

Male Mating Success in *Lemur catta*

by

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Abstract

Dominance rank of males, number of males present during mating and harassment and interruption of mating were each examined to see how they impact male mating success. This study was conducted on four groups of ring-tailed lemur (*Lemur catta*) at Berenty Reserve, Madagascar, with data collected over three mating seasons. I observed six complete estrous periods and four incomplete estrous periods, which represents the largest sample size reported on wild *L. catta* mating behaviour where entire estrous periods were observed. Predictions of the priority-of-access model, the impact of the operational sex ratio (OSR) on mating success, and the relationships between harassment and interruption of mating and mating success were tested. I found that male rank was positively correlated with the number of ejaculations and male mate order. I found no relationship between male dominance rank and number of copulatory partners. My findings do not support the priority-of-access model (that high ranking males will monopolize mating when estrus is asynchronous). My findings show that variation in the OSR during a female's estrous period impacts male mating success, as presence of a greater number of males inhibits ejaculation. This finding raises questions about the value of group membership for non-alpha males. I found the first evidence for primates that aggression directed towards the

mating male directly increases the harassing male's reproductive potential. Occurrence of interruptions decreased the quality of copulations by causing copulatory mounts to be fewer and rates of affiliative behaviour between the mating male and female to be lower. My findings should have implications for reproductive success in *L. catta*, as occurrence of ejaculations with estrous females were used as a measure of mating success. Understanding the relationship between male mating success and mating season dynamics is of key importance in this species.

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1 Chapter 1

Introduction

Mating in ring-tailed lemurs (*Lemur catta*) is intensely competitive, as females come into estrus for only a few hours once per year and typically mate with as many males as possible during this time (Jolly, 1966; Sauther, 1991). Studying this behaviour has its challenges, as females must be monitored closely for subtle behavioural and physiological cues of entering estrus. Perhaps this is one reason why studies reporting mating behaviour in this species typically have small sample sizes and incomplete documentation of estrous periods. In this thesis, I report on data collected during three mating seasons and four lemur groups. During this time, I observed six complete estrous periods and four incomplete estrous periods. As this is the largest sample size for wild *Lemur catta* exploring mating behaviour and mating success in terms of estrous periods observed, I have been able to investigate questions that have not yet been assessed in this species, and in some cases have not yet been evaluated in primates. Each of the following chapters will address questions relating to mating behaviour and mating success while considering questions raised by findings in the previous chapter.

I begin in Chapter Two with a test of the priority-of-access model, something that has previously only been tested in a few primates and never in strepsirrhines. The third chapter addresses the role that the operational sex ratio plays in influencing mating success, and this is only the second time it has been addressed in primates. Following this, the fourth chapter presents an investigation of the role that harassment and interruption of mating bouts play in male mating success. This chapter addresses the question of whether aggression directed towards the mating male directly increases the harassing male's reproductive potential for the first time in primates. Throughout each chapter, I utilize a new model for determining whether or not ejaculation has

occurred during copulation. This model, coupled with the excellent observational conditions at Berenty Reserve, has offered a wealth of new information on *L. catta* mating behaviour. Because Berenty Reserve has been a tourist destination for over 50 years, the lemurs here are very accustomed to human observation, especially those living in the tourist front, allowing for close observation. Although *L. catta* mating behaviour has been especially well studied (e.g., Budnitz and Dainis, 1975; Evans and Goy, 1968; Gould, 1994; Jolly, 1966; 1967; Koyama *et al.*, 1988; Parga, 2003; 2010a; 2010b; Sauther and Sussman, 1993; Sussman, 1992; Taylor, 1986; Van Horn and Resko, 1977), there remains some confusion about this species' mating behaviour that can be addressed in this particularly favourable observational context.

My thesis may clear up some confusion about *L. catta* mating behaviour described in a recent review (Dixson, 2012). Dixson (2012) in his most recent review of primate sexual behavior, lists *L. catta* as exhibiting a single brief intromission copulatory pattern and a multiple ejaculatory pattern based on Jolly (1966) and Koyama's (1988) early research. As will become clear over the following chapters, this is incorrect, as each mating male most typically intromits and thrusts multiple times during copulation and ejaculates only once (Sauther, 1991). Only on the rare occasion of extremely intense competition was a male seen to achieve only a single brief intromission with the estrous female. This incomplete information is especially problematic as *L. catta* is suggested as one of a very small number of strepsirrhines in which mating behaviour has been fully described (Dixson, 2012). Dixson (2012) categorises *L. catta* based in part on Koyama's (1988) incorrect assumption that every copulatory mount between male and female resulted in ejaculation. He explains that what information is lacking, and needs to be documented, is "how frequently males ejaculate with fertile females under natural conditions"

(Dixson 2012, pp. 161). It is quite possible to address this question for *Lemur catta* because the time when each female is fertile is readily observable.

Because confusion exists about what has previously been documented about *L. catta* mating behaviour and what this means for the species' copulatory patterns, I have summarized all previously published work on this topic in a table (Table 1.1). This table shows that, although much is known about *L. catta* mating behaviour, there are still some gaps in our understanding. This thesis aims to continue the tradition of documenting *L. catta* mating behaviour while filling in gaps in the literature in relation to male-male competition and mating success. It is my hope that this thesis sheds some light on topics that have previously been undocumented or incorrectly interpreted in wild groups due in part to small sample sizes and poor observation conditions.

Table 1.1: The history of the study of sexual behaviour in ring-tailed lemurs: published research on mating behaviour

Citation	Key words	Key findings	Sample Size	Location (wild in bold)
Jolly 1966	Aggression, ejaculation, harassment and interruption of copulations	High level of aggression during mating season, friendly interactions between male and female peak at the start of mating season; multiple intromissions	4 incomplete estrous periods	Berenty Reserve
Jolly 1967	Male-female affiliation during mating season	Males groom females more during mating season; multiple copulatory mounts; male-male competition; she theorizes dominance hierarchy is not maintained for mating order	14 adults, unknown how many complete or incomplete estrous periods	Berenty Reserve
Evans and Goy 1968	Mounts	2 to 7 copulatory mounts but only the final mount is the one clearly with intromission	12 adults, unknown estrous periods	Oregon Regional Primate Research Center

Budnitz and Dainis 1975	Male rank and mating frequency	Dominance status does not affect access to estrous females; alpha males do not have a greater number of copulations	10 adults, unknown estrous periods	Berenty Reserve
Van Horn and Resko 1977	Female partner preference	Estrous females do not copulate with all males	12 adults, 9 incomplete estrous periods	Oregon Regional Primate Research Center
Taylor 1986	Male rank and mating frequency	Alpha male had the most copulations	15 copulations observed	Duke University Primate Center
Koyama 1988	Ejaculation, mate order	Each intromission results in ejaculation; 2 nd ranking male first to mate	13 adults, 2 complete estrous periods	Berenty Reserve
Sauther 1991	Single ejaculations	Mate order matches dominance hierarchy	6 complete estrous periods	Beza Mahafaly Special Reserve
Pereira and Weiss 1991	Extra group male mating	Immigrant males sired offspring and received proceptive behaviour from females	15 incomplete estrous periods	Duke Lemur Center
Sussman 1992	Extra group male mating	Females mate with group males, transfer males, males attempting to transfer, temporary visitors and mating season transfer males	6 estrous periods, not clear whether complete or incomplete	Beza Mahafaly Special Reserve
Sauther and Sussman 1993	Mate order, harassment	Mate order matches dominance hierarchy; vigorous and persistent harassment by group males	Unknown	Beza Mahafaly Special Reserve
Gould 1994	Mate order	Alpha male does not always mate first	8 copulations, four of which were at the onset of estrous	Beza Mahafaly Special Reserve
Parga 2003	Copulatory plugs	Copulatory plug displacement occurs	22 copulations	St Catherines Island
Parga 2010a	Inter-group migration	Leaving the natal group is a viable mating strategy	67 copulations	St Catherines Island

Parga 2010b	Mate-guarding	Females solicit mate guarding from males	60 copulations	St Catherines Island
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1.1 Sexual Selection

Darwin (1871) proposed that two forms of sexual selection occur to influence mating outcomes: 1) competition between members of one sex to gain access to the other and 2) choice exerted by one sex on the other. Over the many years of further development of this theory, access to fertile females has been thought of as the limiting factor impacting male reproduction (Andersson, 1994; Bateman, 1948). This leads to competition between males for access to females who, with their higher costs invested in producing offspring, are expected to be the primary individuals exerting mate choice (Trivers, 1972). This leads us to the expectation of observing high male-male competition in the wild, especially in species who are seasonal breeders because the competition between males should be especially concentrated at this time.

1.2 *Lemur catta* as a study species

Lemur catta are Malagasy strepsirrhines that are seasonal breeders, living in complex multimale-multifemale groups exhibiting female dominance (Jolly, 1966; 1984; Kappeler, 1990; Sauther, 1993). Female dominance is an important consideration when studying the effects of female choice on reproductive outcome because it is rare within the primate order (Richard, 1987) and allows females the opportunity to act on their mating preferences prior to copulation without risking male aggression (Sauther, 1991). *Lemur catta* are female philopatric with male dispersal (Sussman, 1991), and females show close affiliation with their daughters (Nakamichi and Koyama, 1997). Female *L. catta* exhibit estrus asynchrony within estrus synchrony, meaning that females enter estrus in close succession but on different days (Pereira, 1991; Sauther, 1991).

Lemur catta live in a harsh environment in which energy must be carefully conserved because severe drought mortality is a constant threat (Gould *et al.*, 1999; Gould *et al.*, 2015). Rainfall will contribute to determine offspring survivorship, but is unpredictable, because amount of rainfall can vary as much as three times between years (Jolly *et al.*, 2002). This has caused a ‘bet-hedging’ lifestyle to evolve in this species, with females often raising just one offspring in good years (Gould *et al.*, 2003; Jolly *et al.*, 2006). Because *L. catta* exhibit strict reproductive seasonality (Koyama *et al.*, 2001), and estrus periods can be as brief as a few hours to less than 24 hours (Sauther, 1991), the mating season represents a short time window of opportunity to reproduce. Within a single group, females will enter into estrus within four weeks of one another, further limiting mating opportunities to a brief time period (Sauther, 1991). Established male dominance hierarchies often predict copulatory priority during the mating season (Parga, 2006; Sauther, 1991), but dominance rank reversals and rank instability among males also occur (Budnitz and Dainis, 1975; Gould, 1994; 1997; Gould *et al.*, 2005; Parga, 2009; Taylor, 1986). This leads to high levels of male-male aggression over access to estrous females (Koyama, 1988; Parga, 2006; Sauther, 1991). Several factors impact male mating success during this time, including male and female mate choice (Gould, 1994; Koyama, 1988; Parga, 2006; 2009; Pereira and Weiss, 1991; Sauther, 1993; Sauther *et al.*, 1999; Sussman, 1991; 1992; Taylor, 1986), and male-male competition (Jolly, 1966; Koyama, 1988; Sauther, 1991). Two factors that potentially impact male mating success are sperm competition (Parga, 2003; Sauther, 1991) and female post-copulatory choice (Birkhead, 1998; Scordato and Drea, 2007). Each of these factors combine so that the mating success of males is impacted by many variables.

Sperm competition (Parker, 1970) is likely to occur in this species, because females mate with multiple partners, and males have one of the largest testes to body size ratios of any strepsirrhine

primate (Kappeler, 1997). Passive mate guarding occurs in the form of copulatory plugs (Dunham and Rudolf, 2009; Sauther, 1991), and behavioural adaptations to this reproductive strategy have been observed in the form of sperm plug displacement (Parga, 2003). Therefore, there is a great deal of evidence to suggest that sperm competition occurs in this species, but very little investigation into how male mating success translates into paternity. Paternity in this species has been examined recently (Parga *et al.*, 2016) and it was found that extra-group males sired between 21% and 33% of offspring. This study did not look at specific behavioral male mating strategies in this species and paternity success. Only one study has examined the relationship between male mating success and paternity in *L. catta* (Pereira and Weiss, 1991). These researchers studied animals in captivity and found that although male dominance rank can be important in determining reproductive success of male *L. catta*, female choice can override male rank (Pereira and Weiss, 1991). It is interesting to note that in this study, alpha males were not found to sire the majority of offspring because three of the study females solicited copulation from, and only mated with, the low ranking new immigrant males. However, this captive study was performed in a constrained environment, where different social groups were separated by fencing. Even still, dominance rank clearly plays a role in mating success of *Lemur catta*.

1.3 Dominance Rank

Although it was stated that social dominance was a universal phenomenon of animal relationships as early as the 1930's (Allee, 1938), whether social dominance has value as a concept defining social behaviour has been thoroughly debated for many decades since (Bernstein, 1981). It was thought for many years that dominance hierarchies were byproducts of the unnaturally stressful conditions of captivity and that dominance hierarchies did not exist in the wild (Rowell, 1974). We now know that linear dominance hierarchies are formed in a wide

range of species, both in the lab and in the wild (Chase *et al.*, 2002). It has generally been concluded that social dominance is a useful concept to describe animals' ability to compete for resources such as food, territory and mates (Benton, 1982). van Kreveld (1970, p. 146) defines dominance as "a priority of access to an approach situation or of leaving an avoidance situation that one individual has over another". When an animal is described as dominant over others, this means that agonistic encounters between the two animals are likely to end with the dominant animal being the receiver of submissive behaviour from the other (Rowell, 1974). Dominance and subordination has also been defined as "a relationship between two individuals in which one (the subordinate) defers to the other (the dominant) in contest situations" (Kaufmann, 1983, p. 2). Social dominance is the state of being dominant over other individuals, and dominance hierarchies are the dominance structures denoting who is dominant to whom in a group. It has been noted that too much emphasis has been placed on aggression within dominance relationships; submission is critically important as well (Bernstein, 1981; Deag, 1977; Kappeler, 1993; Keverne *et al.*, 1982; Lu *et al.*, 2008; Rowell, 1966). When it comes to the outcome of agonistic encounters, without submissive behaviour it is unclear who has won the agonistic interaction. An early review of primate dominance literature pointed out that contradictory findings could be found using different indices for measuring dominance rank (Gartlan, 1964). Such uncertainty about what is meant by social dominance led researchers to question whether anthropomorphism caused hierarchical relationships to be seen in animals where they did not exist (Rowell, 1974), something we now know is not the case (Benton, 1982; Kaufmann, 1983; Rowell, 1966; van Kreveld, 1970).

The first inquiry to describe dominance hierarchies was a pioneering study conducted on chickens. Chickens were observed to engage in direct aggression towards others with impunity

and their social organization in relation to dominance was termed a pecking order (Schjelderup-Ebbe, 1922). For some animals, such as rodents, it is difficult to observe acts of aggression, and thus difficult to ascribe dominance hierarchies (Benton, 1982). This is common for animals that communicate predominantly by scent because dominance interactions may be conducted via olfactory cues which are sometimes difficult to record. Stable dominance hierarchies are often reinforced by ritualized displays of dominance and submission; actual fights are more often seen when an individual's status is disputed (Kaufmann, 1983).

Lemur catta have been found to show linear dominance hierarchies based on avoidance-based matrices when studied in the wild (Norscia and Palagi, 2015; Sauther, 1992) although non-linear dominance hierarchies have been found as well (Nakamichi and Koyama, 1997; Pereira, 1993; Sauther *et al.*, 1999). Hierarchy can be defined as either submission- or aggression-based depending on how it is measured (Norscia and Palagi, 2015). For *L. catta*, dominance hierarchies have been found to be linear based on measuring aggression or submission, and therefore dominance hierarchies are both submission-based and aggression-based for this species (Norscia and Palagi, 2015). Dominance hierarchies are not invariably linear, however, and dominance relationships can also change quite abruptly (Gould, 1994; Nakamichi and Koyama, 1997; Nakamichi and Rakototiana, 1997).

Dominance hierarchies may have an impact on mating outcomes. The priority-of-access model, created in 1962 (Altmann), attempts to predict which males will have access to females based on dominance hierarchies, and was originally studied in *Macaca mulatta* at Cayo Santiago. The model predicts that if a single female is in estrous at one time, only the alpha male has the opportunity to mate. Lower ranking males are predicted to mate in the order of their dominance rank only when more than one female is in estrous at one time. Each male can only monopolize

one female at a time, thus the “rank of the lowest ranking male able to mate with a female on a given day is equal to the number of females simultaneously receptive” (Dubuc et al., 2011, p. 1616). *Lemur catta* are an appropriate animal for studying this model as they live in multi-male, multi-female groups and males show dominance hierarchies (Gould, 1994; Koyama, 1988; Parga, 2006; 2009; Pereira and Weiss, 1991; Sauther, 1993; Sauther *et al.*, 1999; Sussman, 1991; 1992; Taylor, 1986).

A correlation between dominance status and greater mating and reproductive success has been shown in many species (Botero *et al.*, 2009; Côté and Festa-Bianchet, 2001; Cowlshaw and Dunbar, 1991; Curie-Cohen *et al.*, 1983; Dewsbury, 1985; Ellis, 1995; Pusey *et al.*, 1997; Smith, 1981). However, few studies have shown a correlation between each of the three variables: dominance rank, mating success and reproductive success (Huck *et al.*, 1986). My thesis aims to address this issue by assessing the relationship between dominance rank and mating success using a method that may be a direct reflection of reproductive success: ejaculations with estrous females.

The relationship between dominance rank and mating success has been extensively studied in primates (Cowlshaw and Dunbar, 1991; Curie-Cohen *et al.*, 1983; Dewsbury, 1982; Ellis, 1995; Kutsukake and Nunn, 2006; Pusey *et al.*, 1997; Surbeck *et al.*, 2011) with results showing that high ranking males have higher mating success as well as many findings that male rank did not predict mating success (Cowlshaw and Dunbar, 1991). The causes of extreme variation in male reproductive skew in primates is not known, and more information is needed on what factors contribute to paternity in primates (Dubuc *et al.*, 2011). Tests of predictions of the priority-of-access model specifically, have only been carried out in a handful of primate species (rhesus macaques, *Macaca mulatta*, Dubuc *et al.*, 2011; Suarez and Ackerman, 1972; savannah baboons,

Papio cynocephalus, Alberts *et al.*, 2003; 2006; Hausfater, 1975; chacma baboons, *Papio ursinus*, Weingrill *et al.*, 2003; mandrills, *Mandrillus sphinx*, Setchell *et al.*, 2005; chimpanzees, *Pan troglodytes*, Boesch *et al.*, 2006; Wroblewski *et al.*, 2009) and never in strepsirrhines. The findings of these studies have shown that the predictions of the priority-of-access model were upheld, but that the model overestimated the monopolization of females by alpha males (Dubuc *et al.*, 2011). This suggests that there are further factors influencing male mating success. Because *L. catta* are female dominant, female choice may influence male mating success to a greater degree compared with other primate species, which is one reason why a study of how the priority-of-access model predicts mating success in lemurs is an important area of research. Because strepsirrhines are more focused on scent than other primates (Delbarco-Trillo *et al.*, 2011; Drea, 2014; 2015; Schilling, 1979), this heightened ability may play a role in influencing whether alpha males dominate matings. For example, female *Lemur catta* are able to differentiate how genetically compatible they are with a certain male based on the male's scent marks (Charpentier *et al.*, 2010). This would be one way that females could make mate choices for not only the most genetically fit male) but for genetically compatible males.

1.4 Mating Success

Mating success, which is the estimation of how successfully a male has mated with a female, can be measured in many ways simply by observing mating behaviour in primates. In the past, researchers have used a wide array of measures, such as number of copulations (Curie-Cohen *et al.*, 1983; Kuester and Paul, 1992; Paul, 1989; Surbeck *et al.*, 2011), number of consort relationships (Carpenter, 1942), number of days in which copulation occurred (Conaway and Koford, 1965), or even time a male spends with an estrous female (Bercovitch, 1986) as measures of mating success. This variation in ways of assessing mating success may be one

reason why, when mating and reproductive success were both measured in the same groups of primates, it was found that mating success was a poor predictor of reproductive success (Curie-Cohen *et al.*, 1983; Stern and Smith, 1984) although some correlation was found between mating success and reproductive success in male Rhesus Macaques (Berard *et al.*, 1994). No matter how it is assessed, mating success will never be an exact reflection of reproductive success, which is an exact count of how many offspring a male produces, and takes much longer to measure than mating success, as it involves paternity analysis (Parga *et al.*, 2016). By measuring ejaculations with estrous females, we come closest to approximating reproductive success from behavioural observations alone, since males may copulate with females without ejaculating or when the females are not able to conceive. However, when multiple males ejaculate with one estrous female, behavioural observations alone are not enough to estimate reproductive success.

One factor that may affect mating success is harassment of mating (Neimeyer and Anderson, 1983). Harassment of mating has not previously been tested in primates to determine whether aggression directed towards the mating male directly increases the harassing male's reproductive potential. Knowing whether harassment of mating is an important reproductive strategy for males is key to understanding male primate mating behaviour. Previously, the functional significance of harassment of matings in primates was not known. Measuring whether harassment has an impact on the ability of harassed males to ejaculate and whether the harasser goes on to mate to ejaculation with the female is an important area of study.

Determining the incidence of male ejaculation can be problematic in many species by observation alone. Males do not always make audible noises or pause while intromitted when they ejaculate, although this is helpful for determining ejaculation in some species. A systematic protocol for determining ejaculation has occurred is necessary in any measure of male mating

success in the wild just as it is necessary to systematically record female estrous. This thesis addresses this issue by utilizing a new model for determining whether ejaculation has occurred, by systematically documenting relevant observations.

1.5 Operational Sex Ratio

Although the impact of mating behaviour on male mating success has been studied in the wild for *Lemur catta* (Gould, 1994; Koyama, 1988; Sauther and Sussman, 1993 Sussman, 1992; Walker-Bolton, 2010), there has been no investigation of the role that the operational sex ratio plays in male and female mating success. The operational sex ratio (OSR) is the ratio of males to females that are available to mate in a group at a given time. The OSR can be estimated using snapshot censuses counting the number of males and females who are ready to mate at any given time (Kvarnemo and Ahnesjö, 2002). The OSR was first studied in bullfrogs by Emlen (1976). Bullfrogs exhibit highly biased male sex ratios when females go into estrous, estrous is asynchronous during a breeding season, and females are receptive only for one night. This is a very similar scenario to that of *Lemur catta*, who exhibit highly biased male sex ratios when females go into estrous, estrous is asynchronous during a breeding season, and females are receptive only for one day. Because of this similarity to the original study examining OSR, *L. catta* are an ideal study subject to examine the relationship between OSR and mating success. Studying OSR is compelling because it measures male-male competition in a potentially more biologically relevant way. In *Lemur catta*, for example, there are many subtle threat behaviours between males that are difficult to capture during the intense mating period including, for example, two types of stare or grimace (Pereira and Kappeler, 1997). When we study OSR it is possible to potentially capture these subtle threats that are not recorded when we look at contact aggression alone. Another reason OSR is interesting to study in *L. catta* is that it may fluctuate

during a female's estrous period. Not all males that mate with an estrous female copulate under the same competitive social environment (Gould and Ziegler, 2007). This fluctuating level of male-male competition, even though it is more subtle than contact aggression, may follow predictable patterns and/or impact mating outcomes. Operational Sex Ratio has been studied in several social animals (Klemme *et al.*, 2007; Michener and McLean, 1996). Richardson's ground squirrel females (*Spermophilus richardsonii*) mate with multiple males during their estrous and male-male conflict was highest when peak mating occurred and OSRs were least male biased (Michener and McLean, 1996). The movement of estrous females also contributed to the intensity of male-male conflict (Michener and McLean, 1996). Researchers experimentally manipulated OSRs for male bank voles (*Clethrionomys glareolus*) and found that multiple males were more likely to sire offspring when OSRs were male-biased than female-biased. It is expected that *Lemur catta* would experience highly male-biased OSRs during mating unlike what was seen in Richardson's ground squirrels. *Lemur catta* matings are known to be highly contested by group and extra group males (Jolly, 1966; 1967; Gould, 1994; Koyama, 1988; Pereira and Weiss, 1991; Sauther, 1991; Sauther and Sussman, 1993; Sussman, 1992). However, movement of females may contribute to the intensity of male-male conflict in *Lemur catta*, as females have been seen to climb high into the canopy during estrous, which causes an increased risk of injury to males who may fall from this greater height (pers. observ.).

The operational sex ratio and its impact on mating success has been studied only once previously in primates: in Japanese macaques (*Macaca fuscata*) (Takahashi, 2001). In Japanese macaques, several females may enter estrous at one time, thus the OSR fluctuates over time. When the OSR was highly female-biased, extra group males were able to mate and thus had higher mating success than when the OSR was low (Takahashi, 2001). In *L. catta*, two females very rarely are

receptive during the same day (Jolly, 1966; Koyama, 1988; Sauther, 1991) and the number of males present during a female's estrous period fluctuates. Both scenarios affect the defensibility of estrous females, making a study of this metric in *L. catta* an important counter-point to the work done previously on macaques. Moreover, it is important to measure how the OSR may impact mating success for males as this is a factor that is external to the mating male, rather than an intrinsic quality. The OSR may be as important as intrinsic male qualities for impacting mating success.

1.6 Summary

My thesis examines the relationship between certain intrinsic and extrinsic factors affecting males and male mating success in wild *Lemur catta*. For example, I measure whether male dominance rank predicts mating outcomes. Next, I look at factors external to the males, such as number of males present during mating and the incidence of harassment and interruption of mating to mating success. By using an original, multi-step approach to determining whether ejaculation has occurred in this species, I use the measure of mating success that currently most closely predicts reproductive success, since some males do not ejaculate when they mate with estrous females.

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2 Chapter 2

Male dominance rank and mating success in the ring-tailed lemur (*Lemur catta*)

2.1 Abstract

In many species, male-male competition for fertile females determines male mating success. The priority-of-access model predicts male mating success based on male dominance rank, with the highest-ranking group male predicted to monopolize mating when estrus is asynchronous. *Lemur catta* is a species which should support this model, because typically only one female enters estrus at a time in a group, and males form dominance hierarchies. However, the relationship between male dominance rank and mating success is not simple in this species because the previously established male dominance hierarchies can break down during the mating season. I tested the prediction that alpha males will monopolize females during their estrous periods, and tested whether alpha males would mate and ejaculate with the greatest number of females and/or mate first with females.

Observations of mating behaviour and dominance interactions were recorded for four wild, free-ranging groups of *Lemur catta* at Berenty Reserve, Madagascar during three mating seasons. I observed six complete estrous periods and four incomplete estrous periods, which represents the largest sample size reported on wild *L. catta* mating behaviour. Each year was analyzed separately. My findings did not support the priority-of-access model (that high ranking males will monopolize mating when estrus is asynchronous); high-ranking males also did not achieve higher mating success than lower-ranked males, as measured by number of copulatory partners. However, when mating success was measured by mating order and number of ejaculations, the alpha males I studied had the greatest mating success, because male rank was positively correlated with male mate order, and positively associated with incidence of ejaculation.

Therefore, although alpha males do not have the greatest mating success in terms of overall numbers of female mates, they are more likely to mate and ejaculate first with estrous females, which may give them an advantage in fertilization success.

