflicting motivations between individuals or otherwise
inaccessibility of a desired resource to them can create an excess of energy that
releases in the form of an irrelevant SDB. This is contrasted by
van Iersel and Bol (1958), which suggests that the inhibition of two individuals'
conflicting motivations can disinhibit a third motivation, allowing displacement
behavior to occur. Evidence from more recent studies suggest that SDB
responses are linked to changes in attentional state, as SDB frequently occurs in

the context of a behavioral transition (Amselme, 2008; Macfarland, 1966). Irrespective of which of these mechanisms is the likely cause of increased SDB in individual non-human primates, these models all suggest that displacement behavior is intricately connected to emotional and psychological stress and is influenced primarily by stressors originating from sociality/social relationship based stimuli.

Maestripieri et al. (1992) suggests that primates most often exhibit SDB in contexts that would trigger anxiety. This finding is supported by the literature, such as in experiments that stimulated certain brain regions that are known to be associated with anxiety such as the locus coeruleus, which is a region of the brainstem known to influence human stress and anxiety. When this was done on a group of stump-tailed macaques (*Macaca arctoides*), a significant increase in SDB such as self-scratching and yawning was found in individuals with a stimulated brainstem as opposed to an unstimulated one (Redmond & Huand, 1979). Other studies have used drugs that are known to reduce anxiety in humans to show the relationship between SDB and anxiety inducing events. Schino et al. (1996) used lorazepam on long-tailed macaques (*Macaca fascicularis*) and found that administering this drug significantly decreased SDBs such as self-scratching, yawning, and self-grooming without affecting rates of other behaviors such as locomotion, aggression, or social grooming.

While a link between anxiety inducing behavior and SDB does exist, the relationship between SDB rates and glucocorticoid levels continues to elude researchers. A study on a group of wild female olive baboons found that daily changes in SDB rates were not associated with daily changes in fecal cortisol levels (Higham et al., 2009). Another study found that SDB rates did not increase with crowding in a captive hamadryas baboon population, but salivary cortisol levels were significantly elevated (Pearson et al., 2015). While anxiety and physiological stress are commonly thought of as one in the same, there is growing evidence that a distinction between behavior that induces anxiety and behavior that induces increased physiological stress exists and should be studied. One of the primary goals of this study is to look deeper into the relationship between social stressors in male hamadryas baboons stemming from "relational anxiety triggers" rather than physiological stressors.

Agonistic Behaviors

Male hamadryas baboon dominance interactions have been only minorly examined, yet the complexity of the male social dynamic in hamadryas baboons requires a focused set of studies aimed at exploring male social and dominance relationships to more fully understand the nuances of the hamadryas social system. There is a missing component of the hamadryas behavioral ecology literature that investigates male-male social and dominance relationships (Romero & Castellanos, 2010), and of the studies that do exist, they are primarily conducted in a captive setting (Gil-Burmann et al., 1998; Painter, 2018; Romero

& Castellanos, 2010). Of the few studies aiming to examine dominance relations in wild hamadryas males, none have found evidence that a strict linear dominance hierarchy exists (Kummer 1968, 1997). Studies of dominance relationships and the existence of a dominance hierarchy among male hamadryas baboons in captivity have shown mixed results. Several studies have found there to be a linear dominance hierarchy that exists within captive male hamadryas baboon populations (Painter, 2018; Romero & Castellanos, 2010). However, one study by Gil-Burmann et al. (1998) found no existing dominance hierarchy among captive hamadryas males. On the other hand, studies of wild populations consistently suggest no linear dominance hierarchy exists in hamadryas baboons (Abegglen, 1984; Kummer, 1968; Sigg & Stolba, 1982).

These mixed results are often considered to be a result of the differences in behavioral ecological pressures affecting wild versus captive populations. It has been suggested by multiple authors independently (Abegglen, 1984; Sigg & Stolba, 1982) that strict dominance hierarchies may not exist in wild populations of this species because of the uneven distribution of food resources in the hamadryas habitat and because of unclear feeding competition. This would make sense as both Romero and Castellanos (2010) and Painter (2018) found captive hamadryas males to exhibit a dominance hierarchy, but in both studies the captive hamadryas populations were regularly provisioned and had differential access to feeding platforms that may have artificially created sociobiological

pressures pertaining to defense of clumped food resources which do not exist in

wild populations. This could have led to the emergence of a dominance hierarchy

in captive populations not seen in wild populations.

Socio-Positive Behaviors

Another important set of measures to consider when examining primate

social systems is the quality and patterning of socio-positive behaviors. Socio-

positive behaviors consist of socially "positive" situations between two

individuals. Primary examples of socio-positive behaviors are proximity,

notifications, and allogrooming. Allogrooming behavior is defined as when one

individual grooms another individual, rather than self-grooming or autogrooming

(Sparks, 1967). Hypotheses regarding the evolved function

of allogrooming behavior include a "hygienic function" explanation, which

suggests allogrooming behavior serves to curb the spread of parasites and other

disease-causing vectors that may latch onto the body of a non-human primate

(Pérez & Veà, 2000), and the social grooming function that posits that grooming

serves as an "inalienable social currency" which facilitates stronger social bonds

between dyads that allogroom more frequently (Dunbar, 1991). The social

grooming hypothesis has intellectual roots in biological markets theory (Noë &

Hammerstein, 1995), as the proposed functional benefits of the hygienic

grooming hypothesis can be reached via both allogrooming and self-grooming,

but the proposed benefits of social grooming can only be reached

via allogrooming.

