

Sexual Selection in Mantled Howling Monkeys (*Alouatta palliata*), With an Emphasis on  
the Role of Female Mate Choice

by

Randall Thomas Ford

Department of Biological Anthropology and Anatomy  
Duke University

Date: \_\_\_\_\_

Approved:

\_\_\_\_\_  
Kenneth Glander, Supervisor

\_\_\_\_\_  
Christine Drea

\_\_\_\_\_  
Leslie Digby

\_\_\_\_\_  
Daniel Schmitt

Dissertation submitted in partial fulfillment of  
the requirements for the degree of Doctor  
of Philosophy in the Department of  
Biological Anthropology and Anatomy in the Graduate School  
of Duke University

2010

ABSTRACT

Sexual Selection in Mantled Howling Monkeys (*Alouatta palliata*), With an Emphasis on  
the Role of Female Mate Choice

by

Randall Thomas Ford

Department of Biological Anthropology and Anatomy  
Duke University

Date: \_\_\_\_\_

Approved:

\_\_\_\_\_  
Kenneth Glander, Supervisor

\_\_\_\_\_  
Christine Drea

\_\_\_\_\_  
Leslie Digby

\_\_\_\_\_  
Daniel Schmitt

An abstract of a dissertation submitted in partial  
fulfillment of the requirements for the degree  
of Doctor of Philosophy in the Department of  
Biological Anthropology and Anatomy in the Graduate School  
of Duke University

2010

Copyright by  
Randall T. Ford  
2010

## **Abstract**

Despite early neglect, recent studies of sexual selection have shown a renewed interest in female reproductive strategies. Clearly the traditional portrayal of female animals as passive participants in mating is incorrect, but much is still unknown about female reproductive strategies, including the extent of female mate choice. The primary goal of this dissertation is to explore the role of female mate choice in mantled howling monkeys (*Alouatta palliata*), a species in which males have previously been assumed to control mating.

From March 2006 through February 2007, I used focal-animal sampling to record the behavior of adult female mantled howlers at Hacienda La Pacifica, Costa Rica. The focal animals in the study were nine adult females in a social group that has been regularly monitored since 1984. There were also four capture sessions performed by K. Glander to collect blood samples for genetic paternity analysis. A total of 33 individuals in the study group and the eight adult males from surrounding groups were captured.

The genetic paternity analyses were largely inconclusive. Of the eight microsatellite markers used previously in this species, only four were polymorphic in this sample. Additionally, nearly half (7 of 16) of the purported mothers were excluded at one locus. Assuming the mother was unknown allowed determination of genetic paternity in only one case. In terms of behavior, females were largely responsible for soliciting copulations, but the females generally solicited the male who was maintaining

proximity. Females almost never rejected copulations (3.3% of copulation attempts) and mated with multiple males in 77.8% of female cycles.

The lack of conclusive genetic paternity data leaves open alternate possibilities via post-copulatory female choice. However, female mate choice appears to reinforce male competition. In a species with reported infanticide, a multimale mating strategy, with most copulations concentrated among high-ranking males, may be a female's best reproductive strategy.

# Contents

Abstract .....	iv
List of Tables .....	ix
List of Figures .....	x
Acknowledgments .....	xii
1. Introduction.....	1
2. Background.....	4
2.1 Male-male competition.....	5
2.1.1 Male dominance rank and reproductive success .....	5
2.1.2 Constraints on male control.....	7
2.2 Female mate choice .....	10
2.2.1 Mate choice models.....	10
2.2.1.1 Adaptive models .....	10
2.2.1.2 Nonadaptive Models .....	13
2.2.2 Multimale mating .....	14
2.2.3 Constraints on female mate choice.....	16
2.3 Sexual Conflict .....	18
2.4 Other mechanisms of sexual selection .....	20
2.4.1 Male mate choice .....	20
2.4.2. Female-female competition .....	22
2.5 Sexual selection in mantled howling monkeys.....	25

2.6 Hypotheses .....	29
3. Methods .....	32
3.1 Study site .....	32
3.2 Study schedule and subjects .....	34
3.3 Capture .....	35
3.4 Observations.....	37
3.4.1 Observation schedule .....	37
3.4.2 Observation methods.....	39
3.5 Genetic paternity analysis .....	40
3.6 Behavioral Analysis .....	41
3.6.1 Data preparation .....	41
3.6.2 Female mate choice.....	42
3.6.3 Male-male competition.....	44
3.6.4 Female-female competition.....	45
3.6.5 Male mate choice .....	45
4. Results.....	47
4.1 Genetic paternity analysis .....	47
4.2 Behavioral analysis.....	49
4.2.1 Female mate choice .....	50
4.2.2 Male-male competition.....	58
4.2.3 Female-female competition .....	62
4.2.4 Male mate choice .....	64

5. Discussion.....	66
References.....	74
Biography.....	87



## List of Tables

Table 1: Group 2 Animals Captured .....	36
Table 2: Neighboring Males Captured.....	36
Table 3: Behaviors Recorded .....	40
Table 4: Exclusion of Purported Dams for Group 2 Offspring.....	49
Table 5: Statistical Analysis of Female Preference Indicators.....	51

## List of Figures

Figure 1: Map of La Pacifica indicating location of social groups.....	33
Figure 2: Frequency of male-directed approaches by females (number after female code represents the female's dominance rank).....	52
Figure 3: Frequency of male-directed lingual gestures by females (number after female code represents the female's dominance rank).....	53
Figure 4: Frequency of female copulations with males (number after female code represents the female's dominance rank).....	54
Figure 5: Correlation between female approach index and dyadic copulation rate .....	55
Figure 6: Correlation between female lingual gesture rate and dyadic copulation rate...	56
Figure 7: Correlation between proximity maintenance index and dyadic copulation rate .....	57
Figure 8: Average copulation rate for males of various ranks (number in parentheses indicates the number of males contributing to each average).....	58
Figure 9: Percentage of copulations by males of various ranks based on the day of copulation (number in parentheses indicates the number of males contributing to that rank).....	59
Figure 10: Percentage of total copulations performed by males of various ranks based on the day of copulation (number in parentheses indicates the number of males contributing to that rank).....	60
Figure 11: Comparison of male mating success with different alpha males .....	61
Figure 12: Aggression received from females when attractive to males and not attractive to males (● = low-ranking; ■ = mid- and high-ranking) .....	63

Figure 13: Proportion of time alpha male within 3m of female when attractive (numbers indicate female rank) ..... 64

## **Acknowledgments**

This project could not have been completed without the help and support of many people. This brief thank you can never fully express my appreciation for all they have done for me.

I would like to thank the owners and operators of Hacienda La Pacifica for allowing me to conduct this research. I am grateful for funding from the National Science Foundation, the Wenner-Gren Foundation, and the Center for Latin American and Caribbean Studies at Duke University. I must also thank the entire Hagnauer family for their hospitality while I was in Costa Rica. While living alone in a foreign country, the value of knowing that good people are looking out for you cannot be overstated. I thank Margie Clarke for invaluable assistance getting to know Group 2 and for suggestions on numerous aspects of my research. I thank Vanessa Ione Machen for her assistance and friendship in the field, and I thank everyone who was involved in the various capture sessions during my study, especially Mark Teaford and Tim Keith-Lucas. You all made those times some of the most enjoyable times, not just of my study, but of my life.

Thank you to my committee members. I am grateful to Dan Schmitt and Christine Drea for being with me throughout this long process. They provided comments and suggestions that helped me secure funding and improved the final dissertation. I thank Leslie Digby for taking on the burden of being on my committee relatively late in

the process. She nonetheless provided valuable insights and support. I thank Kathleen Smith for filling in at my major paper defense, and I thank Susan Alberts for valuable feedback and for allowing me to spend time in her lab. In fact, I must thank the entire Alberts lab for helping me to better understand the techniques used in molecule genetics. Finally, I thank Ken Glander for being a true mentor during my time at Duke. He has supported me every step of the way, from the very beginning when he took me to Costa Rica (even though I had no intention of studying howlers at the time) to the end when I was trying to write my dissertation while juggling the many wonderful things that life managed to throw my way. I can never thank Ken enough for his support and guidance over the years.

I thank all of the students, faculty, and staff of BAA. You all made my time at Duke more enjoyable than I could have imagined. I would especially like to thank Catherine Workman, Todd Yokley, and Jonathan Perry for their friendship.

I thank my family, especially my parents, for their love and support through my attempts to be a professional student. I am grateful for their patience and their continued support of everything I do. Finally, I thank my amazing wife, Nicole, for encouraging me when I was tired and frustrated. You and Brayden are the greatest things that have ever happened to me.

# 1. Introduction

This dissertation examines mating behavior in mantled howling monkeys (*Alouatta palliata*) in an attempt to better understand sexual selection in this species, particularly in relation to the role of female mate choice. Sexual selection theory has traditionally portrayed female animals as passive participants in mating. In fact, males have generally been assumed to control the mating process, competing with one another for control of females. Trivers (1972) specifically referred to female primates as potentially being unable to exert mate choice because of male control. However, many factors can prevent a dominant male from monopolizing the females in a multimale-multifemale social group. Thus, presumptions of male control may have been overstated, as suggested by the prevalence of multimale mating.

Mantled howling monkeys were chosen to explore these aspects of sexual selection theory because, consistent with traditional sexual selection theory, alpha males in mantled howler social groups have been proposed to control access to females during peak estrus (Glander, 1980). Consequently, it was assumed that the alpha male sires all offspring during his tenure (e.g., Clarke & Glander, 1984), but molecular genetic data demonstrate this is not the case. Ellsworth (2000) showed that the alpha male could be excluded as the father in 60% of the cases in which she performed paternity exclusion. It thus appears that female mating opportunities are not completely controlled by the alpha male, but it remains unclear whether females are exerting mate choice. The goal of the

dissertation was to compare observed mating behavior with molecular paternity data to shed light on this question.

Chapter 2 provides background information on sexual selection theory, tracing the development of traditional theory focusing primarily on male-male competition to more recent ideas recognizing the importance of female mate choice. This shift in thinking included the development of sexual conflict theory, which acknowledges the possibility that male and female reproductive strategies may be incompatible. I then discuss aspects of sexual selection theory that are often neglected, namely male mate choice and female-female competition. The chapter ends with a discussion of the current state of knowledge regarding sexual selection in mantled howlers, leading to a statement of the hypotheses tested in this study.

Chapter 3 discusses the methods used to perform the study. The study site and study group are described, followed by the schedule of captures and observations, as well as the process used to perform the captures and observations. Finally, the plan of analysis (both genetic and behavioral) is discussed.

The results of the study are described in Chapter 4. I begin with the results of the genetic paternity analysis. I then discuss the results of the behavioral analysis, beginning with general information on the mating patterns observed and concluding with a discussion of the results as they relate to my hypotheses.

The final chapter interprets my results in an attempt to determine how these results relate to existing information about sexual selection, especially in mantled howlers. I summarize my ideas about female mate choice in this species and discuss how

female mate choice interacts with other features of sexual selection. The chapter concludes with a discussion of data that are needed to fully understand sexual selection in mantled howling monkeys.



## 2. Background

When Darwin (1871) developed the theory of sexual selection, he identified two mechanisms by which sexual selection can act. First, the members of one sex compete “to drive away or kill their rivals” (Darwin, 1871; Vol. II, p. 398). Darwin stated that males are generally the competing sex while the females remain passive. Alternatively, the members of one sex (again, generally the males) compete “to excite or charm those of the opposite sex, generally the females, [who] no longer remain passive, but select the more agreeable partners” (Darwin, 1871; Vol. II, p. 398). The first mechanism is generally referred to as male-male competition, and the latter is called female mate choice.

Although Darwin identified both mechanisms as important factors in sexual selection, female mate choice was initially neglected, with most emphasis being placed on the idea of males actively competing for passive females. Huxley (1938) dismissed female mate choice as an important evolutionary force, while downplaying the importance of sexual selection in general. Bateman (1948) stated, “Darwin took it as a matter of general observation that males were eager to pair with any female, whereas the female, though passive, exerted choice” (p. 350). This idea of ever-eager males and passive females remained prevalent for the next few decades, leading to numerous studies focusing on male-male competition to explain variance in male mating success (the ability of males to perform copulations) and reproductive success (the ability of males to sire living offspring). However, more recent studies have challenged the idea of passive

females on both theoretical and empirical grounds (e.g., Fedigan, 1983; Gowaty, 1997), leading to renewed interest in the role of female mate choice.

This chapter provides an overview of current thinking on the role of male-male competition and female mate choice. It also explores the sexual conflict that may arise when male and female reproductive strategies are at odds with one another. Finally, it concludes with a brief look at other mechanisms of sexual selection, namely male mate choice and female-female competition.

## ***2.1 Male-male competition***

According to sexual selection theory, most animals are expected to display greater intrasexual competition among males. The most common reasons for this prediction include the greater investment by females in gametes (Bateman, 1948) or more generally in the offspring (Trivers, 1972). In addition, the operational sex ratio (Emlen & Oring, 1977) is often skewed toward males, meaning there are more reproductive males than fertile females at any given time. Because of the presumed importance of male-male competition, many researchers have studied the influence of male dominance rank on mating and reproductive success.

### **2.1.1 Male dominance rank and reproductive success**

Male dominance rank, the formalized representation of the outcome of male-male competition, should be highly correlated with reproductive success if male-male competition determines the outcome of mating. In most mammals, higher male

dominance rank is usually associated with greater mating and reproductive success (Ellis, 1995). However, the relationship is not always as clear in primates (Dixson, 1998). As in other animals, the relationship between male dominance rank and mating success is usually positive (Soltis et al., 2001), but some studies have found no significant relationship (e.g., Huffman, 1987; Noë & Sluijter, 1990; Manson, 1996) or, in rare cases, a negative relationship (Baldwin, 1968). The relationship between male dominance rank and reproductive success is also generally positive (e.g., Smith, 1981; de Ruiter et al., 1994; Gerloff et al., 1999; Constable et al., 2001; Launhardt et al., 2001; Soltis et al., 2001; Engelhardt et al., 2005; Klinkova et al., 2005) but not always (e.g., Berard et al., 1994).

Despite some inconsistency in results, a broad overview suggests dominance rank is an important determinant of male reproductive success in mammals, including primates. Kutsukake and Nunn (2006) reported that 75-78% of the studies they reviewed showed significant mating skew among male primates. However, it is also clear that dominance rank is not the only factor influencing male reproductive success. Although methodological explanations have been given in some cases (e.g., Fedigan, 1983; Bercovitch, 1986; Constable et al., 2001), these explanations cannot explain all the varied results, suggesting there are biological constraints on the ability of high-ranking males to monopolize reproduction.

## **2.1.2 Constraints on male control**

Many factors may influence the relationship between male dominance rank and reproductive success. One suggestion is that male-male competition may take the form of sperm competition, rather than overt physical competition (Ginsberg & Huck, 1989). However, sperm competition can only occur if dominant males have been unsuccessful at monopolizing females in the first place. The underlying causes for this failure may include demographic factors, alternative mating tactics of subordinate males, potential costs of dominance or monopolization, and female reproductive strategies.

Demographic factors influencing the relationship between male dominance rank and reproductive success include the number of males, the number of females, the sex ratio, and the degree of synchrony among females (Cowlshaw & Dunbar, 1991; Bulger, 1993; Setchell et al., 2005). Although the results of demographic analyses sometimes conflict, they give the overall impression that the ability of dominant males to monopolize females decreases as the number of females, the number of males, and estrous overlap increase. Increased female cohort size generally leads to increased male cohort size (Bulger, 1993) and potentially to greater numbers of simultaneously receptive females (Altmann, 1990; Charpentier et al., 2005). The decrease in reproductive skew associated with larger female cohorts may result from the presence of more male competitors (Setchell et al., 2005). The increased number of competitors can lead to numerous repeated challenges, which overwhelm the dominant male, especially since power differentials among males are likely to be smaller with more males present (Cowlshaw & Dunbar, 1991). The presence of more males also increases the likelihood

of alternative reproductive tactics, including coalition formation (Bulger, 1993). Increased synchrony of female estrous periods potentially decreases male reproductive skew because dominant males are unable to monopolize more than one female at a time, without their cooperation (reviewed in Nunn, 1999). Thus, demographic factors have a significant influence on the relationship between male dominance rank and reproductive success, in part, because they can increase opportunities for alternative male mating tactics and female mate choice.

Males with low reproductive success, especially when they are unrelated to the males with high reproductive success, are expected to develop alternative means of improving their reproductive success. The simplest alternative male mating tactic is the use of sneak copulations. Briefer, less conspicuous copulations by subordinate males have been documented in numerous species of mammals (e.g., Cox & LeBoeuf, 1977; Inoue et al., 1991; Amos et al., 1993; Manson, 1996; Coltman et al., 1999). The success of this tactic depends largely on cooperation from the female. If the female chooses not to mate with the male, she can easily draw the attention of higher-ranking males.

A more confrontational alternative tactic involves the formation of male coalitions. This tactic is relatively successful in some species of primates. Male savannah baboons are particularly well known for using this tactic, which allows older, mid-ranking males to achieve higher mating success than expected (Noë & Sluijter, 1990; Alberts et al., 2003). However, proximate and ultimate explanations for coalition formation are unclear. For instance, no satisfactory explanation has been provided for the lack of coalitions in the mating context among chacma baboons (Bulger, 1993). Noë

(1990) suggested coalition formation may be less likely in small male cohorts, but this explanation does not seem adequate in chacma baboons (see Bulger, 1993).

In some cases, active efforts on the part of subordinate males may not be necessary to acquire mating opportunities. Attempts to acquire or maintain high rank may inhibit reproductive activity (Dewsbury, 1982; Alberts et al., 2003), and despite early assumptions to the contrary (e.g., Trivers, 1972), males do not mate without costs. First, spermatogenesis has metabolic costs. The production of sperm in high-ranking *Macaca fuscata* males may represent up to 6% of their basal metabolic rate (Thomsen et al., 2006). Second, spermatogenesis requires time, which means repeated mating can lead to sperm depletion. In Soay sheep, dominant males produced fewer sperm per ejaculate and a greater proportion of abnormal sperm as the rutting season progressed (Preston et al., 2001). Sperm depletion has also been suggested to occur in primates (Small, 1988). Third, mate guarding involves energetic constraints because it reduces the amount of time that a male can forage (Alberts et al., 2003; Matsubara, 2003). Consequently, dominant males in species with non-seasonal mating may be unable to sustain mate guarding during periods when successive females enter estrus on a nearly continuous basis (Setchell et al., 2005). The dominant male would have to refrain from mate guarding some females, allowing subordinate males to obtain mating opportunities not predicted by priority-of-access models (Alberts et al., 2003).