2.2 Introduction

The concept of social dominance has been widely used to explain animal social interactions, such as competition for mating or food resources (Benton, 1982; Kaufmann, 1983; Rowell, 1974; van Kreveld, 1970; Wilson, 1975). Dominance hierarchies were first studied in chickens (*Gallus gallus domesticus*) in the 1920's when it was observed that certain individuals were aggressive towards others without retribution (Schjelderup-Ebbe, 1922). Dominance through the mechanism of agonistic relationships was later suggested as a universal animal phenomenon (Allee, 1938). However, agonism is not as overtly observable in certain animals, such as rodents (e.g., *Mus musculus*) because aggression is often subtly expressed using covert threats, submissive gestures and odours (Benton, 1982). This lack of observed agonism influenced an early definition of dominance as being related to an individual's ability to be the first in the group to approach a reward situation (such as food) and be the first to leave a situation they wish to avoid (van Kreveld, 1970). For many years there was no single accepted definition of dominance as it is exhibited in primates (Bernstein, 1970; de Waal, 1986; Lewis, 2002). When social dominance is considered among primates today, the focus is on the idea that individuals will have unequal numbers of agonistic wins and losses within a group. Male dominance rank has been linked to mating success in many animals (reviewed in Dewsbury, 1982), including primates (reviewed in Bernstein, 1976; Cowlshaw and Dunbar, 1991; Fedigan, 1983; Kolata, 1976; Lancaster, 1978; Pusey *et al.*, 1997; Robinson, 1982; Surbeck *et al.*, 2011). In no other taxon has the relationship

between dominance rank and mating and reproductive success been studied as extensively as in the Order Primates (Fedigan, 1983).

Before genetic analysis became available, mating success was used as a proxy measure of reproductive success (Hughes, 1998; Robinson, 1982). One problem with equating mating success with reproductive success is that some studies which have measured both mating success and reproductive success in the same primate groups have found that measures of mating success were not good predictors of reproductive success (Curie-Cohen *et al.*, 1983; Stern and Smith, 1984). For example, in an eight-year study of captive rhesus monkeys (*Macaca mulatta*), the dominant male only sired 13% to 32% of the offspring, even though he participated in 67% of the observed copulations (Curie-Cohen *et al.*, 1983). The beta male was observed to copulate at a much lower rate but sired a greater number of offspring. In another study of captive rhesus monkeys, findings also indicated that predictions of paternity based on copulatory behaviour were unreliable (Stern and Smith, 1984). Other, more recent studies have found that observed mating behaviour *did* predict reproductive outcome (Berard *et al.*, 1994; Alberts *et al.*, 2006). Berard *et al.* (1994) found some evidence that mating success predicted reproductive success in male rhesus macaques. For high-ranking males, forming long-term consortships resulted in the biggest reproductive pay off; however, the quick, furtive reproductive tactic was also successful for some males (Berard *et al.*, 1994). In a study by Alberts *et al.*, (2006) on wild savannah baboons (*Papio cynocephalus*), observed mating success was generally a good predictor of reproductive success for males (Alberts *et al.*, 2006). One limitation to measuring mating success is that some copulations are hard to see as subordinates attempt to conceal themselves from members of the group (Drickamer, 1974). Another difficulty with the two earlier studies that did not find a correlation between mating and reproductive success, may be that mating success was

not measured in the most accurate way: by measuring ejaculation rate at ovulation (Fedigan, 1983).

Mating success is measured in different ways and much has been written about the discrepancies within primate research on how mating success is measured (Bernstein, 1976; Drickamer, 1974; Fedigan, 1983; Rowell, 1974; Smuts, 1982). Part of the issue lies in the fact that copulatory behaviour can be classified into three types of events: mounts, intromissions, and ejaculation (Dewsbury and Pierce, 1989). Each of these events has been used as a measure of mating success and for each of these classes of events there are several ways in which they can be measured. For example: baboon (*Papio anubis*) mating success has been measured by the amount of time spent in consortships (Bercovitch, 1986) since this had been correlated with ejaculation success in previous research (Bercovitch, 1985). Researchers studying chimpanzees (*Pan troglodytes*) have measured mating success by counting intromissions (Klinkova *et al.*, 2005). These researchers have measured mating success by determining copulation rates, where one copulation was defined as one or more intromissions occurring within 260 seconds (the minimum interval between two ejaculations in this species) (Klinkova *et al.*, 2005). The fact that mating success has been measured in different ways has led to difficulties in intraspecific and interspecific comparisons of primate mating success.

The priority-of-access model (Altmann, 1962) is the most widely used framework for predicting sexual access to females in multi-male, multi-female groups. The priority-of-access model predicts the likelihood that a male will have access to an estrous female based on his position in the dominance hierarchy and the duration of the female's estrus. The model has several assumptions: (1) females of a group have independent estrous cycles; (2) when males are competing for access to an estrous female, the highestranking male will win; (3) males are

ranked on an ordinal scale of dominance; (4) males are continually receptive to mating, while females are receptive for only a fraction of their cycle; (5) males do not consort with more than one female at a time.

When more than one male mates with a receptive female, first-mating males are believed to have greater reproductive success than other males (Pereira and Weiss, 1991; Sauther, 1991). This idea relies on the assumption that these males are ejaculating with fertile and conceiving females and that there is a fertilization advantage for first ejaculating males. Differential fertilization success has been seen experimentally in mice, where the first males to ejaculate of a compatible albino strain were found to sire the most offspring (Levine, 1967). When males of a less compatible, black-agouti strain were allowed to ejaculate first, the number of albino fetuses was reduced. This result showed that there was some advantage to being the first ejaculating male. However, mating order is often difficult to determine in primates, and few studies have considered whether there is a reproductive advantage to being the first ejaculating male (reviewed in Dixson, 2012; Eberle *et al.*, 2007). Early mating males, but not first mating males, were found to be more likely to sire offspring in mouse lemurs (Eberle *et al.*, 2007).

The topic of reproductive success and male dominance rank in primates has been extensively studied, but this research has resulted in conflicting findings. For example, immigrant and neighbouring group males sire a significant proportion of offspring in some primate studies (*Lemur catta*: Pereira and Weiss, 1991; Parga *et al.*, 2016; *Macaca mulatta*: Georgiev *et al.*, 2016) and occasionally low ranking resident males can be significantly successful at reproducing (*Erythrocebus patas*: Ohsawa *et al.*, 1993; *Macaca mulatta*: Smith, 1993). These findings contrast with the majority of primate studies' findings which show a correlation between male

dominance rank and reproductive success (Altmann *et al.*, 1996; Bauers and Hearn, 1994; Bercovitch and Nürnberg, 1996; De Ruiter *et al.*, 1992; Dixson *et al.*, 1993; Pope, 1990).

The species of focus for this study, ring-tailed lemurs (*Lemur catta*), live in complex multimale-multifemale groups exhibiting female dominance (Jolly, 1966; Sauther *et al.*, 1999; Sussman, 1991; 1992), male dispersal (Gould, 1997; 2006; Sussman, 1992), continual status-striving between intrasex group-mates (Pereira, 2006), strict reproductive seasonality (Sauther, 1991) and asynchrony within the broader seasonal estrous synchrony (Jolly, 1966; Pereira and Weiss, 1991; Sauther, 1991). Female *L. catta* experience estrous periods which last from half a day to two days and often mate with multiple male partners from inside and outside their groups (Gould, 1994; Koyama, 1988; Parga, 2006b; Pereira and Weiss, 1991; Sauther, 1991; Sussman, 1992). Females are thought to mate during the night as well as the day during their estrous, although data are lacking on this behaviour (Jolly, 1966; Koyama, 1988; Parga, 2006, 2011; Petter, 1965; Sauther, 1991). *L. catta* live in large groups of several matriline and are highly terrestrial (Jolly, 1966). Olfactory communication is important to *L. catta* and scent marking is used by males and females for a variety of functions, including: marking territorial boundaries (Mertl, 1977; 1988; 2006), identifying individuals (Mertl, 1977), signalling estrus (Gould and Overdorff, 2002), intergroup spacing and intrasexual competition (Scordato and Drea, 2007), and short range communication within a group when they are close together (Oda, 1999).

Lemur catta are highly social and females are consistently dominant to males (Jolly, 1966; 1984; Pereira *et al.*, 1990; Sauther *et al.*, 1999). Males and females have separate dominance hierarchies in each group (Budnitz and Dainis, 1975; Gould, 1994; Koyama *et al.*, 2005; Sauther *et al.*, 1999; Taylor, 1986), and these dominance relationships can be linear or non-linear (Cavigelli *et al.*, 2003; Gould, 1996; 1997; Nakamichi and Koyama, 1997; Sauther, 1992;

Sauther *et al.*, 1999). These dominance hierarchies are steep, consistent, and cohesive (Norscia and Palagi, 2015). This means that the difference between the ability to win an agonistic encounter between adjacent individuals in the hierarchy is great and consistent, and that group members maintain close proximity (within 20m) of the alpha (Nakamichi *et al.*, 1997; Norscia and Palagi, 2015; Sauther, 1992). A female's dominance status is passed on to her daughters, with older sisters being dominant to younger sisters (Jolly, 1966). High dominance status has certain advantages for males and females. Dominant females have priority of access to feeding sites over all group members (Jolly, 1966; Sauther, 1993) whereas dominant males have priority of access to feeding over less dominant males (Sauther, 1993; White *et al.*, 2007).

Alpha males do not maintain their position as most dominant male throughout the mating period, as male dominance hierarchies break down during the mating season (Budnitz and Dainis, 1975; Gould, 1994; 1997; Gould *et al.*, 2005; Parga, 2009; Taylor, 1986). Often, alpha males maintain their dominance until shortly after ejaculation, at which time they are challenged by competitor males and eventually overpowered and lose access to the estrous female (Parga, 2009). Female sexual receptivity shown towards a lower ranking male also was one factor that preceded the break down of the dominance hierarchy in one study (Parga, 2009).

In this species, females often mate with non-natal members of the group as well as extra-group males (Gould, 1994; Sauther, 1991; Sauther and Sussman, 1993), however alpha males have been shown to benefit in certain ways during the mating season. Dominant males have been found to: mate first with females (Sauther, 1991; Sauther and Sussman, 1993; Sussman, 1992), be the only males who engage in precopulatory guarding of females (Sauther, 1991), and engage in post-ejaculatory mate guarding for the longest duration (Sauther, 1991). However, not all studies have confirmed that alpha male *L. catta* mate first, with research at Bezà Mahafaly

Special Reserve (Gould, 1994) and Berenty Reserve in Madagascar (Koyama, 1988) showing that some alpha males did not mate first. At Bezà Mahafaly Special Reserve, data were collected on complete estrous periods of four individual females and it was observed that for two of these estrous periods the first male to mate was not the alpha male of the group (Gould, 1994). At Berenty Reserve, data were collected on two complete estrous periods and it was found that the first mating male in the two instances was not the alpha male but the beta male, and that the mating female refused to mate with the alpha male (Koyama, 1988). The mating success of males can be measured in a number of ways. Mating success in *Lemur catta* has been measured by: counting number of ejaculations (Koyama, 1988; Sauther, 1991; Sauther and Sussman, 1993), number of mounts with intromission (Koyama, 1988), mating order (Sauther, 1991; Sauther and Sussman, 1993), and the duration of pre and post ejaculatory guarding (Sauther, 1991). Multiple ejaculations between single male-female pairs during mating has been reported (Koyama, 1988), but this finding has been disputed as an overestimate of ejaculations and it is now understood that males will ejaculate only once with each female mate during a single estrous period (Parga, 2003; Sauther, 1991). Ejaculations in *L. catta* have been determined using varying criteria (Sauther, 1991; Parga, 2009). Sauther (1991) determined that ejaculation had occurred by watching for the longest thrusting bout and then observing ejaculate on the male's penis, which he then typically grooms. Conversely, Parga (2009) determined ejaculation when ejaculate was visible on the female's genital region or on the male's penis tip. I present additional criteria for measuring ejaculation in this species.

In my study, I addressed three hypotheses to test for evidence supporting the priority-of-access model in *L. catta*. (1) If dominance rank is an accurate indication of male quality (Andersson, 1994; Berglund *et al.*, 1996; Cox and Le Boeuf, 1977; Qvarnström and Forsgren, 1998), I

hypothesize that high ranking males should have the greatest number of copulatory partners due to success at male-male competition and/or due to female choice. Correspondingly, I predict a positive correlation between male dominance status and number of copulatory partners (with the alpha male having the greatest number of partners). (2) Considering that most previous studies of sexual behavior in *L. catta* have found that high ranking males mate in the order of their rank (Sauther, 1991; Parga, 2006c) or that high ranked males mate first (Koyama, 1988; but see Pereira and Weiss, 1991 and Gould, 1994), I hypothesize that high status males will mate earlier in the mating queue. I predict a positive correlation between male dominance rank and mate order (alpha male mates first). (3) Because high ranking males have demonstrated a greater ability to dominate competitor males during the pre-mating period and should be able to complete mating bouts more easily than other males, I predict that higher ranking males will ejaculate more than lower ranking males (measured as a significant difference between the medians of the two groups: ejaculation and no ejaculation, in terms of the rank of males in each category). The null hypothesis is that there is no relationship between male dominance rank and measures of male mating success.

2.3 Methods

2.3.1 Ethical Note

All research protocols were approved by the Animal Care Committee at the University of Toronto (Protocol number: 20010369) and conform to the governing laws of the Malagasy Republic. This study was conducted with the approval of the de Heaulme family, owner of the private nature Reserve of Berenty.

2.3.2 Study Site

Berenty Reserve (24° 58 S, 46° 16 E) is a private nature preserve in the extreme south of Madagascar established in 1936 by the de Heaulme family. The de Heaulme family have a long history of welcoming international researchers to their study site, beginning with Alison Jolly's pioneering study of *Lemur catta* behaviour, which was initiated in 1963 (Jolly *et al.*, 2006). Long term, continuous research has been conducted by Koyama and his colleagues at the reserve since 1989 (Koyama *et al.*, 2001).

The reserve consists of 2 km² of gallery forest containing large tamarind trees (*Tamarindus indica*) with a closed-canopy and 1.5 km² of less ecologically rich scrub and spiny forest (Jolly *et al.*, 2002). The reserve acts as a major tourist destination throughout the year and the main area for tourists in which this study was conducted is known as the Tourist Front. The Tourist Front includes a restaurant and tourist bungalows and has many introduced species of plants and trees which supplement the lemurs' diets (Jolly, 2012). In addition, lemurs are occasionally fed scraps by tourists, although formal provisioning has been discontinued and tourists are warned against feeding the animals. Summers are hot and wet, averaging 40°C at mid-day and winters are cold and dry with temperatures falling at night to 10°C (Jolly, 2012). There is great variability in rainfall from year to year, ranging from 300cm to 900cm annually (Jolly, 2012).

The population of *L. catta* for Berenty Reserve was reported as 562 individuals in 2015, with the largest average group being found in the Tourist Front (Dimilahy *et al.*, 2015; Foulon *et al.*, 2015; Gould and Sauther, 2016). Population density is 5.8 ind/ha for *L. catta* at the Tourist Front, the highest in the reserve (Jolly *et al.*, 2002). This is much higher than the 1-1.5 ind./ha density seen within the Scrub (Jolly *et al.*, 2002). Primates found in Berenty Reserve include the introduced *Eulemur rufus collaris* hybrid, Verreaux's sifaka (*Propithecus verreauxi*), lepilemur

(*Lepilemur leucopus*), and two types of mouse lemur (*Microcebus murinus*, *Microcebus griseorufus*) (Jolly *et al.*, 2002). Potential lemur predators include both mammals (domestic dogs and cats, and the Indian civet [*Viverricula indica*]) (Jolly, 2012) and birds (the harrier hawk [*Polyboroides radiatus*], the Madagascar buzzard [*Buteo madagascariensis*], and the black kite [*Milvus migrans*]) (Crowley, 1995; Karpanty and Goodman, 1999).

2.3.3 Study Subjects

The *L. catta* chosen for this research were not part of any other ongoing research study (Appendix 1). Natural markings (minor pelage coloration differences, old, easily-seen scars from fights with other animals, etc.) were used to identify each lemur. Adult male and female study subjects were selected as focal animals from four groups inhabiting the Tourist Front (Table 2.1). Adults were selected because they are the age category which engages in mating behaviour. Each adult subject has been photographed and drawn to document their distinguishing features.

Table 2.1: *Lemur catta* group composition by adult male (AM) and adult female (AF) study subjects for the three study periods, 2012-2014 at Berenty Reserve, Madagascar.

Group	2012		2013		2014	
	AM	AF	AM	AF	AM	AF
A1	1	6	1	4	0	0
RG	4	4	3	3	4	4
MG	2	2	3	4	3	5
LG	1	3	0	0	0	0
Total	8	15	7	11	7	9

I collected all data for this study during three consecutive field seasons in Berenty, April to June in 2012 to 2014. The observed mating season lasted for at most 10 days in the study groups

(Table 2.2). The mating season was determined to start at the first observed copulation and ended with the last observed copulation. Certainly, some copulations were missed, meaning that the actual mating season was likely longer than the observed mating season. The sample size for study animals fluctuated slightly over the three years of behavioural observations due to deaths, disappearances, emigrations, births, and group membership changes as juveniles matured to adulthood. Adults were defined as sexually mature individuals who have reached full adult body size and were observed mating during the mating season. Juveniles were defined as individuals who were close to adult body size but who did not participate in mating. Yearlings were all individuals that were of smallest body size in the group and exhibited infant-like traits (Sauther and Sussman, 1993). Adults were distinguished from juveniles based on body size estimates, and sexual development. Sexual development was assessed on appearance of genitals as well as whether the individual mated during the mating season. Individuals are known to mate as early as two years, and most females have their first offspring at three or four years of age (Koyama *et al.*, 2001). There were substantial changes in group composition during the three study years (Table 2.1).

Table 2.2: Duration of the observed mating season for each of the study years

Year	First Observed Copulation	Last Observed Copulation	Duration of Mating Season
2012	April 25th	May 4 th	10 days
2013	May 1st	May 7 th	7 days
2014	April 27th	April 27th	1 day

Extra-group males were seen mating with group females. Extra-group males were defined as any males from outside of the group, known to be members of other groups, and not attempting to immigrate into the group. When calculating male dominance rank for correlations with number

of copulatory partners, male mate order and male ejaculation frequency, only resident males were included in calculations of male dominance rank. Male dominance rank was calculated using data from the entire study period except for days when a female entered estrous. In this way, the effect of the break-down of the dominance hierarchy during the mating season was minimized.

2.3.4 Behavioural Data Collection

All behavioural observations were conducted by AWB, supported by two experienced Malagasy field assistants from the University of Antananarivo. AWB trained and supervised both of the field assistants chosen for the research project. Assistants did not collect data but assisted by identifying individuals, monitoring group movement, and locating estrous females. Observations of four groups (A1, RG, MG, LG) were conducted six days per week from 0700 hrs until 1700 hrs, alternating between groups on subsequent days for a total of 414 hours of focal observations over three years. During the study, the mating period was defined as the time between the onset of the first observed estrus and the last observed estrus during the first estrus cycle of the season (Evans and Goy, 1968; Sauther, 1991; Van Horn and Resko, 1977). During the mating period, observations were conducted seven days per week. Prior to the commencement of the mating period, training of assistants and familiarization with all study subjects occurred.

During the mating season, when a female was observed to enter estrus, all occurrences sampling for agonism and sexual behaviour began for the entire duration of estrus. Twenty-two hours of all occurrences sampling data were collected over the three years. All affiliative, mating, and aggressive behaviour was recorded using the all-occurrence group sampling method (Altmann, 1974). Prior to the initiation of each follow, data were recorded on physical manifestations of female reproductive state by noting any changes in genital swelling or colour. *Ad libitum* data

were also collected at all times on such occurrences as presence of any physical injuries, abandonment of infants, infanticide, and predation events.

Using continuous-time focal sampling (Altmann, 1974), data were collected during the non-mating days on all affiliative and aggressive behaviours, and all mating behaviours (courtship, copulations, mate guarding) (Appendix 2). Copulations were defined as mounting with penile intromission and thrusting. Mating bouts were defined as each male's period of copulatory mounts with a female in which he did not lose access to the female to a competitor male. Estrous periods were defined as the entire time a female was sexually receptive to males. Outside of mating periods, focal samples were conducted for 15 minutes each. This focal follow duration allowed each focal individual to be sampled at least twice during each time period of morning or afternoon. Focal animals were selected by always choosing to follow the individuals with the lowest total number of follows and making an attempt to equalize the number of follows completed on each individual during the mornings and afternoons. Data were recorded using data sheets.

Dominance rank was calculated by collecting data on all decided agonistic interactions, displacements and the direction of submissive vocalizations known as the spat call (Jolly, 1966). Focal data on aggression and submission during the mating period were used for the hierarchy matrices. Winners of aggressive interactions and receivers of the submissive vocalization were coded in the same manner for the matrices. For example, within the matrix, rows represent winners of aggression and receivers of spat calls, while columns represent losers of agonistic encounters who give the submissive vocalization. Because some of the dominance hierarchies were non-linear, the dominance index method was chosen following Zumpe and Michael (1986). In this method, the dominance index for each individual was calculated by averaging the

percentage of aggression given and submission received with all the other same-sex animals in the group (Zumpe and Michael, 1986). Dominance indices for males were turned into ordinal ranks for analysis.

Mating success was measured in three ways: number of copulatory partners, mating order, and incidence of ejaculation. Number of copulatory partners was determined by counting the number of females a male mounted and engaged in pelvic thrusting with intromission of the penis. Mating order was the order in which the male was seen to mate with the female relative to her other copulatory partners. Both number of copulatory partners and mate order were relevant only when the entire estrous period of a female was known to be observed. For example, if a female and male were encountered after mating had already commenced, this was coded as an incomplete estrous period because there could have been some mating which occurred prior to the observer arriving. Similarly, if a female was still in estrus at the time that observations ended, this was also coded as an incomplete estrous period.

Table 2.3: Criteria for determining whether ejaculation has occurred or not occurred.

Ejaculation has occurred	Ejaculation has not occurred
Ejaculate seen on male's penis tip	Male with an erection after thrusting bout and none of the criteria for determining ejaculation has occurred are met.
Ejaculate seen on female's genitals	Mating interrupted by competitors and none of the above criteria are met.
The male in question removes a copulatory plug (Parga 2003) from the female during mating and the male who mates directly after the male in question also removes a copulatory plug during mating.	
The male in question is known to be the first mating male and the male who mates directly after the male in question removes a copulatory plug from the estrous female during mating.	
Male seen mate guarding the female without an erection and no further mounts with thrusts and intromission.	

2.3.5 Data Analyses

The number of copulatory partners was translated into rates by dividing by the number of hours of all occurrences observation for each individual. Spearman rank correlations were used to compare the number of copulatory partners and mate order with male rank. The Mann-Whitney U test was used to compare incidence of ejaculation with male rank. All statistical analyses were conducted in SPSS 22.0 for Windows. Significance levels were set at $p < 0.05$ for all correlations and all tests were two-tailed. Data from each of the three years were not pooled, but analysed separately. The reason data were analyzed separately is due to the fact that there were many group composition changes over the years. Changes to male dominance hierarchies also occurred as some males emigrated to new groups.

2.4 Results

Twenty mating bouts in total were observed over the three-year period with eight mating bouts by extra-group males (Appendix 3). Over the three-year period, I was able to observe six complete estrous periods and four incomplete estrous periods. I observed fourteen ejaculations, seven of which were by extra-group males.

In the first mating season, I recorded five complete estrous periods and two incomplete estrous periods. The incomplete estrous periods occurred for females FL and SI. A total of 107 focal observation hours and 15.5 all occurrences hours of observation were recorded (Appendix 4). Ejaculations occurred in 12 of the 17 mating bouts recorded in the first mating season. In 41.2% (N=7) mating bouts recorded, extra-group males were involved (Table 2.4). For the second mating season, 223.75 focal observation hours and 3.8 all occurrences hours of observation were recorded. For the third mating season, 83.25 focal observation hours and 2.65 all occurrence hours of observation were recorded. In the second mating season, I recorded two incomplete estrous cycles and in the third mating season I recorded one complete estrous cycle.

Table 2.4: Summary of mating events from three mating seasons (2012-2014) among four groups at Berenty Reserve, Madagascar.

Season	Mating Bouts	Complete Estrous Cycles	Incomplete Estrous Cycles	Ejaculations	Extra-group Males Mating
2012	17	5	2	12	7
2013	2	0	2	2	1
2014	1	1	0	0	0

2.4.1 Male rank and number of copulatory partners

There was variation among the male study subjects in the number of female mating partners they had each year (Table 2.5). I found no significant relationship between male rank and number of copulatory partners (Spearman Rank: $r_s = -0.086$, $n = 8$, $p = 0.839$) in the first mating season. When the variable of male rank was grouped as a comparison of alpha males with lower ranked males (rank of 1 vs. 2-4), there was again no significant average rate difference between high rank and lower ranks (t-test: $p = 0.628$, two-tailed).

Table 2.5: Range of number of copulatory partners for males over the three mating seasons studied (2012-2014) at Berenty Reserve.

MALES	GROUP	YEAR	# of Partners
AL	A1	2012	4
RY, BK, FO	RG	2012	2
WL, RE	RG	2012	1
FX	MG	2012	0
HY	LG	2012	1
AL	A1	2013	0
WL	A1	2013	1
BK, IY	RG	2013	0
RE, BK	RG	2013	1
BT, BV, BY	MG	2013	0
BK	RG	2014	1
AL, WL, IY	RG	2014	0
BT, BV, BY, BR, BJ	MG	2014	0

There was no significant relationship between male dominance rank and number of copulatory partners (Spearman Rank: $r_s=0.132$, $n=8$, $p=0.755$) during the second mating season. Due to the fact that the two estrous periods observed were incomplete, mate order is marked as unknown (UNK) in Appendix 6.

Due to group mergers, only two study groups remained for mating season three: RG and MG. There was only one male who was observed mating in the third mating season, precluding any statistical analysis of male mating success by dominance rank. The low number of estrous periods observed was due most likely to estrous periods being missed by the observers. BK was clearly the alpha male with seventy acts of aggression towards or submission received from others in the group. The other males are marked with a question mark under rank (Appendix 7) because they were not seen to engage in aggressive or submissive acts towards one another.

2.4.2 Male rank and mate order

Even though the sample size is small, there was still a significant positive relationship between male dominance rank and mate order ($r_s=0.965$, $n=9$, $p=0.0001$) during the first mating season. When a male was higher ranking, he was more likely to mate first (Figure 2.1). Of the five estrous periods where the entire estrous was observed, the alpha male of the mating female's group mated first.