Allogrooming is considered an inalienable resource because you cannot coerce or force an individual into an extended grooming partnership. Thus, to reap the benefits of allogrooming under the social grooming hypothesis a mutual exchange of allogrooming via a relationship which tolerates extended bouts of behavior is necessary (Barrett & Henzi, 2006). This makes allogrooming a reliable indicator of more socio-positive relationships between males and is a particularly well-suited indicator of this in hamadryas baboons due to their general intolerance of other adult males. Research has found that both the hygienic function hypothesis and social grooming hypothesis to not be mutually exclusive (Dunbar, 1991), although evidence suggests that the social grooming hypothesis is a more than viable interpretation of the evolved function of allogrooming. Particularly, Dunbar (1991) conducted a study that examined the frequencies of allogrooming among 44 primate species and compared these data to group size and body size. He found that allogrooming frequency was positively correlated with group size but not body size, which he suggests is indicative that allogrooming serves a more social function than hygienic one. Primates with larger body sizes would have to allogroom more frequently and for longer durations if the hygienic grooming hypothesis were to be supported, as more body mass means more area for an ectoparasite to inhabit (Dunbar, 1991). Studies have also shown that allogrooming relationships are important in maximizing fitness of highly social species (Silk et al., 2003), as well as achieving

and maintaining coalitionary support in times of social unrest or conflict (Schino, 2007; Schino et al., 2007).

Allogrooming is extremely rare between male hamadryas baboons, instead the primary socio-positive behavioral vector is a ritualized greeting behavior termed a notification. There are two primary types of notifications, reciprocated and unreciprocated. Mechanically, the sequence of behaviors that indicates a notification is occurring is as follows: an adult male baboon, called "A", approaches another adult male, called "B", with a rapid stereotyped gait. A presents his hindquarters to B, and B either reciprocates with his own presentation or touches/interacts with A's presented hindquarters in a reciprocated notification. An unreciprocated notification is structurally the same as a reciprocated notification, except individual B will either ignore A's approach/presentation or will respond agonistically towards A as he approaches (Colmenares, 1991). Multiple explanatory mechanisms have been proposed as possible evolved functions of notification behavior.

Fraser and Plowman (2007) evaluated eight different hypothesized functions of notification behavior and found evidence to support three of these hypotheses as viable drivers of this behavior. The three functional explanations that their study supported were submission, which is defined as where notifications serve to signal submission from subordinate to dominant individuals; peacekeeping, which states that notifications serve to reassure potential opponents of the notifier's non-agonistic social objective; and alliance formation,

which is suggested to facilitate confirmation of a peaceful relationship with similar

ranking individuals. It is important to note that Fraser and Plowman collected their

data on a captive population of hamadryas baboons at the Paignton Zoo

Environmental Park in Devon, UK. As we have already discussed, dominance

rankings in hamadryas baboons have been found to exist in captive populations

but not in wild populations (see section "**Agonistic Behavior**). Two of the three

supported hypotheses from their work involve definitions of functional

explanations that include dominance rank in the operationalization of the

hypothesized mechanism's definition (i.e., submission and alliance formation).

Additionally, their definition of alliance formation is not consistent with

the conceptual operationalization of what an alliance is found in the rest of the

literature, as Fraser and Plowman (2007) define alliance as "confirming a

peaceful relationship with a similarly ranked individual" (p. 1448). The prevailing

definition of what an alliance is varies, although it is generally accepted that

alliances are repeated coalitionary endeavors between individuals which rely on

reciprocal altruism to drive the behavior (Packer, 1977; Trivers, 1971) and seem

to have an end-goal or objective (Cheney et al., 1986). An example of this comes

from the baboon species such as olive baboons (*P. hamadryas anubis*),

where two males will simultaneously attack a third male who has access to a

valuable resource, most often a female who is in estrous (Noë, 1992). Broadly,

alliances are an outcome of the cooperative interactions (i.e., coalitions) between

males which result from the pursuit of their self-interests (Bercovitch,

1988). Fraser and Plowman's definition of an alliance do not fulfill these criteria. These considerations can be viewed as further circumstantial evidence to support the "peacekeeping" hypothesis (Fraser & Plowman, 2007), as it is the only supported hypothesis that does not involve dominance rankings.

Finally, proximate behavior is the act of an individual coming within one meter of another individual. Almost all significant social interactions occur while individuals are in proximity to one another, and patterns of spatial tolerance/intolerance have been shown to play major roles in facilitating the emergence of higher-level social structure attributes such as cooperation (Ohtsuki et al., 2006; Voelkl & Kasper, 2009). Additionally, because wild populations of hamadryas baboons do not exhibit a strict dominance hierarchy it has been suggested that the highly intolerant behaviors exhibited by leader males towards males not within a leader's OMU function as a replacement strategy for what would be defined as a dominance hierarchy in other species (Kummer et al., 1974). This makes it of particular interest to examine which individuals are tolerated by leader males in proximity compared to individuals whose presence is not tolerated.

Current Study

The primary hypotheses being tested in this study involve rates of SDB among males of different sex-classes of hamadryas baboons. SDB has been shown to suggest high levels of anxiety in individual primates (Maestripieri, 1992), and according to Sapolsky (2005), the structuring and dynamics of a

primate's social system would influence which individuals of different ranks will experience higher/lower levels of physiological stress and relational anxiety. In many species, a primate's dominance ranking as well as the certainty of that ranking would be a large determinant in which individuals would experience elevated anxiety; however, in species such as hamadryas baboons that have no clear dominance rankings, differentiation of roles such as male sex-class may provide a viable alternative to dominance ranks in situations where the aim is to understand if certain classes of males experience more SDBs than others. In this study, the goal was to investigate hypotheses and questions pertaining to differences in three behavioral dimensions (i.e., agonistic, socio-positive, and self-directed) between and amongst adult male hamadryas baboons of different sex-classes (i.e., leader, follower, or solitary male). I hypothesize that regarding SDBs, there will be significant differences between the different sex-classes which would suggest significant differences in anxiety among males of occupying different social roles. As for patterning of social interactions and relationships, observations of socio-positive and agonistic behaviors among male-male dyads were examined using descriptive analyses to highlight important trends.