The ability of dominant males to monopolize females also depends on the amount of resistance they receive from the females. Females are expected to pursue reproductive strategies that will maximize their fitness (Engelhardt et al., 2006). When female

reproductive interests are not best served by cooperating with dominant males, assuming they will not evolve in response to attempted male control is analogous to assuming prey will not evolve in response to predation (Gowaty, 1997).

## ***2.2 Female mate choice***

According to sexual selection theory, females (in most species) are expected to exert a greater level of mate choice than males because of their greater parental investment (Trivers, 1972). This is especially true for female mammals because pregnancy represents a large investment and a significant threat to a female's survival (Wallen & Zehr, 2004). Although most theories for the evolution of mate choice assume mate choice provides some fitness benefits (adaptive models), some theories propose mate choice does not provide fitness benefits (nonadaptive models; Paul, 2002).

### **2.2.1 Mate choice models**

#### **2.2.1.1 Adaptive models**

Adaptive models of mate choice include direct (non-genetic) or indirect (genetic) benefits (Paul, 2002). An important direct benefit of mate choice may be paternal care. This benefit is often overlooked in mammals because males provide direct paternal care in only a small fraction of mammal species (Wolff & Macdonald, 2004). However, male primates have been shown to selectively support their offspring in agonistic disputes (Buchan et al., 2003) and to protect possible offspring from potentially infanticidal males (Borries et al., 1999a). Biasing paternity toward the male most able to provide assistance

to a female's offspring could provide fitness benefits for a female primate (van Schaik et al., 2000). Alternatively, females may receive services from males in exchange for mating opportunities. Tutin (1979) proposed male chimpanzees at Gombe may provide meat to estrous females in exchange for mating opportunities. Gomes and Boesch (2008) showed that female chimpanzees in the Tai chimpanzee community copulated more frequently with males who had shared meat with them over a 22-month period, but Mitani and Watts (2001) found no evidence to support the meat-for-sex hypothesis at Kibale. Barrett and Henzi (2001) suggested females may receive grooming or support in agonistic encounters in return for mating opportunities. If such a pattern exists, it is difficult to know if the service is truly traded for mating opportunities, and in some cases, the available evidence does not support this mode of interchange (Hemelrijk et al., 1999; Palombit et al., 1997). Finally, female mate choice may allow females to increase the likelihood of successful fertilization (Trivers, 1972; Paul, 2002). Direct benefits of mate choice (if present) would probably have a greater impact on female fitness than indirect benefits (Price et al., 1993), but often they are not readily apparent, leading to the assumption that the female is benefiting indirectly.

Models incorporating indirect benefits of female mate choice assume offspring viability is related to male attractiveness through some genetic mechanism (Paul, 2002). First, females may choose mates because they possess heritable traits that will improve her offspring's fitness. A number of "good gene" or "indicator" models have been proposed (reviewed in Paul, 2002), and they generally assume that males possess honest indicators of their quality (Zahavi, 1975). Studies of birds and fish in which females



choose brightly colored males, who are less parasitized than less brightly colored males, provide support for this mechanism of mate choice (Howard & Lively, 2004). The Fisherian “runaway” or “sexy son” model (Fisher, 1930) is sometimes linked to good gene models (e.g., Kokko et al., 2002). This model assumes a genetic coupling of the attractive male trait and the female preference for the trait which may lead to self-reinforcing coevolution between the trait and preference. In the model, females produce sons who have greater reproductive success (because they possess the attractive trait), regardless of whether the trait is indicative of high overall quality (reviewed in Andersson & Simmons, 2006).

Good gene and sexy son models make two assumptions. First, they assume there is a “best” male and he is the best male for all females. Second, they assume the attractive traits of males are heritable. These assumptions may not be realistic (Brown, 1997). Differing levels of relatedness to a male is one reason why the male may not be an equally suitable mate for all females, and attractive male traits may reflect heterozygosity, which is not directly heritable (Brown, 1997), or a male’s current status (e.g., dominance rank, health,) which is also not heritable. If attractive male traits are indicators of current status, rather than overall quality, female choice for these traits could reflect direct benefits (e.g., ensuring fertilization, providing a good protector for her offspring), rather than indirect benefits.

The recognition that a male may not be an equally suitable mate for all females has led to the development of genetic compatibility models. In these models, females choose mates based on the genetic benefits of the interaction between parental genotypes

(Zeh & Zeh, 1996). Females may selectively mate with males who are genetically dissimilar from themselves to increase the heterozygosity of their offspring (Brown, 1997), or they may mate with several males to reduce the likelihood that they will be fertilized by a genetically incompatible male (Zeh & Zeh, 1996). The major histocompatibility complex (MHC) has been proposed as a target of mate choice based on genetic compatibility (Potts et al., 1991). Regardless of the mechanisms involved, an important aspect of genetic compatibility models is that males differ in their suitability as a mate for different females (Tregenza & Wedell, 2000). Thus, the highest quality male may not be the optimal mate for all females.

#### **2.2.1.2 Nonadaptive Models**

Nonadaptive models of mate choice do not assume the chooser receives any benefit from being choosy. In the “sensory exploitation” model, a male trait is attractive because it exploits a pre-existing sensory bias (Ryan, 1990). Female behavior is thus manipulated in the male’s favor (West-Eberhard, 1984). Holland and Rice (1998) extended the concept to develop a “chase-away” model, in which below optimal female fitness, resulting from sensory exploitation, causes females to develop resistance to the male signal. This resistance causes the male signal to become exaggerated to overcome the new female threshold. Although sensory exploitation is generally included in nonadaptive models of mate choice, pre-existing sensory biases can also be involved in the development of indicator traits (e.g., eye spots on a peacock’s tail; Petrie, 1994).

There are numerous models for the development of mating preferences. These models are not mutually exclusive, and females probably must balance a number of potentially conflicting factors when choosing mates. However, direct evidence of female mate choice is limited, especially in primates (reviewed in Paul, 2002). In part this scarcity of evidence is probably due to difficulties in studying sexual selection in primates (Paul, 2002), but some researchers have begun to question whether females in some primate species exert mate choice (Small, 1992).

### **2.2.2 Multimale mating**

One reason female mate choice has recently been questioned in some primate species is the prevalence of multimale mating. It is not uncommon for primate females to copulate with multiple males during a single ovarian cycle (Tutin, 1979; Cords et al., 1986; Pereira & Weiss, 1991; Small, 1992). However, this pattern is not limited to primates. Multimale mating has been documented in socially monogamous birds and mammals (Palombit, 1994; Reichard, 1995; Fietz et al., 2000; Griffith et al., 2002), as well as birds and mammals living in groups with multiple adults of one or both sexes (reviewed in Wolff & Macdonald, 2004). Mating with multiple males does not necessarily preclude mate choice, though. Within a promiscuous mating strategy females may bias paternity based on the timing of copulations with different males (Matsumoto-Oda, 1999), and post-copulatory (cryptic) female choice (Eberhard, 1996) may represent another means by which females can bias paternity despite mating with multiple males.

Rather than preventing mate choice, multimale mating may allow females to accumulate additional direct and indirect benefits.

One direct benefit females may receive from multimale mating is fertilization insurance (Cox & LeBoeuf, 1977; Hoogland, 1998). But sperm depletion may be a result of, rather than the cause of, promiscuous mating by females. An alternative direct benefit of multimale mating may be reduced harassment of a female's infant. Males who have some probability of paternity are less likely to harm an infant because doing so could reduce their fitness (Soltis et al., 2000). By mating with multiple males, a female can reduce the pool of potentially infanticidal males (Hrdy, 1979). Because males also show an increased willingness to protect the infants of former mates (de Ruiter et al., 1994; Palombit et al., 1997; Borries et al., 1999b), multimale mating may also increase the amount of protection infants receive. However, the probability of paternity required for protection is probably higher than that required to prevent infanticide because the potential cost of protection is likely to be higher than the cost of not committing infanticide. Thus, females may have to balance paternity confusion (to reduce infanticide) and paternity concentration (to increase protection; van Schaik et al, 2000).

Rather than decreasing harassment of their infants, females may mate with multiple males to reduce harassment they receive from males. Avoiding sexual harassment may explain some instances of multimale mating in mammals (reviewed in Wolff & Macdonald, 2004). Because mating with a male to avoid sexual harassment may require the female to copulate with a non-preferred male, this tactic involves a cost to the female. This cost varies with the probability that the copulation will lead to

conception. When conception is not probable, the female's cost of mating is likely to be less than the cost of refusing (i.e., harassment). As the probability of conception increases, the female may be more likely to endure the cost of harassment to avoid the production of less fit offspring. The increased receptiveness of female northern elephant seals as they return to the sea at the end of the breeding season (Mesnick & LeBoeuf, 1991) may represent an attempt to avoid harassment by males.

In addition to direct benefits, females may gain indirect benefits via good genes from multimale mating (Kempnaers et al., 1992; Keller & Reeve, 1995). If females are unable to accurately assess male quality prior to mating, mating with multiple males may allow sperm competition to determine the "best" male (Keller & Reeve, 1995; Yasui, 1997), if the male's "good genes" allow him to produce more competitive sperm. Alternatively, multimale mating may allow the female to "choose" the genetically compatible sperm for fertilization. Genetic compatibility may not be evident at the phenotypic level, requiring females to mate with multiple males to ensure genetic compatibility (Zeh & Zeh, 1996), but odors associated with the major histocompatibility complex may provide a mechanism for assessment (Egid & Brown, 1989).

### **2.2.3 Constraints on female mate choice**

While multimale mating does not prevent females from exerting female mate choice, there are factors that can constrain a female's ability to mate selectively. Many of these factors are demographic, and the factors that increase monopolization by dominant males will decrease the ability of females to exert choice. In conjunction with these

demographic factors, male sexual coercion can reduce female ability to act on their mating preferences. Male sexual coercion is the use of force or threat of force by a male to increase the probability that a female will engage in fertile mating at some cost to the female (Smuts & Smuts, 1993).

Forced copulation and intimidation (male punishment of females who refuse to mate; Clutton-Brock & Parker, 1995) are commonly mentioned forms of sexual coercion in primates, but their success is questionable. In some species, females are able to resist male copulation attempts (e.g., Manson, 1992; Soltis et al., 1997a; Stumpf & Boesch, 2006), and male aggression does not necessarily improve male mating success with the female (Campbell, 2003). Even when there is a correlation between male aggression toward a female and his mating success with her, it may just be a consequence of increased time in proximity, rather than sexual coercion (Soltis et al., 1997a). Infanticide may also be considered a form of sexual coercion because the threat of infanticide may cause a female to copulate with non-preferred males to reduce the risk of infanticide. Infanticide is relatively common among primates (van Schaik & Janson, 2000) and almost certainly influences female reproductive strategies in species with infanticide. Thus, infanticide and male aggression toward females in the mating context (e.g., forced copulation and intimidation) may cause females to mate with non-preferred males, but in most cases, females may still be able to concentrate paternity in favor of preferred males by copulating preferentially with them during peak fertility.

In contrast, mate guarding (usually by dominant males) can severely limit the ability of females to mate with some males (Smuts & Smuts, 1993). Mate guarding can

be considered a form of sexual harassment, where repeated mating attempts by a male impose costs on a female (Clutton-Brock & Parker, 1995). Perhaps the largest cost associated with mate guarding is the limitation placed on female mate choice. The proximity of a dominant male may make it difficult for a female to mate with a lower-ranking preferred male. In fact, mate guarding has been called “one of the strongest forms of male coercion if it is not based on female cooperation” (Engelhardt et al., 2006, p. 741). Female ability to bias paternity in favor of preferred males depends on their ability to overcome male coercion.

### ***2.3 Sexual Conflict***

Female mate choice does not always oppose male-male competition. There are situations in which female choice reinforces male-male competition (e.g., Alfaro, 2005; Setchell, 2005). However, there are situations in which female choice does oppose male-male competition (e.g., Manson, 1992; Soltis et al., 1997b; Stumpf & Boesch, 2005), leading to sexual conflict (Gowaty, 1996). When female choice and male-male competition conflict, female choice may be limited by male mating behavior (Smuts & Smuts, 1993). In turn, females will be under selection to develop counter-strategies to subvert male control. In primates, most discussions of female reproductive counterstrategies focus on infanticide avoidance (e.g., Hrdy, 1979; Soltis et al., 2000; van Schaik et al., 2000). Although infanticide is likely to be an important factor influencing female reproductive strategies (especially in certain species), the ability of females to exert mate choice in the face of attempted male control may be a more general concern

for female primates because female reproductive success is likely to be higher when females have some control over who sires their infants (Gowaty, 1997). In fact, studies in mice have shown that offspring quality is improved when females are able to exert mate choice (Drickamer et al., 2003; Gowaty et al., 2003).

The ability of females to implement their own reproductive strategies depends to a large extent on the balance between female mate choice and male-male competition. When female mate choice reinforces male-male competition, females should not face much difficulty mating with preferred males. When female mate choice and male-male competition conflict, the ability of females to mate with preferred males is likely to be species- and context-dependent. On the species level, two factors that influence the balance of female mate choice and male-male competition are the amount of sexual dimorphism and male ability to detect the fertile phase of the female ovarian cycle. High levels of sexual dimorphism are generally presumed to increase the success of male sexual coercion (Clutton-Brock & Parker, 1995), but this is not necessarily the case. In mandrills, females are able to escape a mate-guarding male using branches that are too small for him (Setchell, 2005). Because mate guarding has associated costs (Alberts et al., 1996; Matsubara, 2003), the ability of males to detect the fertile phase of female cycles would improve the success of this tactic by allowing them to concentrate their efforts during this time (Engelhardt et al., 2006). This ability is likely to vary among species, and possibly males within a species, but in some primate species, males seem to detect the fertile phase with some accuracy (e.g., Engelhardt et al., 2004, Emery Thompson & Wrangham, 2008). The balance of power between the sexes will also vary



within species due to context-dependent factors. As noted earlier, many of these factors will be demographic, but differing abilities of dominant males (e.g., to monopolize females, fight off rival males, detect the fertile phase) will also play a role.

Post-copulatory mechanisms are an aspect of sexual selection that is sure to play a role in sexual conflict but has not yet received enough attention. As with pre-copulatory mechanisms of sexual selection, early studies of post-copulatory selection focused on male-male competition, in the form of sperm competition (Snook, 2005). However, if females are unable to exert mate choice by mating with preferred males, they may rely on selective mechanisms within the female reproductive tract to bias paternity toward a particular male via post-copulatory choice (Eberhard, 1996). Most research on post-copulatory choice has been done with insects, but the presence of antigens on the surface of primate sperm (Batova et al., 1998; Lassere et al., 2003) may provide a means by which the sperm of different individuals can be discriminated (Quiatt & Everett, 1982). Although it is essentially unknown whether post-copulatory choice occurs in primates, the potential seems to exist in the majority of primate species (Birkhead & Kappeler, 2004).

## ***2.4 Other mechanisms of sexual selection***

### **2.4.1 Male mate choice**

Traditionally it had been assumed that males are “eager to pair with any female” (Bateman, 1948, p. 350). This assumption fails to recognize the potential costs incurred

by males through mating. Repeated mating by dominant males can lead to sperm depletion (e.g., Preston et al., 2001), and mate guarding involves energetic costs because males may be limited in the amount of time they can forage (Alberts et al., 2003) and opportunity costs (they can only copulate with one female at a given time). Mate guarding is also associated with the risk of injury from contest competition (Setchell & Wickings, 2006). Not surprisingly, there are times when males fail to respond to sexual solicitations by females (Alfaro, 2005). When multiple females are fertile at the same time, or if females repeatedly enter estrus in succession, dominant males may be forced to choose with which females to mate and when to mate with them (Smuts, 1987; Alfaro, 2005). In such cases it would be advantageous to dominant males to mate selectively with females having the highest reproductive potential (Parga, 2006).

Experimental evidence of male mate choice has been demonstrated in mice (Drickamer et al., 2003; Gowaty et al., 2003), and male preferences for certain females have been reported in primates (reviewed in Parga, 2006). In primates, female age, parity, and dominance status may all affect a female's reproductive potential and thus be used by males to assess her attractiveness (Beach, 1976). In species with sexual swellings, the size of the swelling may also be a signal of female quality (Domb & Pagel, 2001), but this point is controversial (see Nunn et al., 2001). Males often prefer older females to younger females (Anderson, 1986), which could be confounded by a preference for multiparous females (Parga, 2006). In many species, a preference for higher-ranking females (e.g., Kuester & Paul, 1996) may also be confounded by age and therefore parity. In chimpanzees, males preferred older parous females to younger parous females, but

dominance rank was not considered (Muller et al., 2006). In ringtailed lemurs (*Lemur catta*), males showed preferences for older females with high reproductive success and females belonging to the prime reproductive age class (4-9 years), but dominance rank did not affect male preferences (Parga, 2006). And in mandrills, males preferred higher-ranking females to lower-ranking females and parous females to nulliparous females, but age did not affect male preferences (Setchell & Wickings, 2006). The general sense from these studies is that parity may be the primary factor influencing male mate choice.

Although female mammals, and especially female primates, are expected to be the more choosy sex because of their greater parental investment (Trivers, 1972), there is increasing evidence that males often demonstrate some level of mate choice. Because of the interrelatedness of female age, parity, and rank, additional research is needed to determine the basis of male preferences.

#### **2.4.2. Female-female competition**

Female-female competition may be the most overlooked aspect of sexual selection. This phenomenon has received the most attention in species with sex-role reversal, but sex-role reversal is not necessary for female-female competition (Berglund et al., 1993). Female-female competition (as a component of sexual selection) can include competition for mates, as well as competition for resources required to raise offspring (Berglund et al., 1993). Because competition for resources to raise offspring can be difficult to distinguish from competition for resources for the female's own

survival, only competition for mates (and the services they may provide) will be considered here.