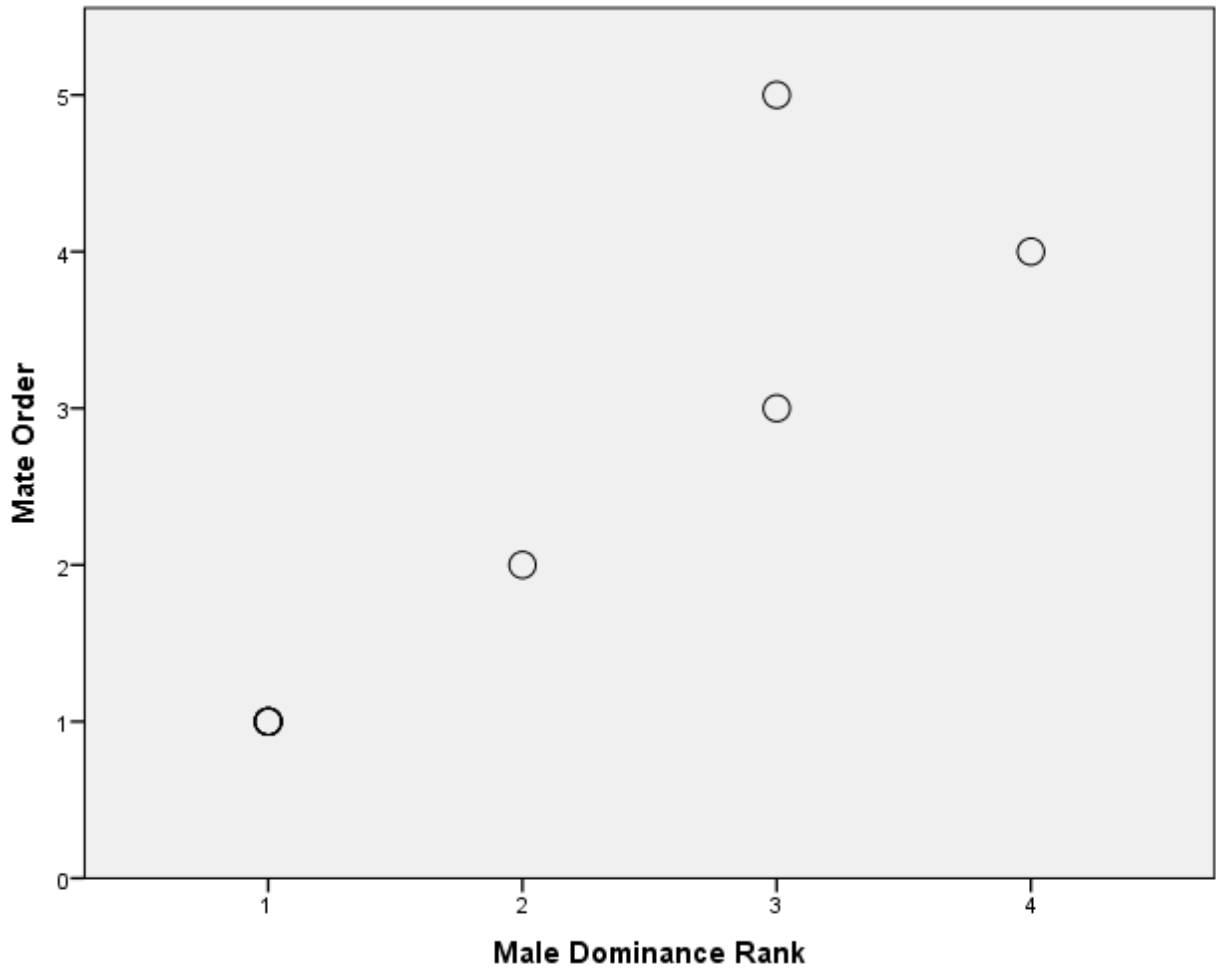


Fig. 2.1: Relationship between male mate order and male dominance rank among *Lemur catta* males from four groups at Berenty Reserve during the 2012 mating season. Bold: represents five data points.

Because only two incomplete estrous periods were observed, the relationship between rank and mate order was not analyzed for the second mating season. During the third mating season, BK, the highest ranking male of RG, was observed mating with one female whose full estrous period was observed. Because only one male mated with this female, mate order was not relevant, although it is interesting to note that the mating male was the alpha of the group.

2.4.3 Male rank and ejaculation

In the first mating season, there was a significant relationship between male dominance rank and incidence of male ejaculation, with males observed to ejaculate showing higher ranks than males

who were observed to mate without ejaculation (Mann-Whitney $U = .0001$, $n_1 = 4$, $n_2 = 6$, $P = 0.004$ two-tailed). When a male was high ranking, he was more likely to ejaculate with his female mating partner.

Because only two incomplete estrous periods were observed during the second mating season and a single estrus period was observed for the third mating season, the relationship between rank and ejaculation was not analyzed for these latter two seasons. Although I did not analyze the relationship between male rank and ejaculation due to the incomplete estrous periods observed, it is interesting to note that in both cases the beta male was able to ejaculate with the female, and male-male competition did not limit his ability to ejaculate.

In the single estrous period observed during the third mating season, the alpha male was not seen to ejaculate with his partner. This was determined to be due to high levels of male-male competition which occurred during the mating bout. Comparing the brief mounts which precede a longer bout in this case, I observed that the longer bout at the end of mating was 52 seconds long. It was determined that this mating did not end in ejaculation because no ejaculate was seen, the male was seen to have an erection after the final mating bout ended, and the final mating bout was interrupted by intense male-male competition.

2.5 Discussion

My study tested whether alpha males would monopolize mating with estrous females as predicted by the priority-of-access model, and whether alpha males would mate with the most females, mate first with those females, and be more likely to ejaculate than lower-status males. My results show that while alpha males did not mate with a greater overall number of females than other males, they did mate first with females and ejaculate with females more frequently. Although mating success is usually measured by the number of mating partners, it is perhaps a

more accurate reflection of true mating success in this species to consider mate order and to measure the number of females with whom a male ejaculated. This is because not all mating bouts culminate in ejaculation in *Lemur catta* and there may exist a fertilization advantage for first mating males (Evans and Goy, 1968; Pereira and Weiss, 1991).

Over a three-year period, I was able to observe six complete estrous periods and four incomplete estrous periods, which represents the largest sample size reported on wild *L. catta* mating behaviour. Although male dominance rank and mating success in *L. catta* has previously been studied, conflicting results have been found. My findings complement those published previously from Bezà Mahafaly Special and Berenty Reserves (Gould, 1994; Koyama, 1988; Sauther, 1991; Sauther and Sussman, 1993; Sussman, 1992). Although Gould (1994) and Koyama (1988) both observed alpha males not being the first males to mate, my study is in agreement with data collected by Sauther (1991), who found that males often mate in the order of their rank.

The priority-of-access hypothesis predicts that if estrus is asynchronous among group females, only the alpha male will copulate. Similar to previous research on the mating behaviour of this species, I found that *Lemur catta* do not fit this model, because females mate with multiple males (Gould, 1994; Koyama, 1988; Parga, 2006b; Pereira and Weiss, 1991; Sauther, 1991; Sussman, 1992). As I predicted, there was no correlation between male dominance rank and number of copulatory partners. Number of copulatory partners may not be a good measure of mating success in this species, as both males and females seem to mate with as many partners as possible. A better measure of mating success may be male mate order.

Mate order was predicted to positively correlate with male dominance rank. Alpha males were indeed seen mating first in every instance where the entire estrous period was observed, and

lower ranking males were generally observed to mate in the order of their rank (Figure 1). These findings match those of Sauther (1991), Sauther and Sussman (1993), and Sussman (1992), who observed alpha males mating first, and were contrary to what was found by Koyama (1988) and Gould (1994), who observed lower ranking males mating first on occasion.

Incidence of ejaculations were predicted to be higher for high ranking males. When a male was high ranking, he was more likely to ejaculate with his female mating partner. These findings were predicted for *L. catta* because one of the benefits of being an alpha male is expected to be greater reproductive success. These findings provide the strongest evidence reported so far of a reproductive advantage for alpha males in this species.

The current study inferred the occurrence of ejaculation using systematic criteria with as few assumptions made as possible. Each mount with thrust and intromission between a male and female was not assumed to result in ejaculation, as was assumed by Koyama (1988). Since his important pioneering study, we have learned that male *L. catta* are capable of ejaculating only once with estrous females (Sauther, 1991; Parga, 2003). I used a five-step process for determining whether ejaculation occurred. This is a less conservative measure than employed by Parga (2009), who classified an ejaculation only when ejaculate was seen on the male's penis tip or the female's genitals. However, my method does capture some ejaculations that would otherwise be missed by using the visual method.

I observed fourteen ejaculations, half of which were by extra-group males. This high rate of ejaculation by extra-group males was unexpected, as previous research on *L. catta* in Berenty, Madagascar has shown that extra-group males were not observed to mate (Jones, 1983; Mertl-Millhollen *et al.*, 1979). On three occasions in 1975, a neighbouring troop male attempted to mate with an estrous female, but these attempts were unsuccessful (Mertl-Millhollen *et al.*,

1979). Female *L. catta* were not seen mating outside of their groups and were classified as not engaging in this behaviour by Jones (1983). Research at Bezà Mahafaly Special Reserve has shown that extra-group males did mate with estrous females, but data on the frequency of ejaculations for these males was lacking (Gould, 1994; Sauther, 1991; 1992; Sussman, 1992). Future research will examine what factors may have led to the high ejaculation rate of extra-group males in my study and what the reproductive success of these males was.

One limitation of the current study is that it can be difficult to determine when a male *L. catta* has ejaculated, and proximate criteria must be used to estimate when it has occurred. For this reason, I may have underestimated low ranking male ejaculations. I rejected the idea that male self-grooming of genitals or white substance visible on the shaft of the penis (versus the tip) were good indicators of male ejaculation. This was based on the data that males would often self-groom their genitals prior to ejaculation and that white substance on the shaft of the penis may have been present due to contact to previous mating males' ejaculate or copulatory plug. It is also not possible to observe ejaculate on the female's genitals or the male's penis tip in every instance.

Another limitation involves the classification of complete and incomplete estrous periods. Mating behaviour was often already initiated by the time mating observations began. Because my study followed four groups of lemurs and I was limited to two observers, it was not always possible to be present at the beginning of a female's behavioural estrus. Four incomplete estrous periods were observed during the three- year study period.

Alpha males were most often found mating with the estrous female in the early morning. One indication that no other group males had mated prior to the alpha male was that all group males were present and in competition for the estrous female. Typically, once a male is overthrown he

participates less in competition for the estrous female. The possibility remains that an extra-group male could have mated prior to the alpha male mating with the female, although this seems highly unlikely because no extra-group males were observed in the vicinity of any estrous female of the group when an alpha was mate guarding her. More importantly, no copulatory plug was removed during any alpha male's mating bout, providing strong evidence that these males were often the first to mate and ejaculate with estrous females. It is therefore highly unlikely that alpha males were overestimated as first mating males in this study.

In conclusion, I predicted that dominance rank would not have a positive correlation with male mating success, as measured by number of copulatory partners for males. I found no correlation between male rank and number of copulatory partners. My findings do not support one of the predictions of the priority-of-access model (that high ranking males will monopolize matings with females if estrous periods are asynchronous). I also tested mating success in two other ways: by mate order and number of ejaculations. When mating success was measured in these ways, alpha males were shown to have an advantage over lower ranking males. My findings add to the literature on male rank and mate order with previous results at Bezà Mahafaly Special Reserve showing alpha males mating first (Sauther, 1991; Sauther and Sussman, 1993 but see Gould, 1994). Previous research from another Malagasy research site, Berenty Reserve, has found alpha males not mating first (Koyama, 1988), while my findings differ. My criteria for determining whether ejaculations occurred differed from those of previous researchers by including instances where no ejaculate was seen. Further studies should continue to explore whether mating order correlates with reproductive success in this species. My findings add to our understanding of the function of male dominance rank in this species.

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Appendices

APPENDIX 1: *Lemur catta* focal subjects and group membership for the three study periods, 2012-2014 at Berenty Reserve, Madagascar. Individuals that emigrated from one group to another are shown under each group they were a member of. Individuals are indicated as not present when they disappeared from the group and were not known to be deceased or present in another group.

Group	Subject	Category	Apr–Jun 2012	Apr-Jun 2013	Apr-Jun 2014
A1	Finch (FI)	AF	Present	Present	Not present
A1	Frances (FR)	AF	Present	Not present	Not present
A1	Flavia (FL)	AF	Present	Deceased	Deceased
A1	Fyawn (FY)	AF	Present	Not present	Not present
A1	Simi (SI)	AF	Present	Not present	Not present
A1	Chris (CH)	AF	Present	Present	Not present
A1	Alec (AL)	AM	Present	Present	Member of RG
A1	William (WL)	AM	Member of RG	Member of A1	Member of RG
A1	Pippa (PI)	AF	Member of LG	Member of A1	Member of RG
A1	Tammy (TA)	AF	Not present	Member of A1	Member of RG
RG	Joyce Parga (JP)	AF	Present	Present	Not present
RG	Erica (EC)	AF	Present	Present	Present
RG	Marie (MI)	AF	Present	Not present	Not present
RG	Muki (MU)	AF	Present	Not present	Not present
RG	Pippa (PI)	AF	Member of LG	Member of A1	Member of RG

RG	Molia (MO)	Female	Juvenile	AF	Present
RG	William (WL)	AM	Present	Member of A1	Member of RG
RG	Ryan (RY)	AM	Present	Not present	Not present
RG	Burke (BK)	AM	Present	Present	Present
RG	Reginald (RE)	AM	Present	Present	Not present
RG	Itchy (IY)	AM	Not present	Present	Present
MG	Laura (LA)	AF	Present	Present	Present
MG	Lisa (LI)	AF	Present	Present	Not present
MG	Juliette (JT)	AF	Not present	Present	Present
MG	Funny Peak (FP)	Female	Juvenile	AF	Present
MG	Frodo (FO)	AM	Present	Not present	Not present
MG	Felix (FX)	AM	Present	Not present	Not present
MG	Borat (BT)	AM	Not present	Present	Present
MG	Bethoven (BV)	AM	Not present	Present	Present
MG	Billy (BY)	AM	Not present	Present	Present
MG	Barry (BA)	AM	Not present	Not present	Present
MG	Benji (BJ)	AM	Not present	Not present	Present
LG	Pippa (PI)	AF	Present	Member of A1	Member of RG
LG	Victoria (VT)	AF	Present	Not present	Not present
LG	S. Shettleworth (SH)	AF	Present	Not present	Not present
LG	Harry (HY)	AM	Present	Not present	Not present

APPENDIX 2: Ethogram adapted from Pereira & Kappeler (1997).

Behaviour	Code	Definition
Adult Female	AF	Sexually mature female
Adult Male	AM	Sexually mature male
Aggression	AG	All incidents of aggression
Anoint Tail	AT	Rub antibrachial glands on tail
Approach	AP	Enter proximity to within 1.5 meters
Block	BL	Block mating attempt with tail
Displace	DI	
Ejaculation	EJ	See text
End Mount/mating	EM	Male or female ends mount
End Mutual Groom	EMG	
Erection	ER	
Face greet	FG	Face greet always includes spat
Female Pace	FP	Female walks back and forth in front of male during mating
Focal	F	
Genital Mark	GM	By male or female
Groom Self	GS	
Grooming	GR	
Huddle Cuddle	HC	Resting in body contact
Infant Female	IF	Up to one year of age
Infant Male	IM	Up to one year of age
Intromission	IN	Visual confirmation of penis entering vagina

Juvenile Block	JVB	When JV interrupts flirting or mating
Juvenile Female	JF	One to two years of age
Juvenile Male	JM	One to two years of age
Leave	LE	Leave proximity of 1.5 meters
Lick Genitals	LG	Lick genitals of conspecific
Lick Substrate	LS	To investigate odour or mark
Mount	MT	
Present	PR	Lift tail and hindquarters in proximity to conspecific
Received	R	
Self Groom	SGR	
Sniff Body	SB	Anywhere except genitals
Sniff Genitals	SG	Nose within 3 cm of genitals
Sniff Invite	SV	Hindquarters placed 3cm from other's nose
Spat	ST	Submissive vocalization hard or soft
Sub Adult Female	SAF	
Sub Adult Male	SAM	
Thrust	TH	With intromission
Tongue Out	TO	Tongue held out of mouth
Tooth Grind	TG	Audible grinding of teeth
Urinate	UR	Emptying bladder
Urine Mark	UM	1-5 drops of urine
Where she sat	WSS	Used with sniff or lick substrate
Waft tail	WT	Waving tail over head at conspecific
Wrist mark	WM	Pulling wrists across substrate twice (usually once per wrist)

Wrist to pit	WP	Rub wrist glands to pit glands
Eye contact	E	Male and female gaze at each other
Proximity	P	The male and female are within 15 meters
Scanning	S	The male scans for conspecifics (looks around)
Not seen (no)	N	Placed before any code or modifier

APPENDIX 3: All mating bouts from three mating seasons. Complete column refers to whether the entire estrous period of the female was observed.

Season	Date	Partners	Complete?	Ejaculation?	Extra-group Male?
2012	April 25 th	FL & AL	No	Yes	No
2012	April 26 th	MI & WL	Yes	Yes	No
2012	April 26 th	MI & RY	Yes	No	No
2012	April 26 th	MI & BK	Yes	No	No
2012	April 26 th	MI & RE	Yes	No	No
2012	April 26 th	MI & BK	Yes	No	No
2012	April 26 th	MI & FO	Yes	Yes	Yes
2012	April 28 th	FI & AL	Yes	Yes	No
2012	April 28 th	FI & RY	Yes	Yes	Yes
2012	April 28 th	FI & BK	Yes	No	Yes
2012	April 28 th	FI & FB	Yes	Yes	Yes
2012	April 28 th	FI & AM 3	Yes	Yes	Yes
2012	April 30 th	SI & RY	No	Yes	Yes
2012	April 30 th	CH & AL	Yes	Yes	No
2012	May 2 nd	FR & AL	Yes	Yes	No
2012	May 2 nd	FR & RY	Yes	Yes	Yes
2012	May 4 th	FP & FO	Yes	Yes	No
2013	May 1 st	EC & RE	No	Yes	No
2013	May 7 th	CH & WL	No	Yes	Yes
2014	April 27 th	MO & BK	Yes	No	No

APPENDIX 4: Hours of observation for each individual during mating season one.

Subjects Male or Female	Group	Observation Hours	All occurrences hours of observation	Rank	Number of Copulatory Partners	Mating Order	Ejaculation
FI (F)	A1	2.25	2.67	2	5		3
FR (F)	A1	2.5	3.72	1	1		
FL (F)	A1	1.5	2.3	3	1		1
FY (F)	A1	2.75	0	4	0		
SI (F)	A1	1.75	0.67	5	0		
CH (F)	A1	1.5	1	6	1		1
AL (M)	A1	2.5	0	1	4	1, 1, 1, 1	3
JP (F)	RG	8.5	0	4	0		
EC (F)	RG	9.25	0	3	0		
MI (F)	RG	10	4.35	1	5		1
MU (F)	RG	9	2	2	0		
WL (M)	RG	9	0	1	1	1	1
RY (M)	RG	9	0	2	2	2,unk	2
BK (M)	RG	9.25	0	3	2	3,5,3	
RE (M)	RG	9.75	0	4	1	4	
LA (F)	MG	3.5	0	1	0		
LI (F)	MG	3.5	0	2	0		
FP (F)	MG	1.5	0.83	3	1		1
FO (M)	MG	5.25	0	1	2	1,5	1
FX (M)	MG	3.25	0	2	0		
PI (F)	LG	0.5	0	2	0		
VT (F)	LG	0.25	0	1	0		
SH (F)	LG	0.25	0	3	0		
HY (M)	LG	0.5	0	1	0		
TOTAL		107	15.54				

APPENDIX 5: Male dominance index scores for mating season one.

Group	Individual Name	Dominance Index Score in %
A1	AL	100
RG	WL	99
RG	RY	64
RG	BK	27
RG	RE	10
MG	FO	100
MG	FX	0
LG	HY	100

APPENDIX 6: Hours of observation for each individual during mating season two.

Subjects	Group	Observation Hours	All occurrences hours of observation	Rank	Number of Copulatory Partners	Mating Order
FI (F)	A1	13	0	3	0	
CH (F)	A1	12.25	2.5	4	1	
AL (M)	A1	12.5	0	1	0	
WL (M)	A1	13.25	0	2	1	UNK
PI (F)	A1	13	0	2	0	
TA (F)	A1	12.75	0	1	0	
JP (F)	RG	13	0	2	0	
EC (F)	RG	12.75	1.3	1	1	
BK (M)	RG	12.75	0	1	0	
RE (M)	RG	12.75	0	2	1	UNK
MO (F)	RG	12.75	0	3	0	
IY (M)	RG	12.75	0	3	0	
LA (F)	MG	11.75	0	4	0	
LI (F)	MG	11.5	0	1	0	

FP (F)	MG	11.5	0	2	0	
JT (F)	MG	12	0	3	0	
BT (M)	MG	11.5	0	3	0	
BV (M)	MG	11.75	0	2	0	
BY (M)	MG	11.75	0	1	0	
TOTAL		223.75	3.8			

APPENDIX 7: Hours of observation for each individual during mating season three.

Subjects	Group	Observation Hours	All occurrences hours of observation	Rank	Number of Copulatory Partners	Mating Order
AL (M)	RG	5.5	0	?	0	
WL (M)	RG	5.25	0	?	0	
PI (F)	RG	4.75	0		0	
TA (F)	RG	5.5	0		0	
EC (F)	RG	5.25	0		0	
BK (M)	RG	5.25	0	1	1	1
MO (F)	RG	5.5	2.65		1	
IY (M)	RG	5.25	0	?	0	
LA (F)	MG	5	0		0	
FP (F)	MG	5.25	0		0	
JT (F)	MG	5.25	0		0	
BT (M)	MG	5	0		0	
BV (M)	MG	5.25	0		0	
BY (M)	MG	5	0		0	

BR (M)	MG	5	0		0	
BJ (M)	MG	5.25	0		0	
TOTAL		83.25	2.65			

3 Chapter 3

Operational Sex Ratio, Dominance Rank and Mating Success of Group and Non-Group Male Ring-tailed Lemurs (*Lemur catta*)

3.1 Abstract

Male mating success depends on intrinsic male qualities, but mating success can also be impacted by extrinsic factors. The operational sex ratio (OSR) is known to impact male mating success in several diverse species. I examined the relationship between OSR, dominance rank, and male mating success in four groups of ring-tailed lemur (*Lemur catta*) at Berenty Reserve, Madagascar based on data collected over three mating seasons. I found significant relationships between the OSR during mating (calculated based on whether males were present and engaged in competition for the estrous female) and mount with thrust duration (Mann–Whitney $U = 0.0001$, $n_1 = 4$, $n_2 = 11$, $P < 0.001$ two-tailed). Incidence of ejaculation was shown to correlate with thrust duration (Mann–Whitney $U = 3.5$, $P = 0.005$ one-tailed). Alpha males copulated (mounts with thrusting) for longer durations than lower ranking group males (Mann–Whitney $U = 0.0001$, $n_1 = 5$, $n_2 = 4$, $P < 0.016$ two-tailed). When alpha males of the estrous female's group were excluded, extra group males were more likely to ejaculate than group males (Fisher's exact test, $p = 0.015$). These findings show that variation in the OSR during a female's estrous period impacts male mating success as presence of a greater number of males inhibits ejaculation and raise questions about the value of group membership for non-alpha males.

3.2 Introduction

Intrinsic male qualities and extrinsic group factors both contribute to create variability in reproductive success among male animals. Intrinsic traits of an individual male are attractive to females, and females are expected to choose the best mate, ensuring their offspring inherit these

qualities of fitness (Andersson, 1994). However, extrinsic factors such as male-male competition and group demographics during a female's estrous period impact male reproductive success as well (Clutton-Brock and Parker, 1992; Enders, 1993). Darwin (1859) described competition among males to reproduce with females in his work on sexual selection, a component of his theory on natural selection. In many species of animals, male dominance hierarchies exist in which winners of agonistic encounters have proven their higher fitness over lower ranking males of the group and outcompete other males for access to estrous females or are often chosen as mates by females (Andersson, 1994; Dewsbury, 1982, Dixson, 1998). Intense male-male competition during mating can occur for mammals that are seasonal breeders (Chism and Rogers, 1997), as agonistic encounters are impacted by group demographics during mating. Female choice can be influenced by an increase in the number of males present during their estrous periods for two reasons 1) more males means greater choice and 2) the increased level of competition tests males at an increased level (Clutton-Brock and Parker, 1992; Enders, 1993; Kvarnemo and Ahnesjö, 1996, 2002). The number of males present and competing for access to estrous females is predicted to impact male reproductive success (Dunbar, 1988; Stearns and Hoekstra, 2000).

The operational sex ratio (OSR) is the ratio of males to females that are available to mate in a group at a given time. As OSR becomes more male-biased, it has been observed that competition among males and agonistic encounters increase (Clutton-Brock and Parker, 1992; Emlen and Oring, 1977; Weir *et al.*, 2011). A study on bullfrogs was the first to examine these ratios. Bullfrogs have highly asynchronous female estrous periods, with females entering estrous for only one night, thus creating highly male-biased OSRs (Emlen, 1976). This research led to the ground-breaking paper by Emlen and Oring (1977) which introduced the term OSR. The OSR

can be estimated using snapshot censuses counting the number of males and females who are ready to mate at any given time (Kvarnemo and Ahnesjö, 2002).

The OSR is known to have an impact on mating behaviour in many animals (Clarke and Grant, 2010; de Jong *et al.*, 2009; Kiritome *et al.*, 2012; McWilliams, 1992; Preston and Stockley, 2006; Shine, 2003; Spence and Smith, 2005; Zhang and Zhang, 2003). In several types of fish and amphibians, the OSR has been found to impact courtship frequency (Clarke and Grant, 2010; de Jong *et al.*, 2009; McWilliams, 1992; Shine *et al.*, 2003; Spence and Smith, 2005). In guppies (*Poecilia reticulata*), the OSR has an impact on how attractive dull males are to females versus the normally preferred bright males. When the OSR is female-biased, dull males are chosen more often than when the OSR is male-biased (at which time bright males have greater mating success) (Kiritome *et al.*, 2012). Brandt's vole (*Lasiopodomys brandtii*) is impacted by the OSR; when there is a male bias, the mating opportunity of the males decreases due to increased male-male interference competition and female mating effort remains the same. However, if the OSR is female-biased, male voles increase their mating effort while female voles do not (Zhang and Zhang, 2003). The sexual behaviour of wild house mice (*Mus musculus domesticus*) is also impacted by OSRs. Thrusting behaviour of male mice was tested with OSRs being even and with a male-biased sex ratio. When the sex ratio was male-biased, males reduced their copulatory stimulation (or duration of thrusting) by a median of 53% before their first ejaculation as compared to when sex ratio was balanced (Preston and Stockley, 2006). These findings show that mating behaviour is impacted by the OSR in various ways: by influencing which males females find most attractive, by changing mating opportunity and the mating effort of males, by changing courtship frequency, and by affecting thrust duration before ejaculation.

Not only has research shown that OSRs impact mating behaviour, but research has also shown that OSRs directly impact mating success of males. A male-biased OSR can be predicted to increase male-male competition for females in estrous (Clutton-Brock and Parker, 1992; Emlen and Oring, 1977; Krupa and Sih, 1993; Weir *et al.*, 2011). The OSR, and therefore the level of male-male competition for sexually available females, has been shown to impact mating success in several animal species (Clutton-Brock *et al.*, 1997; Krupa and Sih, 1993; Takahashi, 2001). For example experiments altering the OSR in water striders (*Aquarius remigi*) showed that large males copulated more in scenarios in which the OSR was balanced but small males copulated more when the OSR showed a male bias (Krupa and Sih, 1993). This result was surprising because a large male mating advantage was expected in both scenarios. The authors hypothesize that female resistance to males is reduced when the OSR is male-biased. When females resist mating, larger males have an advantage over smaller males, but when females reduce their resistance due to heightened harassment by males, smaller males copulate more frequently than larger males (Krupa and Sih, 1993). A study of red deer (*Cervus elaphus*) showed that when a female-biased adult sex ratio developed, immigrant males became more successful at fathering offspring and the proportion of infants sired by the males born in the study area declined (Clutton-Brock *et al.*, 1997).

