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Dominance or Leverage? An Analysis of Female Power in Captive Varecia

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ABSTRACT

DOMINANCE OR LEVERAGE? AN ANALYSIS OF FEMALE POWER IN CAPTIVE *VARECIA*

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Northern Illinois University, 2021

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Lemurs are unusual in that, unlike in most other primates, females have more power than males. This is evident by females receiving priority access to foods and preferred spaces and frequent grooming. Rebecca Lewis provided a framework to analyze the basis of female power that distinguishes between true dominance and leverage. Dominance is defined as the physical ability to overpower an individual, whereas leverage is the ability to influence others based on intangible resources, such as social currency like grooming or the potential for mating. This study aimed to investigate female power in the critically endangered ruffed lemurs (genus *Varecia*). Previous studies have shown that female ruffed lemurs have priority access to food and are groomed more than males, but this research occurred before the power framework was developed, so the mechanisms behind the females' power remain largely unexplored.

I observed captive, mixed-sex groups of *Varecia variegata* and *Varecia rubra* over a two-month period at the Duke Lemur Center in Durham, North Carolina. I used body mass as a proxy to measure a female's physical dominance and used age as a predictor of maturity and leverage, utilizing the center's existing veterinary records. I recorded data via continuous, focal animal sampling for seven hours per day, five days a week for approximately 275 total observation hours. I recorded social behaviors following Pereira's ethogram, including agonism and submission. I classified conflicts as "decided" if only one individual showed unambiguous submissive signaling to the other. I used generalized linear mixed models to evaluate the influence of body mass, age, and reproductive maturity on the outcome of intersexual conflict. I also collected spatial proximity data via a combination of instantaneous and continuous sampling. I analyzed these data using generalized linear mixed models and the Hinde index to determine the responsibility of individuals for maintaining proximity to their group members.

The results of this study indicate that captive *Varecia* exhibit female dominance to a lesser degree than other scientists described previously. While females were significantly more likely to win intersexual conflicts than males, the ratio of decided female victories to male victories was smaller than reported in previous studies. Additionally, these data provide evidence that weight-based dominance is the source of female power rather than leverage. Male *Varecia* were not significantly more likely to approach females than females were to males, and the average distance between males and females was not significantly smaller than that of male pairs. I found no significant difference in conflict outcomes or spatial proximity between *V. variegata* and *V. rubra*. These results show that female power in the genus *Varecia* is not as prominent as other species and that further research is needed to better understand the mechanisms behind it.

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DOMINANCE OR LEVERAGE? AN ANALYSIS OF
FEMALE POWER IN CAPTIVE *VARECIA*

BY

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DEDICATION

For Bill and Betsy Birckelbaw, who taught me that
you can count the seeds in an apple, but you cannot count the apples in a seed.

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CHAPTER 1

INTRODUCTION

Across the primate order, male dominance over females is common, particularly in feeding contexts. This pattern is thought to be a consequence of sexual dimorphism, in that larger males can easily displace smaller females by force (Young et al., 1990; Hemelrijk et al., 2008). However, many primates exhibit patterns of dominance that do not conform to this traditional male dominance model, and with renewed methodologies and conceptual frameworks, researchers can evaluate complex social dynamics in a new light (Young et al., 1990; Kappeler, 1997; Lewis, 2018).

The concept of dominance evokes a variety of definitions and explanations. Originally, the term “dominance” was effectively synonymous with aggression (Mitchell and Maple, 1985). Primates were observed utilizing aggression to maintain control of important resources, namely sexual partners and food (Mitchell and Maple, 1985). Dominance was also considered to be a static aspect of an individual, but more contemporary research has shown that dominance is dynamic and that it varies with age, context, and social structure (Mitchell and Maple, 1985; Young et al., 1990; Watts 2010). Building upon that early definition, researchers began viewing dominance as “the ability to manipulate others’ behavior and the ability to form and recognize

alliances” (Mitchell and Maple, 1985; p. 51). This led to the understanding that dominance hinges on the abilities of the individual and is contextually dependent (Mitchell and Maple, 1985).

Many benefits have been proposed to explain why dominance occurs, but the most important incentives are access to sexual partners and food (Mitchell and Maple, 1985; Majolo et al., 2012). Both access to sexual partners and food ultimately contribute to reproductive success (Majolo et al., 2012). Individuals may maintain control of these critical resources in two primary ways. One of the most common methods, especially in male dominance, is the use of aggression. Through aggressive displays and combat, primates can protect mates and food as well as displace their competitors (Muehlenbein and Watts, 2010). Additionally, primates may form alliances within their group to improve their rank in the dominance hierarchy (Mitchell and Maple, 1985; Surbeck et al., 2011). Alliances are common among females in some species, but males also use this tactic to improve their dominance and reproductive success in a group (Surbeck et al., 2011; Schülke et al., 2010).