Females should compete for males if there is variation in male quality that affects female fecundity and the benefits received from competition outweigh the costs of competition (Palombit et al., 2001). Variation in male ability to enhance offspring survival and male fertilizing ability are likely aspects of male quality that may attract female competition.

Some aspects of a male's ability to enhance offspring survival (e.g., protection from infanticide) may be limited resources. As the number of a male's offspring increases, his ability to protect them all will likely decrease. Consequently, females may compete over the protection provided by dominant males. This competition can occur during mating and after the offspring are born. During mating, high-ranking females could attempt to disrupt copulation attempts by lower-ranking females to reduce the number of offspring the dominant male has to protect. Once the offspring are born, females could compete over access to the dominant male, strengthening social bonds and maintaining proximity to increase the protection received by their offspring. The available evidence suggests female-female competition over male "friends" in chacma baboons (*Papio ursinus*) is to attain protection for the offspring from the male friend (Palombit et al., 2001).

Another limited resource possessed by high-quality males is sperm. Repeated copulation can lead to sperm depletion (Preston et al., 2001). Thus, dominant females may interrupt copulation attempts by subordinate females to ensure the male has

sufficient sperm reserves for their own fertilization (Berglund et al., 1993). As part of female competition over sperm, females may engage in multiple copulations with a male to deplete his sperm reserves, preventing the fertilization of other females (Small, 1988). This hypothesis is difficult to test, though, because it is not possible to distinguish between a female copulating multiple times to ensure fertilization and a female copulating multiple times to cause sperm depletion.

Evidence of female-female competition in species without sex-role reversal is limited, and evidence that it has an effect on female fecundity is even rarer. In baboons, Dunbar and Sharman (1983) demonstrated a negative correlation between birth rates and female-to-male ratio across a number of populations. They attributed this relationship to increased female-female competition at higher female-to-male ratios. In talapoin monkeys (*Miopithecus sp.*), subordinate females received higher rates of aggression and, unlike dominant females, did not produce an LH surge following estrogen stimulation (Bowman et al., 1978). The authors suggested the LH surge may have been blocked by high prolactin levels because isolating the subordinate female from aggression caused a drop in prolactin levels and allowed the LH surge to occur.

There are theoretical reasons to believe female-female competition should occur and limited evidence suggesting it does. However, the area of female-female competition remains largely unexplored.

## ***2.5 Sexual selection in mantled howling monkeys***

Mantled howling monkeys are members of the family Atelidae (Schneider et al., 1993). They are found throughout much of Central America from southern Mexico to the west coasts of Colombia and Ecuador (Crockett & Eisenberg, 1987). Mantled howlers typically live in multimale-multifemale groups of unrelated adults, although single-male groups also occur. Group sizes are variable among and within sites. At Hacienda La Pacifica, Costa Rica, Clarke et al. (1999) reported group sizes ranging from 4 to 28 individuals. The mean group size was 10.6 individuals, consisting of 1.5 adult males and 4.7 adult females. The skewed sex ratio appears to be due primarily to differential mortality, rather than differential birth rates, between the sexes. Based on data collected from 1970-1981, Clarke and Glander (1984) reported a skewed sex ratio at one year of age despite observing equal numbers of male and female infants born. Not counting cases in which an infant died with its mother, 100% of female infants survived beyond one year, but only 39% of males survived to this age (Clarke & Glander, 1984).

Mantled howler social groups are characterized by linear dominance hierarchies, in which adult rank is inversely related to age (Glander, 1980; Jones, 1980). Both male and female mantled howlers disperse as juveniles and live as solitaries until they enter a new group. To enter and remain in a new group, individuals must attain alpha status. Females begin by challenging the lowest-ranking female and work their way up the dominance hierarchy. Males, on the other hand, generally attack the highest-ranking male only (Glander, 1992). Glander (1992) reported never observing secondary dispersal

by males and only four cases of secondary dispersal by females in approximately 20 years of study. Although relatively uncommon, secondary dispersal by males and females has been documented in recent years and may occur in response to changes in a group's sex ratio (Clarke & Glander, 2004). Clarke and Glander (2010) demonstrated that females tend to leave groups in which the sex ratio exceeds 4 females per male, and males leave a group when the sex ratio falls below 2 females per male.

Mantled howlers are non-seasonal breeders (Clarke & Glander, 1984). There are birth clusters, but there is no consistency in the timing of these clusters from year to year. Mantled howler males and females are not believed to reproduce until successfully entering the dominance hierarchy (Jones, 1985). Male mantled howlers generally immigrate successfully at approximately 5-6 years of age, and successful female immigrants are approximately 3.5 years old (Glander, 1992). This is consistent with reports that age at first reproduction is approximately 4 years for female mantled howlers (Glander, 1980).

The female ovarian cycle is accompanied by a cyclic swelling and color change of the sexual skin (Glander, 1980). By measuring the interval from the midpoint of one maximal sexual swelling to the next, Glander calculated a mean cycle length of 16 days. During each cycle, females exhibit proceptive and receptive behavior (Beach, 1976) for two to four days. Gestation length is approximately 186 days. Following birth, there is a 3-4 month anovulatory period associated with lactation; however, females quickly resume cycling (within three weeks) if the infant dies. In addition, females generally spend 8-15 months cycling before becoming pregnant again. Consequently, the average

interbirth interval following infant survival is approximately 22.5 months, but may be as short as 9 months following the death of an infant (Glander, 1980). Fedigan and Rose (1995) reported an interbirth interval of 19.9 months for all pregnancies.

Male-male competition is a conspicuous feature of mantled howling monkey reproduction. Alpha males attempt to prevent subordinate males from mating with females who are in peak estrus (Glander, 1980). This interference is reported to occur prior to copulation, as the use of direct aggression to interrupt copulation is reported to be rare or absent in this species (Jones, 1985). Before and after the midpoint of a female's receptive period, alpha males reject solicitations by females and do not prevent subordinate males from mating (Glander, 1980). Consequently, a significantly higher proportion of an alpha male's copulations occur during peak estrus (Jones, 1985). The ability of males to accurately determine the ovulatory state of females may be aided by the presence of a functional vomeronasal organ in this species (Starck, 1975).

The relatively small adult male and female cohorts in mantled howler social groups (Clarke, 1983) and the relative lack of overlap in peak estrus among females (Glander, 1980) should increase the ability of dominant males to monopolize females. However, limited genetic paternity data show dominant males may be less successful than previously believed (Ellsworth, 2000). One possibility is that the brief copulatory pattern and arboreal habitat of this species favor the use of sneak copulations. Additionally, male-male coalitions have been reported between older, low-ranking males and young males attempting a takeover. These coalitions are reported to allow the older male to gain mating opportunities they would not otherwise obtain (Clarke, 2005).



Female mate choice is less clear in this species. Females have been reported to show social preferences for certain males (Zucker & Clarke, 2007), but there was no indication of how this affected mating. The preferences were reported to change over time, which may indicate the flexibility to adjust to changing social situations (Zucker & Clarke, 2007). It also suggests that females may be more responsive to a male's current status, rather than his inherent quality. Male mate choice, on the other hand, has not been addressed in this species. Males are reported to prefer females in peak estrus (Glander, 1980), but no preferences for individual females have been reported.

Female mantled howlers appear to engage in female-female competition by directing aggression toward the infants of other females. The adaptive significance of birth clusters is suggested by the fact that infants are more likely to survive when part of a cluster (Clarke & Glander, 1984). Having an infant during a birth cluster may reduce aggression toward the infant because other females are caring for their own infants (Clarke et al., 1998).

Male and female mantled howlers may experience sexual conflict resulting from attempts by dominant males to monopolize females. Although estrous overlap is minimal, females often enter estrus in close succession (Glander, 1980). Thus, males may encounter costs of mate guarding in terms of foraging and sperm depletion. Avoidance of sperm depletion may explain the relatively short period of time the alpha male mate guards each female. Alpha males only mate guard females during a portion of the two to four days during which they are receptive and refuse female solicitations outside this window (Glander, 1980).

Infanticide may be another aspect of sexual conflict in this species. One case of infanticide and numerous infant disappearances coinciding with male takeovers have been reported in mantled howlers, and these “eliminations” of a female’s offspring resulted in decreased interbirth intervals, consistent with the sexual selection hypothesis (Clarke, 1983).

In summary, limited evidence exists for nearly every mechanism of sexual selection in mantled howling monkeys. However, the limited nature of the evidence does not provide a clear picture of sexual selection in this species. This dissertation attempts to supplement the existing information by exploring the following hypotheses.

## ***2.6 Hypotheses***

Regarding female mate choice, patterns of female proceptivity, proximity, and copulation were used to assess female preferences for males. These patterns were then used to determine whether females showed preferences for males and whether the preferences were consistent across females. Consistent preferences across females would be consistent with a good genes explanation, but it does not necessarily rule out genetic compatibility because the same male could theoretically be the most compatible mate for all of the females in the sample. Preferences for males that differ across females would support a genetic compatibility explanation for female mate choice. Because female mantled howlers engage in multimale mating, behavioral preferences may not translate into paternity by the preferred male. Genetic paternity exclusion was attempted to determine whether a preferred male was the sire of a female’s offspring.

In order to explore the impact of male-male competition on mating patterns, the copulation rates for males of different ranks was assessed. If male-male competition is largely responsible for determining mating patterns, the alpha male should have the highest copulation rate, with the copulation rate decreasing as rank decreases. Because multimale mating occurs in this species, the timing of copulations was examined to determine whether there were rank-related patterns in the timing of copulations. Finally, the possibility that a relationship between copulatory success and male coalition formation was explored to assess whether the lower-ranking coalition partner achieved improved copulatory success by participating in a coalition.

An important aspect of male-male competition appears to be male following behavior, in which a male moves in synchrony with a female to maintain proximity to that female for an extended period of time. When high-ranking males follow a female, it may limit the female's ability to mate with lower-ranking males. However, a female may attract a high-ranking male as part of her own reproductive strategy. Thus, it is difficult to differentiate between male-male competition and female mate choice when females prefer high-ranking males. In an attempt to determine whether female mate choice or male-male competition was the impetus behind male following of females, the timing of male following was compared with the start of female proceptive behaviors. If male following began before the start of female proceptivity, it would suggest that male-male competition was the driving force behind male following behavior.

The possibility that females compete by harassing the infants of other females was investigated by looking at levels of aggression directed toward infants. Presumably the

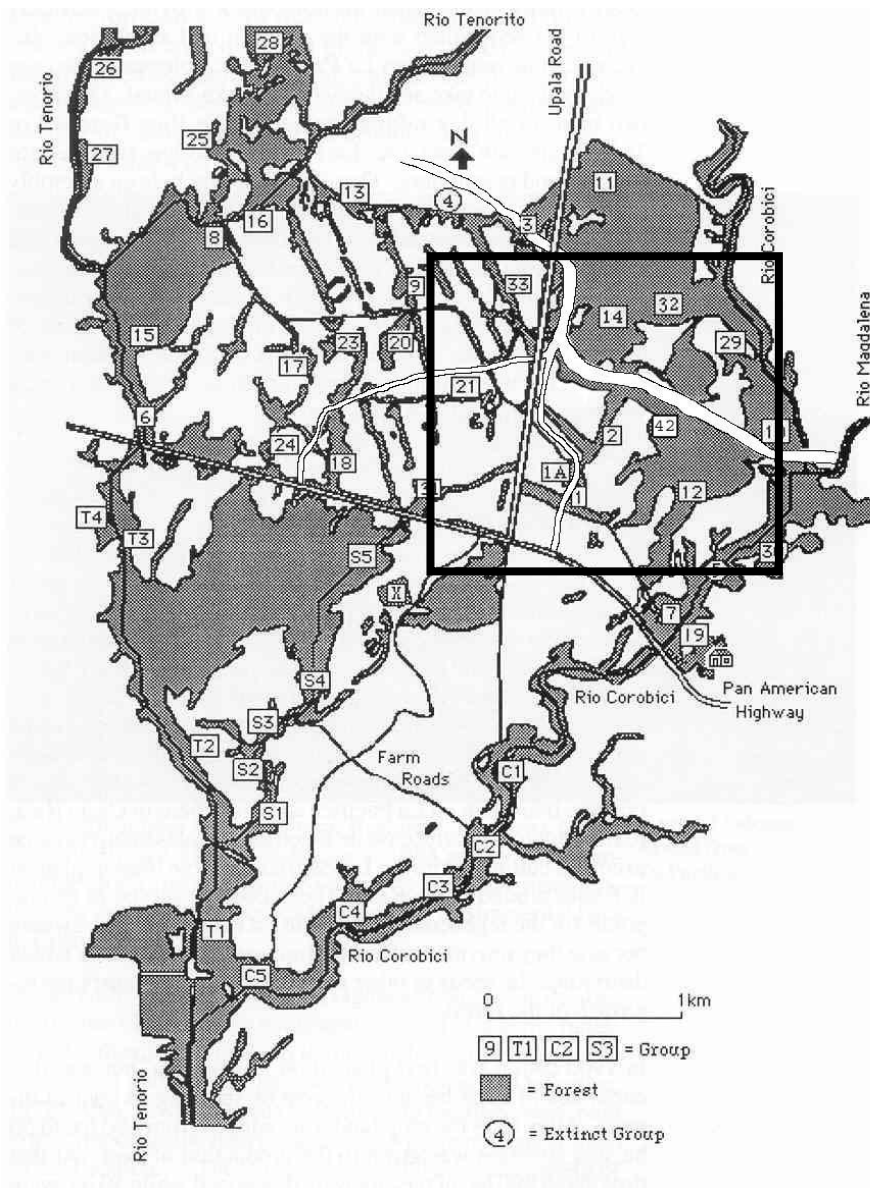
infants of lower-ranking females would receive more aggression than the infants of higher-ranking females. Although not addressed in previous studies, female-female competition in the mating context was assessed by determining whether rates of female-female aggression were higher in the mating context versus the non-mating context.

Finally, patterns of male following behavior were used to look for the existence of male mate choice. Determining whether male preferences are related to rank versus parity should be relatively clear, but parity and age are confounded because of the reverse age-graded dominance hierarchy in this species.

## **3. Methods**

### ***3.1 Study site***

Hacienda La Pacifica is a 1,980 hectare cattle ranch and tilapia/rice farm located at the base of the Cordillera de Tilarán, five km northwest of Cañas, Guanacaste, Costa Rica. It lies within the lowland tropical dry forest life zone (Holdridge, 1967) and consists of 600 hectares of semi-deciduous forest remaining in several large tracts as well as windbreak strips and riparian forests (Figure 1). The howler population density of 63.8/km<sup>2</sup> (Clarke et al., 2002) falls at the upper end of the range reported for mantled howlers at other sites. The population size of howlers on La Pacifica (370 in 1998) has remained stable since the mid-1970s, but the number of groups has increased, causing a decrease in mean group size (Clarke et al., 1999). The increased number of groups may have been caused by altered land use following the sale of the farm in 1986 (Clarke et al., 2002). This hypothesis is supported by the most recent survey which showed group sizes have increased and the number of groups has decreased following recent, stable land use (Clarke et al., 2007).



**Figure 1: Map of La Pacifica indicating location of social groups**

La Pacifica has been the site of numerous studies over the past 35 years, providing extensive demographic data for this population. The animals are highly observable because they are well habituated and the forest has a low canopy. Glander

(1975) reported that focal animals were lost a total of 72.4 hours out of 1,986 hours of observation or an average of 26 minutes out of 709 minutes per day over 168 days.

### ***3.2 Study schedule and subjects***

The present study took place from March 2006 – March 2007. It consisted of three capture periods and two observation periods. Captures were performed in March 2006, July 2006, and March 2007. Observations were performed from 21 March 2006 – 16 July 2006 and from 31 July 2006 – 27 February 2007.

The study focused on the adult females in Group 2 (Figure 1). This group has been regularly monitored since 1984 (Clarke et al., 2002). Individual animals in the group were marked before the start of the project (see description below). All areas of Group 2's home range were accessible for observation, and the group's home range is in upland habitat with a relatively short canopy. The group's home range overlapped that of three adjacent groups (1, 12, and 33). In addition, a group consisting of one adult male and two adult females (Group 2a) occupied the home range of Group 2.

At the beginning of the study, the group consisted of eight adult females, one subadult female, and five adult males (one of which was peripheral until July 2006). The subadult female emigrated in late May 2006 and is not included as a focal animal. In early May 2006, an adult female immigrated to the group and had successfully integrated herself into the group by early June 2006. The nine adult females (eight original and one immigrant) served as focal animals (Table 1). Of these nine females, six were observed to cycle during the study.

### ***3.3 Capture***

Study animals were captured to collect blood samples for genetic analyses and to mark the animals for individual identification. All captures in this study were performed by K. Glander. Twenty-nine individuals in Group 2 (including all 5 adult males and all 9 adult females) and all adult males in Groups 1, 2a, 12, and 33 (Table 2) were captured during at least one capture period. In addition, Glander returned in February 2008 and captured four additional immature individuals (from Group 2's home range) who were not caught during the study period. Table 2 lists all individuals captured in Group 2.

Capture of the animals was accomplished using the Pneu-Dart™ system (Pneu-Dart, Inc., HC 31, Williamsport, PA 17701). The Pneu-Dart system employs disposable non-barbed darts with a 9mm needle delivered by a carbon dioxide powered gun. The darts were loaded with Telazol®, a nonnarcotic, nonbarbiturate, injectable anesthetic. (Telazol® is a Schedule IIIN drug; Glander's DEA Registration Number is RG 0138619). It is a combination of equal parts by weight of tiletamine hydrochloride (an arylaminocycloalkanone dissociative anesthetic) and zolazepam hydrochloride (a nonphenothiazine diazepamone with tranquilizing properties; Fort Dodge, Fort Dodge, IA 50501-0518). The dosage was 25mg/kg. This dosage has been safe and effective for more than 2,600 primate captures (see Glander et al., 1991 for a detailed description of the capture protocol).