Among primates, the impact of OSRs on mating behaviour has been measured in several primate species exhibiting a range of mating systems. This research ~~spans~~ includes the following species: Japanese macaques (*Macaca fuscata*), a group-living primate for whom more than one female comes into estrous at a time (Takahashi, 2001); gray mouse lemurs (*Microcebus murinus*), a solitary species in which mating is asynchronous (Eberle and Kappeler, 2004); and owl monkeys (*Aotus azarai*), pair-living and genetically monogamous primates (Fernandez-Duque and Huck,

2013). In Japanese macaques, when the OSR was low, and ratios of estrous females to adult males was more even, group males were able to monopolize matings and had higher mating success than extra group males. When the OSR was highly female-biased, extra group males were able to mate and thus had higher mating success than when the OSR was low (Takahashi, 2001). In gray mouse lemurs, adults are solitary and males have to make decisions regarding their mating tactics based on several factors, including the OSR (Eberle and Kappeler, 2004). Researchers found that males who were ultimately successful at siring offspring would roam extensively in search of mates, had superior finding ability and mated as early as possible (Eberle and Kappeler, 2004). Males would switch tactics, however, based on several factors, including the OSR. In this way, OSR contributes to whether gray mouse lemurs experience reproductive success. In socially monogamous owl monkeys, OSRs have been assumed to be equal in the past. Solitary floaters, however, play an important role in mating dynamics (Fernandez-Duque and Huck, 2013). Fernandez-Duque and Huck (2013) argue that flexible, context specific OSRs should be assumed for monogamous primates. Presence of solitary floaters (young males who had dispersed from their natal groups) was found to have a negative impact on pair-mates' reproductive success, both male and female (Fernandez-Duque and Huck, 2013). The impact of OSRs on mating behaviour has never been studied in a group living primate which exhibits asynchronous estrous, such as *Lemur catta* in Madagascar.

In order to assess the importance of the OSR in terms of its impact on reproduction, reproductive success must be estimated. Mating success is a good proxy measure of reproductive success in some species (Altmann *et al.*, 1996; Robinson, 1982) and mating success can be measured using several types of copulatory behaviour. Copulatory behaviour can be classified into three types of events: mounts, penile intromissions, and ejaculation (Dewsbury and Pierce, 1989). Although

looser classifications of mating success have been used in the past, measuring mating success based on ejaculations with estrous females is the closest estimate for reproductive success when paternity data are unavailable since males may copulate with females without ejaculating or when the females are not able to conceive. This method is employed here because it is more accurate than some previously employed methodologies that do not determine either whether the estrous female was conceptive or the male ejaculated during mating. Male *Lemur catta* mount females multiple times before a single ejaculation (Sauther, 1991), although they have been improperly classified as engaging in a single brief intromission (SBI) copulatory pattern (Dixon, 2012).

Since different animal studies use different copulatory behaviours as measures of mating success, it is often difficult to make comparisons between these studies. In the study of primates, mating success has been measured in different ways and much has been written about these measurement discrepancies (Alberts *et al.*, 2003; Bercovitch, 1995; Bernstein, 1976; Bogusław *et al.*, 1998; Cowlshaw and Dunbar, 1991; Drickamer, 1974; Fedigan, 1983; Kuester and Paul, 1992; Rowell, 1974; Smuts, 1982; Surbeck *et al.*, 2011). One problem with equating mating success with reproductive success is that the few studies which have measured both mating success and reproductive success in the same primate groups have found that previous measures of mating success were not good predictors of reproductive success (Curie-Cohen *et al.*, 1983; Stern and Smith, 1984). Two studies of rhesus macaques found similar results. In the earlier study, researchers found that even though an alpha male participated in the greatest number of matings (their measure of mating success), he did not sire the majority of the offspring (Curie-Cohen *et al.*, 1983). In a study published a year later, researchers found that they could not predictably determine the father of offspring based on copulations alone or consort activity alone

(Stern and Smith, 1984). Improper estimation of ejaculation in primates may be one reason why inconsistent results are being seen in studies of male mating success in primates. Altmann *et al.*, (1996) found, however, that mating behaviour was a good predictor of reproductive success. The paternity analysis the researchers conducted provided strong support “for the validity of estimating variance in reproductive success using consortships on fertile days of conception cycles” (p. 5799). Observations of females mating on their conceptive days seems to be of critical importance.

Mating success has been measured using the cumulative duration of all mounts showing thrusting as well as number of ejaculations, yet few studies have tested whether a correlation exists between duration of mounts with thrust and ejaculation. In guppies (*Poecilia reticulata*), copulation duration positively correlates with the number of sperm deposited (Pilastro *et al.*, 2007). Differing results have been found for rabbits, however. Ejaculatory mounts lasted for a shorter duration than non-ejaculatory mounts in New Zealand white rabbits (*Oryctolagus cuniculus*) (Contreras and Beyer, 1979). In orangutans (*Pongo abelii*), copulations in which ejaculation occurred lasted from three to 28 minutes with a mean of 10.8 minutes, while copulations without ejaculations lasted from ten seconds to one minute (Galdikas, 1981). Ejaculatory mounts can be classified as occurring as a single brief intromission (SBI) or a single prolonged intromission (SPI) copulatory pattern, and data have been collected on these patterns in over 30 primate species (Dixson, 2012). Although *Lemur catta* is not listed in Dixson’s (2012) table of intromission duration in primates, previously published data would classify their ejaculatory mounts as being brief (approximately one minute) although these ejaculatory mounts are preceded by many non-ejaculatory mounts (Evans and Goy, 1968; Jolly, 1966; Koyama,

1988; Sauther, 1991). It has yet to be examined in *L. catta* whether entire thrusting durations of males who do not ejaculate are shorter than those who do ejaculate.

Lemur catta is an important study species for testing OSRs and mating success, as they live in multimale-multifemale groups exhibiting female dominance (Jolly, 1966; 1984; Kappeler, 1990; Sauther, 1993), a characteristic seen in most lemur species but rarely in primates (Kappeler, 1993). With female dominance, it is expected that females will be able to more effectively choose their mates and avoid male harassment. Male dispersal, strict reproductive seasonality (Sauther, 1991) and asynchrony within estrous synchrony (Pereira and Weiss, 1991) are all traits of *L. catta*. Female *L. catta* experience estrous periods which last from half a day to two days and often mate with multiple male partners from inside and outside their groups during estrus (Gould, 1994; Koyama, 1988; Parga, 2006b; Pereira and Weiss, 1991; Sauther, 1991; Sussman, 1992). Because female estrous periods are asynchronous within groups, highly male-biased OSRs exist, as most males in a group (and some non-group members) tend to compete for access to the estrous female. Not all males who engage in copulations ejaculate (Sauther *et al.*, 1999; Walker-Bolton, unpub. data). For those occasions in which ejaculation does occur, a copulatory plug is deposited in the female's vaginal tract and subsequent mating males may remove this plug (Dixson, 1998; Parga, 2003; Parga *et al.*, 2006; Sauther, 1991). Females mate during the night as well as the day during estrous, although data are lacking on nocturnal mating behaviour (Jolly, 1966; Koyama, 1988; Parga, 2006, 2011; Sauther, 1991). Although there is usually only one female available to mate at a time in each *L. catta* group, the number of males present and competing for a female in estrous varies considerably for each individual estrous female and for each copulation. Not all group males are present and competing for each estrous female, as some

males leave their group during the mating season to monitor females in other groups (Sussman, 1992).

The OSR is expected to be highly male-biased when alpha females are in estrus, particularly in *L. catta*, who enter estrous asynchronously during a brief annual mating season. Male competition for access to estrous alpha females in particular is expected to be high for several reasons. Female *L. catta* of high rank have priority access to food resources and therefore should have a higher caloric intake and better health than other females (Parga, 2006), leading to higher fecundity. Higher ranking females have greater offspring survivorship in captive *L. catta* (Taylor, 1986), although captivity is known to have an impact on infant mortality as individuals are free from predation pressures, extra-group encounters and do not need to forage for food. Surprisingly, in one study, males did not show the highest mating effort for the highest ranking females in this species, preferring instead middle aged and older females who had a history of successfully raising offspring (Parga, 2006).

Male *L. catta* emigrate into neighbouring groups during a six month period ending just after the mating season (Budnitz and Dainis, 1975; Gould, 1994; 2006; Jones, 1983; Sauther, 1991; Sussman, 1991; 1992). The migration of males is thought to be motivated by mate choice and sexual competition (Sussman, 1992) and evidence supports the theory that males leave their groups to avoid inbreeding (Jones, 1983). While males are attempting to enter a new group, they are known as transferring males (Sauther, 1991, Sussman, 1992). Females are known to mate with newly transferred males and those attempting to transfer (Koyama, 1988; Parga, 2006b; Pereira and Weiss, 1991; Sauther, 1991; Sussman, 1992). In addition, two other types of males are known to mate with group females: temporary visitors from neighbouring groups who return to their own groups of current residency at night, and mating season transfers who join a new

group for the duration of the mating season and return to their original group when the mating period is over in that group (Gould, 1994; Sussman, 1992). The mating success of extra group males (transferring males, temporary visitors and mating season transfers) has been documented in several primate studies (Dixson *et al.*, 1993; Jones, 1983; Mertl-Millhollen *et al.*, 1979; Parga, 2006; Sauther, 1991). A study of male mandrills (*Mandrillus sphinx*) has shown solitary males lingering at the edge of the group in the hopes of mating opportunistically (Dixson *et al.*, 1993). This strategy is effective at avoiding the costs of emigrating into a new group (Dixson, 1998). Transferring male *L. catta* have been found to receive persistent harassment by group males; however, females approached, presented to, and mated with these transferring males at Bezà Mahafaly Special Reserve (Sauther, 1991). Contradictory findings have also been reported: in other studies, extra group *L. catta* males either were not present during female estrous periods or were unable to mate (Jones, 1983; Mertl-Millhollen *et al.*, 1979; Parga, 2006).

3.2.1 Questions and Predictions

In the present study, I addressed the following hypotheses to test that a more male-biased OSR will negatively affect male mating opportunities and copulatory success in *L. catta*: (1) Male-biased OSRs will decrease thrust duration due to increased competition (2) High dominance rank of the mating male will decrease OSR while high dominance rank of the mating female will increase the OSR. This is expected because the alpha is the known winner of past agonistic encounters and fewer males are expected to challenge his mating bout because of this. More males are expected to compete for access to high ranking estrous females because high ranking females have a greater ability to provide their offspring with high quality nutrition and thus experience greater infant survivorship (Parga, 2006; Taylor, 1986). (3) When the OSR is more male-biased, lower ranking males and extra group males will experience greater mating success

as measured by thrust duration and incidence of ejaculation, due to the fact that these males will not be able to sequester the estrous female as alpha males are often able to and therefore will only experience mating success when OSRs are highly male-biased (4) Longer thrust duration will lead to incidence of ejaculation in this species as male-male competition often interrupts mating attempts, potentially before ejaculation is possible (5) Higher ranked males will thrust for a longer period of time and therefore ejaculate more than lower ranked group males (6) Higher ranking females will receive fewer ejaculations than lower ranking females because of increased male-male competition (7) Group males will have a mating advantage over extra-group males because group membership will confer a mating advantage on males who are known to females. The null hypothesis is that there is no relationship between OSR, dominance rank, thrust duration, and male copulatory success. I predict that: (1) Thrust duration is shorter when OSRs are more male-biased (2) The dominance rank of the mating male or female will impact OSR with high ranking males experiencing low OSRs during mating and high ranking females experiencing high OSRs while mating (3) When the OSR is more male-biased, lower ranking group males and extra group males will experience greater mating success (as measured by thrust duration and ejaculation) than when the OSR is low (4) Longer thrust duration will lead to ejaculation (5) Male dominance rank will impact thrust duration with higher ranking males thrusting for longer (6) High ranking females will receive fewer ejaculations due to male-male competition (7) Group males will ejaculate more than extra-group males.

3.3 Methods

3.3.1 Ethical Note

All research protocols were approved by the Animal Care Committee at the University of Toronto and conform to the governing laws of the Malagasy Republic. This study was conducted with the approval of the De Heulme family, owner of the private nature Reserve of Berenty.

3.3.2 Study Site

Berenty Reserve (24° 58 S, 46° 16 E) is a private nature preserve in the extreme south of Madagascar established by the de Heaulme family in 1936. The de Heaulme family have a long history of welcoming international researchers to their study site, beginning with Alison Jolly's pioneering study of *L. catta* behaviour that was initiated in 1963 (Jolly *et al.*, 2006). Long term, continuous research has been conducted by Koyama and his colleagues at the reserve since 1989 (Koyama *et al.*, 2001).

The reserve consists of 2 km² of gallery forest containing large tamarind trees (*Tamarindus indica*) with a closed-canopy and 1.5 km² of less ecologically rich scrub and spiny forest (Jolly *et al.*, 2002). The reserve acts as a major tourist destination throughout the year and the main area for tourists in which this study was conducted is known as the Tourist Front. The Tourist Front includes a restaurant and tourist bungalows and has many introduced species of plants and trees which supplement the lemurs' diets (Jolly, 2012). In addition, lemurs are occasionally fed scraps by tourists, although formal provisioning has been discontinued and tourists are warned against feeding the animals. Summers are hot and wet, averaging 40°C at mid-day and winters are cold and dry with temperatures falling at night to 10°C (Jolly, 2012). There is great variability in rainfall from year to year, ranging from 300cm to 900cm annually (Jolly, 2012).

The population of *L. catta* for Berenty Reserve was reported as 941 individuals in 2015, with the largest average group being found in the Tourist Front (Dimilahy *et al.*, 2015). Population density is 5.8/ha for *L. catta* at the Tourist Front, the highest in the reserve (Jolly *et al.*, 2002). This is much higher than the 1-1.5/ha density seen within the Spiny Desert and Scrub (Jolly *et al.*, 2002). Density in the Spiny Desert and Scrub is comparable to density found at Bezà Mahafaly (Sussman, 1991). Primates found in this reserve include the introduced *Eulemur rufus collaris* hybrid, Verreaux's sifaka (*Propithecus verreauxi*), Lepilemur (*Lepilemur leucopus*), and

two types of mouse lemur (*Microcebus murinus*, *Microcebus griseorufus*) (Jolly *et al.*, 2002). Potential lemur predators include both mammals (domestic dogs and cats, and the Indian civet [*Viverricula indica*]) (Jolly, 2012) and birds (the harrier hawk [*Polyboroides radiatus*], the Madagascar buzzard [*Buteo madagascariensis*], and the black kite [*Milvus migrans*]) (Crowley, 1995; Karpanty and Goodman, 1999).

3.3.3 Study Subjects

Natural markings (minor pelage coloration differences, old, easily-seen scars from fights with other animals, etc.) were used to identify each individual (Appendix 1). Adult male and female study subjects were selected as focal animals from four groups inhabiting the Tourist Front (Table 3.1). Adults were selected because they are the age category that engages in mating behaviour and the groups that were chosen were used because they were currently not part of any long-term field research. Each adult subject had been photographed and drawn to document their distinguishing features.

Table 3.1: *L. catta* group composition by adult male (AM) and adult female (AF) study subjects for the three study periods, 2012-2014 at Berenty Reserve, Madagascar. The four study groups are: A1, Restaurant Group (RG), Museum Group (MG), and Lost Group (LG). Two groups dissolved during the study, which is indicated by 0 members in later years.

Group	2012		2013		2014	
	AM	AF	AM	AF	AM	AF
A1	1	6	1	4	0	0
RG	4	4	3	3	4	4
MG	2	2	3	4	3	5
LG	1	3	0	0	0	0
Total	8	15	7	11	7	9

I collected all data for this study during three consecutive mating seasons (April to June, 2012 to 2014). The sample size for my study animals fluctuated slightly over the three years of behavioural observations due to deaths, disappearances, emigrations, births, and group

membership changes as juveniles matured to adulthood. Adults were defined as sexually mature individuals who participated in mating during the mating season. Subadults were defined as individuals who were close to adult body size but who did not participate in mating. Yearlings were all individuals that were of smallest body size in the group and exhibited infant-like traits (Sauther and Sussman, 1993). Adults were distinguished from subadults based on body size, and degree of sexual development. Sexual development was assessed on appearance of genitals as well as whether the individual mated during the mating season. Individuals are known to mate as early as two years in the wild, and most females have their first offspring at three or four years of age (Koyama *et al.*, 2001). There were significant changes in group composition during the three study years (Table 3.1; Appendix 1). Data points from each of the three mating seasons varied significantly. Sixteen mating bouts were seen in 2012, two mating bouts were seen in 2013 and one mating bout was seen in 2014. Each year I had a single field assistant who did not collect data but who watched for females entering estrous and then alerted me so that I could begin data collection on that female. In 2012 I had the field assistant cover separate groups from myself during the mating season. This method allowed us to observe double the groups for individual females entering estrous. In 2013 and 2014 the field assistants and I followed the same groups during the mating season, decreasing the number of individual females monitored for estrous status. In 2014 my primary focus was on collecting hair samples from juveniles to analyse for paternity data and we may have missed some females entering estrous due to this shift in focus. Because of the unpredictable nature of observing mating behaviour, it is also difficult to consistently observe the majority of matings which occur.

Extra group males were seen mating with group females. Extra group males were defined as any males from outside of the group, known to be members of other groups, and not sleeping in the

same sleep tree as the group. Extra group males were not assigned a rank, since male dominance rank is not known to transfer over from the home group to the new group.

3.3.4 Behavioural Data Collection

I conducted all behavioural observations, supported by two experienced Malagasy field assistants from the University of Antananarivo. I trained and supervised both of the field assistants chosen for the research project. Assistants did not collect data but assisted by identifying individuals, monitoring group movement, and locating estrous females. Observations of four groups (A1, RG, MG, LG) were conducted six days per week from 0700 hrs until 1700 hrs, alternating between groups on subsequent days for a total of 414 hours of focal observations over three years. During the study, the mating period is defined as the time between the onset of the first observed estrus and the last observed estrus during the first estrus cycle of the season. Female *L. catta* will cycle three times if no pregnancy occurs during the mating period (Evans and Goy, 1968). During the mating period, observations were conducted seven days per week. Prior to the commencement of the mating period, training of assistants and familiarization with all study subjects occurred.

Using continuous-time focal sampling (Altmann, 1974), data were collected on all affiliative and aggressive behaviours, and all mating behaviours (courtship, copulations, mate guarding) (Appendix 1). Copulations were defined as mounting with penile intromission and thrusting. Mating bouts were defined as each male's entire period of copulations with a female. Estrous periods were defined as the entire time a female was sexually receptive to males. Focal samples were conducted for 15 minutes each when no females were in estrous. This focal follow duration allowed each focal individual to be sampled at least twice during each time period of morning or afternoon. Focal animals were selected by always choosing to follow the individuals with the lowest total number of follows and making an attempt to equalize the number of follows

completed on each individual during the mornings and afternoons. Data were recorded using data sheets (Appendix 5).

During the mating season, when a female was observed to enter estrus, all occurrences sampling for agonism and sexual behaviour began for the entire duration of estrus (Altmann, 1974). A female was monitored more closely if she ceased to act aggressively when a male would mark and waft his tail towards her. A female was considered to enter estrous when she first performed a sexual present towards a male and allowed him to mount her. Twenty-two hours of all occurrences sampling data were collected over the three years. Prior to the initiation of each follow, data were recorded on physical manifestations of female reproductive state by noting any changes in genital swelling or colour. *Ad libitum* data were also collected at all times on such occurrences as presence of any physical injuries, abandonment of infants, infanticide, and predation events.

Dominance rank was calculated by collecting data on all decided agonistic interactions, displacements and the direction of submissive vocalizations known as the spat call (Jolly, 1966). Focal data on aggression and submission during the mating period were used for the hierarchy matrices. Winners of aggressive interactions and receivers of the submissive vocalization were coded in the same manner for the matrices. For example, within the matrix, rows represent winners of aggression and receivers of spat calls, while columns represent losers of agonistic encounters who give the submissive vocalization.

Various studies measure mating success differently. Each of the studies examining OSR and mating behaviour in animals measured mating success in a different manner: the experiments with water striders (Krupa and Sih, 1993) measured whether mating occurred or not, the study of red deer (Clutton-Brock *et al.*, 1997) measured which male maintained the longest access to a

female during an estimated conception date, and the study of Japanese macaques (Takahashi, 2001) measured mating success as ejaculations with estrous females. I have also measured mating success as ejaculations with estrous females (Table 3.2).

Table 3.2: Criteria for determining whether ejaculation has occurred or not occurred.

Ejaculation has occurred	Ejaculation has not occurred
Ejaculate seen on male's penis tip	Male with an erection after thrusting bout and none of the criteria for determining ejaculation has occurred are met.
Ejaculate seen on female's genitals	Mating interrupted by competitors and none of the above criteria are met.
The male in question removes a copulatory plug (Parga 2003) from the female during mating and the male who mates directly after the male in question also removes a copulatory plug during mating.	
The male in question is known to be the first mating male and the male who mates directly after the male in question removes a copulatory plug from the estrous female during mating.	
Male seen mate guarding the female without an erection and no further mounts with thrusts and intromission.	

Operational sex ratio is defined here as the ratio between estrous females and males available in a group for mating during copulation. OSRs are meant to be snapshot censuses of sex ratio during a specific time period (Kvarnemo and Ahnesjö, 2002). OSRs can be time and place specific, especially in the wild (Grant and Foam, 2002).

3.3.5 Data Analyses

All statistical analyses were conducted in SPSS 22.0 for Windows. Non-parametric statistics were used because of small sample sizes and because data were not normally distributed.

Significance levels were set at $p < 0.05$ and tests were one or two-tailed based on the null hypothesis. Data from each of the three years were not pooled, and the data from 2012 was analysed separately. The reason the data were not pooled is due to the fact that there were many group composition changes over the years. Changes to male dominance hierarchies also occurred, as some males emigrated to new groups.

To answer the question “does rank impact the OSR and/or duration of thrust events”, the males present during a male’s mating bout with a female were counted and the mating bout was classified as having males present or having no males present. A mating bout was defined as starting with the first mount with intromission and thrusting and ending at ejaculation. If ejaculation did not occur, the mating bout was defined as ending when the mating male was displaced from the estrous female by a male competitor. Thrust duration was calculated by adding together the duration of all copulatory mounts with a single female for an individual mating male.

3.4 Results

For a summary of the mating events from the three mating seasons (2012-2014), see Chapter 2, Table 2.3.

Operational sex ratios (OSRs) varied for different males’ mating bouts (Table 3.3). The maximum number of males who were present and competing for access to an estrous female at one time was five, and the minimum was one male. The male who most frequently had OSRs of 1:1 was AL, the lone male of A1 group.

Table 3.3: Operational sex ratios of *L. catta* during the three mating seasons.

Year	Sex Ratio (males: females)	Number of Instances	Mating Pairs
2012	1:1	6	(AL and FL), (AL and FI), (RY and SI), (AL and CH), (AL and FR), (FO and FP)
2012	2:1	2	(BK and MI), (RY and FI)
2012	3:1	4	(WL and MI), (BK and FI), (AM3 and FI), (RY and FR)
2012	4:1	2	(BK and MI), (FO and MI)
2012	5:1	3	(RY and MI), (RE and MI), (FB and FI)
2013	2:1	1	(WL and CH)
2013	4:1	1	(RE and EC)
2014	4:1	1	(BK and MO)

3.4.1 Prediction One

The median duration of mounts with thrusting in the two groups: no males present and one or more males present, were 453.5 and 78.0 seconds; the distributions in the two categories differed significantly (Mann–Whitney $U = 0.0001$, $n_1 = 4, n_2 = 11$, $P < 0.001$ two-tailed). When one or more males were present during mating, thrust durations were shorter (Figure 3.1).

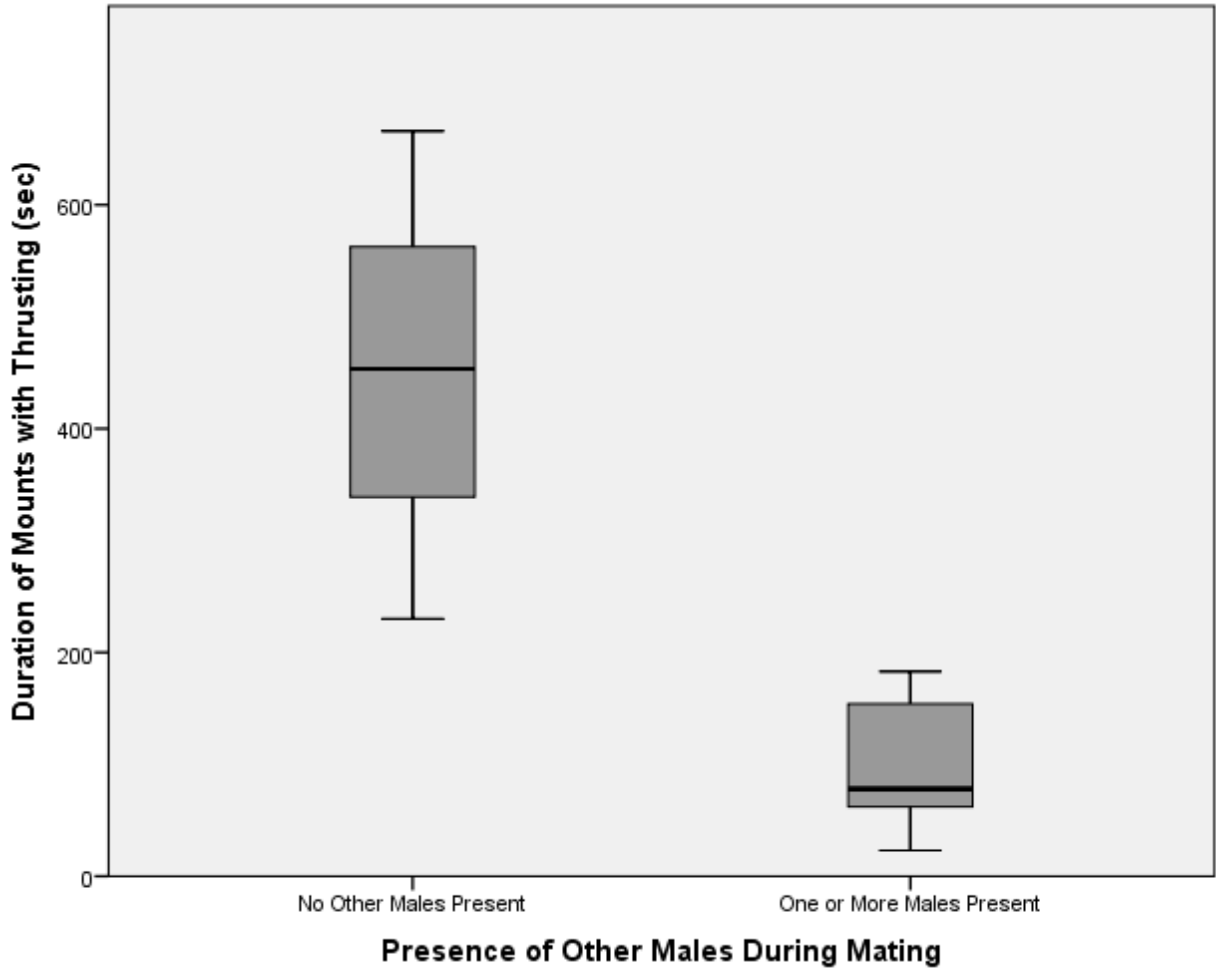


Fig 3.1: Duration of male thrusting in seconds from data collected during the 2012 mating season at Berenty Reserve for situations where no other males were present and situations where one or more males were present. Bold lines represent the median, box represents the interquartile range, whiskers show minimum and maximum values.

For the second mating season (2013), I found that when the number of males present and engaged in competition for the estrous female was higher, thrust durations were shorter (Table 3.4). This relationship supported findings from the first mating season (2012).

Table 3.4: Data from Mating Season Two on OSRs, Thrust Duration, Male and Female Rank, and Ejaculation for all observations.