CHAPTER II

METHODS

Subjects and Study Site

Behavioral observations were conducted at the Filoha research outpost which is on the northern boundary of Awash National Park, Ethiopia by Matthew Pines and other key members of Larissa Swedell's lab group from 2007-2009 (Pines et al., 2011). Video data collection for this project was classified as an archive exemption by Central Washington University's Institutional Animal Care and Use Committee (IACUC) before data collection began, as the video recordings fell under the City University of New York's approved IACUC protocol from data collection for Pines et al. (2011). During these behavioral observations a video camcorder was used to record the entirety of a focal observation of one individual. These video recordings are the source of the data for this project. The recordings used for this study were taken between June 2007 and May 2009. Video recordings were uploaded to the video sharing platform Vimeo. A total of 242 focal recordings were available. Because this study is concerned with male-male interactions, any videos that had a female as a focal follow were eliminated resulting in 127 videos. Of the 127 videos with male focal individuals, 80 of the focal follows were of leader males, 30 were of follower males, and 17 were of solitary males. The recordings lasted from the start of the focal to the end, which lasted for 15 minutes each. Some of the earlier recorded video samples were 30 minutes in length and were cut into two 15-

minute video samples for this study. The number of individuals that data were collected from in this study is 62, with the mean number of samples from each individual being ~1.8. The range of the number of samples taken from any given male is from one to five, with ten individuals only having one sample and one individual having five samples.

Data Collection

Data for this study were collected according to the focal sampling schema (Altmann, 1974). Recorded focal samples were viewed for interobserver reliability between scoring individuals and for data collection. Before data collection began, an undergraduate research assistant and I coded nine separate five minute increments, taken from three of the 15 minute recordings, and assessed these videos for an interobserver reliability (IoR) rating of >90%. Once this threshold was reached, we would exchange coded videos and re-do IoR weekly to ensure that we still had an IoR rating over the 90% threshold throughout the remainder of the study. We maintained an average IoR of 93% across coding. According to a personal communication between myself and Larissa Swedell, a random sampling schema was applied when collecting video observations in the 2007- 2009 period by creating a randomized list of individuals and sampling individuals from this list in the random order produced, and then repeating the randomization procedure for the next round of sampling. Given this information, all 127 focals were used, as it is assumed that these videos had already been collected in a

way that eliminates sampling bias before we coded the videos. Additionally, we coded all of the videos that were available.

Data collection focused on collecting behaviors of interest that were outlined in an ethogram (see **Appendix A**) that was constructed prior to data collection. There were three main classes of data that were collected using this ethogram. These classes were: SDB, socio-positive behavior, and agonistic behaviors. Time of day and season were recorded to supplement analyses and provide a temporal dimension to the dataset. Time was recorded as either morning (i.e., focal began before noon) or afternoon (i.e., focal began after noon). Season was recorded as wet or dry, with the wet season being applied to focals conducted in October to March and dry season focals being conducted in April to September. Random variables for both analysis of variances (ANOVAs) were fitted using the lm() function in R (lme4 package).

SDB Analysis

SDBs were coded for by observing focal individuals for self-grooming, self-scratching, and yawning behaviors. A composite measure of SDB that was called "Rate of Self-Directed Behavior" (rSDB) was used as well which was the sum of the frequency of yawns, self-scratches, and self-grooming events divided by the total time of observation for each focal individual. The composite measure, as well as the mean frequencies of each individual measure, were used as independent variables in all SDB analyses. Analysis was conducted in Statistica initially and analyses were re-run in Rstudio afterwards.

Correlations between the SDB behavioral variables were tested using a Pearson-correlation to ensure each of the behavioral variables of interest were related in a way that justified their usage as a composite measurement of SDB. QQ plots and boxplots in R (base package) were generated to ensure data were normally distributed. The data were not normally distributed, and to correct for this I applied a log transformation (Chanyong et al., 2014) to correct the distribution of the data in order for parametric statistics to be applied to these data. The log transformation corrected the issue based on visual examination of corrected QQ plots, allowing the use of the parametric Pearson correlation as opposed to the non-parametric Spearman-rank correlation.

Two-way ANOVAs were run to examine if there were differences in rSDB between sex-classes of males. Time and season were run as random variables to see if there were any temporal or ecological components to differences found between rSDB. Two analyses applied to the SDB data were ANOVAs that used rSDB as the dependent variable and used sex-class as the primary independent variable. The additional independent variables time of day (morning versus afternoon) and season (wet versus dry) were also used. The decision to use multiple two-way ANOVAs to examine this data rather than a regression that could include all three independent variables is due to missing portions of data that are necessary for a regression (e.g., The data was missing focals of follower males in the morning and afternoon during the dry season, as well as solitary males in the morning during the wet season).

Socio-Positive Behavior Analysis

Measures of socio-positive behaviors such as allogrooming, proximity, and notification behaviors were coded by observing focal video observations for the socio-positive behaviors listed in the ethogram (**Appendix A**). The identity of the initiator of the socio-positive behavior, the recipient of the socio-positive behavior, the sex-classes of initiator and recipient, the type of socio-positive behavior, and if applicable the duration of behavior were all recorded for each instance of a socio-positive interaction.

For socio-positive data, a total of 67 interactions between individuals were collected. Some of these interactions involved males whose identification was not available, or their sex-class could not be definitively determined. These samples were removed from the analysis resulting in an updated total of total of 41 socio-positive interactions. To analyze these data, descriptive statistics were conducted (Table 8-10) on the directionality, duration, and dyad composition of these behaviors.

Agonistic Behavior Analysis

Agonistic behaviors were the final class of data that was chosen for collection. Rather than collecting explicit behaviors, a tiered system of aggression was constructed and used to collect agonistic data. Level one included displacements and threats, level two included prolonged chases and brief aggressive contact (e.g., hit, bite, slap), while level three aggression included bouts of extended contest competition.

The identity of the initiating male, the recipient male, the pattern of behavior at each interaction (i.e., if an agonistic encounter was coded as level two, the sequence of events that indicated the interaction was a level two interaction was recorded), and the identity of the individuals that were determined to be the winner and loser of the interaction were recorded for each bout of agonism. If an agonistic interaction contained a sequence of behavior which spanned multiple levels, the highest level of agonism reached during the interaction was recorded.

A total of seven agonistic interactions were observed throughout the course of this study, and in two of these interactions individual identity or sex-class was unknown of at least one of the adult male participants, limiting the number of viable observations to five instances.