**Table 1: Group 2 Animals Captured**

Adult Females		Adult Males		Immature Females		Immature Males	
ID	Age <sup>1</sup>	ID	Age <sup>1</sup>	ID	Age <sup>1</sup>	ID	Age <sup>1</sup>
WI	19	VO	22	PE	3	WG	3
AZ	17	RA	19	TA	3	SG	2
JU	15	OR	14	WY	3	357	3
SA	15	AC	8	DI	3	JO	7/1/06 <sup>2</sup>
SC	13	HO	5	SO	2.5	381	3/07 <sup>2</sup>
HI	10			AN	2		
SI	7			SD	1.5		
ZA	7			AI	1.5		
AT	6			HP	1.5		
				ZY	1.5		
				GA	1		
				074	1		
				021	1		
				SP	7/14/06 <sup>2</sup>		

<sup>1</sup> at beginning of study (in years)

<sup>2</sup> date of birth

**Table 2: Neighboring Males Captured**

Group 1		Group 2a		Group 12		Group 33	
ID	Age	ID	Age	ID	Age	ID	Age
DY	3	JA	5	CO	4	MA	12
RU	17			KA	5	CB	12
				HE	22		

Once captured, the monkeys were weighed and measured. In addition, less than 0.5 mL of blood was collected from the femoral vein using a 20-gauge needle and blotted on Whatman FTA<sup>®</sup> cards. Cards were placed in an envelope with silica gel and stored at ambient temperature until analysis. The animals were then marked with collars for

females and anklets for males. Immature animals did not receive collars or anklets because they were still growing. Instead, a patch of fur was dyed to provide a means of individual identification. Although many individuals possess identifying features that can be used if collars and anklets are lost, the collars and anklets make rapid, accurate identifications possible, allowing the observer's focus to remain on the behavior of the focal animal. An Avid<sup>®</sup> microchip was also placed subcutaneously between the shoulder blades to ensure proper identification in subsequent captures when collars and anklets have been lost (see Glander et al., 1991 for a detailed description of the marking protocol).

Animals that recovered from the capture dosage before the procedures were completed were given injections of 1-3mg/kg of Telazol<sup>®</sup>, repeated as often as needed. After all procedures were completed the animals were placed in burlap bags until they recovered enough to walk or climb unaided. The bags were kept in the shade and are the best means of holding an animal until it recovers because the bag reduces visual stimulation. Following recovery, the animals were released in their home range near the capture site.

### ***3.4 Observations***

#### **3.4.1 Observation schedule**

Observations were performed from approximately 0630-1700 on five days per week. On each observation day from 21 March – 27 June 2006, six females were

observed for one hour each unless a male was noticed shadowing a female, possibly indicating estrus. If a male continued to follow a female for more than one hour, she became the focal animal for the remainder of that day and each subsequent day until she was no longer attractive (Beach, 1976). The order in which females were observed was determined randomly, but the randomization was constrained to ensure that observations on each female were balanced regarding time of day and no females were observed twice on the same day. If more than one female was attractive at the same time, the female being followed by the alpha male was chosen as the focal animal and observations of the other estrous female(s) were performed *ad libitum*.

Beginning on 29 June 2006 and continuing through the end of observations on 27 February 2007, I began observing two females per day when no females showed signs of estrus. One female was observed in the morning (0700-1130), and one female was observed in the afternoon (1130-1600). The primary reason for this change was the difficulty of switching focal animals during the wet season. During the dry season, search time was negligible, but in the wet season, search time could be significant (greater than 30 minutes). Thus, the number of females observed per day was reduced to improve the ratio of observation time to search time. In addition, it was possible to reduce the number of females observed per day because fewer females were cycling at this point. From March through May 2006, as many as four females were cycling, but by June 2006 there were at most two females cycling at the same time. Consequently, there were more days on which to observe non-estrous females, meaning not as many females had to be observed per day.

### 3.4.2 Observation methods

This study used focal animal sampling (Altmann, 1974; focal sampling with continuous recording, Martin & Bateson, 1993) of adult female mantled howling monkeys. Table 3 lists the behaviors that were recorded during focal observations. The frequency and duration of behavioral states and the frequency of events (Martin & Bateson, 1993) were recorded. Also, the initiator and receiver of interactions were noted. Focal observations were supplemented with *ad libitum* observations of other group members and all occurrences recording of behaviors (Altmann, 1974) that may be used by males to determine a female's ovulatory state (e.g., inspection of genitalia) or demonstrate sexual interest (e.g., lingual gesturing). Extensive *ad lib* sampling was possible during focal animal rest time (focal animals rested approximately 70% of total observation time). Data collected on agonistic interactions (from focal and *ad lib* observations) were used to assess the dominance hierarchy on a weekly basis.

**Table 3: Behaviors Recorded**

Behavior Name	Behavior type <sup>1</sup>	Behavior name	Behavior type
<b><u>Activities</u></b>		<b><u>Interactions (cont.)</u></b>	
Rest	state	<i>Subordinance</i>	
Locomotion	state	avoid (be supplanted)	event
Feed	state	cower	event
Play	state	flee	event
genital rub	event	<i>Male-related</i>	
break branch	event	present	event
sniff/lick (urine)	event	lingual gesture	event
		approach (move to < 3 m)	event
		leave (move to > 3 m)	event
		follow (maintain proximity)	event
<b><u>Interactions<sup>2</sup></u></b>		<i>Infant-related</i>	
<i>Affiliation</i>		infant transfer	event
groom	state	carry	state
sit close (< 1 m)	state	<i>Other</i>	
<i>Contact Aggression</i>		sniff/lick (axilla, genitalia)	event
bat/hit	event	<b><u>Sexual<sup>3</sup></u></b>	
push	event	mount	state
grab	event	intromission	state
bite	event	thrusting	state
<i>Noncontact</i>		ejaculation <sup>4</sup>	event
<i>Aggression</i>			
chase	event		
supplant	event		

<sup>1</sup> Use of the terms event and state follows Martin & Bateson (1993).

<sup>2</sup> The identity of the initiator and recipient of interactions was recorded.

<sup>3</sup> The focal animal was the recipient for all sexual behaviors.

<sup>4</sup> Ejaculation was indicated by the presence of an ejaculatory pause.

### 3.5 Genetic paternity analysis

Ideally this study would include hormone analyses to determine the probable timing of peak fertility, in addition to the genetic paternity analyses. However, budgetary constraints forced a choice between the two types of data. Because the duration of

female receptivity was previously reported to be so brief (Glander, 1980) and because male behavior was reported to be a good indicator of ovulation (Clarke et al., 1991), the decision was made to include genetic data at the expense of endocrine data.

Blood samples were sent to Therion International for genetic analysis. Analyses used eight microsatellite markers (Ap6, Ap68, Ap74, D5S111, D6S260, D8S165, D14S51, D17S804) previously identified as polymorphic in mantled howling monkeys (Ellsworth & Hoelzer, 1998). For each natal individual sampled in the study group paternity exclusion was performed in an attempt to determine genetic paternity. In this analysis, all males from the study group as well as all males in neighboring groups were included as potential sires.

### ***3.6 Behavioral Analysis***

#### **3.6.1 Data preparation**

Two different proximity indices were calculated as possible indicators of female preference for males. The first index is a female approach index. For each male-female dyad, I calculated the proportion of male-directed approaches by the female toward a given male. Higher values indicate that the female approached that male relatively more than other males. The second index is a proximity maintenance index. For each male-female dyad, I calculated the proportion of total approaches between the members of the dyad that were performed by the female. Values above 0.5 indicate the female approached the male more than the male approached the female. The proximity

maintenance index is useful because it controls for the possibility that a female approached a male often because he spent a lot of time maintaining proximity to her.

A number of rates were also used in the following analyses. In all cases the rates show the number of instances per hour. The lingual gesture rate for a dyad was calculated as the number of times the female directed a lingual gesture toward the male per hour of time the female was observed on days when she was proceptive. Copulation rates were calculated as the number of copulations per hour of time females were observed on days when they copulated. Finally, aggression rates were calculated for female-female aggression. Rates were calculated as the number of instances of aggression per hour on days when the female was followed by a male and on days when the female was not followed.

When testing for female mate choice, the above-mentioned statistics were calculated for the observations during which females were followed by males, proceptive toward males, and/or copulating with males. The statistics were also calculated for observations during which females were cycling but not mating (i.e., not followed by males, proceptive toward males, nor copulating with males,) pregnant, and lactating. These statistics were used to determine how female reproductive state influenced affiliation with males.

### **3.6.2 Female mate choice**

A Kruskal-Wallis test was used to test the hypothesis that all females prefer the same male. Three separate measures of female proceptivity (female approach index,

proximity maintenance index, and lingual gesture rate) were tested, as was male copulation rate. For these analyses, I tested for a significant difference among males based on male identity. Because male rank changed during the observation period, I performed another Kruskal-Wallis test for copulation rate to test for differences among males based on male rank. This test was performed to determine if females chose the same male based on rank, rather than male identity.

In order to test the hypothesis that females show preferences for males but the preferences are not consistent across females, I used a chi-square test. I compared the observed frequency of male-directed approaches by females, male-directed lingual gestures by females, and female copulations with males with the expected frequencies assuming an equal distributions of the behaviors across males. I also tested whether there was a significant correlation between possible indicators of female preference (female approach index, proximity maintenance index, and lingual gesture rate) and copulation rate.

Because the dyads in the previous analysis are not independent, I also performed a computer simulation similar to that created by Soltis (Soltis et al., 1997a). For each female, males were ranked according to the given indicator of female preference. Because most females in my study copulated with all males (preventing a comparison between copulatory partners and non-copulatory partners) I then weighted male rank based on the proportion of a female's copulations performed by the male. The computer simulation thus tested whether the males with whom females copulated most often were more likely to have higher indices of female preference.



The computer simulation was run for 10,000 trials. During each trial, a rank was assigned randomly to each male from all possible ranks for each female, and the mean rank for six females was calculated. The mean weighted rank was determined by multiplying the mean rank by 0.20, the proportion of copulations per male if copulations are distributed evenly among the males. The p-value was calculated as the proportion of trials in which the simulated mean weighted rank was farther from the expected mean weighted rank than the observed mean weighted rank.

### **3.6.3 Male-male competition**

The relationship between rank and copulatory success was assessed by pooling the copulations by males of a given rank. Because male rank changed during the observation period, multiple males contributed to each rank. I then plotted the copulation rate against male rank to explore the relationship between these variables. To look for rank-related patterns in the timing of copulation, I calculated the proportion of copulations performed by males of each rank for each day of female cycles (with day 1 representing the first day copulations were observed). I also plotted the proportion of total copulations performed by males of each rank as a function of the day of a female's cycle.

I compared the copulatory success of males (measured as the proportion of total copulations performed by each male) during the tenures of the different alpha males to explore the use of male coalitions to improve mating success.

In an attempt to determine whether female proceptivity caused a male to begin following that female, I scored each female cycle based on which occurred first, male following or female proceptivity. I looked at the first day on which female proceptivity, male following, or a combination of the two occurred for each female cycle. The cycle was scored as being initiated by male following or female proceptivity if only one of those behaviors occurred on the first day. If both behaviors occurred on the first day, the cycle was scored inconclusive. I then calculated the proportion of cycles that were initiated by male following versus female proceptivity.

#### **3.6.4 Female-female competition**

To look for evidence of female-female competition, I calculated the rate of aggression directed by females toward the infants of other females, and I examined the nature of the aggression in an attempt to understand the impact on the infant. I also compared the amount of aggression a female received when she was being followed by a male (suggesting the presence of estrus) to the amount received when she was cycling but not being followed, using a Wilcoxon signed-ranks test.

#### **3.6.5 Male mate choice**

Finally, I examined whether there were differences among females in terms of the proportion of time they were followed by the alpha male using a Kruskal-Wallis test. Specifically, I examined the proportion of time the alpha male was within 3m of the

female on days when he followed the female. This measure was used as a proxy for male preference, assuming the male would maintain closer proximity to preferred females.

## 4. Results

### *4.1 Genetic paternity analysis*

Of the eight microsatellite markers, only four (Ap74, D5S111, D6S260, D17S804) were polymorphic in this sample, and the overall level of heterozygosity was relatively low. Upon examination of the genetic data, I determined that in many cases (7 out of 16) where maternity was believed to be known, the purported mother was excluded at one locus (Table 4). Of these seven offspring, one could not be assigned to any females in the group. There were three cases in which two females could not be excluded as the mother, two cases in which four females could not be excluded as the mother, and one case in which six females could not be excluded.

Four of the cases in which the purported mother was excluded were particularly confusing. Two of the offspring were approximately one year old when captured. There were only two females in the group with infants that age, but both of these females were excluded as mothers for both of these infants. Also, two offspring were captured as infants. Both were less than one month old when captured, and both were captured because they were clinging to a female (presumably the mother) when she was captured. At the time, these were the only infants less than five months old in the group. For both infants, the female to which the infant was clinging was excluded as the mother. In both cases, the other female known to have a young infant could not be excluded as the

mother. However, the females were captured on different days so it is unlikely that the infants (or their samples) were mixed up.

Despite the problems with maternity assignment, I still attempted to assign paternity. Using a conservative approach (i.e., assuming the mother was unknown), allowed determination of genetic paternity in only one case. This individual, believed to have been conceived during the observation period of this study, appears to have been sired by a male from Group 1. A second analysis, in which purported mothers who could not be excluded were assumed to be the actual mother, resulted in only one additional paternity assignment. The offspring in this case was approximately 14 months old at the beginning of this study and appears to have been sired by the top-ranked male at the time of conception (M. Clarke, *personal communication*).

In two other cases, paternity exclusion did not identify a single possible sire, but it did point toward a probable sire. In each case, the offspring shared a rare allele (allele 167 at locus D5S111) with only one potential sire. Because none of the females in the study group possessed this allele, the most likely source of the allele was the probable sire (the top-ranked male immediately prior to the observation period; M. Clarke, *personal communication*). One offspring was approximately 22 months old at the beginning of the study, and the other was conceived around the beginning of the observation period.

**Table 4: Exclusion of Purported Dams for Group 2 Offspring**

Offspring Loci		Alleles		Dam	Loci		Alleles	
AT	D17S804	163	165	AZ	D17S804	163	167	
	D5S111	165			D5S111	165		
	AP74	154			AP74	152	154	
	D6S260	185			D6S260	181		
AI	D17S804	163	165	AZ	D17S804	163	167	
	D5S111	165			D5S111	165		
	AP74	152			AP74	152	154	
	D6S260	187	189		D6S260	181		
HP	D17S804	165	167	HI	D17S804	163		
	D5S111	165			D5S111	165		
	AP74	152	154		AP74	152	155	
	D6S260	181			D6S260	181	185	
JO	D17S804	163	167	JU	D17S804	163	167	
	D5S111	165			D5S111	165		
	AP74	154			AP74	152		
	D6S260	181	183		D6S260	181	189	
WG	D17S804	163		WI	D17S804	163		
	D5S111	165	167		D5S111	165		
	AP74	152			AP74	154		
	D6S260	181	183		D6S260	181		
WD	D17S804	163	167	WI	D17S804	163		
	D5S111	165	167		D5S111	165		
	AP74	152	154		AP74	154		
	D6S260	185	189		D6S260	181		
ZY	D17S804	163		ZA	D17S804	163	165	
	D5S111	165			D5S111	165		
	AP74	152	154		AP74	152	154	
	D6S260	183			D6S260	187	189	

## ***4.2 Behavioral analysis***

During the observations periods, I accumulated over 1566 hours of focal animal observations. I observed a total of 27 female cycles, indicated by female attractivity and

at least one copulation, for 6 of the 9 focal females. During these cycles I witnessed 150 copulation attempts, of which 134 (89.3%) were ejaculatory copulations, 14 (9.3%) were nonejaculatory copulations, and 2 (1.3%) were rejections prior to intromission.

#### **4.2.1 Female mate choice**

Females were largely responsible for initiating copulation. Of the 134 ejaculatory copulations observed, 88 (65.7%) were solicited by females. Only 6 (4.5%) of the copulations were solicited by males, with the remaining 40 (29.9%) copulations not clearly initiated by either sex. Consistent with the fact that females actively solicited most copulations, female resistance to copulations was essentially absent. Of the 150 attempted copulations, only 5 (3.3%) were rejected. The remaining copulation attempts (that did not result in ejaculation) were interrupted by an adult male (5), interrupted by the female's infant (1), or terminated for no obvious external reason (5). Multimale mating was also very common. Females copulated with more than one male during 21 of 27 ovarian cycles (77.8%). Associated with this high level of multimale mating were extended periods of mating during female cycles. Females copulated an average of 3.37 days per cycle, but the range extended up to 8 days.

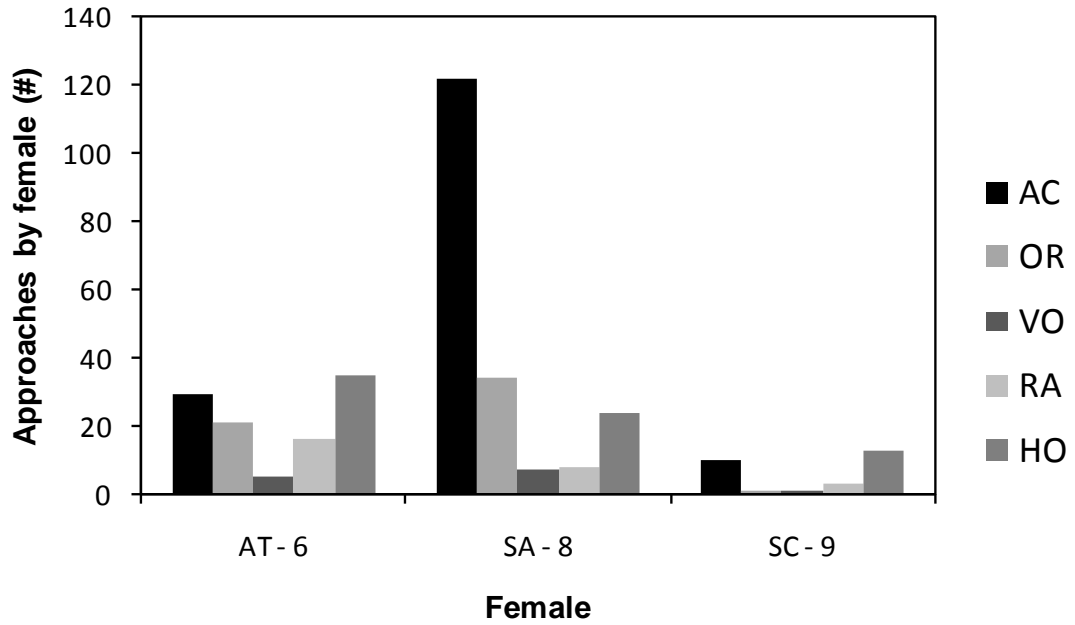
A “good genes” explanation of female mate choice, in which female preference converges on a single male, was not supported by the data. There was not a significant difference among the males in any of the preference indicators (Table 5), and there were no significant differences among males in copulation rate based on male identity ( $H/D = 6.600$ ,  $df = 4$ ,  $p = 0.159$ ) or male rank ( $H/D$ ,  $df = 4$ ,  $p = 0.170$ ).