Mating Pair	OSR	Thrust Duration in Seconds	Male Rank	Female Rank	Ejaculation
RE and EC	4	230	2	1	Yes
WL and CH	2	304	2	4	Yes

The one mating bout that was observed in the third mating season (2014) was partly consistent with findings from the previous two years. There was a highly male-biased OSR and thrust duration was short: 1.15 minutes compared to the average duration of alpha males, which was roughly 7 minutes.

3.4.2 Prediction Two

When an alpha male was mating, there were fewer males present in competition than when non-alpha group males were mating. Fewer males were present during the mating of extra-group males than for non-alpha group males (Figure 3.2). There was a statistically significant difference between groups (Kruskal-Wallis test: $P = 0.016$); specifically, post hoc tests showed this difference was between alpha males and non-alpha group males (Poisson Regression: $P=0.004$) and alpha males and extra group males (Poisson Regression: $P=0.017$). The difference between non-alpha group males and extra-group males was not significant.

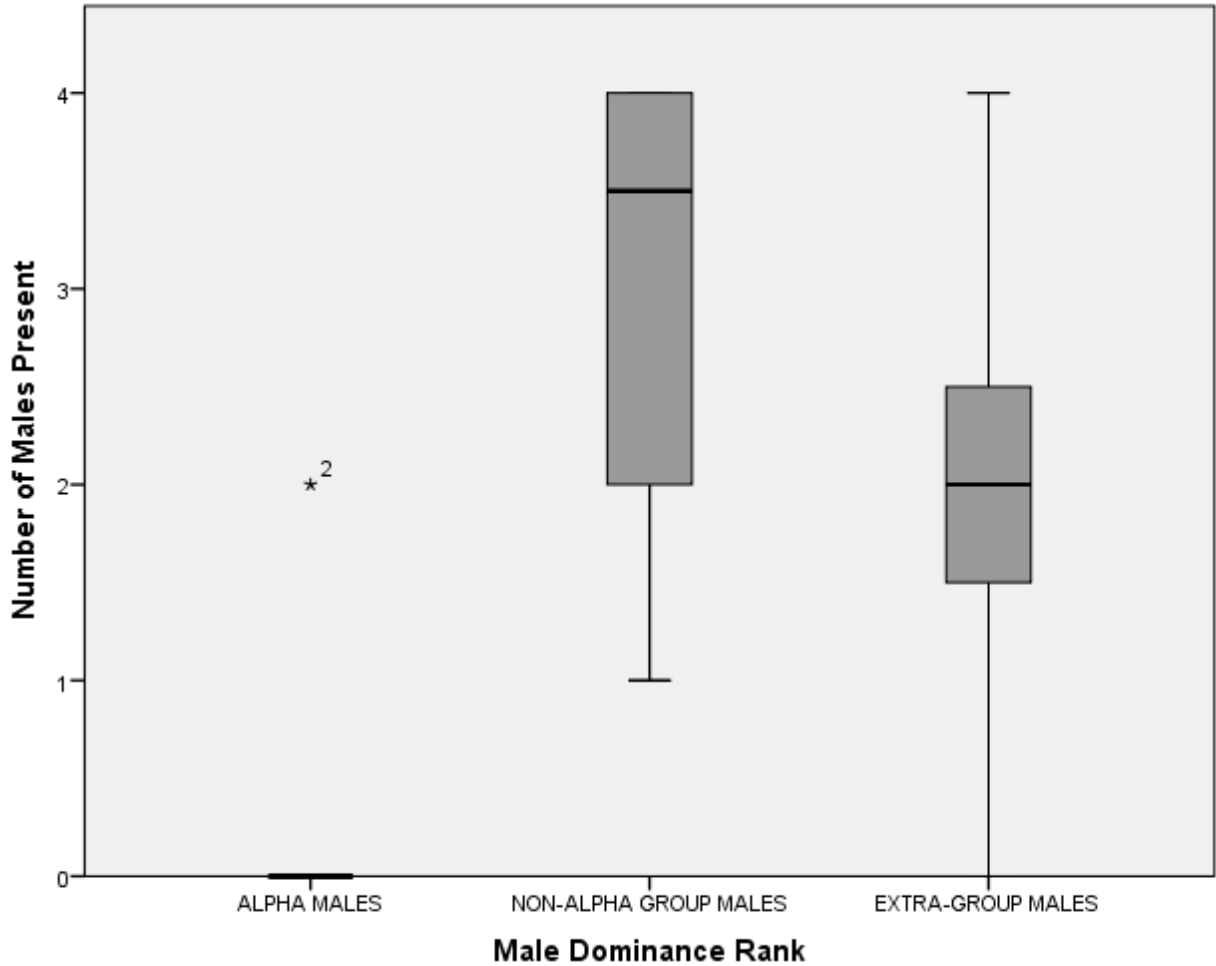


Fig 3.2: Relationship between dominance rank of the mating male and number of non-mating males present (OSR) for *L. catta* at Berenty Reserve during the mating season 2012. Alpha males, non-alpha group males, and extra-group males are shown. Bold lines represent the median, box represents the interquartile range, whiskers show minimum and maximum values.

In 2014, the mating male was an alpha, mating with a female from his group, and the OSR was highly male-biased. This finding did not match with what was typical of the previous two years in that the OSR was highly male-biased. In the previous two years the OSR was not male biased during an alpha male's mating period. Only once, during the first mating season, was a similar result found (mating of WL and MI, with two non-mating males present).

When a higher-ranking female is in estrous there are more males present in competition. The average number of males present for an alpha female was 2.4 males, while the average present for lower ranking females was one male (Table 3.5).

Table 3.5: Relationship between dominance rank of the mating female and number of non-mating males present (OSR) for *L. catta* at Berenty Reserve during the mating season 2012.

Female Dominance Rank	Number of Females of this Rank	Total Number of Males Present During Mating	Average Number of Males Present Per Female
1	8	19	2.4
2-6	9	9	1

In 2013, I found that when the higher-ranking female was in estrous there were more males present in competition. This relationship supported findings from the first mating season (2012) (Table 3.5).

3.4.3 Prediction Three

Out of eleven incidences recorded in which lower ranked group males or extra group males mated, in ten of the cases the OSR was male-biased. In other words, when the OSR is more male-biased, lower ranking males and extra group males experienced greater mating success as measured by thrust duration and incidence of ejaculation.

3.4.4 Prediction Four

Males who thrust for a longer duration overall were more likely to ejaculate with their mating partner (Mann–Whitney $U = 3.5$, $P = 0.005$ one-tailed) (Figure 3.3). Duration of all mounts with thrusting during copulation ranged from 23 seconds to 666 seconds (11.1 minutes), with a mean duration of 193 seconds (3.2 minutes) and standard deviation 186.4. Males who

were interrupted by other males being present were not the only individuals that stopped and started mounts with thrusting. Males who successfully sequestered their female mating partner also stopped and started copulations, resulting in multiple copulatory mounts before ejaculation.

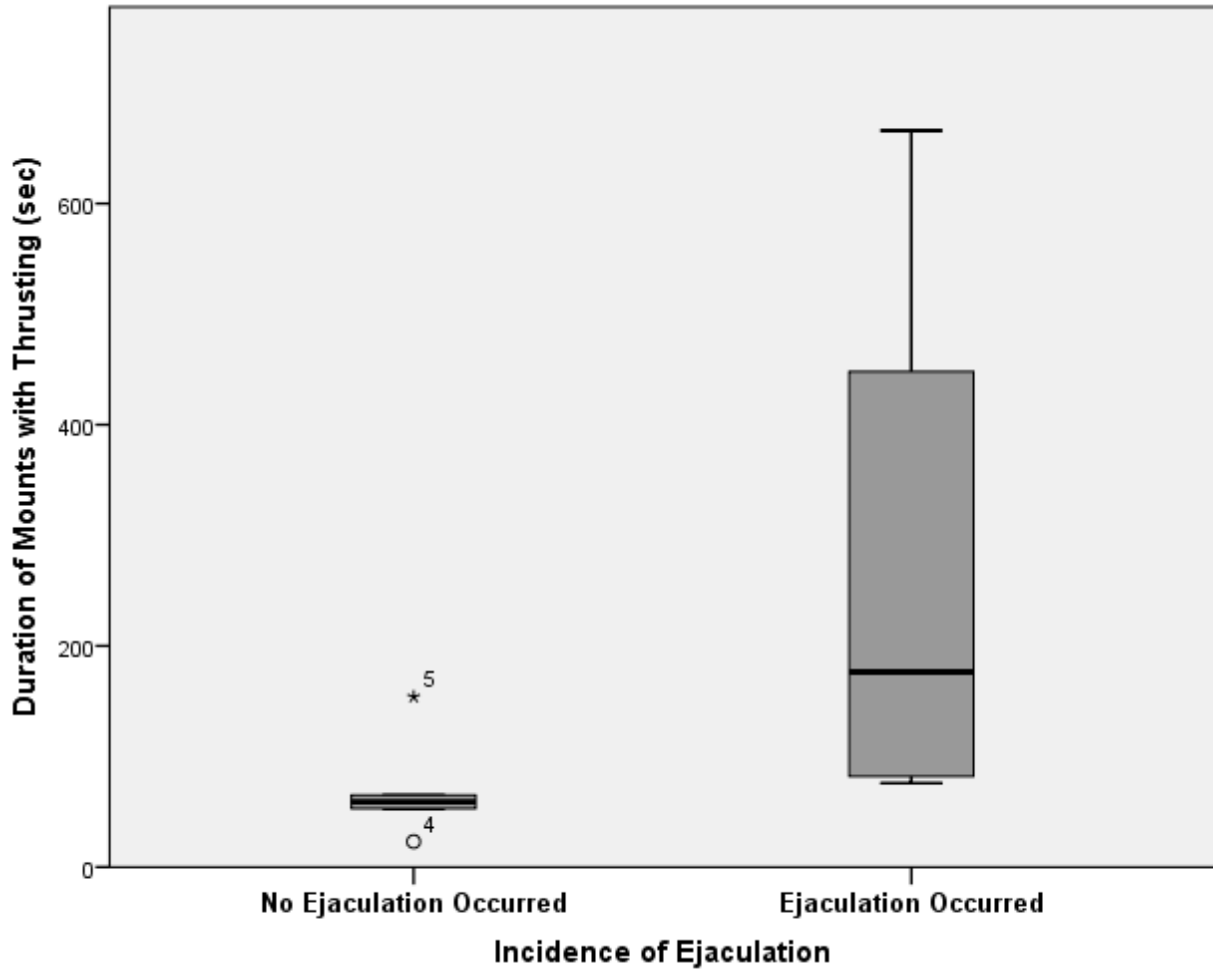


Fig 3.3: Duration of male thrusting in seconds and incidence of ejaculation from data collected during the 2012 mating season at Berenty Reserve. Bold lines represent the median, box represents the interquartile range, whiskers show minimum and maximum values.

I found that thrusting started with a series of shorter thrusting bouts, culminating in one longer thrusting bout in which ejaculation occurred. I found that for the mating bouts that culminated in ejaculation among my study males during the first mating season, the long mount and thrusting had a mean length of 1 min 57 sec (N = 12, range 0.67- 6.60 min).

3.4.5 Prediction Five

The median duration of mounts with thrusting in the two groups (alpha male mating and lower ranking group male mating) were 448 and 62 seconds. The distributions in the two groups differed significantly (Mann–Whitney $U = 0.0001$, $n_1 = 5$, $n_2 = 4$, $P < 0.014$ two-tailed). Fewer males were present during an alpha male’s mating bouts, and thrust durations were longer when fewer males were present. Alpha males had the most variability in their thrust durations (Figure 3.4).

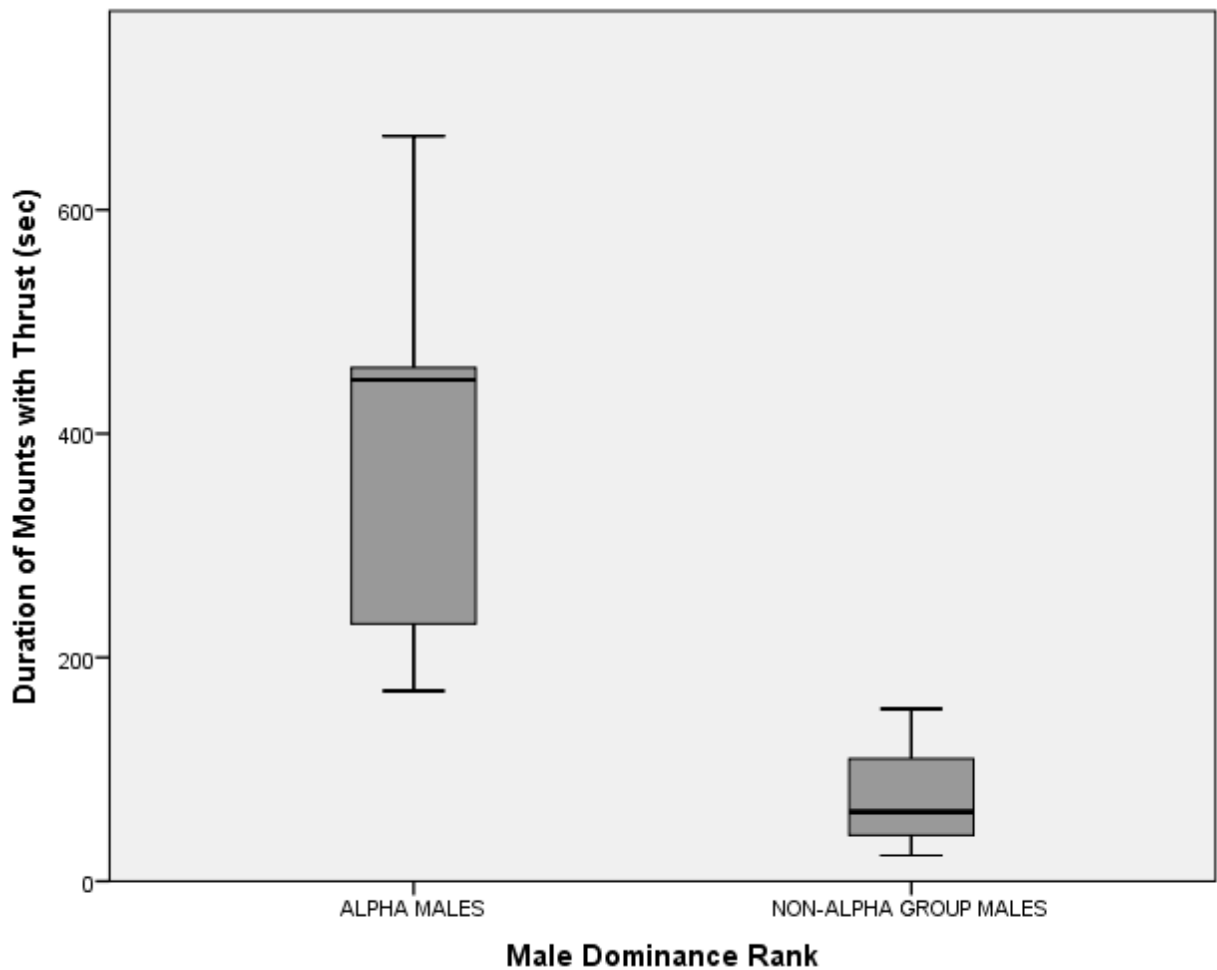


Fig 3.4: Mean duration of male thrusting in seconds from data collected during the 2012 mating season at Berenty Reserve for situations where the alpha male was mating and situations where a lower ranking group male was mating. Bold lines represent the median, box represents the

interquartile range, whiskers show minimum and maximum values. Alpha males were the only group males to be observed ejaculating (N=6) (Table 3.6).

Table 3.6: Male dominance rank and ejaculation frequency among study groups during the 2012 mating season at Berenty Reserve.

Male Rank	Incidence of Ejaculation	Total Males Observed Mating
1	6	6
2	0	1
3	0	2
4	0	1

For one study group (A1) the lone male of the group was not contested by other males during mating. This low level of male-male competition allowed for longer duration of thrusting. When the analysis was completed with this male excluded from calculations, there was no longer a significant relationship between rank and thrust duration (Mann–Whitney $U = 0.0001$, $n_1 = 2$, $n_2 = 4$, $P < 0.064$ two-tailed).

3.4.6 Prediction Six

Female rank showed no significant relationship with incidence of ejaculations (Mann–Whitney $U = 14.0$, $P = 0.104$, one-tailed) meaning that males did not ejaculate less frequently with lower ranked females.

3.4.7 Prediction Seven

When lower ranking and extra group males were considered (non-alphas of the estrous female’s group and males from outside the female’s group), extra group males were significantly more likely to ejaculate than group males (Fisher’s exact test, $p = 0.015$) (Table 3.7).

Table 3.7: Male group status and incidence of ejaculation during the 2012 mating season at Berenty Reserve.

Male Group Status	Incidence of Ejaculation	Total Males Observed
Non-alpha group males	0	4
Extra group males	6	7

When I analyzed my data in terms of copulations rather than ejaculations, I found no link between male group status and mating success (Mann–Whitney $U = 16.0$, $n_1 = 5$, $n_2 = 7$, $P = 0.802$ two-tailed).

Table 3.8: Male group status and incidence of copulations during the 2012 mating season at Berenty Reserve.

Male Group Status	Copulations	Total Males Observed
Non-alpha group males	29	4
Extra group males	22	7

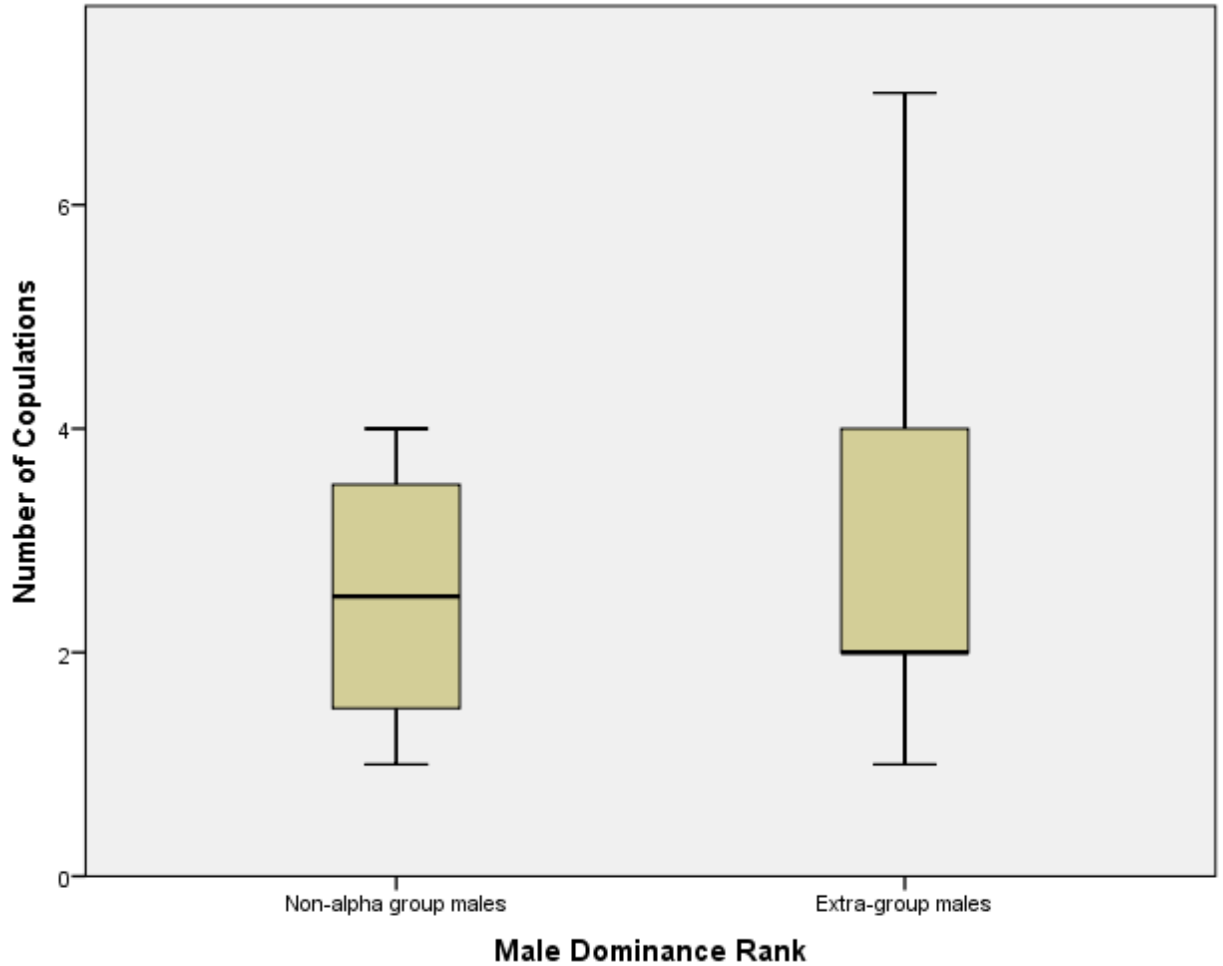


Fig 3.5: Male group status and number of copulations during the 2012 mating season.

3.5 Discussion

3.5.1 Prediction One: Thrust duration will be shorter when OSRs are more male-biased

When other males were present during mating bouts, the total duration of mounts with thrusting was shorter. This is potentially due to the fact that male-male competition increases as OSRs increase, as I examine in chapter four. I observed that when OSRs were male-biased, the number of ejaculations were low. This was most evident for lower ranking group males (non alphas). These males engaged in the most intense competition for estrous females of their group and were the least likely to ejaculate. Alpha males almost always had no males present during their mating

and these males had longer thrusting bouts. It was a trend that other males tended to stay away during alpha males' mating bouts, leading to greater mating success for alpha males.

The *L. catta* literature is lacking on the impact of OSR on mating behaviour; however, there has been some research conducted on other primates on the topic. Male Japanese macaques (*Macaca fuscata*) are able to monopolize their matings with females within their groups when the OSR is balanced. When the OSR is female-biased however, males from outside of the group are able to mate with females. This showed that when males were unable to defend their estrous females, non-troop males had the opportunity to mate (Takahashi, 2001). Male mouse lemurs (*Microcebus murinus*) will switch mating tactics from defending a mate to searching for a new mate in part due to fluctuations in the OSR (Eberle and Kappeler, 2004). The researchers found, however, that male body mass was an important factor determining mating success, regardless of OSR (Eberle and Kappeler, 2004). My finding that a male-biased OSR led to a decrease in total duration of mounts with thrusting is an important finding in terms of reproductive success, as thrust duration correlates with ejaculation (prediction four).

3.5.2 Prediction Two: Male and female dominance rank will have an impact on the OSR

Fewer males were present during alpha male mating bouts than all other males' mating bouts and more males were present during alpha female estrous periods than all other females' estrous periods. Females are known during intertroop agonistic encounters to genital mark at territorial boundaries (Jolly, 1966; 1972; Sussman and Richard, 1974; Budnitz and Dainis, 1975; Mertil-Millhollen *et al.*, 1979) and males are more attracted to these scent marks during female estrous periods (Evans and Goy, 1968; Kappeler, 1998; Palagi *et al.*, 2004; Scordato and Drea, 2007). Ring-tailed lemurs are able to recognize familiar individuals through matching scents and

vocalizations (Kulahci *et al.*, 2014) and relatedness is conveyed in the scent of female genital marks (Boulet *et al.*, 2009). It is possible that group males and males in neighbouring groups know when certain females are going into estrus based on the investigation of their genital marks alone. It is also possible that the female's body scent is detected by males in neighbouring groups. Males are showing greater interest in the estrous females who are high ranking by staying in their groups when these females go into estrous and visiting from neighbouring groups. This greater male interest is also causing greater competition for these females, resulting in copulatory mounts being terminated prior to ejaculation.

My results showed that the average number of non-mating males present was lowest when alpha males were mating and then increased for lower ranking group males and decreased slightly for extra-group males. The difference between the number of males present when alpha males mated versus when non-alpha males mated was statistically significant (Figure 2). A low number of competitors present is one advantage that mating alpha males experience over mating non-alpha group males. One reason why OSRs may have been lower while extra-group males mated than for non-alpha group males could have been that all competitors for the estrous female had experienced agonistic losses during their time sequestering the estrous female and therefore stopped competing for the estrous female. I use the term "overthrowing" to refer to the intense male-male competition which typically results in the end of sequestering of an estrous female. Out of the 7 extra-group males who mated in 2012, only one mated with a female from a group where more than one male was resident. In this case, all of the group males had been overthrown prior to the extra-group male mating. In the cases where extra-group males were mating with females from a uni-male group, the alpha male had been overthrown prior to the extra-group male's mating.

Interestingly, in instances in which there is a lack of competition, the number of times mating was discontinued and resumed when a male dismounted and then remounted the same female did not decrease, meaning the number of copulatory mounts was still as high as when males ended mating bouts in order to chase off competitor males. This supports the argument that *L. catta* mating tends to involve many non-ejaculatory mounts with thrusting before ejaculation can occur (Sauther, 1991). Multiple shorter intromissions before an ejaculatory mount are one characteristic of primate species in which sperm competition is likely, complex penis morphology exists, females mate with multiple males, and larger testes in relation to body size is exhibited; all are characteristics of *L. catta* (Dixon, 2012; Kappeler, 1997; Parga, 2003; Sauther, 1991; Sauther *et al.*, 1999).

3.5.3 Prediction Three: When the OSR is more male-biased, lower ranking males and extra group males will experience greater mating success as measured by thrust duration and incidence of ejaculation

It was found that when the OSR was more male-biased, lower ranking males and extra group males experienced greater mating success as measured by thrust duration and incidence of ejaculation. This finding was predicted because low OSRs were only expected for alpha males. When lower ranking males are mating, these copulations are highly contested by group and extra-group males (Cavigelli and Pereira, 2000; Gould, 1994; Gould *et al.*, 2005; Gould and Ziegler, 2007; Jolly, 1966; Koyama, 1988; Sauther, 1991; Sauther *et al.*, 1999). Although this prediction has not been addressed in primates, this finding contrasts with those of Eberle and Kappeler (2004) who found that male mouse lemurs whose centers of activity were closer to that of the estrous female were more likely to mate in general, regardless of OSR. These mouse lemur males are comparable to group males in *L. catta* who experience spatial familiarity. For owl monkeys, solitary floaters mate only when they supplant a pair-bonded male (Fernandez-Duque

and Huck, 2013), so in this way higher male-biased OSR (two males to one estrous female) is associated with greater mating success for outsider males. The relationship between male rank and OSR was biased by one of the four study groups in which the alpha male was the only resident male of the group (A1 group, AL alpha male). AL had six females in his group and was not challenged by extra group males during his mating bouts. One reason he was not challenged by extra group males was that the mating females stayed in one location and did not travel to neighbouring territories to attract male attention. However, not all females remained in one location in proximity to the sequestering alpha male; on two occasions, females were observed to run away from the alpha male who was sequestering them towards other males.

3.5.4 Prediction Four: Thrust duration will correlate with incidence of ejaculation in this species as male-male competition often interrupts mating attempts

My analyses show duration of mounts with thrust correlated with ejaculation in this species. This finding was expected because the longer a male had to mate with a female without being contested by competitor males, the more likely he was able to complete the mating bout by ejaculating. When comparing mating behaviour among mammals generally and among primates specifically it is useful to classify copulatory behaviour based on whether four types of behaviour are seen: genital locking, thrusting, multiple intromissions, and multiple ejaculations (Dewsbury, 1972). *L. catta* experience repetitive, deep thrusting and rocking behaviour while intromitted, multiple intromissions, an inability to achieve multiple ejaculations and no genital locking (Sauther, 1991). Among strepsirrhines, it is common to have no locking between males and females and thrusting, although multiple intromissions and single ejaculations seem to be less common (Dewsbury and Pierce, 1989).