Descriptive statistics of the patterning, directionality, and winner/loser outcomes for each agonistic interaction were then examined to find patterns in the data that suggest relevant trends for this project and considerations for future research.

CHAPTER III

RESULTS

SDB Data

Tables 1 to 4 provide descriptive statistics of the composite measure of rSDB (Table 1) as well as for observed frequencies of three sub-categories of SDB (Tables 2-4). These data include measurements from both within and across males of all sex-classes. Based on descriptive statistics alone, we can see there is very little difference in mean rates of SDB across sex-classes. On average, leader males exhibited the most self-scratches, while solitary males were observed self-grooming and yawning the most often.

Table 1
Descriptive Statistics of rSDB Across Sex-Classes

Sex-Class	Sample Size	Mean	Minimum	Maximum	SD
All Sex-Classes	127	0.57	0.00	5.54	0.63
Follower Male	30	0.50	0.00	2.47	0.50
Leader Male	80	0.59	0.00	5.53	0.71
Solitary Male	17	0.60	0.07	1.40	0.37

Note. *rSDB = composite measure of the rate of all SDB measures*

Table 2
Descriptive Statistics for Frequency of S.S. Among Males

Sex-Class	Sample Size	Mean	Minimum	Maximum	SD
All Sex-Classes	127	6.86	0.00	77.0	8.38
Follower Male	30	5.96	0.00	25.0	5.47
Leader Male	80	7.23	0.00	77.0	9.76
Solitary Male	17	6.41	0.00	18.00	5.00

Note. S.S. = Self-scratch

Table 3

Descriptive Statistics for Frequency of S.G Among Males

Sex-Class	Sample Size	Mean	Minimum	Maximum	SD
All Sex-Classes	127	0.75	0.00	7.0	1.22
Follower Male	30	0.80	0.00	5.00	1.24
Leader Male	80	0.64	0.00	4.00	1.06
Solitary Male	17	1.18	0.00	7.00	1.74

Note. S.G. = Self-Groom

Table 4

Descriptive Statistics for Frequency of Yawns Among Males

Sex-Class	Sample Size	Mean	Minimum	Maximum	SD
All Sex-Classes	127	0.96	0.00	9.00	1.59
Follower Male	30	0.67	0.00	9.00	1.75
Leader Male	80	1.00	0.00	8.00	1.55
Solitary Male	17	1.35	0.00	5.00	1.46

Pearson correlations were run to ensure the variables used in calculating the composite measure of rSDB were correlated, which would suggest that the composite measure was a valid indicator of SDBs. Three correlations were conducted, the results of which are shown in Table 5. These results showed that frequency of self-scratches was significantly positively correlated with both the frequency of self-grooms, $r(125) = 0.26$, $p < 0.05$, and yawns, $r(125) = 0.34$, $p < 0.001$. Additionally, the frequency of self-grooms was not significantly correlated with yawns but showed a trend, $r(125) = 0.15$, $p < 0.1$. These findings validate the usage of the sum of the frequencies of each individual SDB category as a representative measure of overall rSDB in this population.

Table 5
Pearson Correlations Between Measures of Self-Directed Behavior

Variable	Freq of SS	Freq of SG	Freq of Y
Freq of SS	---	0.26, p=0.04	0.34, p=0.0001
Freq of SG	---	---	0.15, p=0.09
Freq of Y	---	---	---

To look at differences in rSDB across sex-classes of males, a two-way ANOVA was performed to examine the rSDB between sex-classes, with an added fixed variable of time (Table 6). No relationship between male sex-class and rSDB was found, $F(2,121) = 0.16$, $p = 0.84$. The relationship between time and rSDB was also not significant, $F(1,121) = 0.05$, $p = 0.82$.

Table 6
ANOVA for rSDB Between Sex-Classes Across Times

Effect	SS	Deg. Of Freedom	MS	F	P
Intercept	24.7	1	24.7	60.6	0.00
Sex_Class	0.13	2	0.06	0.17	0.84
Time	0.02	1	0.02	0.06	0.82
*Sex_Class*Time*	0.20	2	0.07	0.24	0.79
Error	49.3	121	0.41		

A second two-way ANOVA (Table 7) was conducted followed the same design as the previous ANOVA, except the random variable in this analysis was season as opposed to time. This second ANOVA was conducted due to the structuring of the data not allowing a linear model to be run that incorporated both time and season as random variables into a single model. The relationship between season and rSDB was found to be non-significant, $F(1,121) = 0.19$, $p =$

0.65, and the relationship between rSDB to the combined independent variables of sex-class and season to be non-significant, $F(2,121) = 0.34$, $p = 0.70$.

Table 7
ANOVA for rSDB Between Sex-Classes Across Seasons

Effect	SS	Deg. Of Freedom	MS	F	P
Intercept	11.7	1	11.7	29.2	0
Sex_Class	0.13	2	0.07	0.17	0.84
Season	0.08	1	0.08	0.20	0.65
*Sex_Class*Season*	0.28	2	0.14	0.35	0.70
Error	48.4	121	0.40		

Socio-Positive and Agonism Data

A total of 41 socio-positive interactions were recorded. Four of these were instances of allogrooming, six were notifications (i.e., four reciprocated, two unreciprocated), and 31 were instances of proximity between males.

Table 8 below shows the directionality of these behaviors and between males of which sex-class the behaviors occurred. In the two observations of leader-follower male grooming, a leader male initiated a grooming bout directed towards a follower once and a follower male directed grooming towards a leader once. Solitary males were not observed to groom any other sex-class of male, and in both instances the solitary male who initiated the grooming bout was directing it towards the same solitary male who was the recipient.

Table 8
Frequencies of Allogrooming Interactions Among Male Sex-Class

	Recipient's Sex-Class		
Initiator's Sex-Class	Follower	Leader	Solitary
Follower	0	1	0
Leader	1	0	0
Solitary	0	0	2

Note. The initiator's sex-class is listed down the rows, while the recipient's sex-class is listed across the columns.