In the case of male dominance, researchers often point to chimpanzees (*Pan troglodytes*) as a primary example. Male chimpanzees exhibit a high degree of intrasexual competition and aggression with strict dominance hierarchies (Muller and Wrangham, 2004; Muehlenbein and Watts, 2010). Chimpanzee dominance hierarchies greatly affect reproduction, and high-ranking males maintain priority, if not exclusive, access to receptive females (Muller and Wrangham, 2004). Mountain gorillas (*Gorilla gorilla beringei*) show a pattern similar to the chimpanzees, but with more flexibility in their group structure (Bradley et al., 2005). Most commonly, mountain gorillas live in single-male, multiple-female groups where the male maintains

exclusive access to the females in his group and relies on contest competition with other males to keep his rank (Bradley et al., 2005). However, not all primates maintain male dominance through aggression alone. Schülke et al. (2010) found that male Assamese macaques (*Macaca assamensis*), regardless of rank, benefited from the formation of alliances. Despite living in societies with strict dominance hierarchies, this study showed that both dominant and subordinate males experienced increased reproductive success when they formed social bonds, thereby maintaining dominance through coalitions (Schülke et al., 2010).

Codominance is another social structure found among primates in which neither sex fully dominates the other (Lewis, 2018). Generally, in codominant species, intersexual conflict is low (Lewis, 2018). The term “codominance” can be used to describe a variety of scenarios. For example, species in which females form coalitions to dominate males, such as bonobos (*Pan paniscus*), could be categorized as codominant (Lewis, 2018; Toda et al., 2021). These coalitions are an important aspect of bonobos’ sociality, and the rank of related females greatly influences the rank of males (Toda et al., 2021). Codominance in bonobo groups also facilitates increased tolerance of unrelated females, both within the group and outside of it (Toda et al., 2021). Additionally, species that are pair living, such as gibbons, are considered to be codominant (Reichard and Barelli, 2008). Codominance can also include species that have overlapping male and female hierarchies, such as the common brown lemur (*Eulemur fulvus*; del Barco-Trillo et al., 2012; Lewis, 2018).

Researchers have documented male dominance, codominance, and female dominance in primates, but the only superfamily in which females consistently dominate males is the Malagasy lemurs (Young et al., 1990; Kappeler 1997). Scientists have offered three explanations for this

phenomenon. First, males allow females to be dominant to conserve energy for intense intrasexual competition during the breeding season (Young et al., 1990). Second, male subordination serves as a form of paternal investment where females have greater access to resources that would trickle down to their offspring (Young et al., 1990). Lastly, female dominance is a behavioral strategy that alleviates unusually high reproductive costs (Young et al., 1990).

Lemurs vary in how and why females dominate males, and each of these explanations may have a role in this behavioral phenomenon (Kappeler 1990, 1997). Among the most prominently female dominant lemurs are the ring-tailed lemurs (*Lemur catta*; Kappeler 1990; Pereira et al., 1990; Von Engelhard and Kappeler, 2000). Sifakas are broadly considered to be female dominant as well, but within this group, there is notable variation in the degree of dominance that females possess (Kappeler and Schäßler, 2008; Rasolonjatovo and Irwin, 2020). Additionally, some lemur species do not exhibit female dominance (Pereira et al., 1990). As previously described, common brown lemurs appear to lack dominance from either sex (del Barco-Trillo et al., 2012). Other lemurs, such as the blue-eyed black lemurs (*Eulemur flavifrons*) and grey bamboo lemurs (*Hapalemur griseus griseus*), exhibit female dominance, but the mechanisms by which that dominance is maintained differ between species (Digby and Stevens, 2007). Due to this variation, a more sophisticated model should be used to investigate the root causes of female dominance in lemurs.

In 2002, Rebecca Lewis published the first of many articles on the “power framework,” in which she suggested a more inclusive model for analyzing social relationships (Lewis, 2002). As she stated, “Power...more accurately describes asymmetries in relationships between

individuals than the narrowly defined traditional concept of dominance” (Lewis, 2002; p. 150). These power asymmetries can be based on dominance, the ability to physically overpower another individual, or leverage, which is an individual’s potential to hold resources that cannot be obtained by force, such as reproductive potential or social currency like grooming (Lewis 2002). This framework is much more specific than the traditional dominance concept because it explores both proximate and ultimate causes of power (Lewis, 2002). This framework is particularly interesting to apply to the lemurs as females often have power over males but rarely show true physical dominance. Lewis’s power framework allows researchers to investigate and clearly define the root causes behind female power, which has great implications for conservation efforts as well as animal welfare in captivity (Lewis, 2002).