When thrusting length prior to ejaculation is considered, data are lacking in strepsirrhines. Research has shown that prior to ejaculation, all primates engage in some thrusting behaviour (with intromission), however, not all animals engage in thrusting prior to ejaculation (Dewsbury and Pierce, 1989). Eulipotyphlans, rodents, lagomorphs, bats, carnivores, pinnipeds, and artiodactyls have all been shown to be able to ejaculate without thrusting (Dewsbury and Pierce, 1989). When it comes to the average duration of thrust prior to ejaculation, my results match previous studies on wild *L. catta* at Bezà Mahafaly Special Reserve (Sauther, 1991). Like Sauther (1991), I also found that males thrust for longer just prior to ejaculation, however, when entire duration of thrusting was considered, my documented durations were much greater. I found greater variability in the duration of alpha males' thrust duration than was found by Sauther (1991), with one alpha male's combined mounts with thrusting totalling 11.1 minutes.

3.5.5 Prediction Five: Higher ranked males will thrust for longer

I found that fewer males were present during alpha males' mating bouts and thrust durations were longer when fewer males were present. Alpha males had the most variability in their thrust durations. Mating for a longer duration has been shown to have benefits for males in other species when sperm competition is likely. For example, insects that prolong copulation increase the number of sperm transferred to the female (Parker, 1970). A similar result is seen in several types of reptiles; longer copulations lead to greater sperm transfer (Olsson, 2001; Olsson and Madsen, 1998). Longer thrust durations, and the corresponding greater genital stimulation, have been shown to create a neuroendocrine response in female house mice, causing the female to be less receptive to future mates (Birkhead and Møller, 1998). In primates, it is likely that sperm competition has led to males who copulate longer being favoured by females, as prolonged copulations and multiple intromissions during copulation are associated with species who

experience sperm competition (Dixson, 1991). The stimulation provided by multiple intromissions is considered part of normal sexual function in rodents (Stockley and Preston, 2004) and may be necessary to facilitate sperm transfer (Chester and Zucker, 1970; Wilson *et al.*, 1965). In *L. catta* it is unlikely that the longer thrust durations of alpha males create the neuroendocrine response seen in house mice because females often go on to mate with multiple partners after mating with the alpha male. It is not clear whether *L. catta* require a certain amount of stimulation in order to facilitate sperm transfer. If this is needed, alpha males, who mate for the longest duration, could have an advantage over other males. However, if stimulation from multiple males leads to greater sperm transfer of late mating males, then extra group males who mate last could have a reproductive advantage, even though they were found as individuals to thrust for shorter durations.

The relationship between male rank and OSR could have been biased by one of the four study groups in which the alpha male was the only resident male of the group (A1 group, AL alpha male). AL had six females in his group and was not challenged by extra group males during his mating bouts. Males were present before and after this male's copulations, but they stayed away during his copulations. One reason he was not challenged by extra group males was that the mating females stayed in one location and did not approach other males while AL was mating with them. AL was also very effective at keeping other males away from his group. This low level of male-male competition allowed for longer duration of thrusting.

3.5.6 Prediction Six: Higher ranking females will receive fewer ejaculations than lower ranking females because of increased competition

Males were not more likely to ejaculate with lower ranking females. I expected that the increased competition for alpha females would inhibit ejaculation due to interruption of mating, and this

was not the case. This result is not due to a lack of data on alpha female mating bouts. I witnessed one alpha female (MI) mate with five males in close succession. MI's estrus was characterized by highly male-biased OSRs and heightened male-male competition. This heightened competition was due in part to the fact that MI ran from the alpha male (WL), who was mate guarding her post ejaculation. When WL was challenged by and engaged in aggression with the fourth ranked male of the group RE, MI quickly ran from WL, who had been actively mate guarding her and was followed by the beta male, RY. She then quickly presented to RY and mating began with this male. MI later climbed to the canopy of the tallest tree in her territory, causing four of the males who were competing for access to her to each fall five meters during aggressive encounters. The behaviour of the alpha female increased the threat of injury to the males pursuing her. The lower ranking group males were forced to abort their mating efforts prior to ejaculation due to the high levels of aggression which occurred after the alpha male had mated to ejaculation. Although this female mated with the most males out of the female estrous periods I observed, she only received ejaculate from one male, the alpha of her group. Because it was 1300 hrs when MI's behavioural estrous ended, it is unlikely that she continued to mate with one or more males after my observations ended that day. She was followed later in the afternoon at 1528 hrs for fifteen minutes and showed no signs of estrous. In this way, female choice may be limited by male-male competition. For example, females may run from a mate guarding male and approach another male in order to mate to ejaculation with them, but the resulting increase in male-male competition can cause mating males to be interrupted prior to ejaculating.

3.5.7 Prediction Seven: Group males will ejaculate more than extra group males

Extra group males were significantly more likely to ejaculate than lower ranking group males (non alphas), which was contrary to my prediction. Koyama (1988) predicted that as time passes,

the number of males that have not ejaculated will decrease and competition intensity will likewise decrease. My results do show what Koyama predicted: as time passes, extra group males are more likely to have the opportunity to mate and there were fewer males present in competition during extra group males' mating bouts on average than there were for non-alpha group males. These results raise the questions: Why were fewer males present to contest the mating of extra group males? Could female choice for outsider males play a role in their ability to ejaculate?

Researchers at Bezà Mahafaly found that extra group males were vigorously contested by group males but achieved ejaculation anyway (Sauther, 1991). Other researchers working at Berenty Reserve have found that males were unsuccessful in their attempts to mate outside of their groups (Mertl-Millhollen *et al.*, 1979; Jones, 1983). Future research will attempt to determine what factors played a role in allowing extra group males to ejaculate at higher rates than non-alpha group members. One possibility is that because the dominance position of these outsider males is unknown to the group males they are not prepared to take the chance of aggression with a superior male. Another possibility is that because these males often mate last, all of the other males have been overthrown during agonistic encounters and thus no males are left to contest the mating, which allows these males to mate to ejaculation.

My findings suggest that mating with females from outside of the group is a beneficial strategy. Of the five extra group males who were observed to mate during mating season one, three of the males were from one of the study groups and thus their dominance rank in their home group was known. One of the males was top ranking, one was second, and one was third ranking. The top ranking male did not ejaculate while the two lower ranking males did. Monitoring receptivity of females outside of one's group and mating with these females once they come into estrous may

be an advantageous strategy for lower ranking males. This is supported by findings of a recent study where up to 33% of infant ring-tailed lemurs were sired by non-group males (Parga *et al.*, 2016). Greater mating success is thought to be an advantage of group membership because females mate first with group members and then with extra group males, potentially giving first mating males a fertilization advantage (Gould, 1994; Koyama, 1988; Sauther, 1991). However, this advantage is nullified if group males are unable to ejaculate with females due to high levels of competition, as seen in my study. Gould (1994) observed eight mating bouts and one of these mating bouts was with an extra group male. This mating occurred at the end of the female's estrous period, which is consistent with my findings that extra group males were the last to mate with the estrous female. Four males from adjacent troops were seen mating with study females at Bezà Mahafaly Reserve (Sauther, 1991); each of these males was the final mating male and was seen to ejaculate. These findings are consistent with my results. Sussman (1992) observed seven mating bouts, including one mating season visiting male and one mating season transfer male. The visiting male and mating season transfer male were both the last to mate. Sussman (1992) found no link between male migration (group status) and mating success in *L. catta*. However, Sussman measured mating success by copulations alone rather than measuring whether the copulating male ejaculated or not. When I analyzed my data in terms of copulations rather than ejaculations, I also found no link between male group status and mating success.

3.5.8 Conclusions

I found that variation in the OSR during a female's estrous period impacts male reproductive success. My findings highlight the advantages of both being an alpha male and of mating with females from outside of one's group, since in both cases these males had the highest likelihood of ejaculating with estrous females. These results raise questions about the value of group

membership for non-alpha males and offer an explanation for why males often leave their groups during the mating season to pursue mating opportunities in neighbouring groups. *L. catta* males tend not to win agonistic encounters once they have been overthrown by a competitor male during a female's estrous (pers. observ). An adaptive mating strategy for extra group males is waiting until competition between group males has ended and overthrowing the lowest ranking male of a group for access to an estrous female, since they are unlikely to be contested in mating and are as likely as alpha males to ejaculate. Future research will examine male interference during copulations and the relationship with mating success. Currently the relationship between male ejaculate order and fertilization success in this species is unknown (Parga, 2003). Further research should continue the investigation into whether first ejaculating males have a fertilization advantage over later ejaculating males.

My findings have implications for mate choice being limited by male-male competition, as females would approach and mate with desirable males only to have the copulation interrupted prior to ejaculation. This was most evident for alpha females. My study is the first analysis of OSRs and mating success in *L. catta* and adds to the limited primate literature in this area. My findings offer important insight into how male-male competition impacts mating outcomes in a model taxon with large group sizes and female dominance.

3.6 Bibliography

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4 Chapter 4

Sexual Interruptions and Harassment in the Ring-tailed Lemur (*Lemur catta*)

4.1 Abstract

Males who harass and/or interrupt copulations are expected to experience improved mating success while decreasing the mating success of other males, although this has not been consistently investigated for primates. I tested this idea in four groups of ring-tailed lemurs (*Lemur catta*) at Berenty Reserve by observing three consecutive mating seasons. I found that interrupting males reduce the mating success (ejaculations) of those they interrupt (Mann-Whitney $U = 11$, $n_1 = 5$, $n_2 = 14$ $P = 0.022$). The intensity of harassment directed towards mating males impacted mating success for the aggressor, as these harassing males were more likely to go on to mate and ejaculate with the estrous female (Mann-Whitney $U = 5.5$, $n_1 = 7$, $n_2 = 5$, $P = 0.036$). This is the first evidence for primates that aggression directed towards the mating male directly increases the harassing male's reproductive potential. Occurrence of interruptions decreased the quality of copulations by causing copulatory mounts to be fewer and rates of affiliative behaviour between mating male and female to be lower (Mann-Whitney $U = 0.5$, $n_1 = 4$, $n_2 = 5$, $P = 0.017$). Extra-group mating males did not experience fewer interruptions during mating, even though these males had more ejaculations than other low ranking males. There was no significant relationship between sexual interruptions and access to estrous females. I found some support for the hypothesis that interruption and harassment of copulations improves mating success for harassers and decreases mating success for harassed males in this species. Harassment was found to increase an aggressor's mating success while interruption was found to decrease the mating success of the mating male. In addition, if the rate of affiliative behaviour

from the male to the female during mating has an impact on reproductive success, interruption of copulations will play a role in which males sire offspring.

4.2 Introduction

Males compete over females because females are the limiting resource for males to achieve reproductive success (Andersson, 1994). This is a prediction of Darwin's (1859) theory of sexual selection. Typically, in species which live in social groups, males compete to form dominance hierarchies which determine reproductive success (Girman *et al.*, 1993; Haley *et al.*, 1992; Maslow, 1936; Pemberton *et al.*, 1992; Wroblewski *et al.*, 2009; Zuckerman, 1932). Non-dominant males also develop alternative mating strategies in order to compensate for their lack of alpha status. One such alternative mating strategy is the harassment and interruption of mating. Harassment and interruption of mating are two distinct concepts. Harassment of mating, when individuals show aggressive behaviour toward the mating pair, does not always lead to interruption of mating, the temporary or permanent cessation of copulatory mounts (Neimeyer and Anderson, 1983). Harassment and interruption of mating may alter the behaviour of the mating male and female as compared to mating that occurs void of interference. One area that has had little attention is the level of affiliative behaviour that occurs between the mating male and female (such as total number of affiliative events during mating) and whether this behaviour decreases in relation to harassment. In *L. catta*, levels of affiliative behaviour from male to female are higher for groups that have fewer males in them (Gould, 1996). Level of affiliative behaviour could be associated with length of postcopulatory guarding if males persuade females to stay in proximity during and after mating by using affiliative behaviour.

Harassment and interruption of mating occurs in many diverse species: insects (Gröening and Hochkirch, 2008; Simmons, 2001; Thornhill and Alcock, 1983; Walker, 1974), earthworms (*Lumbricus terrestris*) (Nuutinen and Butt, 1997), salamanders (*Notophthalmus viridescens*) and newts (*Cynops ensicauda popei*) (Sparreboom, 1996; Verrell, 1983), crayfish (*Orconectes rusticus*) (Berrill and Arsenault, 1984), several species of birds (Chardine, 1986; Davies, 1985; Gratson *et al.*, 1991; Tryjanowski *et al.*, 2007), guinea pigs (*Cavia porcellus*) (Gerall, 1958), Belding's ground squirrels (*Spermophilus beldingi*) (Hanken and Sherman, 1981), yellow toothed caviies (*Galea musteloides*) (Rood, 1972), and black-tailed prairie dogs (*Cynomys ludovicianus*) (Hoogland, 1981), but has been most extensively studied in non-human primates (Neimeyer and Anderson, 1983). Harassment in relation to mating occurs in over 30 primate species (Neimeyer and Anderson, 1983).

Sexual interference by adult males, females and immature animals has been studied extensively in primates, in captivity as well as in the wild (Dixson, 1998). Interruption of copulations is performed by all age-sex classes in non-human primates, including alpha males, alpha females, juveniles, and other lower ranking adults (Neimeyer and Anderson, 1983). There is a discrepancy among primate species as to who is more likely to interfere with copulation: alpha males or subordinates. Alpha male rhesus macaques (*Macaca mulatta*) (Lindburg, 1973, Wilson, 1981), Japanese macaques (*Macaca fuscata*) (Hanby *et al.*, 1971, Stephenson, 1975, Takahata, 1982), crab-eating macaques (*Macaca fascicularis*) (Wheatley, 1982), stumptail macaques (*Macaca arctoides*) (Brereton, 1994; Bruce and Estep, 1992; Gouzoules, 1974), savanna baboons (*Papio cynocephalus*) (Hall and DeVore, 1965), marmosets (*Callithrix jacchus*) (Abbott and Hearne, 1978), capuchins (*Cebus apella nigrinus*) (Alfaro, 2005), squirrel monkeys (*Saimiri sciureus*) (Baldwin, 1968; DuMond, 1968), gray langurs (*Presbytis entellus*) (Boggess, 1980), orangutans

(*Pongo pygmaeus*) (Mitani, 1985; Galdikas, 1985), bonobos (*Pan paniscus*) (Kano, 1992) and chimpanzees (*Pan troglodytes*) (Nishida, 1997) interrupt lower ranking males during copulations. Subordinate male savanna baboons (*Papio cynocephalus*) (Smuts, 1985), gray-cheeked mangabeys (*Lophocebus albigena*) (Wallis, 1983) and ring-tailed lemurs (*Lemur catta*) (Jolly, 1966; Koyama, 1988; Sauther, 1991) interrupt higher ranking males during copulations.

It has been hypothesized that harassment and interruption of copulations may be an attempt by the interfering individual to stop or delay the mating, thus increasing the harasser's own reproductive potential if they are able to subsequently mate with the estrous female, while decreasing that of the mating individual (Brereton, 1994; Brown *et al.*, 1997; DeVore, 1965; Drukker *et al.*, 1991; Himuro and Fujisaki, 2012; Hohmann and Fruth, 2003; Hrdy, 1977; Niemeyer and Chamove, 1983). A review of the primate literature (Neimeyer and Anderson, 1983) showed some support for this hypothesis, and argued that further research was needed. In the years since the review, researchers have found support for this hypothesis in their studies of some primates: Hanuman langurs (*Semnopithecus entellus*) (Sommer, 1989), golden snub-nosed monkey (*Rhinopithecus roxellana*) (Qi *et al.*, 2011), and bonobos (*Pan paniscus*) (Hohmann and Fruth, 2003); while others have shown no support for the hypothesis: stumptail macaques (*Macaca arctoides*) (Drukker *et al.*, 1991), Japanese macaques (*Macaca fuscata*) (Huffman, 1987), and rhesus macaques (*Macaca mulatta*) (Berard *et al.*, 1994).

Harassment may limit the amount of affiliative behaviour, such as grooming, sitting in contact etc., that occurs between males and females during mating. In chimpanzees, consortships may be an adaptation to avoid the harassment and interruption of mating, and correlate with increased reproductive success (Tutin, 1979). Consortships have historically been so loosely defined that

one researcher described the term as defining ‘any relationship between an estrous female and adult male’ (Manson 1997, pp. 356). In chimpanzees, a consortship involves isolation for a period of time from the rest of the group (Manson, 1997; Tutin, 1979). Consorting male chimpanzees are more likely to engage in the affiliative behaviours of grooming the estrous female and sharing food with her (Tutin, 1979). In chimpanzees, at least, it has been documented that an absence of harassment and interruption of mating leads to potentially higher quality mating, including affiliative behaviour from male to female.

The study of harassment and interruption of copulation has been studied predominantly in stump-tail macaques (*Macaca arctoides*) (Brereton, 1994; Bruce and Estep, 1992; Drukker *et al.*, 1991; Estep *et al.*, 1988; Gouzoules, 1974; Niemeyer and Chamove, 1983). When harassment is considered in the stump-tail macaque, it was found that the post-ejaculatory tie was longer when there was interference (harassment) and number of mounts to reach ejaculation were greater during matings with interference – although this finding was not statistically significant (Brereton, 1994). Harassing individuals were ineffective in reducing the reproductive potential of the mating pair, unless the harasser was more dominant than the mating male (Estep *et al.*, 1988; Niemeyer and Chamove, 1983). Harassment has been described as functioning for stump-tail macaque individuals to seek revenge for past aggression (Drukker *et al.*, 1991) and as a ritual that redirects potential aggression away from the mating female and onto the harassing individuals (Gouzoules, 1974). Interruption, on the other hand, is shown to never be directed towards alpha males (Bruce and Estep, 1992) and can successfully prevent ejaculation (Niemeyer and Chamove, 1983). It is unclear why this topic has been so thoroughly examined in *M. arctoides* but not in other primate species.

Testing the relationship between harassment and interruption of mating and male mating success in other primates is important, as it is unclear whether the patterns observed in *M. arctoides* apply more broadly. *L. catta* is an ideal model species for evaluating this relationship, as this species experiences seasonal mating in which intense male-male competition occurs, including both harassment and interruption of mating (Gould and Ziegler, 2007; Koyama, 1988; Sauther, 1991; Parga, 2009). *L. catta* live in complex multimale-multifemale groups exhibiting female dominance (Jolly, 1966; 1984; Kappeler, 1990; Sauther, 1993), a quality seen only in some lemurs among primates (Pereira *et al.*, 1990). Female *L. catta* experience estrous periods which last from half a day to two days and often mate with multiple male partners from inside and outside their groups during estrous (Gould, 1994; Koyama, 1988; Parga, 2006b; Pereira and Weiss, 1991; Sauther, 1991; Sussman, 1992). Not all males ejaculate following copulations. For those occasions in which ejaculation does occur, a copulatory plug is deposited in the female's vaginal tract and subsequent mating males attempt to remove this plug (Dixson, 1998; Parga, 2003; 2010; Sauther, 1991). Females mate during the night as well as the day during estrous, although data are lacking on nocturnal mating behaviour (Jolly, 1966; Koyama, 1988; Parga, 2006; Sauther, 1991). Although there is usually only one female available to mate at a time in each *L. catta* group, the number of males present and competing for a female in estrous varies considerably for each individual estrous female. Not all group males are always present and competing for each estrous female, as some males leave their group during the mating season to monitor females in other groups (Sussman, 1992; Gould, 1994).

The typical mating pattern of *L. catta* is described as a series of brief mounts without intromission before short mounts with intromission, during both of which the mating male is harassed by competitor males (Dixson, 1998). The mating male must then disengage with the

estrous female in order to chase off the competitor(s), thus interrupting the mating attempt (Sauther, 1991). Harassment and the resulting interruption of copulations are described by Jolly (1966; 1967), Koyama (1988), and Sauther (1991). Jolly briefly mentions that a male and female of the same group were observed mating while being challenged by another group male. After the successful mating of the pair, a male from an adjoining troop approached the estrous female who then chased the extra-group male off (Jolly, 1966). This example differs from the more typical scenario in which the mating male chases off the competitor male. Observations made by Koyama (1988) show that many copulatory mounts between the mating male and female were interrupted in order for the mating male to chase off competitors. Males engaged in chases, displacements, anoint and waft tail displays to other males, and jump fights as well as hitting, biting and pulling the tail of the mating male (Koyama, 1988). Interruptions in mating are also reported by Sauther (1991): when the alpha male is mating with an estrous female, he is harassed by a group male and stops copulatory behaviour in order to chase this competitor away. When the estrous female later mated with an extra group male, two adult troop males and a juvenile male harassed the mating male.

Lemur catta sexual behaviour has been widely studied (Budnitz and Dainis, 1975; Gould, 1994 and 1996; Jolly, 1966; Koyama, 1988; Parga, 2006b; Pereira and Weiss, 1991; Sauther, 1991; Sussman, 1992; Sauther and Sussman, 1993; Taylor, 1986), however, affiliative behaviour during mating has not received as much attention as other behaviours (Gould, 1996). Male and female pairs have been observed to groom each other's fur between copulatory mounts (Jolly, 1966). Detailed affiliative behaviour during mating was reported by Koyama (1988). Males were observed to sniff and lick the female's genitals and face during copulations (Koyama, 1988). A mating male is documented as licking the genitals of the estrous female for a full two minutes

(Koyama 1988). Gould (1996) found no increase in affiliative relationships during the mating season between male and female. What was found was that three males exhibited their highest rates of affiliative behaviour during the mating season, while four males exhibited their lowest rates of affiliative behaviour during this time (Gould, 1996). The males with high rates were mainly alpha males, while the others were transferring out of their group during the mating season (Gould, 1996). It is currently unknown whether harassment and interruption of mating have an impact on these affiliative behaviours. This first study of the impact of harassment and interruption of copulation in strepsirrhines offers an important addition to the primate literature.

In order to assess the impact of adult male harassment and interruption of mating on reproduction, reproductive success must be estimated. The only study to report male reproductive success measures among wild *L. catta* did not have accompanying behavioral data, so the effect of male harassment and interruption of mating on male reproductive success is currently unknown (Parga *et al.*, 2016). Mating success can sometimes be used as a proxy measure of reproductive success (Robinson, 1982) and can be measured using several types of copulatory behaviour. Copulatory behaviour can be classified into three types of events: mounts, intromissions, and ejaculation (Dewsbury and Pierce, 1989). Since different animal studies use different copulatory behaviours as measures of mating success, it is often difficult to make comparisons. In primates, mating success has been measured in different ways, and much has been written about these measurement discrepancies (e.g., Bernstein, 1976; Drickamer, 1974; Fedigan, 1983; Rowell, 1974; Smuts, 1982). One problem with equating mating success with reproductive success is that the few studies which have measured both mating success and reproductive success in the same primate groups have found that some previous measures of mating success were not good predictors of reproductive success (Curie-Cohen *et al.*, 1983;

Stern and Smith, 1984). Two studies of rhesus macaques found similar results (Curie-Cohen *et al.*, 1983; Stern and Smith, 1984). In the earlier study, researchers found that even though an alpha male participated in the most matings (their measure of mating success), he did not sire the majority of the offspring (Curie-Cohen *et al.*, 1983). In a study published a year later, researchers found that they could not reliably determine the father of offspring based on copulations alone or consort activity alone (Stern and Smith, 1984). Altmann *et al.* (1996) found however, that mating behaviour was a good predictor of reproductive success. The paternity analysis the researchers conducted provided strong support “for the validity of estimating variance in reproductive success using consortships on fertile days of conception cycles” (p. 5799). Measuring mating success based on ejaculations with estrous females is the closest estimate for reproductive success when paternity data are unavailable, since males may copulate with females without ejaculating. This method is employed here because it is more accurate than previous methodology.

In the present study, I address the hypothesis that harassment and interruption of copulations increases mating success of the harasser, decreases mating success of the harassed, and affects the quality of copulations in *L. catta*. The null hypothesis is that there is no relationship between harassment and/or interruption of mating and mating success. I predict the following results: 1) Individuals with the highest rates of interrupting copulations should have the highest rates of mating success (ejaculations with estrous females) if interruption of copulations is used to improve an individual aggressor’s mating success, 2) The frequency of mating to ejaculation in interrupted mating pairs should be significantly lower than the frequency of mating to ejaculation in uninterrupted mating pairs if interruption of copulations is an effective behavioural tactic used by *L. catta* to reduce the mating success of competitors, 3) Males who interrupt mating pairs

should gain access to the estrous female soon after the interruption(s), 4) Males who show a greater intensity of harassment (intensity level of individual aggressive actions and number of aggressive actions) towards mating pairs will have greater mating success and males who are harassed at the greatest intensity will experience the lowest mating success, 5) Interruption of copulations will decrease the quality of copulations by decreasing the duration and the number of affiliative behaviours during mating between the estrous female and mating male, 6) Extra group males will experience lower rates of copulation interruption than low ranking group males since extra group males at this site are known to have higher rates of ejaculation with estrous females than low ranking group males (Chapter 3), and 7) Incidence of ejaculation or losing access to the estrous female will not have an impact on whether males harass other mating males.

4.3 Methods

4.3.1 Ethical Note

All research protocols were approved by the Animal Care Committee at the University of Toronto and conform to the governing laws of the Malagasy Republic. This study was conducted with the approval of the De Heaulme family, owner of the private nature Reserve of Berenty.

4.3.2 Study Site

Berenty Reserve (24° 58 S, 46° 16 E) is a private nature preserve in the extreme south of Madagascar established by the de Heaulme family in 1936. The de Heaulme family have a long history of welcoming international researchers to their study site, beginning with Alison Jolly's pioneering study of *L. catta* behaviour, which was initiated in 1963 (Jolly *et al.*, 2006). Long term, continuous research has been conducted by Koyama and his colleagues at the reserve since 1989 (Koyama *et al.*, 2001).

The reserve consists of 2 km² of gallery forest containing large tamarind trees (*Tamarindus indica*) with a closed-canopy and 1.5 km² of less ecologically rich scrub and spiny forest (Jolly *et al.*, 2002). The reserve acts as a major tourist destination throughout the year and the main area for tourists, in which this study was conducted, is known as the tourist front. The tourist front includes a restaurant and tourist bungalows and has many introduced species of plants and trees which supplement the lemurs' diets (Jolly, 2012). In addition, lemurs are occasionally fed scraps by tourists, although formal provisioning has been discontinued and tourists are warned against feeding the animals. Summers are hot and wet, averaging 40°C at mid-day and winters are cold and dry with temperatures falling at night to 10°C (Jolly, 2012). There is great variability in rainfall from year to year, ranging from 300cm to 900cm annually (Jolly, 2012).

The population of *L. catta* for Berenty Reserve was reported as 941 individuals in 2015, with the largest group being found in the tourist front (Dimilahy *et al.*, 2015). Population density is 5.8 ind/ha for *L. catta* at the tourist front, the highest in the reserve (Jolly *et al.*, 2002). This is much higher than the 1-1.5 ind./ha density seen within the spiny desert and scrub (Jolly *et al.*, 2002). Density seen in the spiny desert and scrub is comparable to density found at Bezà Mahafaly (Sussman, 1991). Primates found in Berenty Reserve include the introduced *Eulemur rufus collaris* hybrid, Verreaux's sifaka (*Propithecus verreauxi*), lepilemur (*Lepilemur leucopus*), and two types of mouse lemur (*Microcebus murinus*, *Microcebus griseorufus*) (Jolly *et al.*, 2002). Potential lemur predators include both mammals (domestic dogs and cats, and the Indian civet [*Viverricula indica*]) (Jolly, 2012) and birds (the harrier hawk [*Polyboroides radiatus*], the Madagascar buzzard [*Buteo madagascariensis*], and the black kite [*Milvus migrans*]) (Crowley, 1995; Karpanty and Goodman, 1999).