Of the six notification behaviors where both partners in the dyad were identifiable, five of those interactions were initiated by a follower male. Table 9 below shows the pattern of directionality and among which sex-classes the behavior occurred. Three of the five notifications initiated by followers were directed towards leader males, and all three of those notifications were reciprocated by the leader male being notified. The other two notifications initiated by followers were directed at a different follower male on one occasion and a solitary male on another occasion. A single solitary male was observed notifying another solitary male, although the recipient of this notification did not reciprocate and ignored the behavior altogether. Leader males were never observed to initiate a notification, but always reciprocated notifications when they were approached.

Table 9
Frequencies of Notification Interactions Among Male Sex-Class

	Recipient's Sex-Class		
Initiator's Sex-Class	Follower	Leader	Solitary
Follower	1	3	1
Leader	0	0	0
Solitary	0	0	1

Note. The initiator's sex-class is listed down the rows, while the recipient's sex-class is listed across the columns.

Proximity to another male where both individuals could be identified was observed 31 times. Table 10 shows the number of times proximate interactions were recorded between sex-classes.

Table 10
Frequencies of Proximate Interactions Among Male Sex-Class

	Recipient's Sex-Class		
Initiator's Sex-Class	Follower	Leader	Solitary
Follower	2	13	0
Leader	8	5	0
Solitary	0	1	2

Note. The initiator's sex-class is listed down the rows, while the recipient's sex-class is listed across the columns.

The mean amount of time in seconds a follower male who initiated proximity with a leader male stayed in proximity was ($M = 516.15$, $SD = 101.13$), while the mean time that followers spent with other followers was ($M = 452.5$, $SD = 447.5$). The mean duration of time leader males who initiated a proximate interaction with a follower male was ($M = 750.38$, $SD = 190.7$), while the mean duration of time leaders who initiated proximity with another leader male was ($M = 324.2$, $SD = 142.71$). The interaction where the solitary male was proximate to a leader male lasted for 396 seconds, while the mean duration of the two solitary-solitary proximate dyads was ($M = 491.0$, $SD = 409.0$).

Of these five agonistic encounters where all individuals were able to be identified, four were initiated by leader males and one was initiated by a follower male. Follower males received aggression three times while leader males received aggression twice. Of the situations where leader males were the recipients of aggression, one encounter was initiated by a follower male while the other was initiated by another leader male. Regardless of who initiated the

conflict, the leader male was determined to be the winner of the interaction in all five encounters. Of the five conflicts that were observed, two were coded as displacement behavior (i.e., level one aggression), one was coded as a threat which escalated to a chase (i.e., level two aggression), and the remaining two interactions were coded as extended bouts of contest competition (i.e., level three aggression). All level one and three aggressive behaviors were between leader and follower males, while the level two aggression occurred between the two leader males.

CHAPTER IV

DISCUSSION

Interpreting SDB Analyses

In the analyses of SDB, I found that there was no significant difference in rSDB among males of any sex-class. It had been hypothesized that there would be significant differences, particularly among follower males in comparison to other sex-classes of male, because leader males are known to experience lower rates of anxiety centered on uncertainty in who their female OMU members are in comparison to follower males who recently obtained their first female (Pines et al., 2011). Follower males were also found to exhibit more SDB than solitary males in situations where a non-leader male is attempting to acquire his first female. It has been suggested that this is a result of the risks a follower male takes when trying to obtain his first female, where if he fails can result in his "banishment" from his leaders OMU thus causing him to lose out on both his first female as well as socio-positive access to the rest of the members of the OMU in which he was a follower. Solitary males do not have access to the socio-positive interactions of an OMU that a follower male does so there is less risk, and by extension relational anxiety, about attempts to obtain a female to start his own OMU (Pines et al., 2011).

Contrary to my hypotheses, it was found that there was very little difference in the mean rSDB between the sex classes. There are several possible explanations as to why no significant differences were observed across

male sex-classes. It is possible that indicators of physiological stress measured by fecal glucocorticoids or heartrate are more appropriate avenues for detecting differences among males rather than measures of anxiety like SDB. It may also be because rSDB was not examined in different contexts, as there may be different rSDB among sex-classes immediately following agonistic situations or in situations where a non-social tension causing event has occurred.

The Pearson correlations comparing relatedness of the measures of self-scratches, self-grooms, and yawns suggests that these variables are all significant correlated with the exception of self-groom and yawn which were not significantly correlated but showed a trend towards significance. This non-significant trend may have occurred since yawning could be recorded as a threat behavior or a SDB depending on the context the yawn was observed in, contributing to why there were so few SDB specific yawns in comparison to other SDBs. This suggests that the measures used for the composite rSDB score were a valid way of measuring relational anxiety, as all the behaviors occurred more often together independent of sex class. Essentially, as the number of self-scratches observed during a focal increased, the more self-grooming and yawning behaviors were observed during the same focal. This suite of behaviors should be used in future studies to ensure reliability of the composite measure of rSDB employed in this study. Future studies should also aim to examine the relationship between SDBs and socio-positive or agonistic behaviors. This study did not test any hypotheses related to the occurrence of SDBs in relation to

behaviors such as notifications or agonistic interactions directly, although the

trends discussed in the following sections may suggest studies of SDB and

events that involve potential stressors may be fruitful (e.g., since notifications

occur in "peacekeeping" context perhaps there would be more relational anxiety,

and by extension SDB, in the minutes before a notification event occurs).

While these results do not suggest that sex class is indicative of how

much relational anxiety an individual will experience, the dataset that was

analyzed for this project lacked the necessary re-sampling of individuals to get

the proper depth of data required for analyzing the SDB. Individuals are bound to

experience different levels of anxiety throughout their lives (Pryce et al., 2002;

Sapolsky, 1993), and these data analyzed here sampled each individual less

than two instances on average. This amounts to measures of SDB that are mere

fifteen-minute snapshots of a single day in that individual's life. By sampling

individuals' multiple times over extended time periods, the composite measure of

SDB rate for each individual with each sex class would be far more accurate.