**Table 5: Statistical Analysis of Female Preference Indicators**

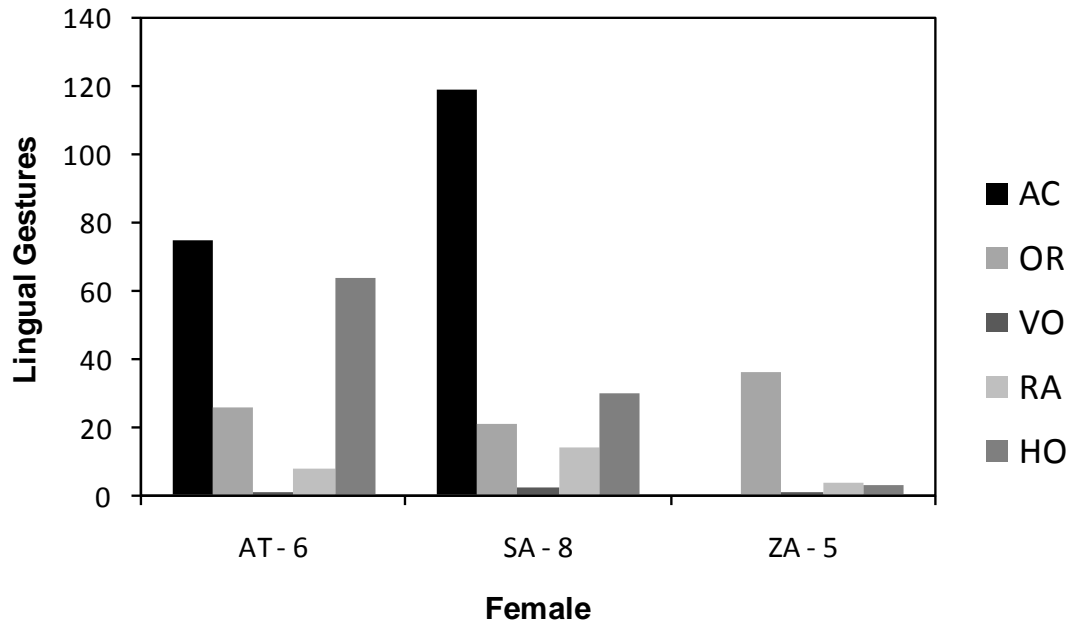
Proceptivity Index	H/D	df	p
female approach index	5.962	4	0.202
proximity maintenance index	5.670	4	0.225
lingual gesture rate	5.221	4	0.265

A “genetic compatibility” explanation of female mate choice, in which female preferences for males are not consistent across females, received some support from the data. The chi-square tests were only performed for a female if the expected frequency of the behavior was at least 5 per male. For male-directed approaches by the female, this left three females (AT, SA, SC) for the analysis. The chi-square test was highly significant ( $p < 0.0001$ ) for all three females (Figure 2). For male-directed lingual gestures by the female, three females (AT, SA, ZA) were again included in the analysis, and again the chi-square test was highly significant ( $p < 0.0001$ ) for all of the females (Figure 3). Only two females (AT, SA) had enough copulations to be included in the chi-square analysis. The chi-square test was significant for AT ( $\chi^2 = 10.68$ ,  $df = 4$ ,  $p < 0.05$ ) and highly significant for SA ( $\chi^2 = 33.04$ ,  $df = 4$ ,  $p < 0.0001$ ; Figure 4).

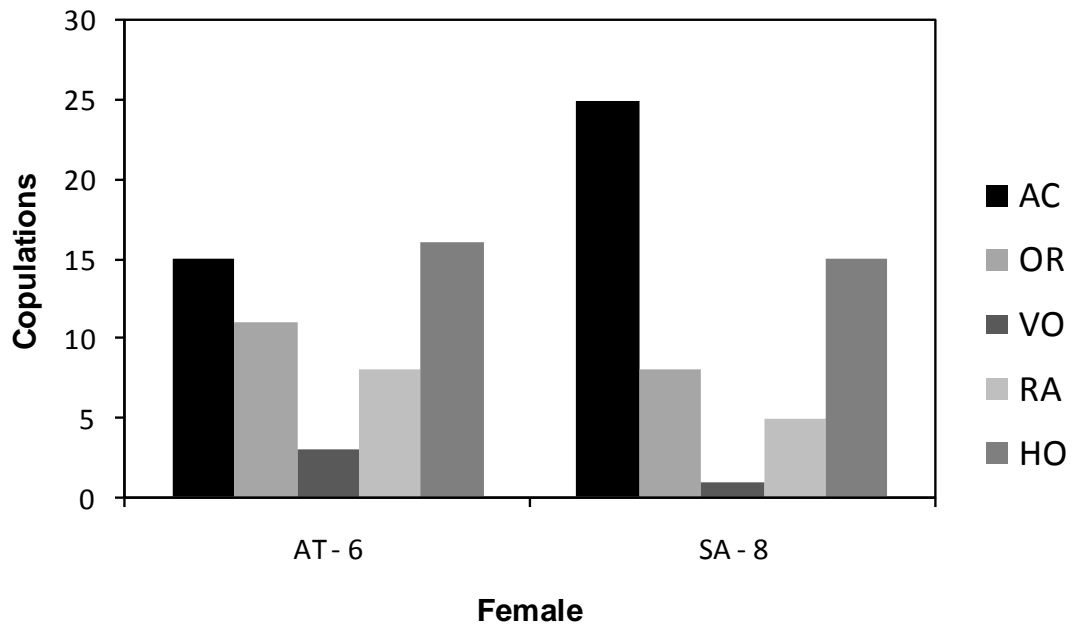




**Figure 2: Frequency of male-directed approaches by females (number after female code represents the female's dominance rank)**



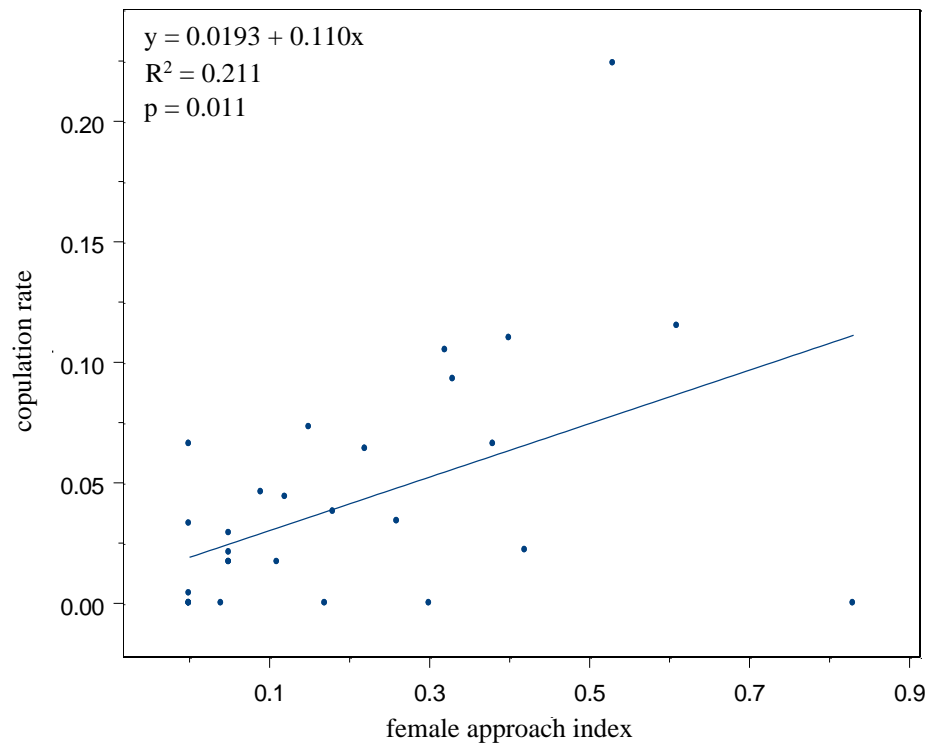
**Figure 3: Frequency of male-directed lingual gestures by females (number after female code represents the female's dominance rank)**



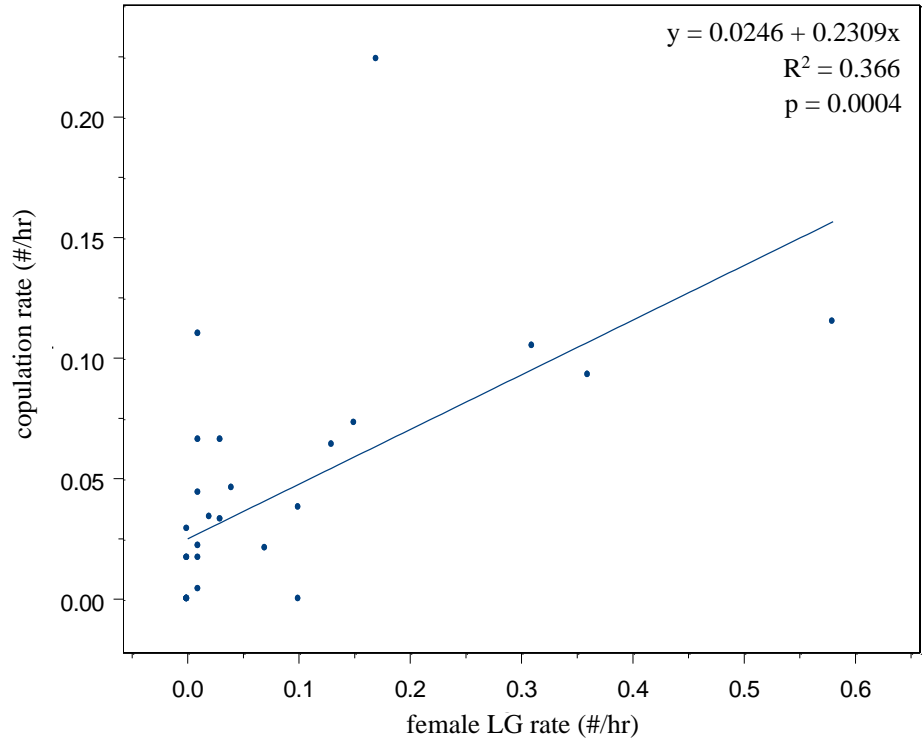
**Figure 4: Frequency of female copulations with males (number after female code represents the female's dominance rank)**

The computer simulations showed that there was a significant relationship between the female approach index and dyadic copulation rate (avg. weighted rank = 0.443,  $p = 0.042$ ) and between female lingual gesture rate and dyadic copulation rate (avg. weighted rank = 0.38,  $p = 0.007$ ). However, the relationship between the proximity maintenance index and dyadic copulation rate was not significant (avg. weighted rank = 0.72,  $p = 0.102$ ). These patterns were also supported by the correlation analysis. The correlations between female approach index and dyadic copulation rate ( $p = 0.011$ ; Figure 5) and female lingual gesture rate and dyadic copulation rate ( $p = 0.0004$ ; Figure

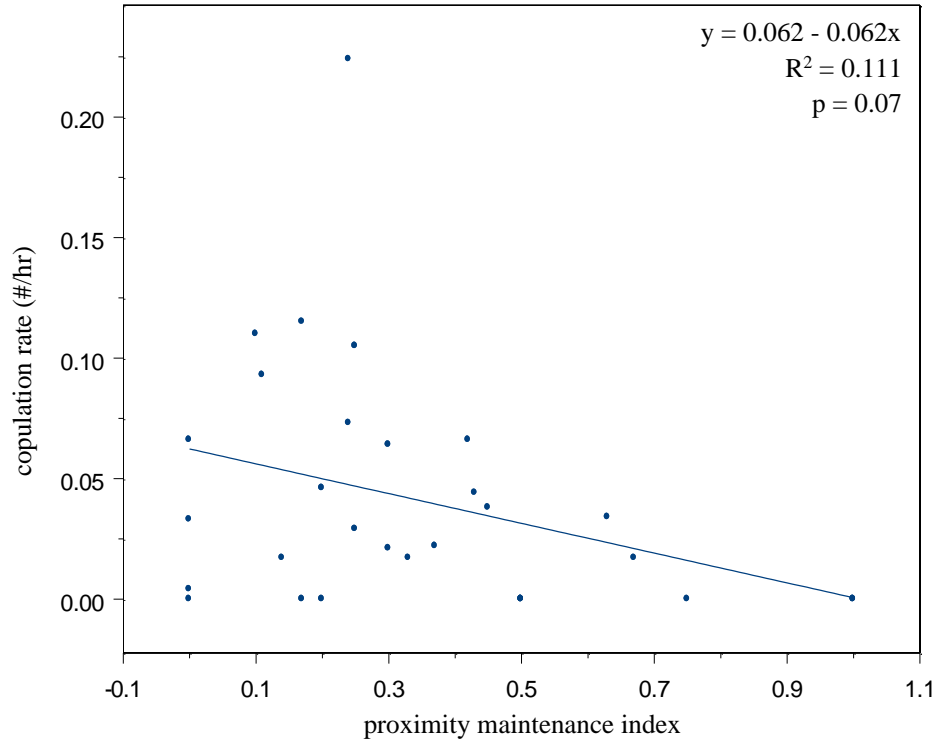
6) were significant, but the correlation between proximity maintenance index and dyadic copulation rate ( $p = 0.072$ ; Figure 7) was not.



**Figure 5: Correlation between female approach index and dyadic copulation rate**



**Figure 6: Correlation between female lingual gesture rate and dyadic copulation rate**

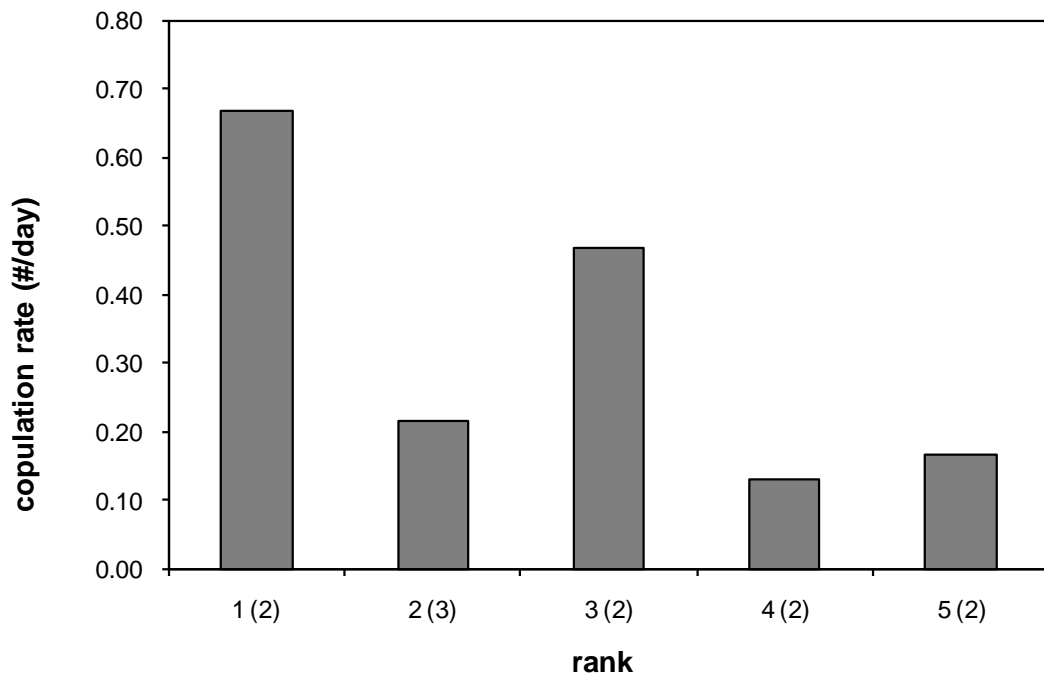


**Figure 7: Correlation between proximity maintenance index and dyadic copulation rate**

Although the relationship between proximity maintenance index and male copulation rate was not significant, it does provide important information. There was an inverse relationship between proximity maintenance index and male copulation rate (Figure 7). Thus, females had the highest copulation rates with males who maintained proximity to them.