4.3.3 Study Subjects

Natural markings (minor pelage coloration differences, old, easily-seen scars from fights with other animals, etc.) have been used to identify each lemur (Appendix 2). Adult male and female study subjects were selected as focal animals from four groups inhabiting the Tourist Front (Table 4.1). Adults were selected because they are the age category which engages in mating behaviour and the groups that were chosen were used because they were currently not part of any long-term field research. Each adult subject has been photographed and drawn to document their distinguishing features.

Table 4.1: *Lemur catta* group composition by adult male (AM) and adult female (AF) study subjects for the three study periods, 2012-2014 at Berenty Reserve, Madagascar.

Group	2012		2013		2014	
	AM	AF	AM	AF	AM	AF
A1	1	6	1	4	0	0
RG	4	4	3	3	4	4
MG	2	2	3	4	3	5
LG	1	3	0	0	0	0
Total	8	15	7	11	7	9

I collected all data for this study during three consecutive mating seasons (April to June, 2012 to 2014). The sample size fluctuated over the three years of behavioural observations due to deaths, disappearances, emigrations, births, and group membership changes as juveniles matured to

adulthood (Table 4.1). Adults were defined as sexually mature individuals who participated in mating during the mating season. Juveniles were defined as individuals who were close to adult body size but who did not participate in mating. Yearlings were all individuals that were of immature body size. Adults were distinguished from juveniles based on body size estimates, and sexual development. Sexual development was assessed on appearance of genitals as well as whether the individual mated during the mating season. Individuals are known to mate as early as two years, and most females have their first offspring at three or four years of age (Koyama *et al.*, 2001). Extra group males were defined as any males from outside of the group and those who were known to be members of other groups but who did not attempt to immigrate into the study groups.

4.3.4 Behavioural Data Collection

I conducted all behavioural observations, supported by two experienced Malagasy field assistants from the University of Antananarivo. I trained and supervised both of the field assistants chosen for the research project. Assistants did not collect data but assisted by identifying individuals, monitoring group movement, and locating estrous females. Observations of four groups (A1, RG, MG, LG) were conducted six days per week from 0700 hrs until 1700 hrs, alternating between groups on subsequent days for a total of 414 hours of focal observations over three years. During the study, the mating period is defined as the time between the onset of the first observed estrus and the last observed estrus during the first estrus cycle of the season. During the mating period, observations were conducted seven days per week. Prior to the commencement of the mating period, training of assistants and familiarization with all study subjects occurred.

Using continuous-time focal sampling (Altmann, 1974), data were collected on all affiliative and aggressive behaviours. Focal samples were conducted for 15 minutes each. This focal follow duration allows each focal individual to be sampled at least twice during each time period of morning or afternoon. Focal animals were selected by always choosing to follow the individuals with the lowest total number of follows and making an attempt to equalize the number of follows completed on each individual during the mornings and afternoons. Data were recorded using data sheets.

During the mating season, when a female was observed to enter estrus, 15 minute focal sampling ended and all occurrences sampling for agonism and sexual behaviour began for the entire duration of estrus. Twenty-two hours of all occurrences sampling data were collected over the three years. All affiliative, mating, and aggressive behaviour was recorded using the all-occurrence group sampling method (Altmann, 1974). Copulations are defined as mounting with penile intromission and thrusting. Mating bouts were defined as each male's entire period of copulations with a female. Estrous periods were defined as the entire time a female was sexually receptive to males. Prior to the initiation of each follow, data were recorded on physical manifestations of female reproductive state by noting any changes in genital swelling or colour. Ad libitum data were also collected at all times on such occurrences as presence of any physical injuries, abandonment of infants, infanticide, and predation events.

Dominance rank was calculated by collecting data on all decided agonistic interactions, displacements and the direction of submissive vocalizations known as the spat call (Jolly, 1966). Focal data on aggression and submission during the mating period were used for the hierarchy matrices. Winners of aggressive interactions and receivers of the submissive vocalization were

coded in the same manner for the matrices. For example, within the matrix, rows represent winners of aggression and receivers of spat calls, while columns represent losers of agonistic encounters who give the submissive vocalization. Because some of the dominance hierarchies were non-linear, the dominance index method was chosen following Zumpe and Michael (1986). In this method, the dominance index for each individual is calculated by averaging the percentage of aggression given and submission received with all the other same sex animals in the group (Zumpe and Michael, 1986). Dominance indices for males were turned into ordinal ranks for analysis. This was possible because male dominance hierarchies were linear. Male dominance rank was calculated using data from the entire study period except for days when a female entered estrous. In this way, the effect of the break-down of the dominance hierarchy during the mating season was minimized (Budnitz and Dainis, 1975; Gould, 1994; 1997; Gould *et al.*, 2005; Parga, 2009; Taylor, 1986). Mating success was measured by ejaculation. Criteria for determining ejaculation has occurred are shown in Table 4.2.

Table 4.2: Criteria for determining whether ejaculation has occurred or not occurred.

Ejaculation has occurred	Ejaculation has not occurred
Ejaculate seen on male's penis tip	Male with an erection after thrusting bout and none of the criteria for determining ejaculation has occurred are met.
Ejaculate seen on female's genitals	Mating interrupted by competitors and none of the above criteria are met.
The male in question removes a copulatory plug (Parga 2003) from the female during mating and the male who mates directly after the male in question also removes a copulatory plug during mating.	
The male in question is known to be the first mating male and the male who mates directly after the male in question removes a copulatory plug from the estrous female during mating.	
Male seen mate guarding the female without an erection after copulation, and no further mounts with thrusts and intromission.	

Female estrous periods were defined as complete or incomplete depending on whether they were observed from beginning to end. In other words, if no male mating partners were missed during observations, then the estrous period was defined as complete. If mating started prior to the observer encountering the mating pair or if mating continued after observations ended, this mating bout was defined as incomplete. Four incomplete mating bouts were observed during the three-year study period. This methodology was conservative in that it may have overestimated incomplete estrous periods and underestimated the complete estrous periods seen.

4.3.5 Data Analyses

In order to test whether individual males who interrupted copulatory mounts achieved more ejaculations (prediction one), an interruption ratio was calculated for each of these males (Bruce

and Estep, 1992). This ratio was calculated as the number of copulatory mounts an individual interrupts, divided by the number of copulatory mounts witnessed. Interruption ratios were calculated for each male for the entire mating period and also for each individual mating bout. Interruption ratios were calculated for individual mating bouts in order to determine whether higher ratios led to a greater likelihood that the interrupting male would gain access to the estrous female during that estrous period. In order to test whether males of interrupted mating pairs achieved fewer ejaculations (prediction two), the percentage of copulatory mounts interrupted by aggression for each mating bout was calculated.

To address the question of whether males who interrupt mating gain access to the estrous female soon after the interruption(s) (prediction three), the number of copulatory interruptions were counted per interrupting male for each mating pair and compared with the duration it took for the interrupting male to gain access to the estrous female after the first interruption.

In order to test whether the intensity of harassment during mating bouts impacted mating success of mating males or those who harassed them (prediction four), aggression was categorized into two levels of intensity: contact or no contact (Parga, 2006a) and each mating bout was ranked based on the level of aggression received. A mating bout included the entire duration a male maintained proximity to the estrous female, including pre and post-copulatory guarding, where applicable. These rankings were correlated with ejaculations to determine whether higher intensity aggression led to fewer ejaculations for the mating male. This ratio was calculated as the number of aggressive events with contact, divided by the total number of aggressive events during the mating bout. This ratio was calculated in order to determine whether higher intensity

of aggression during a mating bout led to the male aggressor gaining access to the estrous female.

Affiliative behaviours between mating males and females during copulations were measured in order to determine if interruption of copulation had an effect on the level of affiliation between mating pairs (prediction five). Copulation was defined as starting at the time of the first mount with intromission and ending with the final mount with intromission. Affiliative behaviour included: sniff genitals, sniff body, lick genitals, nuzzle, sit in contact with, face greet, mutual groom, anoint tail, waft tail, and purr to female (Gould, 1996; Pereira and Kappeler, 1997; Appendix 1).

In order to determine if extra group males experienced fewer interruptions to copulation than lower ranked group males, males of different residence status (non-alpha resident males versus extra group males) were compared with respect to the percentage of their copulatory mounts that were interrupted by aggression for each mating bout (prediction six). Finally, in order to determine if incidence of ejaculation or losing access to the female impacts how much males harass other mating males (prediction seven), each male was categorized based on his group status and whether or not he ejaculated with his mating partner. The average number of males who mated before and after each male was calculated and averaged for each male category (resident versus extra group male). This allowed for a calculation of the rate of harassment of mating males before and after ejaculation and/or losing access to the female.

Spearman rank correlations and Mann-Whitney U tests were used when ordinal data were included in the analysis. A Spearman partial correlation was conducted when the effect of rank was controlled for. All statistical analyses were conducted in SPSS 22.0 for Windows.

Significance levels were set at $p < 0.05$, and all tests were two-tailed. Data from each of the three years were pooled for analyses.

4.4 Results

4.4.1 Do adult males who interrupt copulations experience improved mating success (ejaculations with estrous females)?

There was no correlation between the interruption ratio of individual males and their total ejaculations with estrous females ($r_s = -0.049$, $N = 6$, $P = 0.926$) for the three mating seasons.

Table 4.3: All males who interrupted copulatory mounts, their interruption ratio, and their total observed ejaculations (EJ) during three mating seasons at Berenty Reserve.

Interrupting Male	Interruption Ratio	Total EJ of interrupting male during three mating seasons
BK	0.38	0
RY	0.50	3
WL	1.00	1
RE	1.00	0
AL	0.88	4
IY	0.84	0

4.4.2 Do interrupting males reduce the mating success (ejaculations) of those they interrupt?

There was a significant relationship between percentage of copulatory mounts interrupted by aggression, and ejaculation of the mating male (Mann–Whitney $U = 11$, $n_1 = 5$, $n_2 = 14$ $P = 0.022$). For four out of five instances, when a mating bout (all copulatory mounts between an

individual male and estrous female) did not end in ejaculation, it was because all of the copulatory mounts were interrupted (Figure 4.1). There was a great deal of variation in the percent of copulatory mounts interrupted for instances where the mating male ejaculated (Figure 4.1).

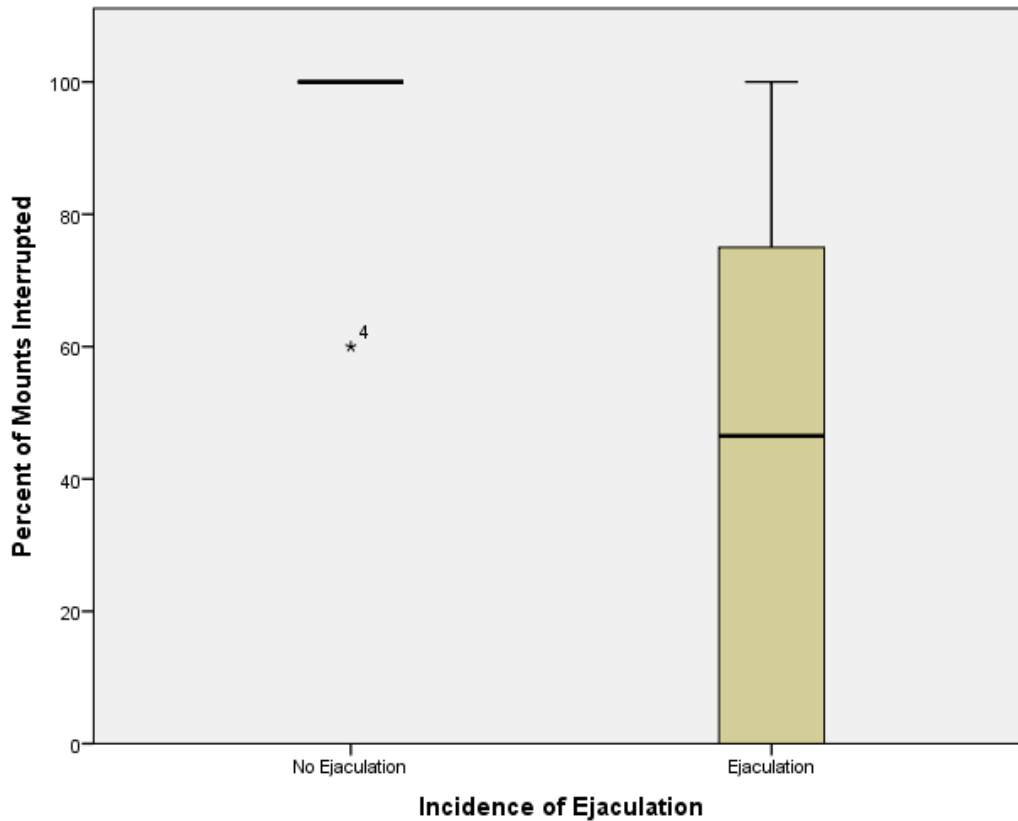


Figure 4.1: Relationship between percentage of mounts interrupted and incidence of ejaculation for mating males at Berenty Reserve during the three observed mating seasons. Bold lines represent the median, box represents the interquartile range, whiskers show minimum and maximum values.

4.4.3 Do interrupting males gain access to estrous females soon after interrupting the mating pair?

Interrupting males do not gain access to estrous females soon after interrupting the mating pair.

Out of nine instances of males interrupting copulations, the interrupting male gained access to

the estrous female directly after interrupting on only one occasion. Often, the interrupting male did not ever gain access to the estrous female (Table 4.4).

Table 4.4: All occasions where males interrupted mating bouts and incidences where the interrupting male gained access to the estrous female during the three mating seasons observed at Berenty Reserve.

Year	Interrupting Male	Mating Pair	Number of Interruptions	How long before access gained hh:mm:ss
2012	BK	WL and MI	2	Never
2012	RY	WL and MI	1	2:07:45
2012	WL	RY and MI	1	Never
2012	RE	BK and MI	1	0:00:47
2012	RY	RE and MI	2	Never
2012	BK	FO and MI	1	Never
2012	RY	FO and MI	1	Never
2012	RY	AL and FI	1	00:53:00
2012	AL	RY and FR	3	Never
2013	IY	RE and EC	1	Never
2013	AL	WL and CH	2	Never
2014	IY	BK and MO	2	Never

4.4.4 Does the intensity of harassment directed towards mating males impact mating success for the aggressor or for the receiver of the harassment?

There was no correlation between the intensity ratio of each individual harassing male and the two measures of mating success: the number of minutes it took for the harassing male to gain access to the estrous female ($r_s = -0.097$, $N = 12$, $P = 0.764$), and incidence of ejaculation by the harassing male: Mann Whitney U test ($U = 9.5$, $n_1 = 7$, $n_2 = 5$, $P = 0.165$). Intensity ratios were calculated by counting the number of aggressive interactions involving contact during the mating bout and the total number of aggressive interactions during the mating bout. Duration until access to the estrous female was gained by the interrupting male ranged from 47 seconds to over 2 hours and 39 minutes. Intensity ratios ranged from 0 to 1.

When intensity of aggression was considered, without calculating it as a ratio of total aggressive incidents, a significant relationship was found with incidence of ejaculation of the harassing male (Mann-Whitney $U = 5.5$, $n_1 = 7$, $n_2 = 5$, $P = 0.036$) (Figure 4.2).

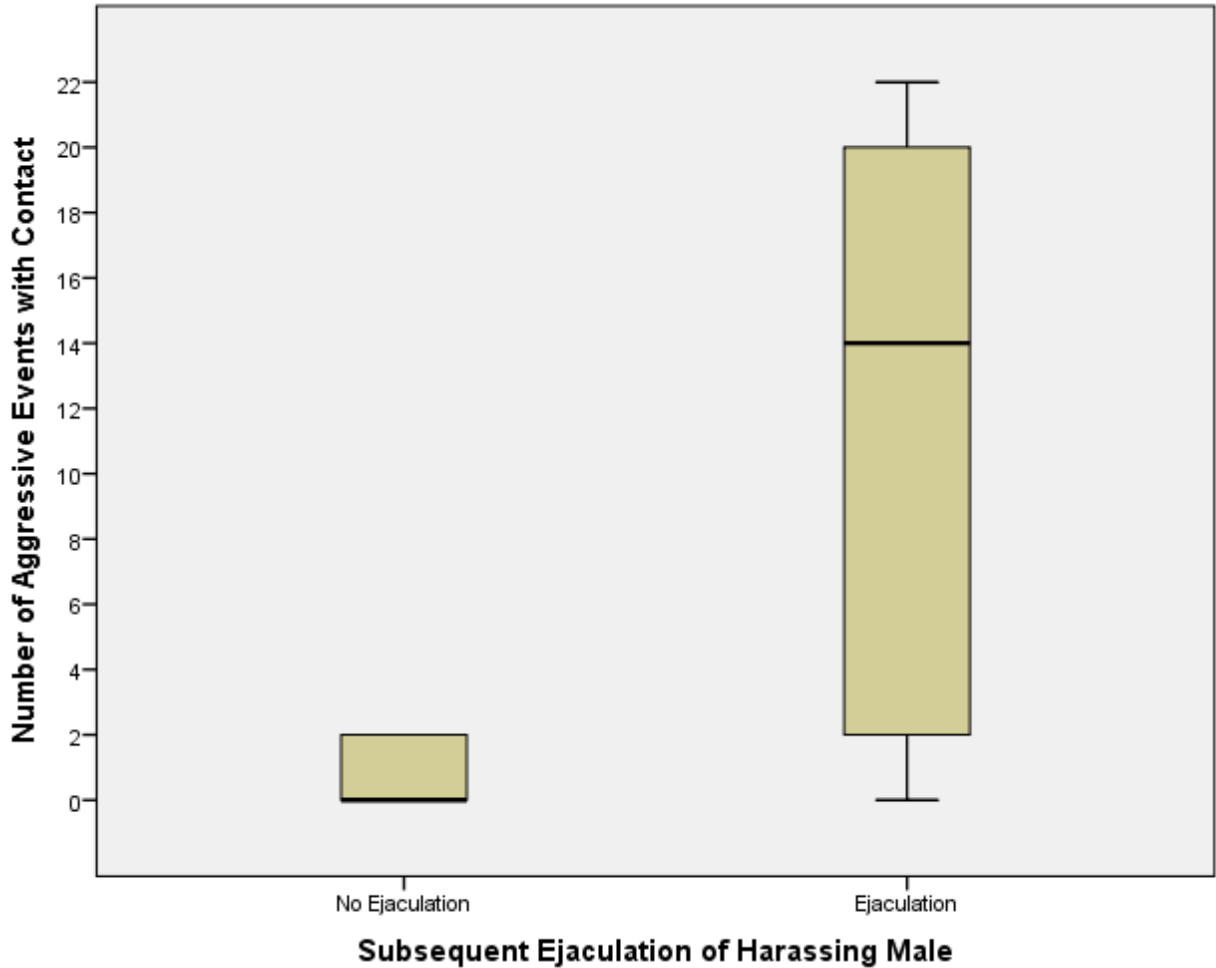


Figure 4.2: Relationship between number of contact aggressive events with the mating male and incidence of later ejaculation with the estrous female for harassing males at Berenty Reserve during the three observed mating seasons. Bold lines represent the median, box represents the interquartile range, whiskers show minimum and maximum values.

There was no significant relationship between intensity of harassment and mating success of the mating male (Mann-Whitney $U = 16.5$, $n_1 = 7$, $n_2 = 5$, $P = 0.861$). When mating males were harassed by competitor males at a higher rate and with more intensity, they were not less likely to ejaculate. Rate of aggression ranged from 0 to 1.37 incidents per minute and rate of aggression weighted for intensity ranged from 0 to 3.95 incidents per minute.

4.4.5 Does interruption of copulations affect the quality of copulations as measured by the duration of mating and the number of affiliative behaviours observed during mating between the estrous female and her mate?

Males engaged in more affiliative behaviours towards their female mating partners when they were not interrupted during mating (Mann-Whitney $U = 5.5$, $n_1 = 4$, $n_2 = 15$, $P = 0.010$) (Figure 4.3).

To test whether this relationship of uninterrupted males engaging in more affiliative behaviour was a reflection of the fact that alpha males tended to engage in more affiliative behaviour towards their mating partners, a partial correlation was conducted between the variables of affiliative behaviour from male to female and whether mounts were interrupted or not. This showed that the relationship did not remain when male rank was controlled for ($r_s = -0.138$, $N = 19$, $P = 0.585$).

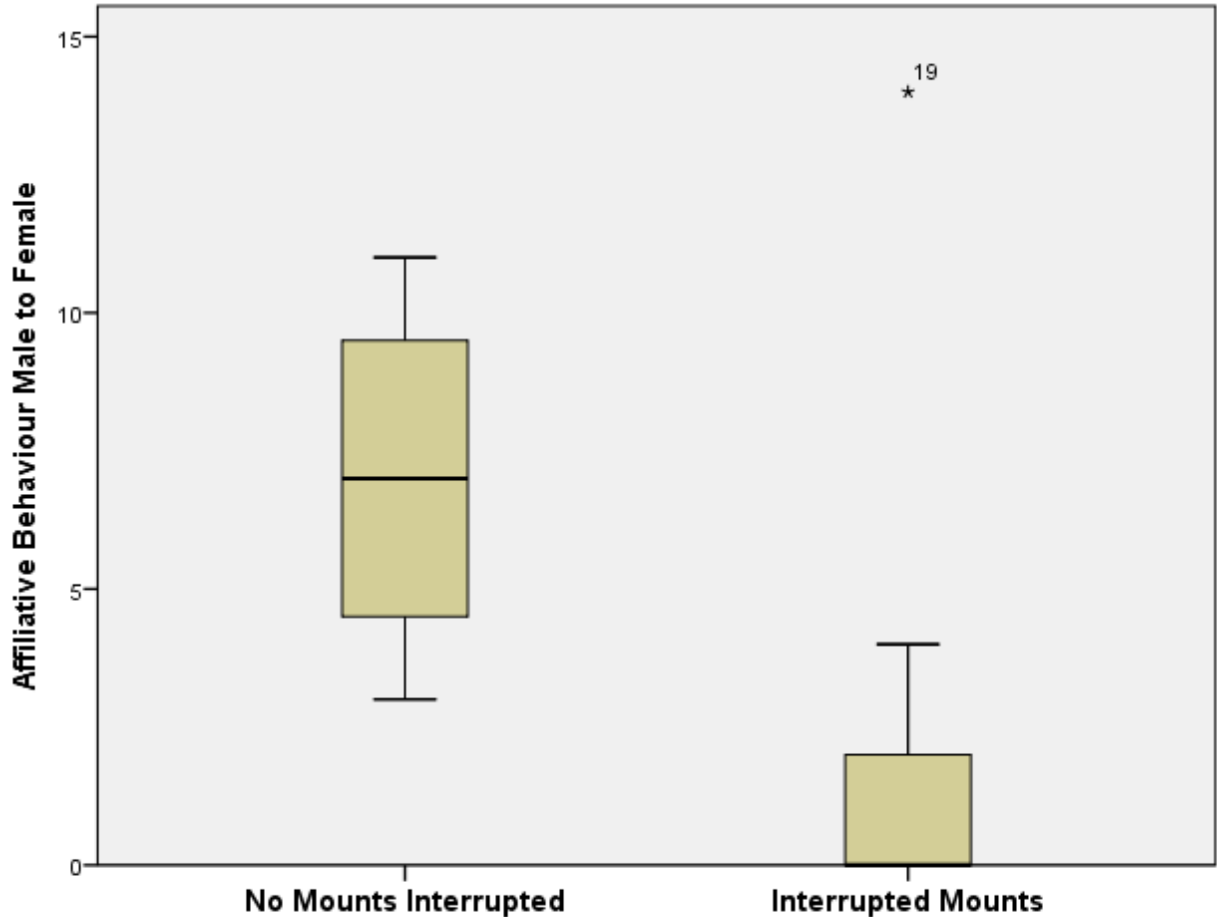


Figure 4.3: Relationship between whether copulatory mounts were interrupted or not interrupted during mating and number of affiliative behaviours from mating male to mating female during the three mating seasons at Berenty Reserve. Bold lines represent the median, box represents the interquartile range, whiskers show minimum and maximum values.

4.4.6 Do extra group males experience more interrupted copulations than group males?

There was no significant relationship between male status as non-alpha group male and extra group male and % of copulatory mounts interrupted (Mann-Whitney $U = 21$, $n_1 = 6$, $n_2 = 7$, $P = 1.0$). Extra-group males did not experience significantly more interruptions than low ranking group males.

There was no significant relationship between male status as a group male and an extra group male and % of copulatory mounts interrupted (Mann-Whitney $U = 28$, $n_1 = 12$, $n_2 = 7$, $P = 0.222$). Extra-group males did not experience significantly more interruptions than group males.

There was a significant relationship between male dominance status (alpha or non-alpha) and % of copulatory mounts interrupted (Mann-Whitney $U = 10$, $n_1 = 13$, $n_2 = 6$, $P = 0.009$). Alpha males experienced significantly fewer interruptions of their copulations than all other males (Figure 4.4).

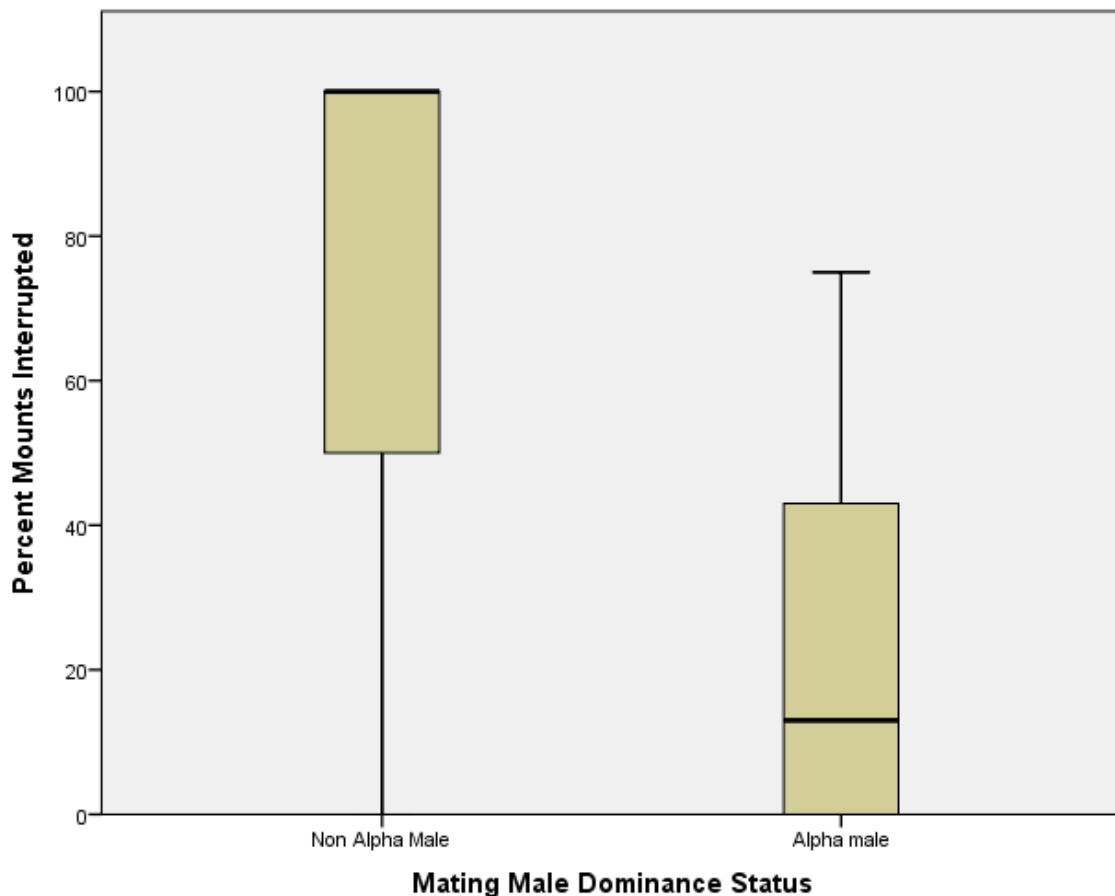


Figure 4.4: Relationship between mating male dominance status and percent of copulatory mounts interrupted during mating during the three mating seasons at Berenty Reserve. Bold lines represent the median, box represents the interquartile range, whiskers show minimum and maximum values.