Interpreting Socio-Positive Analyses

Socio-positive behavioral data violate one of the fundamental assumptions

of traditional parametric statistical techniques by their very nature. Specifically,

parametric statistics assume that data collected for analysis are independent,

meaning data collected on any given subject is not dependent on variables from

other subjects. Socio-positive and agonistic behaviors fundamentally occur at the

dyadic level or higher, meaning any social data collected on an individual does

not fulfill the assumption of independence (Whitehead, 2008). To counter this issue, I attempted to apply analytical techniques that do not assume independence of the data, rather, these techniques rely on dependent data to operate.

Descriptive statistics allowed for extraction of some general patterns from the data that may indicate trends. Tables 8-10 show frequencies of socio-positive behaviors across dyads of the three different sex classes. More than half of all socio-positive interactions were between leader and follower males (62%), and for each sub-category of socio-positive behavior (i.e., allogrooming, notifications, and proximity) leader-follower dyads participated in these behaviors more often than or equally as often as any other combination of male sex-class dyad (Tables 8-10). The larger number of leader-follower male socio-positive interactions can be understood as a result of what Schreier and Swedell (2012) suggested is a male-male system of increased spatial intolerance for other males, rather than a strict dominance hierarchy that is maintained by directed agonism. The leader-follower male relationship has been found to be adaptive for males of both sex-classes (Chowdhury et al., 2015), while leader-leader or leader-solitary male dyads would not convey adaptive benefits and would only increase the likelihood of one of the leader males female's being taken from him. Therefore, it follows that leader males were observed being more spatially tolerant of their followers and engaging in increased rates of socio-positive behaviors with them as opposed to other leader or solitary males.

While the leader-follower dynamic has adaptive value, it also comes with costs. Leader males who are too tolerant of their followers' risk losing a female to their follower if the employs the challenge or opportunistic strategies (Pines et al., 2011), while followers who encroach beyond the limits of their leader male's tolerance of them risk serious injury due to directed agonism by leaders. Although directed agonism is rare, it occurred in my observations and has been suggested in other studies (Pines & Swedell, 2011; Romero & Castellanos, 2010) as a potential cause of fitness and health costs that can be incurred by follower males. In order to reap the adaptive value of the leader-follower relationship while also buffering against potential costs stemming from this relationship, a conflict mitigation mechanism would be necessary. Since dominance rankings are not existent in this population, differentiation in social roles, particularly among patterns and directionality of socio-positive behavior across sex-classes, can supplement the understanding of these data. The pattern and directionality of notifications between leader and follower males was particularly revealing.

Per Fraser and Plowman (2007), the most likely explanation for the mechanism driving the evolution of notification behaviors is the "peacekeeping" mechanism, which states that notifications serve as a signal to other males that the notifier's social objectives are non-confrontational in nature. Of all notification behaviors observed, 42% were directed to leader males by follower males, with the second highest percent of notifications (26%) directed by leader males towards their followers, for a total of 68% of all notifications observed. The

observation that most notifications occur between leader and follower males support the idea that notification behaviors signal the initiator's non-threatening social objective and may ease tensions in this specific class of dyadic relationship, allowing for other socio-positive behaviors to occur and the adaptive benefits of this relationship to be exploited while buffering any potential costs that either leader or follower males may incur.

Solitary males were observed to interact socio-positively with other solitary males more often than leader or follower males, which supports previous literature's findings (Swedell et al., 2014) that solitary males spend most of their time on the periphery of a band and interact with members of a band's OMUs far less often than other solitary males. Apart from one instance of a solitary male initiating a proximate interaction with a leader male, solitary males initiated allogrooming, notification, and proximate behaviors exclusively with other solitary males. Interestingly, of the four allogrooming instances observed out of the 42 total sociopositive interactions, allogrooming was much more evenly distributed among sex-class dyads than notifications or proximate interactions. Exactly half of all allogrooming observation occurred among solitary male dyads, while only 16.7% of notifications occurred among solitary male dyads, and a mere 6.5% of the total observed proximate interactions occurred among solitary males. This trend is indicative of leader and follower male's access to the females of their OMU for allogrooming behavior, as a vast majority of allogrooming in this species occurs between leader/follower males and the

females of an OMU (Swedell, 2002), while solitary males have no social access to females and, therefore, must rely on other solitary males for social grooming purposes.

Durations of timed socio-positive behavioral interactions also suggest trends which are indicative of more intense socio-positive interactions among the expected sex classes of male. Mean durations of time leader males spent in proximity to follower males were higher than that of the time spent together between a dyad of just leader males or just follower males. This further confirms the perceived importance of and increased tolerance towards the leader-follower male relationship in this species. Solitary males spent more time in proximity and allogrooming other solitary males than any other sex class, which supports the trend in the descriptive data which suggests that the majority of male-male interactions occur between either leader males and their follower males or between two solitary males. The patterning of socio-positive interactions overall is suggestive that limited spatial tolerance by leader males may determine which individuals are able to interact socio-positively.

Interpreting Agonistic Analyses

Descriptive statistics of agonistic behaviors from this study are also suggestive of interesting behavioral trends and patterns. According to Schreier and Swedell (2012) strict dominance relationships are either not present or extremely subtle in this species as opposed to in other *Papionin* species, even though hamadryas males are extremely despotic. It is suggested that due to the

clan of organization mainly consisting of related males, the aggressive herding

tactics used by males, and given the sparse/arid ecosystem and scarce

distribution of food resources, males of this species do not use a strict linear

dominance hierarchy as a way of securing mates. Instead, males "respect" the

boundaries of other's OMUs and focus on maintaining their own status as a

leader male to secure future mating opportunities. However, there has been

evidence produced by studies of captive hamadryas troops that suggests the

existence of a dominance hierarchy in this species (Painter, 2018; Romero &

Castellanos, 2010). I postulate that this difference is due to feeding platforms that

allow for captive males to defend resource patches more effectively than in wild

populations, leading to increased agonistic encounters stemming from

resource defensive aggression over feeding platform access. This may be what

causes captive populations to exhibit a dominance hierarchy while wild

populations do not.