## 4.2.2 Male-male competition

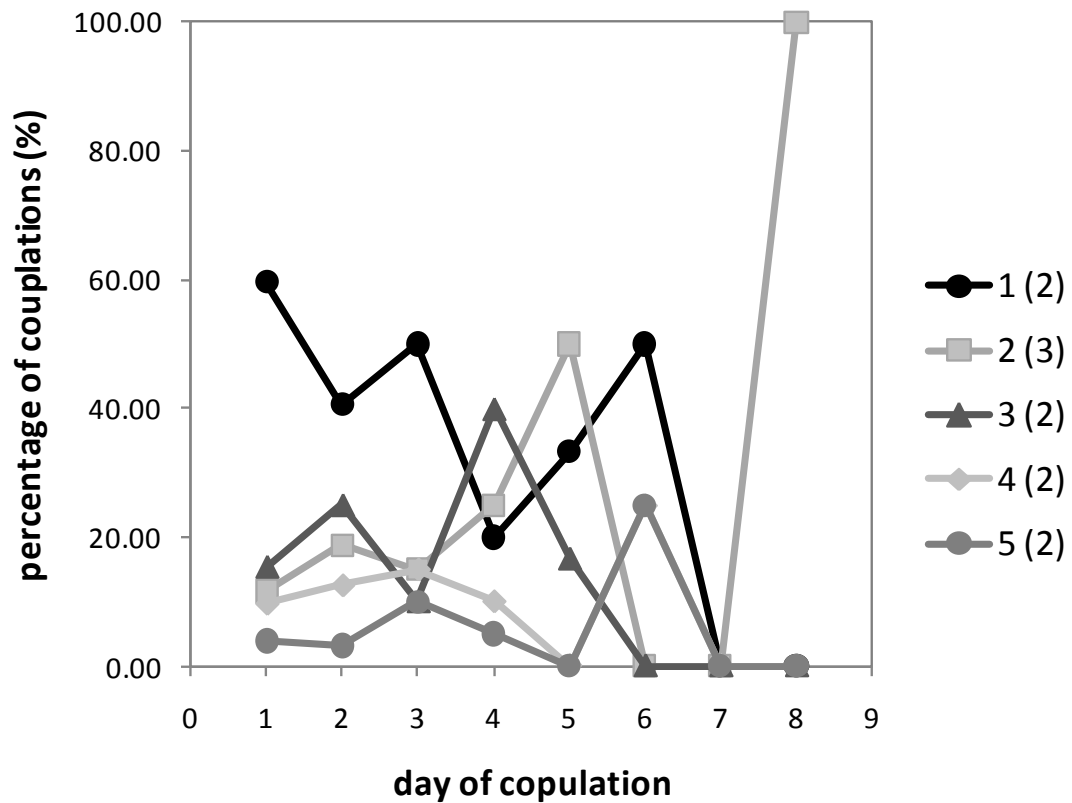
As expected, males of the highest rank had the highest average copulation rate (Figure 8). The surprising finding was that males of rank 3 had a higher average copulation rate than males of rank 2. Males of rank 2 had a copulation rate similar to that of males holding the fourth and fifth ranks.



**Figure 8: Average copulation rate for males of various ranks (number in parentheses indicates the number of males contributing to each average)**

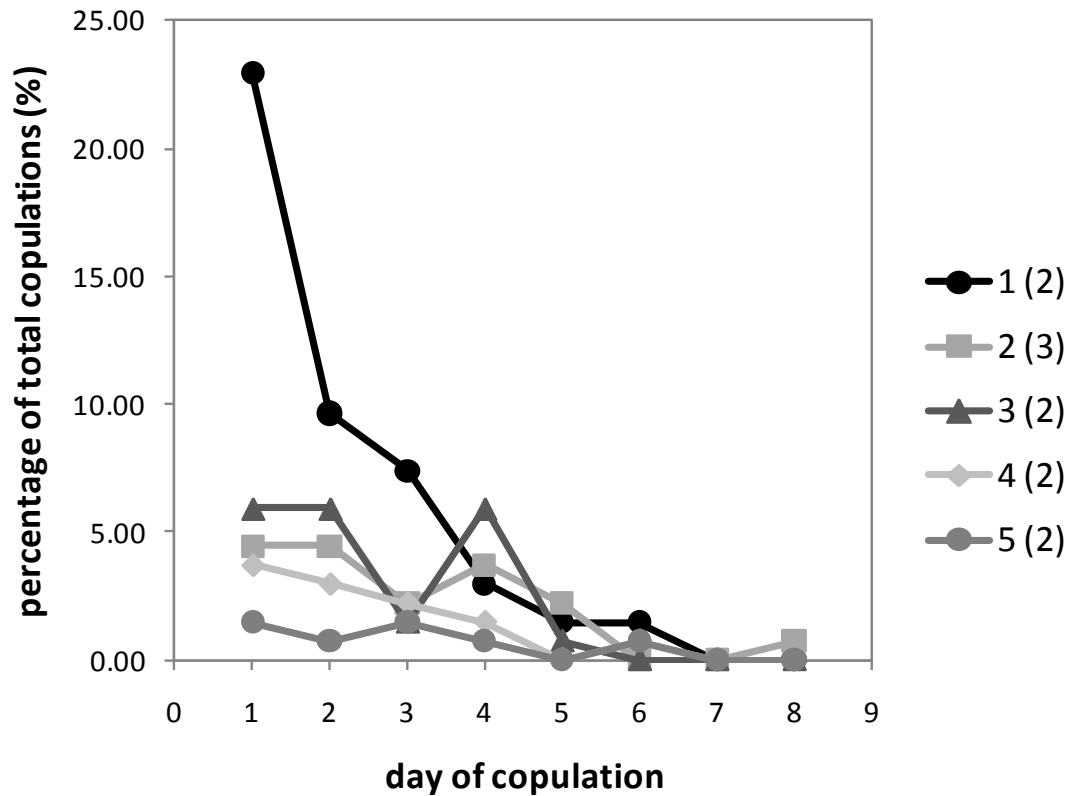
Males of the highest rank performed the highest percentage of copulations on the first three days of copulation. However, the highest-ranked males performed only 60% of the copulations on day 1 and an even lower percentage on days 2 and 3. Males of rank

3 then performed the highest percentage of copulations on day 4 (Figure 9). Days 1-4 accounted for over 90% of total copulations (Figure 10). Males of the highest rank performed 46.8% of these copulations. Thus, the highest-ranked male performed the highest percentage of copulations, especially early in the cycle, but other males were also able to copulate on these days.



**Figure 9: Percentage of copulations by males of various ranks based on the day of copulation (number in parentheses indicates the number of males contributing to that rank)**



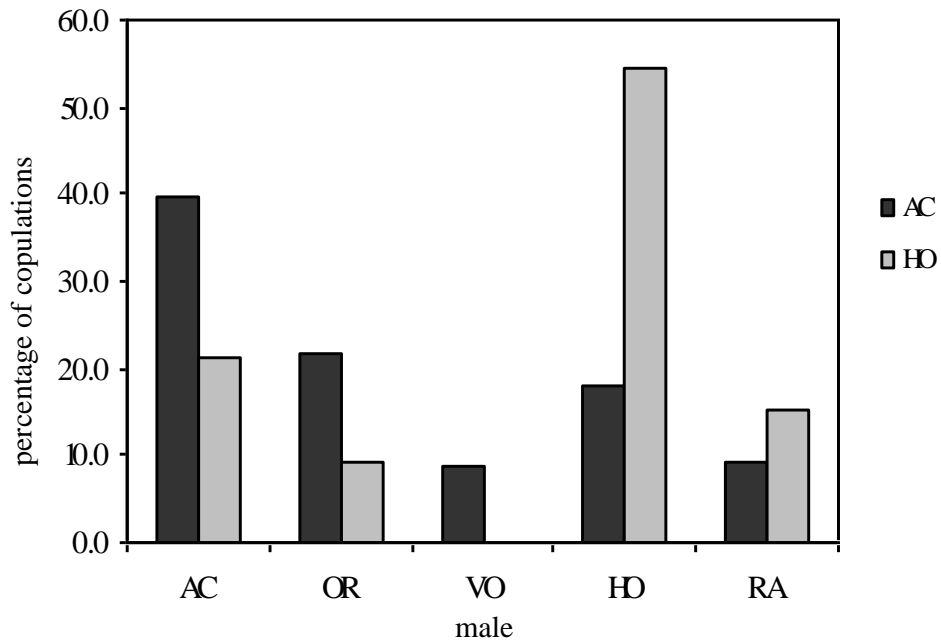


**Figure 10: Percentage of total copulations performed by males of various ranks based on the day of copulation (number in parentheses indicates the number of males contributing to that rank)**

Between the initial capture period and the beginning of formal observations, a natal male (AC) overthrew the previous alpha male (RA). Then approximately 4 months into the observation period, AC was overthrown by a male who had been present on the periphery of the group since the beginning of the observation period (HO). The overthrow by HO was not a typical overthrow. Perhaps because AC was prime-aged and

had only recently become alpha male, AC and HO fought for control of the group for approximately the next 6 months.

During these fights for top rank, males often formed consistent coalitions. Males AC and OR formed one coalition, and males HO and RA formed the other coalition. The final male, VO, did not consistently join either coalition, but he did tend to support the AC-OR coalition more frequently. The coalitions appeared to have an influence on mating success because both OR and RA accounted for a higher percentage of copulations when their coalition partner was alpha male (Figure 11).



**Figure 11: Comparison of male mating success with different alpha males**

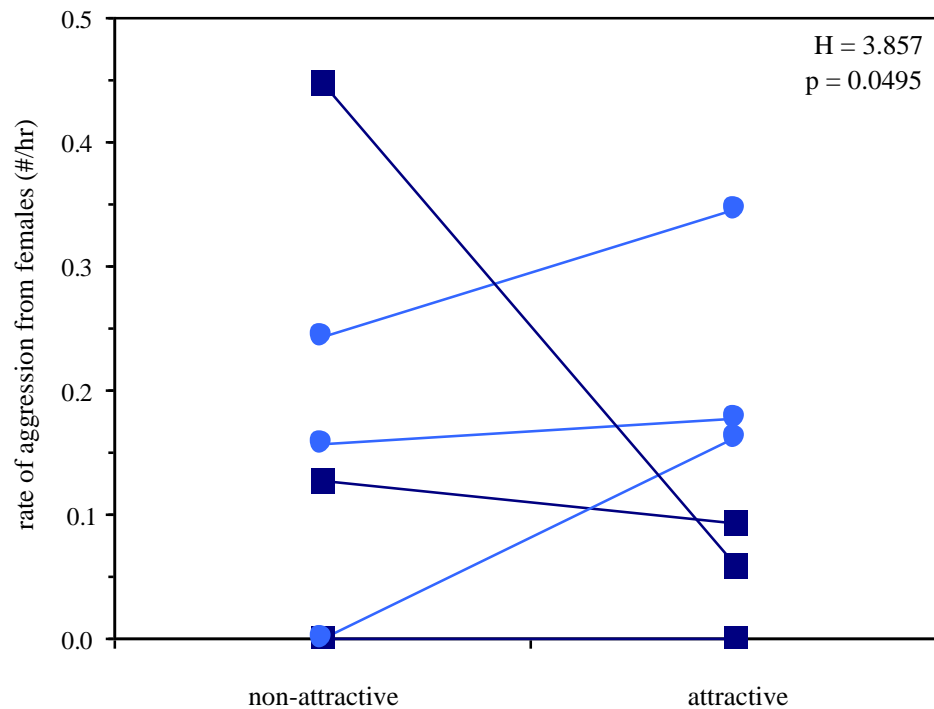
It is difficult to determine why males begin following females as the females become fertile. Looking at the 20 cycles from the three females for whom at least four cycles were observed, 10 appeared to be initiated by the male. In these cycles, male following was observed for at least one day before the female was observed lingual gesturing at him. For the remaining cycles, male following and female lingual gesturing were first observed on the same day, making it difficult to determine which came first. In all 10 cases, the male was observed following the female before she was observed lingual gesturing at the male; however, the possibility that the female lingual gestured at the male before the observation began cannot be ruled out.

#### **4.2.3 Female-female competition**

No overt aggression directed toward infants was observed. For the first few days following the birth of an infant, mothers (regardless of dominance rank) stayed on the periphery of the group. Mothers also experienced a temporary decrease in dominance status as they avoided conflict with other females. When mothers rejoined the group, the other females did show high interest in her infant. Females would often attempt (repeatedly) to get infants to transfer to them and would sometimes take an infant from a lower-ranked female. Although the females often held the infant away from its mother, while the infant was crying out, the behavior did not appear overtly aggressive.

For the six females who cycled during the study, I tested for an increase in the amount of aggression received from other females when females were attractive to males versus when they were cycling but not attractive to males. A Wilcoxon signed ranks test

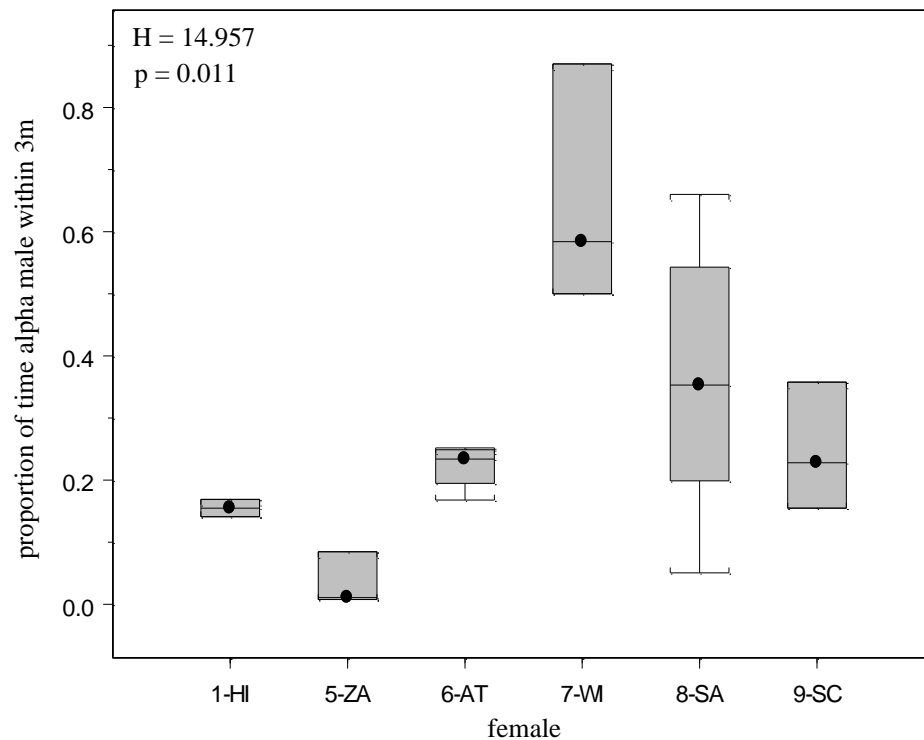
showed that across all ranks, there was not a significant increase in received aggression ( $T_s = 9, p > 0.95$ ). In fact, only the three lowest ranking females received more aggression when attractive versus non-attractive. Using a Kruskal-Wallis test to compare the difference in received aggression between the low-ranking females and the mid- and high-ranking females showed a significant difference between these groups ( $H = 3.857, df = 1, p = 0.0495$ ; Figure 12).



**Figure 12: Aggression received from females when attractive to males and not attractive to males (● = low-ranking; ■ = mid- and high-ranking)**

#### 4.2.4 Male mate choice

Because the alpha male is the only male able to express his mating preferences without interference from higher-ranked males, I analyzed the proportion of time the alpha male was within 3m of a female when she was attractive. A Kruskal-Wallis test showed a significant difference among females in the proportion of time the alpha male remained in proximity while she was attractive ( $H = 14.957$ ,  $df = 5$ ,  $p = 0.0105$ ). Alpha males tended to spend more time in proximity to older, lower-ranking females (Figure 13).



**Figure 13: Proportion of time alpha male within 3m of female when attractive (numbers indicate female rank)**

In addition, there were seven days on which multiple females engaged in ejaculatory copulations. On 5 of 7 days the alpha male (AC) copulated only with the older of the females. On the remaining days the alpha male copulated with both females on one day and neither female on the other day.

## 5. Discussion

The primary purpose of this study was to assess the role of female mate choice in mantled howling monkeys. From a behavioral perspective, there was no support for a good genes hypothesis of female mate choice, but there was some support for a genetic compatibility hypothesis. Females (for whom sufficient data were available) showed clear differences in the number of approaches to, proceptive behaviors toward, and copulations with different males. These results were consistent with the observation that females actively solicited most copulations. However, females seemed to solicit copulations with the male who was maintaining proximity to her. This impression is supported by the trend for females to have higher copulation rates with males who were most responsible for the maintenance of proximity. These findings lead to two possible interpretations. Female mate choice may coincide with the outcome of male-male competition, or male-male competition may limit the ability of females to choose their mates.

The high levels of female proceptivity observed in this study show females play an active role in the mating process, which would suggest that female mate choice coincides with the outcome of male-male competition. Combined with the high levels of multimale mating, this pattern of female mating behavior could reflect a strategy of infanticide avoidance. Females may mate with the male who is able to follow her without interference because he will usually be the male most able to protect her offspring from infanticide. Cases in which the female was followed by a male other than

the alpha male (because he was following another female) and she did not solicit copulations with the alpha male seem to challenge this explanation, but they may reflect the female choosing the best available male. In this scenario, copulations with other males would serve to confuse paternity, reducing the likelihood of them committing infanticide.

An infanticide avoidance hypothesis receives further support from the extended periods of mating observed in this group. The study group is at the high end for male cohort size, whereas previous reports (e.g., Glander, 1980) came from groups with fewer males. As has been suggested in Hanuman langurs, females may require more time to mate when there are more males with whom to mate (van Schaik et al., 2000). However, infanticide has been reported following takeovers and takeovers occur from outside the group (Clarke, 1983). Considering no extra-group copulations were observed, the primary reason for multimale mating may not be infanticide avoidance. This conclusion is consistent with reports from the black and gold howler (*A. caraya*; Kowalewski & Garber, 2010).

In addition to infanticide avoidance, benefits of multimale mating in primates include fertilization insurance (Cox & LeBoeuf, 1977; Hoogland, 1998) and promotion of sperm competition for good gene (Keller & Reeve, 1995; Yasui, 1997) or genetic compatibility (Zeh & Zeh, 1996) reasons. None of these possibilities are mutually exclusive. Furthermore, multimale mating does not preclude female mate choice. Within a promiscuous mating strategy, females may bias paternity by the timing of copulations with different males (Matsumoto-Oda, 1999) and by post-copulatory (cryptic) female



choice (Eberhard, 1996). Unfortunately, this study cannot address either of these possibilities.

As an alternative to the explanation that female mate choice coincides with the outcome of male-male competition, the possibility exists that male-male competition, and the following behavior to which it leads, limits female mate choice. The fact that most periods of male following seemed to begin prior to the onset of female proceptivity would support this explanation. If this is the case, it begs the question of why a female is proceptive toward the male who is following her. One possible explanation is that just conceiving an offspring may be a more important part of the female's reproductive strategy than choosing the father of the offspring. This possibility is strengthened by the fact that males must take over a group to remain in the group (Glander, 1992), meaning a male cannot be a life-long subordinate in this species. This aspect of mantled howler social structure may serve to weed out low-quality males who are unable to take over a group. In addition, females disperse from their natal group, meaning they may be able to exercise a certain amount of mate choice during dispersal. Finally, male monopolization is not absolute. As was the case in the black and gold howler (Kowalewski & Garber, 2010), male following did not prevent other males from copulating with the female. Under these circumstances cooperating with the male while he is following may be the best strategy.