4.4.7 Does incidence of ejaculation or losing access to the estrous female have an impact on whether males harass other mating males?

There were only two instances from the three years where an interrupting male gained access to a female, ejaculated and then other males mated with the female afterwards. There were four instances from the three years where an interrupting male gained access to the estrous female, mated but did not ejaculate, and then went on to challenge other mating males. Because of the small sample size, the data were pooled from the two types of instances: incidence of ejaculation and losing access to the estrous female. Incidence of ejaculation or losing access to the estrous female reduced the rate of harassment, with the average rate before ejaculating or losing access being 31 incidents of aggression per hour and the average rate after ejaculating being 13 incidents of aggression per hour. Thus, the difference between the two means was not statistically significant (Mann Whitney $U= 13.5$, $P=0.155$).

4.5 Discussion

In this study, I present results of a first examination of harassment and interruption of copulations by adult males during three consecutive mating seasons in *L. catta*. Seven predictions of the hypothesis that harassment and interruption of copulations increases mating success of the harasser and decreases mating success of the harassed were tested and support was found for three of the predictions. Males reduce the mating success of those they interrupt. Interruption of copulations is an effective behavioural tactic used by male *L. catta* to reduce the mating success of competitors. Harassment, on the other hand, is an effective behavioural tactic used by some male *L. catta* to increase their own mating success. When a harassing male engages in contact aggression with the mating male, the harassing male is likely to go on to mate to ejaculation with the estrous female. Quality of mating, as measured by number of affiliative

behaviours directed by the mating male towards the mating female, increases when there are no interruptions to the copulation. Alpha males have their copulations interrupted less often than all other males.

I predicted that those individuals with the highest rates of interrupting copulations would have the highest rates of mating success (ejaculations with estrous females). This is because males may interrupt other males in order to improve their own mating success. My results showed that this was not the case; males who interrupted copulations at the highest rates did not have the greatest number of ejaculations with estrous females. This result may have been because mating success depends more on male dominance status than on aggression during mating (Chapter 2).

Interruption of copulations reduced the mating success of those males who were interrupted. When males had 100% of their copulatory mounts interrupted by competitor males, they were unlikely to ejaculate. Although this seems intuitive, it was unknown whether males would ejaculate quickly when faced with harassment and/or interruption by other males. This shows that interrupting individuals are successful at reducing the reproductive potential of mating males. Bruce and Estep (1992) found that for captive stumptail macaques, alpha male copulations were interrupted 0% of the time, beta males were interrupted 33% of the time and lower ranking males were interrupted 39% of time. In comparison, I found that alpha male copulations were interrupted 24% of the time, beta males were interrupted 100% of the time and lower ranking and extra group males were interrupted 76% of the time.

Males who interrupted copulations did not gain access to the estrous female soon after their interruptions, with one case out of nine being the exception. For this reason, it seems that interruption of copulations functions more to decrease the mating success of a competitor (the

mating male) rather than to increase one's own mating success. Harassment, however, was seen to increase the mating success of the harassing male when the aggression was intense, involving contact.

In terms of harassment of mating pairs, I predicted that males who showed a greater intensity of harassment towards mating pairs would have greater mating success. Intensity of harassment was measured by contact versus no contact aggression and those males who engaged in the greatest amount of contact aggression had the greatest mating success. When intensity of aggression was considered as an overall value, without calculating it as a ratio of total aggressive incidents, it was significantly correlated with mating success. The incidence of a major fight with contact dramatically increases the chance that the harassing male will later ejaculate. There were three major fights witnessed with 14, 20 and 22 instances of contact aggression, respectively. Contact aggression often meant a jump fight between males in which the males leap in the air and scratch and grapple with each other (Jolly, 1966), sometimes high in the canopy. These incidents can result in serious injury for either male. In each of these cases, the harassing male later went on to ejaculate with the estrous female. It may also be the case that males who engage in a greater number of contact aggressive behaviours have overall greater fecal testosterone levels. Gould and Zeigler (2007) found that there was a strong relationship between levels of fecal testosterone and rates of male-male competition overall during the mating season although there was no correlation between individual rates of aggression and fecal testosterone levels.

Contact aggression during harassment of a competitor's mating bout, including jump fights, can be considered an effective reproductive strategy for male *L. catta*. I predicted that those individual males who were harassed at the greatest intensity will experience the lowest mating

success; however, this was not found to be true. Some males may be better than others at fighting off harassers and maintaining proximity with the estrous female until ejaculation. Unlike what is observed in stumptail macaques (Niemeyer and Chamove, 1983), *L. catta* males will harass other males at every stage of the mating bout. In stumptail macaques (Niemeyer and Chamove, 1983), sexual interference rarely occurs prior to ejaculation. In *L. catta*, harassment and interruption seems to be an attempt to decrease the likelihood that the mating male ejaculates. Stumptail macaques are thought to perform harassment and interruption of copulation out of 'spite' (Brereton, 1994; Drukker *et al.*, 1991). This interpretation does not fit for *L. catta* because in the case of males who engage in high levels of contact aggression, aggressors are increasing their own mating success (thus directly benefitting) while decreasing that of their competitor.

When males were uninterrupted during mating, their average number of mounts before ejaculation was greater and they engaged in more affiliative behaviour with the estrous female during mating. This shows that when males have the opportunity to mate for an unlimited amount of time they will mate longer than when their mating duration is limited by other competitor males. It is known that *L. catta* are a species in which multiple mounts are required before ejaculation (Parga, 2006b; Sauther, 1991). What is interesting, is that males in my study mated for longer and engaged in more affiliative behaviour when given the opportunity. Interruptions of copulations limit affiliative behaviour of mating males towards mating females. Because male ring-tailed lemurs can determine female reproductive state from genital secretions and regularly lick female genital marks (Scordato and Drea, 2007), it is thought that males lick females' genitals in this species to test their estrous status rather than to function in a way that grooming does - to form social bonds. My data on genital licking during mating is not consistent with this hypothesis, as some males repeatedly licked their partner's genitals during mating. In

one case, the mating male licked the mating female's genitals for 27 seconds, much longer than the average duration of several seconds. If genital licking were to function for solely conveying information relating to female estrous status, it would be unnecessary for this behaviour to be prolonged. Findings by Koyama (1988) support this idea that male licking of female genitals does more than convey estrous status, as he observed a mating male licking an estrous female's genitals for 2 minutes. Genital licking from male to female has also been seen in other primates, including bonobos and orangutans (Palagi *et al.*, 2004, Schurmann, 1982).

Male-to-female affiliative behaviour during mating may be an attempt by the mating male to keep the estrous female in close proximity to him or to coax her to cooperate with his mating attempts. Sauther (1991) describes similar behaviour in relation to pre-copulatory mate-guarding. Males will sit near and rest in contact with females who have not yet gone into estrous (Sauther, 1991). This is especially true of the alpha male, who monitors females closely before they go into estrous (Sauther, 1991). In my study, in one of the instances with a high number of affiliative behaviours from male to female, the female was seen struggling to disengage with the male's copulatory mounts. Each time she attempted to struggle from his grasp he would groom her on her back, while still intromitted. This male engaged in 11 affiliative behaviours during his mating bout with this female, including: face greet, grooming during copulation, and lick genitals. This affiliative behaviour from male to female may be a strategy used by males to prolong sequestering of females, thus improving their chances of ejaculating as well as lengthening the duration that their copulatory plug remains in the female's reproductive tract post-ejaculation.

Extra group males at this site are known to have higher rates of ejaculation with estrous females than low ranking group males (Chapter 3), and therefore, I expected to find lower rates of copulation interruption for these males than low ranking group males. Extra group males were found to be interrupted during copulation at the same rate as other low ranking group males. It remains unclear why extra group males ejaculate more than low ranking group males. Other studies have shown that estrous females show preference, or mate choice, for extra group males (Sauther, 1991). Another typical behaviour of estrous females is that they often change their location during mating when their mate leaves to fight off harassers (Jolly, 1966; Sauther, 1991; personal observation). This movement can increase male-male aggression when the female runs towards competitor males and the mating male loses access to her. Although I did not record instances of estrous females showing mate preference for extra group males, perhaps they move less during copulation with these males than they do during mating with group males. Future research should investigate how far estrous females travel during mating with each male. For example, Jolly (1966) reported that females were often seen to move one branch during mating interruptions, which may not be far enough to cause the mating male difficulty in returning to her. I observed estrous females moving much farther distances, across their entire group's range during mating for example, but did not systematically record these data.

Incidence of ejaculation was found to not have an impact on whether males harass other males and losing access to the estrous female did not impact whether males harass other males. Males were observed to harass others at a lesser rate after losing access to the female than before, regardless of whether they ejaculated or not. This may be because both ejaculating and non-ejaculating males have an incentive to protect their investment in the estrous female: for males who have ejaculated, they will want to reduce the likelihood of sperm competition (Birkhead and

Moller, 1992) if other males are able to ejaculate; for those who have not ejaculated, they will want to regain their opportunity to do so. The fact that harassment is less frequent after losing access to the female may show that males become fatigued over time. Dominant males have been observed to harass lower ranking males after the lower ranking males gain access to the estrous female at St Catherines Island (Parga, 2009). I also observed dominant males continuing to harass lower ranking males after they had ejaculated and lost access to the estrous female.

This chapter examined both harassment and interruption of copulations. Harassment may or may not lead to interruption. I also examined the two mating strategies of increasing one's own mating success or limiting the mating success of others. I found that interruption of copulations reduced the mating success of the males who were interrupted. I found that *harassment* of copulation increased the mating success of the males who engaged in the harassment, when that harassment involved contact aggression. Interruption of copulation functions more to decrease the mating success of a competitor than to increase one's own mating success. Harassment on the other hand, does function to increase one's own mating success (Table 4.5). The difference between these two behaviours can be further illustrated by the occurrence of intense physical fights. These fights were observed occurring during a male's mating bout, but did not always occur as an interruption of a copulatory mount. If a fight involves multiple instances of contact aggression, this intensity is better understood as harassment rather than interruption. It is this type of harassment, intense physical fights, that were found to increase the challenging male's mating success. These fights corresponded with the transfer of access to the estrous female from one male to another.

Table 4.5: The way in which harassment of copulations and interruption of copulations differ in their function to increase one’s own mating success (M.S.) or decrease the M.S. of a competitor.

	Harassment	Interruption
Increase one’s own M.S.	YES	NO
Decrease other’s M.S.	NO	YES

In conclusion, I found some support for the hypothesis that harassment and interruption of mating both increases the harasser’s mating success and decreases the mating success of the harassed individual. I provide the first evidence in this species that sexual harassment and interruption are reproductive strategies which may function to increase one’s own reproductive success and decrease the reproductive success of a competitor. I present the first examination of affiliative behaviour from mating male to estrous female during copulation and found that there was a significant difference in rate of this behaviour between interrupted pairs and non-interrupted pairs. When males are left alone by competitor males during mating, they mate for longer and engage in more affiliative behaviour with the estrous female, potentially impacting reproductive outcomes. My findings represent the first evidence in primates that contact aggression directed towards the mating male directly increases the harassing male’s reproductive potential.

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5 Chapter 5 Discussion

My thesis examines mating behaviour of *L. catta* in terms of how certain factors affect mating success of males. Unlike what has been reported in Dixson (2012), *L. catta* does not exhibit a single brief intromission copulatory pattern or multiple ejaculations. As has been shown in the previous chapters (and previously described in Sauther 1991 and Sauther *et al.* 1999), mating males typically have multiple intromissions and always single ejaculations. My thesis has addressed the question posed by Dixson (2012) as to how frequently males ejaculate with fertile females under natural conditions. Although data relevant to this question has been published by other researchers (Gould, 1994; Parga, 2003; 2010a; 2010b; Sauther and Sussman, 1993; Sussman, 1992; Taylor 1986), my work helps to add new nuances to our understanding of *L. catta* mating behaviour.

5.1 Chapter 2:

In chapter two I report that male rank is positively correlated with the number of ejaculations and male mate order. I found no relationship between male dominance rank (as calculated during the mating season) and number of copulatory partners. My findings do not support one of the predictions of the priority-of-access model - that high ranking males will achieve higher mating success, as measured by number of copulatory partners. I also tested mating success in two other ways: by mate order and number of ejaculations. When mating success was measured in these ways, alpha males were shown to have an advantage over lower ranking males. These findings are significant because alpha males are predicted to have the greatest mating success by sexual selection theory. The fact that there are additional factors affecting male mating success other than male rank raises the question of what extrinsic factors affect male mating success.

5.2 Chapter 3:

In chapter three I report significant relationships between the OSR during mating (calculated based on whether males were present and engaged in competition for the estrous female) and the duration of mounts with thrusting. When fewer males are present during mating, males thrust for a longer period of time. In addition, the longer time a male spent thrusting during a mount, the more likely he was to ejaculate. Alpha males copulated (mounts with thrusting) for longer durations than lower ranking group males. When alpha males were excluded from the calculations, extra group males were more likely to ejaculate than group males. Extra group males have also been found to sire a large proportion of offspring in this species (Parga *et al.*, 2016). Variation in the OSR during a female's estrous period may impact male reproductive success because the OSR has an impact on whether males ejaculate or not, although without paternity data it is not possible to know. My findings highlight the advantages of both being an alpha male and of being an extra-group male, since in both cases these males had a greater likelihood of ejaculating with estrous females than lower ranking group males. My findings also pose the question as to how do the males present during mating bouts interact with the mating pair to interfere with the mating bout.

5.3 Chapter 4:

In chapter four I report that interrupting males reduce the mating success (ejaculations) of those they interrupt. The intensity of harassment directed towards mating males impacted mating success for the aggressor, as these harassing males were more likely to go on to mate and ejaculate with the estrous female. This is the first evidence for primates that aggression directed towards the mating male directly increases the harassing male's mating potential. Occurrence of interruptions decreased the quality of copulations by causing copulatory mounts to be fewer and

rates of affiliative behaviour between the mating male and female to be lower. These findings are significant because it was previously unknown what the functional significance of harassment of mating in primates was.

5.4 Discussion of my findings and directions for future study

The most important next step for my research is to report on findings once the reproductive success of males from this study is known. The DNA of all study group males and the offspring born to the study groups has been collected in the form of hair samples, now analysis of these samples must begin. This will allow me to determine whether A) first mating males have a reproductive advantage over later mating males B) predictions of the priority-of-access model are upheld in terms of reproductive success C) female choice impacts reproductive outcomes D) females make post-copulatory “choices” for the most genetically compatible sperm E) extra-group males sire more offspring than group males F) males who are close kin are less likely to sire offspring, and G) affiliative behaviour plays a role in reproduction. Currently the relationship between male ejaculate order and fertilization success in this species is unknown (Parga, 2003). It is expected that reproductive skew will be high if there is a reproductive advantage for first ejaculating males (Pereira and Weiss, 1991) and the same male tends to ejaculate first with every female in the group; however, one recent study evaluating the level of male reproductive skew among wild *L. catta* has shown high skew in only some groups (Parga *et al.*, 2016). Reproductive skew relates to the distribution of reproductive success among same-sex individuals in a population (Clutton-Brock, 1998). Providing results on whether a reproductive advantage exists for first ejaculating males would be a major contribution in understanding *Lemur catta* mating behaviour.

5.4.1 Do first mating males have a reproductive advantage?

I found that alpha males ejaculated more frequently and first. What does this mean for reproductive success? Although other studies of primates have shown that mating success is not predictive of reproductive success (Curie-Cohen *et al.*, 1983; Stern and Smith, 1984, but see Altmann *et al.*, 1996 and Dubuc *et al.*, 2011), those studies were not measuring ejaculations with estrous females. Because females may receive ejaculate from several males, it is important to determine whether first ejaculating males have a reproductive advantage over later ejaculating males. If the first mating male has an advantage, then the alpha males in my study will have sired more offspring. A fertilization advantage for first mating males has been shown in wild house mice (Levine, 1967), and although it has been argued that it may also exist in ring-tailed lemurs (Pereira and Weiss, 1991), whether or not this is actually true is unknown for this species.

5.4.2 Are predictions of the priority-of-access model upheld in terms of reproductive success?

There are several hypotheses present in the literature with predictions about which male will sire the offspring when a female receives ejaculate from several males. One idea is that the ejaculate from the first ejaculating male would reach the ovum first and thus this male would be the one to sire the offspring. If this is the case, it would make little sense for males to compete aggressively for access to the female after a previous male has ejaculated, as is the case in *Lemur catta*. Another idea is that a female needs a certain level of stimulation to facilitate sperm transfer (Chester and Zucker, 1970; Wilson *et al.*, 1965). It could be possible that greater stimulation in total leads to the greater sperm transfer of later ejaculating males. However, for *L. catta* it seems counterintuitive for later ejaculating males to be favoured. Since all male ring-tailed lemurs of an

estrous female's group fight to mate as early as possible, it seems doubtful that these early mating males would turn out to have the lowest opportunity for causing conception.

5.4.3 Does female choice impact reproductive outcomes?

It was observed that the behaviour of the estrous female caused the intensity of the competition for access to her to increase. For example, estrous females were seen to uncharacteristically run to the edge of their territories and into neighbouring groups' territories where males from other groups were present, and those males then joined in the mating competition. This behaviour caused an increase in the intensity of competition by adding competitors as well as increasing aggression to include more contact. This was true for the female who received the highest number of ejaculations during her estrous period (Finch - FI). This increase in competition may have not been the intention of the estrous female, who may have just been attracted to mate with extra group males. Another female was seen to run away from the alpha male who was guarding her, toward a lower ranking group male, who then began mating with her. Soon this female climbed to the tallest canopy in the area and male aggressive attempts to gain access to her were staged at a great height, where the risk of injury was greatly heightened as well. Female langurs also may incite male-male competition by behaving promiscuously (Sommer, 1988). Other female animals are known to behaviourally incite male competition as well. Female elephant seals will protest or not protest the mount of a male to varying degrees (Cox and Le Boeuf, 1977). It is argued that these females incite males to compete for them by their behaviour of rejecting mounts (Cox and Le Boeuf, 1977). Female red jungle fowl (*Gallus gallus*) and Lapland longspurs (*Calcarius lapponicus*), advertise fertility with a vocalization which incites male-male competition (Montgomerie and Thornhill, 1989). The female emei music frog (*Babina daunchina*) also emits a novel call when she is ready to mate that increases male-male

competition (Cui et al 2010). Future research that I will conduct at Berenty Reserve will look at both the distance an estrous female travels between copulatory mounts, the height she travels in the canopy, and to what extent she approaches other males to determine to what degree she incites male-male competition during her estrous period. Future research should not only investigate how far estrous females travel during mating with each male, but also how much aggression or receptive behaviour each female shows to each mating male because this behaviour would indicate female preference and may be related to reproductive success.

5.4.4 Do females make post copulatory “choices” for most genetically compatible sperm?

It is also possible that because females are able to determine male quality and compatibility from male scent they are also able to make post-copulatory “choices” about whether to accept or reject their sperm after ejaculation. Few studies have been conducted in primates to assess the effects of mating order on reproductive success (Dixon, 2012; Eberle and Kappeler, 2004). Researchers studying mouse lemurs found that males who mated early were more successful at reproducing (Eberle and Kappeler, 2004). Studies in mammals have shown an advantage for first mating males (Guinea pigs, *Cavia porcellus*, Martan and Shepherd, 1976), second mating males (prairie voles, *Microtus ochrogaster*, Dewsbury and Baumgardner, 1981), or a lottery effect (Golden hamsters, *Mesocricetus auratus*, Ginsberg and Huck, 1989) (Dixon, 2012). With each of these outcomes there are attendant theoretical implications. Determining whether first ejaculating males have a reproductive advantage in *L. catta* is a major focus of my future research. If my future results were to show a seemingly random outcome of males who sired offspring when there were multiple ejaculations, it would be important to take the next step and determine whether the males who became fathers of offspring were the most genetically compatible with

the mother. I have collected the relevant genetic material in order to test paternity. In three cases, females that I observed received ejaculate from multiple males, making it possible to test these predictions, even though this is a small sample size.

5.4.5 Do extra-group males sire more offspring than group males?

I observed that there were fewer males present to contest the mating of extra group males. But why was this the case? One possibility is that the group males were physically exhausted by this point. Alternatively, if mating order plays a role in reproductive success maybe they “know” this and are not concerned with a late mating male because he has a very low chance of siring offspring, even though these extra-group males had high likelihoods of ejaculating. Another possibility is that female choice for outsider males plays a role in their ability to ejaculate. I observed females approaching and showing interest in extra-group males, but then the group males would quickly displace the extra-group male from the female. It is possible that females show preference for these males which may or may not have implications for mating or reproductive success for males. Parga *et al.* 2016 showed that extra group *Lemur catta* males sired a substantial proportion of offspring. One way I observed females’ behaviour potentially impacting reproductive outcomes was that females incite less competition during mating with these extra-group males. This could have been the defining factor for why there was less male-male competition during the mating of these males and a greater ability of these males to ejaculate (over lower ranking group males). Future research will attempt to determine what factors played a role in allowing extra group males to ejaculate at higher rates than non-alpha group members and determine what the reproductive success of these males was.

My findings suggest that mating with females from outside of the male's group is a beneficial strategy, as has been demonstrated previously by Parga *et al.* 2016. This result is expected from the observed behaviour of males often leaving their groups during the mating season (Gould, 1994; Koyama, 1988; Parga, 2010; Sauther, 1991; Sussman, 1992). Extra-group mating has been observed in other species of primates as well (*Verreaux's sifaka*: Lawler, 2007, *Erythrocebus patas*: Ohsawa *et al.*, 1993, *Rhinopithecus roxellana*: Zhao *et al.*, 2004). For male sifakas, pursuing mating opportunities outside of one's group is a major component of fitness (Lawler, 2007). Some patas monkey males will join the group of a resident male strictly during the breeding season and then leave, opportunistically mating with group females (Ohsawa *et al.*, 1993). These extra-group males have high mating success as "paternity discrimination by DNA typing revealed that 50% of infants (2/4) were sired by outsider males in a one-male situation" (Ohsawa *et al.*, 1993 pp. 542). Clearly, for some primate males it is advantageous to leave their group during the mating season to seek out alternative mating opportunities. When the paternity of all infants born to the study groups is known, it will be possible to determine the percentage sired by extra-group males.

5.4.6 Are males who are close kin less likely to sire offspring?

The alpha males in my study were observed to mate first and were most likely not natal males. Natal males are predicted to not mate because they are related to the females in their group by being the brother or potentially the father of the estrous female (Sussman, 1992); indeed, active inbreeding avoidance and rejection of natal male mating attempts has been practiced by female *L. catta* at other research sites (Sauther, 1991; Taylor and Sussman, 1985). By examining the genetic relationship between mating pairs I will provide important information on the incidences of inbreeding at Berenty Reserve.

5.4.7 Does affiliative behaviour play a role in reproduction?

The fact that uninterrupted mating events were accompanied by greater affiliative behaviour leads to the question, does affiliative behaviour play a role in reproduction? For example, does affiliative behaviour lead to orgasm and does orgasm increase chance of reproducing? Female orgasm is observed in several primates (Dixson, 2012; Kappeler and van Schaik, 2004) and may or may not exist in lemurs. It has been argued that orgasm requires stimulation from multiple sexual encounters, and evidence has been found in Japanese macaques (*Macaca fuscata*) that frequency of orgasm positively correlated with duration of copulation (Troisi and Carosi, 1998). It is logical that oral stimulation of the genitals by males to females may contribute the extra stimulation required for female orgasm. Therefore, affiliative behaviour from male to female during mating may contribute to female orgasm in this species if it exists. On the other hand, this affiliative behaviour may be an attempt by the mating male to keep the estrous female in close proximity to him or to coax her to cooperate with his mating attempts as *L. catta* are known to sequester females (Jolly, 1966; Sauther, 1991; Sauther *et al.*, 1999) Future research will examine how closely a female's resistance to mating accompanies affiliative behaviour from the male to the female. *L. catta* mating tends to involve many non-ejaculatory mounts with thrusting before ejaculation can occur, independent of whether the copulations are interrupted. This may be because females need a certain amount of stimulation before orgasm, if it occurs in this species.

5.4.8 Broader implication for male mating strategies in primates

Males use a number of tactics to outcompete one another for access to estrous females. Exploiting high dominance status to achieve agonistic wins over competing males is just one of these means by which male primates gain access to receptive females (Kappeler and van Schaik, 2004). This is what the priority of access model predicts, that dominance ranking in a group

operates as a queue to accessing receptive females (Altmann, 1962; Kappeler and van Schaik, 2004). Males of different dominance rank not only mate in different orders but also sequester females for different amounts of time. This is seen in *Lemur catta* through mate guarding both before and after ejaculation (Sauther, 1991). I report that male rank is positively correlated with the number of ejaculations and male mate order, reiterating the important role that achieving high dominance status has on mating success.

I also report significant relationships between the OSR during mating and the duration of mounts with thrusting. When fewer males are present during a male's mating bout he thrusts for longer and is therefore more likely to ejaculate. This goes along with the hypothesis that harassing individuals reduce the mating success of those mating (Gouzoules, 1974). Harassment in ring-tailed lemurs can be as simple as sitting nearby and staring at the copulating pair, and does not have to include contact. Harassment and interruption of copulations occurs in over 30 primate species (Dixson, 2012).

Harassment and interruption of mating may be strategies used by males to increase their own reproductive success. I found that interrupting males reduce the mating success (ejaculations) of those they interrupt. Furthermore, the intensity of harassment directed towards mating males impacted mating success for the aggressor, as these harassing males were more likely to go on to mate and ejaculate with the estrous female. This lends support to the hypothesis that interruption reduces the mating success of copulating animals (Neimeyer and Chamove, 1983) and that harassment is a way for the harasser to attempt to gain future access to the estrous female (Hall, 1965; Loy and Loy, 1977). This is an understudied topic (Dixson, 2012) and an important finding in understanding *Lemur catta* behaviour.

5.5 Conclusion

In this thesis, I present results on how certain factors impact male mating success. These findings have shown that although male dominance rank and male-male competition both play a role in impacting mating outcomes, further factors are at play. My findings have added to the current literature on primate mating behaviour by presenting a larger sample size of estrous periods than previously reported. These findings fill a gap in the literature by addressing in detail how intrinsic male qualities and group dynamics affect mating outcomes, and provide much fruitful fodder to stimulate future research on *L. catta* mating behaviour.

5.6 Bibliography

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