The descriptive analyses that were conducted on the agonistic data were

revealing. Agonistic encounters in which both individuals could be identified

showed that leader and follower males were the most likely sex-classes to

engage in any level of agonistic behavior. Solitary males were not observed to be

the initiator or recipient of any form of aggression, and while the sample size is

quite small, this does suggest that solitary male's occupation of the periphery of

hamadryas bands, as opposed to occupying space near the band's OMUs, may

be a contributing factor as to why no aggression was witnessed involving this

sex-class. More aggression is expected to occur near areas occupied by an OMU as females are the main resource that males would exhibit competitive behavior over (Kummer, 1974). Thus, solitary males inhabiting areas that are furthest from a leader male's females as opposed to males of other sex-classes would explain why no agonism was witnessed for the solitary sex-class. Among the sex-classes that agonistic encounters were observed for, all but one agonistic interaction was initiated by leader males, and follower males were the target of this aggression slightly more often than other leader males were the target (i.e., followers were targeted three times while other leaders twice). Additionally, leader males were the exclusive victors in these contests.

Viewing these trends within the context of the behavioral ecology of this species elucidates potential explanations for what was observed. The primary limiting resource for males is reproductive females (van Schaik, 1996), hence aggression should occur in contexts where reproductively viable females are present. All instances of agonistic behavior observed occurred between or among leader and follower males while solitary males were never observed in these interactions. This is consistent with behavioral ecology theory, as leader and follower males are inherently parts of the OMU structure and females will spend virtually all their time in close spatial cohesion with her leader male and, potentially, her leader's follower male. Thus, it follows that directed aggression would occur more frequently between males of sex-classes that have less limited

social or sexual access to females than among the sex class which has little to

no access to females.

The overall rarity of agonistic behaviors suggests that Schreier

and Swedell's (2012) interpretation that spatial cohesion and "respect" of spatial

boundaries among OMU leaders could take the place of a strict linear dominance

hierarchy in this species, as even though agonistic interactions are rare,

hamadryas baboons are still classified as a highly despotic species. However,

the pattern that was observed in which leader males were the exclusive winners

of all agonistic interactions is similar to patterns we see in highly despotic species

with strict linear dominance hierarchies. Leader males winning all agonistic

encounters could be interpreted as an analogue to high-ranking individuals in a

dominance hierarchy winning most or all agonistic interactions against low-

ranking individuals. It is the very fact that high-ranking individuals win

consistently more than low-ranking individuals that allows for the construction of

a dominance hierarchy. Thus, if more agonistic interactions were observed a

linear dominance hierarchy could be constructed. These findings are

contradictory but not mutually exclusive, as it could be the case that due to

current analytical methodologies used to generate dominance hierarchies it is

impossible to detect the existence of a linear dominance hierarchy in this

species. This does not mean a dominance hierarchy does not exist, just that the

current methodologies aren't properly tuned to be able to detect it. If a more

subtle dominance hierarchy does exist, it could still include the system of spatial

tolerance suggested by Scheier and Swedell (2012). While it is impossible to eliminate the possibility of a cryptic dominance system existing in this species, our observations and the findings of others in the literature (Abegglen, 1984; Sigg & Stolba, 1981) suggest that a system of spatial tolerance/intolerance that varies among males of different sex-classes acts as a conflict mitigator and drive the specific structuring and patterning of both agonistic and socio-positive behaviors.

Findings on hamadryas baboons in captivity suggest that dominance hierarchies do exist in hamadryas baboons (Painter, 2018; Romero & Castellanos, 2010). However, in these studies the space that the baboons inhabited was much smaller than in wild populations and they had access to feeding platforms that can be defended by a male against other males in the enclosure, as opposed to in the wild where spatial cohesion is much more fluid and there are no distinct feeding areas where males can compete over differential access to food resources. These variables made it significantly easier to generate data on agonistic encounters in the captive populations and may have led to artificial behavioral ecological pressures which cause the formation of a dominance hierarchy among captive males while not among males in wild populations. Future research should aim to collect a wider array of data on agonistic interactions between males in the wild to disseminate the mechanism driving the high levels of despotism yet absence of a dominance hierarchy.

Limitations

Throughout the course of this study, there were several limitations placed upon our viable analytical methods stemming from the data being collected from pre-recorded tapes only. SDB data collected from the videos was limited to which focals were recorded during the 2007-2009 field seasons, and there was a large difference in the number of samples between sex-classes. Leader males had almost double the number of observations compared to the follower and solitary male sex-classes put together. While transformations and non-parametric analyses were able to be used to examine the data, it would be ideal for there to be a more similar number of samples from each sex-class for SDB. Additionally, a greater depth of re-sampling of individuals across a larger time period would be very helpful for socio-positive and agonistic behavioral analyses. If this study were conducted in the field, the sampling schema could have been adjusted in order to obtain a relatively equal number of samples from each sex-class, rather than having to manipulate the data before analysis to make the data that already existed in the videos fit the study design.

Another benefit of a long term field study would be the ability to incorporate more information regarding individual life history development into analyses. If re-sampling of individuals over a long time period was possible, changes in social strategies and patterns of interactions throughout an individual's life could be more accurately analyzed, which would provide a richer component to the dataset for analysis of differences between individuals.

Ultimately, this would allow for examination of patterning, content, and quality of interactions and relationships of an individual throughout time, as opposed to what video data allowed which was the patterning, content, and quality of interactions of individual sex-classes over a short time period.

Scan and all-occurrence sampling are fundamental techniques for collecting a large breadth of behavioral data (Altmann, 1974), but they could not be used in this study. This is because the only data that could be collected with certainty were data on individuals who were within the frame of the video during the course of the behavior. This negatively impacted the ability to collect both agonistic and socio-positive data, such as agonistic events that occurred off screen or socio-positive interactions occurring in groups around the focal individual but outside of the camera's view. This led to the lack of breadth of interactional data across all these dyads which is necessary to calculate higher level agonistic data such as dominance hierarchy ordering and broad socio-positive trends such as preferred partners and network analytic measures of socio-positive behavior. Elo-ratings are one of the primary methods for calculating dominance rankings, while social network analysis allows for examination of dyadic and higher-level social behavior without violating the assumptions of independence that examining social data using parametric statistics would violate. These analytical techniques are preferred over the descriptive analyses conducted here, but they require very large sample sizes

and repeated measures of social interactions among individuals to calculate that were not possible due to use of archived videos for this study.