Unfortunately, attempts to assign genetic paternity were largely unsuccessful. The small number of microsatellite loci that successfully amplified and were polymorphic in this sample prevented the assignment of paternity in most cases. Genetic

mismatches between purported dams and offspring further limited the ability to assign paternity. Even the limited results that were possible must be questioned based on the four cases in which infants could not be assigned to either of the females with infants of the appropriate age.

Although the reproductive success of males in this study could not be determined, male mating success is clearly influenced by male-male competition. The alpha male had the highest copulation rate and performed the highest percentage of copulations on the first three days of the female copulatory cycle. However, the alpha male performed only 60% or less of the copulations on those days. This pattern was primarily caused by estrous overlap among the females. Most of the infants conceived during the observation period (3 of 5) were conceived at a time when multiple females were cycling, producing considerable overlap in estrus. This pattern may improve infant survival by ensuring that the infants are born during birth clusters (Clarke et al., 1998), but it also reduces the ability of the alpha male to monopolize females. When multiple females were attractive at once, the alpha male chose to follow one female, providing other males the opportunity to copulate with the female(s) he did not follow. Consequently, female synchrony may have reduced reproductive skew among the males in this group.

Another influence of male-male competition on mating patterns was the lower-than-expected mating success of males occupying the second rank. This pattern seemed to occur because the second rank was filled by recently overthrown alpha males, whose presence was not tolerated by the new alpha male. Consequently, the third-ranked male was able to move up in the mating queue. This pattern is likely to occur following any

takeover, but it is presumably a temporary phenomenon, with the new alpha male gradually tolerating the presence of the previous alpha male. During this study, tolerance never developed because of instability at the top of the dominance hierarchy.

The temporary inability of these males to occupy the position in the mating order associated with their dominance rank may provide incentive for coalition formation. As this male dropped in the mating order, the lower-ranking member of the successful coalition enjoyed higher mating success. However, it did not appear that the new alpha male was “rewarding” his coalition partner by allowing him to copulate (Clarke, 2005). The pattern appeared to reflect differences in male tolerance by the new alpha male, rather than an attempt to trade opportunities to copulate for support.

Another possible aspect of male competition is the amount of time the alpha male followed females. Glander (1980) reported that females were receptive for 2-4 days during each cycle and alpha males only mate guarded around the midpoint of this period. During this study, the alpha male followed females for up to eight days, and females remained attractive for up to ten days. The presence of more males may have caused the females to extend their receptive periods, which in turn may have caused the alpha male to increase the duration of his following efforts. This increased duration of male following calls into question the ability of males to accurately determine the timing of a female’s periovulatory period.

Female competition has been proposed to influence female reproductive success as a result of infant harassment (Clarke et al., 1998). During this study, females did show high interest in other females’ infants. Females would often attempt (repeatedly) to get

infants to transfer to them and would sometimes take an infant from a lower-ranked female. Although the females often held the infant away from its mother, while the infant was crying out, the behavior did not appear overtly aggressive. It is unclear what impact this behavior has on the infant's well-being. However, mothers often moved away from the group for a period of time and experienced a temporary decline in dominance status following the birth of their infants, supporting the idea that there is a cost associated with the interest other females show toward infants.

My observations suggested another possible aspect of female competition in this species. The lowest-ranking female at the start of the study (SA) was noticeably harassed by other females while she was being mate-guarded. They would follow her and supplant her whenever she was close to the male. Often a female would move to sit between her and the male that was mate-guarding her. Comparing the amount of aggression females received from other females when they were followed by a male compared to when they were cycling but not followed by a male showed that not all females were harassed while trying to mate. However, the three lowest-ranking females did receive more aggression when they were being followed. At this point, it is not possible to determine what impact this aggression has on a female's ability to conceive.

As mentioned previously, when multiple females were attractive at once, the alpha male (AC) chose to follow only one of the females, spending more time in proximity to the older female. Furthermore, when the alpha male (AC & HO) was following females he spent a greater proportion of time within 3m of older females than he did younger females. These results suggest that male mantled howlers may prefer to

mate with older females, as reported in chimpanzees (Muller et al., 2006). However, the results are based on data that were not collected to address this topic and that came mostly from one male (AC). More research is needed to determine whether this is a consistent pattern for this species.

Unfortunately, the strength of the conclusions made in this dissertation is limited by the lack of genetic paternity data. Without these data, it is not possible to determine the relationship between mating behavior and paternity. Because the genetic analyses were largely inconclusive, the decision to sacrifice endocrine data for the genetic data was unfortunate but sound at the time it was made. Endocrine analyses can usually identify a 4-6 day fertile phase (e.g., Strier & Ziegler, 1997; Deschner et al., 2003; Engelhardt et al., 2005) because of variability in the excretion of hormone metabolites (Carosi et al., 1999) and the life span of sperm (Wilcox et al., 1995). This 4-6 day window is longer than the previously reported duration of receptivity in mantled howlers (Glander, 1980). Consequently, the possibility existed that all of the observed receptivity may have taken place in the estimated window of fertility. Given the possibility of longer periods of receptivity and male following, future studies of mantled howler mating should incorporate endocrine data to place the timing of these behaviors in the context of female fertility.

In conclusion, females actively solicit copulations with males and engage in multimale mating, but the reasons behind these behaviors are still unclear. Females appeared to copulate with the male who was maintaining proximity to them and rarely resisted male copulation attempts. Because males tended to start following females

before the females showed signs of proceptivity, it seems that male behavior may limit the ability of females to freely choose their mates. In addition, there may be reasons why females are not under strong selection pressure to develop strategies against male following behavior and may even benefit from cooperating with the males.

## References

- Alberts, S. C., Altmann, J. & Wilson, M. L. 1996. Mate guarding constrains foraging activity of male baboons. *Animal Behaviour*, **51**, 1269-1277.
- Alberts, S. C., Watts, H. E. & Altmann, J. 2003. Queuing and queue-jumping: long-term patterns of reproductive skew in male savannah baboons, *Papio cynocephalus*. *Animal Behaviour*, **65**, 821-840.
- Alfaro, J. W. L. 2005. Male mating strategies and reproductive constraints in a group of wild tufted capuchin monkeys (*Cebus apella nigrinus*). *American Journal of Primatology*, **67**, 313-328.
- Altmann, J. 1974. Observational study of behavior: sampling methods. *Behaviour*, **49**, 227-267.
- Altmann, J. 1990. Primate males go where the females are. *Animal Behaviour*, **39**, 193-195.
- Amos, W., Twiss, S. D., Pomeroy, P. P. & Anderson, S. S. 1993. Male mating success and paternity in the grey seal, *Halichoerus grypus*: a study using DNA fingerprinting. *Proc. R. Soc. Lond. B*, **252**, 199-207.
- Anderson, C. M. 1986. Female age: male preference and reproductive success in primates. *International Journal of Primatology*, **7**, 305-326.
- Andersson, M. & Simmons, L. W. 2006. Sexual selection and mate choice. *TREE*, **21**, 296-302.
- Baldwin, J. D. 1968. The social behavior of adult male squirrel monkeys (*Saimiri sciureus*) in a seminatural environment. *Folia Primatol*, **9**, 281-314.
- Barrett, L. & Henzi, S. P. 2001. The utility of grooming in baboon troops. In: *Economics in Nature* (Ed. by Noë, R., van Hooff, J. A. R. A. M. & Hammerstein, P.), pp. 119-145. Cambridge: Cambridge University Press.
- Bateman, A. J. 1948. Intra-sexual selection in *Drosophila*. *Heredity*, **2**, 349-368.
- Batova, I. N., Ivanova, M. D., Mollova, M. V. & Kyurkchiev, S. D. 1998. Human sperm surface glycoprotein involved in sperm-zona pellucida interaction. *International Journal of Andrology*, **21**, 141-153.

- Beach, F. A. 1976. Sexual attractivity, proceptivity, and receptivity in female mammals. *Hormones and Behavior*, 7, 195-138.
- Berard, J. D., Nurnberg, P., Epplen, J. T. & Schmidtke, J. 1994. Alternative reproductive tactics and reproductive success in male rhesus macaques. *Behaviour*, **129**, 177-201.
- Bercovitch, F. B. 1986. Male rank and reproductive activity in savanna baboons. *International Journal of Primatology*, **7**, 533-550.
- Berglund, A., Magnhagen, C., Bisazza, A., König, B., & Huntingford, F. 1993. Female-female competition over reproduction. *Behavioral Ecology*, 4, 184-187.
- Birkhead, T. R. & Kappeler, P. M. 2004. Post-copulatory sexual selection in birds and primates. In: *Sexual Selection in Primates* (Ed. by Kappeler, P. M. & van Schaik, C. P.). Cambridge: Cambridge University Press.
- Borries, C., Launhardt, K., Epplen, C., Epplen, J. T. & Winkler, P. 1999a. DNA analyses support the hypothesis that infanticide is adaptive in langur monkeys. *Proc. R. Soc. Lond. B*, **26**, 901-904.
- Borries, C., Launhardt, K., Epplen, C., Epplen, J. T. & Winkler, P. 1999b. Males as infant protectors in Hanuman langurs (*Presbytis entellus*) living in multimale groups - defence pattern, paternity and sexual behaviour. *Behav Ecol Sociobiol*, **46**, 350-356.
- Bowman, L. A., Dilley, S. R., & Keverne, E. B. 1978. Suppression of estrogen-induced LH surges by social subordination in talapoin monkeys. *Nature*, 275, 56-58.
- Brown, J. L. 1997. A theory of mate choice based on heterozygosity. *Behavioral Ecology*, 8, 60-65.
- Buchan, J. C., Alberts, S. C., Silk, J. B., & Altmann, J. 2003. True paternal care in a multi-male primate society. *Nature*, 425, 179-181.
- Bulger, J. B. 1993. Dominance rank and access to estrous females in male savanna baboons. *Behaviour*, 127, 67-103.
- Campbell, C. J. 2003. Female-directed aggression in free-ranging *Ateles geoffroyi*. *International Journal of Primatology*, 24, 223-237.
- Carosi, M., Heistermann, M., & Visalberghi, E. 1999. Display of proceptive behaviors in relation to urinary and fecal progesterone levels over the ovarian cycle in female tufted capuchin monkeys. *Hormones and Behavior*, 36, 252-265.



- Charpentier, M., Peignot, P., Hossaert-McKey, M., Gimenez, O., Setchell, J. M., & Wickings, E. J. 2005. Constraints on control: factors influencing reproductive success in male mandrills (*Mandrillus sphinx*). *Behavioral Ecology*, 16, 614-623.
- Clarke, M. R. 1983. Infant-killing and infant disappearance following male takeovers in a group of free-ranging howling monkeys (*Alouatta palliata*) in Costa Rica. *American Journal of Primatology*, 5, 241-247.
- Clarke, M. R. 2005. Testing the model for male-male coalitions: data from male mantled howling monkeys (*Alouatta palliata*). *American Journal of Physical Anthropology*, 126(Suppl. 40), 87.
- Clarke, M. R. & Glander, K. E. 1984. Female reproductive success in a group of free-ranging howling monkeys (*Alouatta palliata*) in Costa Rica. In: *Female Primates: Studies by Women Primatologists*, pp. 111-126. New York: Alan R. Liss, Inc.
- Clarke, M. R. & Glander, K. E. 2004. Adult migration patterns of the mantled howlers of La Pacifica. *American Journal of Primatology*, 62(Suppl. 1), 87.
- Clarke, M. R. & Glander, K. E. 2010. Secondary transfer of adult mantled howlers (*Alouatta palliata*) on Hacienda La Pacifica, Costa Rica: 1975-2009. *Primates*, 51, 241-249.
- Clarke, M. R., Zucker, E. L. & Harrison, R. M. 1991. Fecal estradiol, sexual swelling, and sociosexual behavior of free-ranging female howling monkeys in Costa Rica. *American Journal of Primatology*, 24, 93.
- Clarke, M. R., Glander, K. E. & Zucker, E. L. 1998. Infant-nonmother interactions of free-ranging mantled howlers (*Alouatta palliata*) in Costa Rica. *International Journal of Primatology*, 19, 451-472.
- Clarke, M. R., Zucker, E. L., Crockett, C. M. & Zaldivar, M. 1999. Assessment of the howling monkey (*Alouatta palliata*) population on Hacienda La Pacifica, Guanacaste, Costa Rica. *American Journal of Physical Anthropology*, S28, 108-109.
- Clarke, M. R., Crockett, C. M., Zucker, E. L. & Zaldivar, M. 2002. Mantled howler population of Hacienda La Pacifica, Costa Rica, between 1991 and 1998: effects of deforestation. *American Journal of Primatology*, 56, 155-163.
- Clarke, M. R., Ford, R., Arden, D., & Glander, K. E. 2007. Survey of the howler population of La Pacifica, 2006. *American Journal of Primatology*, 69 (Suppl. 1), 55-56.

- Clutton-Brock, T. H. & Parker, G. A. 1995. Sexual coercion in animal societies. *Animal Behaviour*, 49, 1345-1365.
- Coltman, D. W., Bancroft, D. R., Robertson, A., Smith, J. A., Clutton-Brock, T. H. & Pemberton, J. M. 1999. Male reproductive success in a promiscuous mammal: behavioural estimates compared with genetic paternity. *Molecular Ecology*, 8, 1199-1209.
- Constable, J. L., Ashley, M. V., Goodall, J. & Pusey, A. E. 2001. Noninvasive paternity assignment in Gombe chimpanzees. *Molecular Ecology*, 10, 1279-1300.
- Cords, M., Mitchell, B. J., Tsingalia, H. M., & Rowell, T. E. Promiscuous mating among blue monkeys in the Kakamega Forest, Kenya. *Ethology*, 72, 214-226.
- Cowlshaw, G. & Dunbar, R. I. M. 1991. Dominance rank and mating success in male primates. *Animal Behaviour*, 41, 1045-1056.
- Cox, C. R. & Le Boeuf, B. J. 1977. Female incitation of male competition: a mechanism in sexual selection. *American Naturalist*, 111, 317-335.
- Crockett, C. M. & Eisenberg, J. F. 1987. Howlers: variation in group size and demography. In: *Primate Societies* (Ed. by Smuts, B. B., Cheney, D. L., Seyfarth, R. M., Wrangham, R. W. & Struhsaker, T. T.), pp. 54-68. Chicago: University of Chicago Press.
- Darwin, C. 1871. *The Descent of Man, and Selection in Relation to Sex*. London: John Murray.
- de Ruiter, J. R., van Hooff, J. A. R. A. M. & Scheffrahn, W. 1994. Social and genetic aspects of paternity in wild long-tailed macaques (*Macaca fascicularis*). *Behaviour*, 129, 203-224.
- Deschner, T., Heistermann, M., Hodges, K. & Boesche, C. 2003. Timing and probability of ovulation in relation to sex skin swelling in wild West African chimpanzees, *Pan troglodytes verus*. *Animal Behaviour*, 66, 551-560.
- Dewsbury, D. A. 1982. Dominance rank, copulatory behavior, and differential reproduction. *Quarterly Review of Biology*, 57, 135-159.
- Dixson, A. F. 1998. *Primate Sexuality: Comparative Studies of the Prosimians, Monkeys, Apes, and Human Beings*. Oxford: Oxford University Press.
- Domb, L. G. & Pagel, M. 2001. Sexual swellings advertise female quality in wild baboons. *Nature*, 410, 204-206.

- Drickamer, L. C., Gowaty, P. A. & Wagner, D. M. 2003. Free mutual mate preferences in house mice affect reproductive success and offspring performance. *Animal Behaviour*, 65, 105-114.
- Dunbar, R. I. M. & Sharman, M. 1983. Female competition for access to males affects birth-rate in baboons. *Behavioral Ecology and Sociobiology*, 13, 157-159.
- Eberhard, W. G. 1996. *Female Control: Sexual Selection by Cryptic Female Choice*. Princeton: Princeton University Press.
- Egid, K. & Brown, J. L. 1989. The major histocompatibility complex and female mating preferences in mice. *Animal Behaviour*, 38, 548-550.
- Ellis, L. 1995. Dominance and reproductive success among nonhuman animals: a cross-species comparison. *Ethology & Sociobiology*, 16, 257-333.
- Ellsworth, J. A. 2000. Molecular evolution, social structure, and phylogeography of the mantled howler monkey (*Alouatta palliata*). Ph.D. Thesis, University of Nevada, Reno.
- Ellsworth, J. A. & Hoelzer, G. A. 1998. Characterization of microsatellite loci in a New World primate, the mantled howler monkey (*Alouatta palliata*). *Molecular Ecology*, 7, 657-666.
- Emery Thompson, M. & Wrangham, R. W. 2008. Male mating interest varies with female fecundity in *Pan troglodytes schweinfurthii* of Kanyawara, Kibale National Park. *International Journal of Primatology*, 29, 885-905.
- Emlen, S. T. & Oring, L. W. 1977. Ecology, sexual selection, and the evolution of mating systems. *Science*, 197, 215-223.
- Engelhardt, A., Pfeifer, A. B., Heistermann, M., Niemitz, C. van Hooff J. A. R. A. M., & Hodges, J. K. 2004. Assessment of female reproductive status by male longtailed macaques, *Macaca fascicularis*, under natural conditions. *Animal Behaviour*, 67, 915-924.
- Engelhardt, A., Hodges, J. K., Niemitz, C., & Heistermann, M. 2005. Female sexual behavior, but not sex skin swelling, reliably indicates the timing of the fertile phase in wild long-tailed macaques (*Macaca fascicularis*). *Hormones and Behavior*, 47, 195-204.
- Engelhardt, A., Heistermann, M., Hodges, J. K., Nurnberg, P., & Niemitz, C. 2006. Determinants of male reproductive success in wild long-tailed macaques (*Macaca fascicularis*)—male monopolization, female mate choice or post-copulatory mechanisms? *Behavioral Ecology and Sociobiology*, 59, 740-752.

- Fedigan, L. M. 1983. Dominance and reproductive success in primates. *Yearbook of Physical Anthropology*, 26, 91-129.
- Fedigan, L. M. & Rose, L. M. 1995. Interbirth interval variation in three sympatric species of neotropical monkey. *American Journal of Primatology*, 37, 9-24.
- Fietz, J., Zischler, H., Schwiegk, C., Tomiuk, J., Dausmann, K. H. & Ganzhorn, J. U. 2000. High rates of extra-pair young in the pair-living fat-tailed dwarf lemur, *Cheirogaleus medius*. *Behav Ecol Sociobiol*, 49, 8-17.
- Fisher, R. A. 1930. *The Genetical Theory of Natural Selection*. Oxford: Clarendon Press.
- Gerloff, U., Hartung, B., Fruth, B., Hohmann, G. & Tautz, D. 1999. Intracommunity relationships, dispersal pattern and paternity success in a wild living community of Bonobos (*Pan paniscus*) determined from DNA analysis of faecal samples. *Proc. R. Soc. Lond. B*, 266, 1189-1195.
- Ginsberg, J. R. & Huck, U. W. 1989. Sperm competition in mammals. *TREE*, 4.
- Glander, K. E. 1975. Habitat and resource utilization: an ecological view of social organization in mantled howling monkeys. Ph.D. dissertation. University of Chicago.
- Glander, K. E. 1980. Reproduction and population growth in free-ranging mantled howling monkeys. *American Journal of Physical Anthropology*, 53, 25-36.
- Glander, K. E. 1992. Dispersal patterns in Costa Rican mantled howling monkeys. *International Journal of Primatology*, 13, 415-436.
- Glander, K. E., Fedigan, L. M., Fedigan, L. & Chapman, C. 1991. Field methods for capture and measurement of three monkey species in Costa Rica. *Folia Primatol*, 57, 70-82.
- Gomes, C. M. & Boesch, C. 2008. Wild chimpanzees exchange meat for sex on a long-term basis. *PLoS ONE*, 4, e5116.
- Gowaty, P. A. 1996. Multiple mating by females selects for males that stay: another hypothesis for social monogamy in passerine birds. *Animal Behaviour*, 51, 482-484.
- Gowaty, P. A. 1997. Sexual dialectics, sexual selection, and variation in reproductive behavior. In: *Feminism and Evolutionary Biology: Boundaries, Intersections, and Frontiers* (Ed. by Gowaty, P. A.), pp. 351-384. New York: Chapman & Hall.

- Gowaty, P. A., Drickamer, L. C. & Schmid-Holmes, S. 2003. Male house mice produce fewer offspring with lower viability and poorer performance when mated with females they do not prefer. *Animal Behaviour*, 65, 95-103.
- Griffith, S. C., Owens, I. P. F. & Thuman, K. A. 2002. Extrapair paternity in birds: a review of interspecific variation and adaptive function. *Molecular Ecology*, 11, 2195-2212.
- Hemelrijk, C. K., Meier, C. & Martin, R. D. 1999. 'Friendship' for fitness in chimpanzees? *Animal Behaviour*, 58, 1223-1229.
- Holdridge, L. R. 1967. *Life Zone Ecology*. San Jose, Costa Rica: Tropical Science Center.
- Holland, B. & Rice, W. R. 1998. Perspective: chase-away sexual selection: antagonistic seduction versus resistance. *Evolution*, 52, 1-7.
- Hoogland, J. L. 1998. Why do female Gunnison's prairie dogs copulate with more than one male? *Animal Behaviour*, 55, 351-359.
- Howard, R. S. & Lively, C. M. 2004. Good vs complementary genes for parasite resistance and the evolution of mate choice. *BMC Evolutionary Biology*, 4: 48.
- Hrdy, S. B. 1979. Infanticide among animals: a review, classification, and examination of the implications for the reproductive strategies of females. *Ethology and Sociobiology*, 1, 13-40.
- Huffman, M. A. 1987. Consort intrusion and female mate choice in Japanese macaques (*Macaca fuscata*). *Ethology*, 75, 221-234.
- Huxley, J. S. 1938. Darwin's theory of sexual selection and the data subsumed by it, in the light of recent research. *American Naturalist*, 72, 416-433.
- Inoue, M., Mitsunaga, F., Ohsawa, H., Takenaka, A., Sugiyama, Y., Gaspard, S. A. & Takenaka, O. 1991. Male mating behaviour and paternity discrimination by DNA fingerprinting in a Japanese macaque group. *Folia Primatol*, 56, 202-210.
- Jones, C. B. 1980. The functions of status in the mantled howler monkey, *Alouatta palliata* Gray: intraspecific competition for group membership in a folivorous neotropical primate. *Primates*, 21, 389-405.
- Jones, C. B. 1985. Reproductive patterns in mantled howler monkeys: estrus, mate choice and copulation. *Primates*, 26, 130-142.

- Kappeler, P. M. & van Schaik, C. P. 2004. Sexual selection in primates: review and selective preview. In: *Sexual Selection in Primates* (Ed. by Kappeler, P. M. & van Schaik, C. P.). Cambridge: Cambridge University Press.
- Keller, L. & Reeve, H. K. 1995. Why do females mate with multiple males? The sexually selected sperm hypothesis. *Adv. Stud. Behav.*, 24, 291-315.
- Kempnaers, B., Verheyen, G. R., Van den Broeck, M., Burke, T., Van Broeckhoven, C. & Dhondt, A. A. 1992. Extra-pair paternity results from female preference for high-quality males in the blue tit. *Nature*, 357, 494-496.
- Klinkova, E., Hodges, J. K., Fuhrmann, K., de Jong, T., & Heistermann, M. 2005. Male dominance rank, female mate choice and male mating and reproductive success in captive chimpanzees. *International Journal of Primatology*, 26, 357-384.
- Kokko, H., Brooks, R., McNamara, J. M., & Houston, A. I. 2002. The sexual selection continuum. *Proceedings of the Royal Society of London Series B-Biological Sciences*, 269, 1331-1340.
- Kowalewski, M. & Garber, P. 2010. Mating promiscuity and reproductive tactics in female black and gold howler monkeys (*Alouatta caraya*) inhabiting an island on the Parana River, Argentina. *American Journal of Primatology*, 72, 734-748.
- Kuester, J. & Paul, A. Female-female competition and male mate choice in Barbary macaques (*Macaca sylvanus*). *Behaviour*, 133, 763-790.
- Kutsukake, N. & Nunn, C. L. 2006. Comparative tests of reproductive skew in male primates: the roles of demographic factors and incomplete control. *Behavioral Ecology and Sociobiology*, 60, 695-706.
- Lasserre, A., González-Echeverría, F., Moules, C., Tezón, J. G., Miranda, P. V. & Vazquez-Levin, M. 2003. Identification of human sperm proteins involved in the interaction with homologous zona pellucida. *Fertility and Sterility*, 79, 1606-1615.
- Launhardt, K., Borries, C., Hardt, C., Epplen, J. T. & Winkler, P. 2001. Paternity analysis of alternative male reproductive routes among the langurs (*Semnopithecus entellus*) of Ramnagar. *Animal Behaviour*, 61, 53-64.
- Manson, J. H. 1992. Measuring female mate choice in Cayo Santiago rhesus macaques. *Animal Behaviour*, 44, 405-416.
- Manson, J. H. 1996. Male dominance and mount series duration in Cayo Santiago rhesus macaques. *Animal Behaviour*, 51, 1219-1231.

- Martin, P. & Bateson, P. 1993. *Measuring Behaviour: An Introductory Guide*. Cambridge: Cambridge University Press.
- Matsubara, M. 2003. Costs of mate guarding and opportunistic mating among wild male Japanese macaques. *International Journal of Primatology*, 24, 1057-1075.
- Matsumoto-Oda, A. 1999. Female choice in the opportunistic mating of wild chimpanzees (*Pan troglodytes schweinfurthii*) at Mahale. *Behav Ecol Sociobiol*, 46, 258-266.
- Mesnick, S. & Le Boeuf, B. J. 1991. Sexual behavior of male northern elephant seals: II. Female response to potentially injurious encounters. *Behaviour*, 117, 262-280.
- Mitani, J. C. & Watts, D. P. 2001. Why do chimpanzees hunt and share meat? *Animal Behaviour*, 61, 915-924.
- Muller, M. N., Thompson, M. E., & Wrangham, R. W. 2006. Male chimpanzees prefer mating with old females. *Current Biology*, 16, 2234-2238.
- Noë, R. 1990. A veto game played by baboons: a challenge to the use of the Prisoner's Dilemma as a paradigm for reciprocity and cooperation. *Animal Behaviour*, 39, 78-90.
- Noë, R. & Sluijter, A. A. 1990. Reproductive tactics of male savanna baboons. *Behaviour*, 113, 117-169.
- Nunn, C. L. 1999. The number of males in primate social groups: a comparative test of the socioecological model. *Behavioral Ecology and Sociobiology*, 46, 1-13.
- Nunn, C. L., van Schaik, C. P., & Zinner, D. 2001. Do exaggerated sexual swellings function in female mating competition in primates? A comparative test of the reliable indicator hypothesis. *Behavioral Ecology*, 12, 646-654.
- Palombit, R. A. 1994. Extra-pair copulations in a monogamous ape. *Animal Behaviour*, 47, 721-723.
- Palombit, R. A., Cheney, D. L. & Seyfarth, R. M. 2001. Female-female competition for male 'friends' in wild chacma baboons, *Papio cynocephalus ursinus*. *Animal Behaviour*, 61, 1159-1171.
- Palombit, R. A., Seyfarth, R. M. & Cheney, D. L. 1997. The adaptive value of 'friendships' to female baboons: experimental and observational evidence. *Animal Behaviour*, 54, 599-614.

- Parga, J. A. 2006. Male mate choice in *Lemur catta*. *International Journal of Primatology*, 27, 107-131.
- Paul, A. 2002. Sexual selection and mate choice. *International Journal of Primatology*, 23, 877-904.
- Pereira, M. E. & Weiss, M. L. 1991. Female mate choice, male migration, and the threat of infanticide in ringtailed lemurs. *Behavioral Ecology and Sociobiology*, 28, 141-152.
- Petrie, M. 1994. Improved growth and survival of offspring of peacocks with more elaborate trains. *Nature*, 371, 598-599.
- Potts, W. K., Manning, C. J. & Wakeland, E. K. 1991. Mating patterns in seminatural populations of mice influenced by MHC genotype. *Nature*, 352, 619-621.
- Preston, B. T., Stevenson, I. R., Pemberton, J. M. & Wilson, K. 2001. Dominant rams lose out by sperm depletion. *Nature*, 409, 681-682.
- Price, T., Schluter, D., & Heckman, N. E. 1993. Sexual selection when the female directly benefits. *Biological Journal of the Linnean Society*, 48, 187-211.
- Quiatt, D. & Everett, J. 1982. How can sperm competition work? *American Journal of Primatology*, 2(Suppl. 1), 161-169.
- Reichard, U. 1995. Extra-pair copulations in a monogamous gibbon (*Hylobates lar*). *Ethology*, 100, 99-112.
- Ryan, M. J. 1990. Sexual selection, sensory systems and sensory exploitation. *Oxford Surveys in Evolutionary Biology*, 7, 157-195.
- Schneider, H., Schneider, M. P. C., Sampaio, I., Harada, M. L., Stanhope, M., Czelusniak, J. & Goodman, M. 1993. Molecular phylogeny of the new world monkeys (Platyrrhini, Primates). *Molecular Phylogenetics and Evolution*, 2, 225-242.
- Setchell, J. M. 2005. Do female mandrills prefer brightly colored males? *International Journal of Primatology*, 26, 715-735.
- Setchell, J. M., Charpentier, M., & Wickings, E. J. 2005. Mate guarding and paternity in mandrills: factors influencing alpha male monopoly. *Animal Behaviour*, 70, 1105-1120.
- Setchell, J. M. & Wickings, E. J. 2006. Mate choice in male mandrills (*Mandrillus sphinx*). *Ethology*, 112, 91-99.



- Small, M. F. 1988. Female primate sexual behavior and conception: are there really sperm to spare? *Current Anthropology*, 29, 81-88.
- Small, M. F. 1992. Female choice in mating. *American Scientist*, 80, 142-151.
- Smith, D. G. 1981. The association between rank and reproductive success of male rhesus monkeys. *American Journal of Primatology*, 1, 83-90.
- Smuts, B. B. 1987. Sexual competition and mate choice. In: *Primate Societies* (Ed. by Smuts, B. B., Cheney, D. L., Seyfarth, R. M., Wrangham, R. W. & Struhsaker, T. T.). Chicago: University of Chicago Press.
- Smuts, B. B. & Smuts, R. W. 1993. Male aggression and sexual coercion of females in nonhuman primates and other mammals: evidence and theoretical implications. *Adv. Stud. Behav.*, 22, 1-63.
- Snook, R. R. 2005. Sperm in competition: not playing by the numbers. *TREE*, 20, 46-53.
- Soltis, J., Mitsunaga, F., Shimizu, K., Nozaki, M., Yanagihara, Y., Domingo-Roura, X. & Takenaka, O. 1997a. Sexual selection in Japanese macaques II: female mate choice and male-male competition. *Animal Behaviour*, 54, 737-746.
- Soltis, J., Mitsunaga, F., Shimizu, K., Yanagihara, Y. & Nozaki, M. 1997b. Sexual selection in Japanese macaques I: female mate choice or male sexual coercion? *Animal Behaviour*, 54, 725-736.
- Soltis, J., Thomsen, R., Matsubayashi, K. & Takenaka, O. 2000. Infanticide by resident males and female counter-strategies in wild Japanese macaques (*Macaca fuscata*). *Behav Ecol Sociobiol*, 48, 195-202.
- Soltis, J., Thomsen, R. & Takenaka, O. 2001. The interaction of male and female reproductive strategies and paternity in wild Japanese macaques. *Animal Behaviour*, 62, 485-494.
- Starck, D. 1975. The development of the chondrocranium in primates. In: *Phylogeny of the Primates* (Ed. by Lockett, W. P. & Szalay, F. S.), pp. 127-155. New York: Plenum Press.
- Strier, K. B. & Ziegler, T. E. 1997. Behavioral and endocrine characteristics of the reproductive cycle in wild murrelet monkeys, *Brachyteles arachnoides*. *American Journal of Primatology*, 42, 299-310.
- Stumpf, R. M. & Boesche, C. 2005. Does promiscuous mating preclude female choice? Female sexual strategies in chimpanzees (*Pan troglodytes verus*) of the Tai National Park, Côte d'Ivoire. *Behav Ecol Sociobiol*, 57, 511-524.

- Stumpf, R. M. & Boesch, C. 2006. The efficacy of female choice in chimpanzees of the Tai Forest, Cote d'Ivoire. *Behavioral Ecology and Sociobiology*, 60, 749-765.
- Thomsen, R., Soltis, J., Matsubara, M., Matsubayashi, K., Onuma, M., & Takenaka, O. 2006. How costly are ejaculates for Japanese macaques? *Primates*, 47, 272-274.
- Tregenza, T. & Wedell, N. 2000. Genetic compatibility, mate choice and patterns of parentage: invited review. *Molecular Ecology*, 9, 1013-1027.
- Trivers, R. L. 1972. Parental investment and sexual selection. In: *Sexual selection and the descent of man, 1871-1971* (Ed. by Campbell, B.), pp. 136-179. Chicago: Aldine.
- Tutin, C. E. G. 1979. Mating patterns and reproductive strategies in a community of wild chimpanzees (*Pan troglodytes schweinfurthii*). *Behav Ecol Sociobiol*, 6, 29-38.
- van Schaik, C. P., Hodges, J. K. & Nunn, C. L. 2000. Paternity confusion and the ovarian cycles of female primates. In: *Infanticide by Males and Its Implications* (Ed. by van Schaik, C. P. & Janson, C. H.), pp. 361-387. Cambridge: Cambridge University Press.
- van Schaik, C. P. & Janson, C. H. 2000. *Infanticide by Males and Its Implications*. Cambridge: Cambridge University Press.
- Wallen, K. & Zehr, J. L. 2004. Hormones and history: the evolution and development of primate female sexuality. *Journal of Sex Research*, 41, 101-112.
- West-Eberhard, M. J. 1984. Sexual selection, competitive communication and species-specific signals in insects. In: *Insect Communication* (Ed. by Lewis, T.), pp. 283-324. New York: Academic Press.
- Wilcox, A. J., Weinberg, C. R., & Baird, D. D. 1995. Timing of sexual intercourse in relation to ovulation—effects on the probability of conception, survival of the pregnancy, and sex of the baby. *New England Journal of Medicine*, 333, 1517-1522.
- Wolff, J. O. & Macdonald, D. W. 2004. Promiscuous females protect their offspring. *TREE*, 19, 127-134.
- Yasui, Y. 1997. A "good sperm" model can explain the evolution of costly multiple mating by females. *American Naturalist*, 149, 573-584.
- Zahavi, A. 1975. Mate selection—a selection for a handicap. *J. Theor. Biol.*, 53, 205-214.
- Zeh, J. A. & Zeh, D. W. 1996. The evolution of polyandry I: intragenomic conflict and genetic incompatibility. *Proc. R. Soc. Lond. B*, 263, 1711-1717.

Zucker, E. & Clarke, M. 2007. Proximities to specific adult males by adult female howling monkeys (*Alouatta palliata*) in Costa Rica. *American Journal of Primatology*, 69(Suppl. 1), 110.

## **Biography**

Randy Ford was born on February 26, 1976 in Metairie, Louisiana to Tom and Patty Ford. He grew up in Metairie with his older sister, Michelle, and younger brother, Kenny, and graduated from Archbishop Rummel High School in 1994. He attended Rhodes College in Memphis, Tennessee where he was a two-sport letterman in football and baseball and graduated cum laude with a degree in biology in 1998. He then earned a Master of Science in biology from the University of New Orleans in 2002. Randy began his Ph.D. work at Duke University in 2002. Since returning from the field in 2007, Randy has returned home to the New Orleans area, where he married his wife, Nicole, in 2008 and was blessed with the birth of their son, Brayden, in 2010. He currently teaches high school biology at Archbishop Rummel.