Future Directions

I believe that the approach outlined here has validity and should be re-purposed in future studies, particularly in a study that has access to live data collection rather than pre-recorded video tapes. While video data analysis is a beneficial alternative for primatological researchers who are unable to go into the field, it also has multiple drawbacks that were experienced throughout this study (see section **Limitations**).

Due to a lack of depth in the data able to be collected, future studies with access to data collected in the field should focus on using all-occurrence and scan sampling to further examine these behavioral trends. One further way of examining questions regarding the conflict management mechanism in this species would be to implement an elo-rating procedure used by Neumann et al. (2011) and improved by Newton-Fisher (2017). The implementation of varying tiers of agonistic intensity (e.g., level one, two, and three) in this study can be extended to improving a potential elo-rating procedure. In essence, future researchers could set differing point values for each level of aggression, so that an individual who won a level one interaction will gain less points to their overall elo-rating as opposed to an individual who won a level three interaction. Even though I was unable to collect enough data for the elo-rating procedure to create a dominance hierarchy, this extension to the elo-rating

procedure has potential to be a lucrative research methodology for future studies that collect data in the field and can use scan/all-occurrence sampling to collect a larger pool of agonistic interactions could be done.

The descriptive analyses of patterning of socio-positive and affiliative behavior indicate emerging patterns of behavioral patterning like those suggested previously in the literature (Abegglen, 1984; Schreier & Swedell, 2009; Sigg et al., 1981) Descriptive analysis of socio-positive behaviors suggests leader males are more tolerant of their follower's presence and socio-positive interactions, while they are much less welcoming towards solitary males and rival leader males. Patterns in descriptions of agonistic interactions do not explicitly suggest either interpretation of the social dynamics of dominance hierarchies in this species (i.e., spatial tolerance or a strict linear dominance hierarchy), however the descriptive data do suggest that both routes may still be viable explanations for the structure and patterning of male social dynamics in this species. Future studies should focus on disseminating these two mechanisms and testing hypotheses to see if there truly is a difference between captive and wild social dynamics or if the behavioral ecological variables present in wild populations have made it more difficult to detect the existence of a dominance hierarchy.

I encourage future research initiatives to explore the patterning of behaviors among male hamadryas baboons, particularly by collecting data that is structured in a way that would allow for more sophisticated analytical techniques

to be applied. In doing this, researchers can continue to explore the intricacies of social organization and dynamics in this species as well as more broadly across the primate order.

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Appendix A—Ethogram

Non-Social Behavior

Behavior Name	Class of Behavior	Data Type	Behavior Description
Self-Scratch	Self-Directed	Frequency (event)	Individual A quickly scratches their own body quickly. Lasts less than 3 seconds and isn't as precise as self-grooming, as it is just a scratching motion rather than dexterous palpation of their own body.
Self-Groom	Self-Directed	Duration (state)	Individual A grooms their own body by manipulating their fur/skin for an extended period of time, manually moving the fur and removing debris with fingers or teeth
Yawn	Self-directed	Frequency (event)	Individual yawns, specifically outside the context of an aggressive interaction. (See threat behaviors, as yawn accompanied by a cheek pump is coded differently)

Social Behaviors

Behavior Name	Class of Behavior	Data Type	Behavior Description
Proximity	Affiliative	Duration (state)	Focal Individual is within approximately **1 meter** of another individual for at least **5 seconds.** This can be approximated by looking at the individuals and imagining them reaching out their arms towards one another. If their fingers would touch, they are within proximity to one another.

Notification	Ritualized Greeting	Frequency (event & pattern of behavior)	Focal individual approaches or is approached by another individual using a rapid, stereotyped gait while looking directly at the other male. Lip smacking, repeated eyebrow squinting, and the laying of his ears flat against his head are common components of the greeting. If accepted, the initiator presents his hindquarters. Allogrooming or rear/genital touching may subsequently occur. Interaction may also end with mounting.

Agonistic Behavior

Behavior Name	Level of Aggression	Data Type	Behavior Description
Displace	Level 1	Frequency (event)	Upon Individual A approaching another male, Individual B (the male being approached) gets up and leaves the area because of Individual A's approach
Threaten	Level 1	Frequency (event & pattern of behavior)	Individual A either threatens or is threatened by another individual without making physical contact, which constitutes a range of aggressive warning signals such as: · **Lunging**: like charge but Individual A does not pursue individual B · **ground slapping** · **yawn accompanied by cheek pumping** · **bearing canines at another individual** · **aggressive vocalizations:** A screech or scream directed at another male

			· **stare threat**: A looks at B intensely; A may also sharply move its head toward B and/or eyebrow raise.
Chase/Charge	Level 2	Frequency (event)	Individual A runs towards and chases individual B in a "tense" manner, individual B may flee/submit, which would end the conflict with individual A being marked as the winner, or stands his ground to fight (which would escalate this behavior to a level 3 conflict).
Aggressive Contact	Level 2	Frequency (event & pattern of behavior)	Focal individual either gives or receives any kind of aggressive physical contact to/from another individual, including a slap, punch, kick, bite. For this event to advance to stage 3 aggression, the receiving individual must respond with an equal level of aggressive behavior.
Contest Competition	Level 3	Duration (state & pattern of behavior)	When an individual is the initial recipient of a level 2 aggressive behavior and they choose to reciprocate by responding with an equal level of aggression rather than submitting or fleeing, this indicates a challenge has been accepted and these two individuals have moved into the third level of aggressive interaction. A winner is decided based on which individual submits, flees, or is unable to continue fighting first (marking that individual as the loser).