Previous research has shown that ruffed lemurs exhibit female power both in the wild and in captivity, but many of these studies were published before Lewis’s female power model existed (Kaufman 1991; Raps and White, 1995; Meyer et al., 1999). Therefore, the source of female power (i.e., dominance or leverage) in the genus *Varecia* is largely unknown. Furthermore, although previous research shows a general trend in intersexual conflict interactions where females receive priority access to food and preferred spaces, the intricacies of ruffed lemur female power remain unclear. *Varecia* diverges from other lemurs in notable ways, including their larger size, high degree of frugivory, litter-bearing reproduction, and importance of alloparental care; thus, power dynamics in this taxon may differ from those observed in other lemurs. Some evidence exists for power differences between the two species, *Varecia variegata* (black and white ruffed lemur) and *Varecia rubra* (red ruffed lemur), but these data have not yet

been verified (Raps and White, 1995). Continued investigation of ruffed lemur female power is crucial to understand why and when it occurs and how the two species differ.

Lemurs are the most threatened mammal group on the planet, and between the five families, they make up over 20% of the world's primate diversity (Schwitzer et al., 2014; Herrera, 2017; Borgerson et al., 2021). Lemurs are ecologically important to Madagascar and their loss would likely cause extinction cascades (Schwitzer et al., 2014; Herrera, 2017). Lemurs are in urgent need of conservation action, but the challenges are great. Madagascar is one of the poorest countries in the world and has few protected areas to keep lemurs safe. Even in those protected areas, illegal logging and mining, unsustainable agricultural practices, and hunting pressures push lemurs toward the brink of extinction (Schwitzer et al., 2014). With these persistent threats, the continuation of lemur research grows in both importance and urgency, and *in situ* and *ex situ* conservation efforts must work together to preserve these unique primates (Schwitzer et al., 2013).

The Genus *Varecia*

Habitat and Distribution

Ruffed lemurs are endemic to Madagascar and their primary habitat is found in the country's eastern rainforests (Vasey, 2005; Hekkala et al., 2007; Baden, 2011). *Varecia rubra* is

found primarily on Madagascar's northeast, in the Masoala Peninsula, and along the Bay of Antongil (Vasey, 2005; Hekkala et al., 2007). *Varecia variegata* also inhabit the area around the Bay of Antongil, but their range is much larger, stretching south to the Mananara River (Hekkala et al., 2007; Baden, 2011). Both species have patchy distributions throughout lowland to mid-altitude primary and secondary rain forests (Vasey, 2005; Baden, 2011). Habitat suitability for ruffed lemurs hinges on the presence of large, mature trees; forests with greater total crown volume have larger ruffed lemur populations than those with lower crown volume (Borgerson, 2016).

Diet in the Wild and in Captivity

Ruffed lemurs are among the most frugivorous of all Malagasy lemur species, but there is considerable seasonality in their dietary repertoire. A recent study in Ranomafana National Park in Madagascar found that black and white ruffed lemur diets consisted of up to 99% fruits during the wet season (Beeby and Baden, 2021). However, during the dry season, fruit consumption decreased to around 25% and the lemurs became more folivorous, with leaves and flowers making up approximately half of their diet (Beeby and Baden, 2021). Ruffed lemurs were also seen consuming flower buds and occasionally nectar during the dry season (Beeby and Baden, 2021).

In captivity, ruffed lemurs are commonly fed a wide range of food items including fruit, leaves, and primate-formulated chow or biscuits, but there is significant variation across institutions. Some differences in zoo animals' diets can be explained by differences in which zoo personnel feed them. For example, diets can be crafted by veterinarians, nutritionists, or sometimes the animal care team itself, who may differ in their approach (Donadeo et al., 2016). A study in the United Kingdom compared the diets of ruffed lemurs between six institutions and found that no two diets were alike (Caravaggi et al., 2018). However, all six diets exceeded the suggested energy requirements for ruffed lemurs due to the high sugar content of commercially available fruits (Caravaggi et al., 2018). Research has shown that Malagasy wild fruits are more nutritionally similar to the vegetables that humans eat, so when lemurs eat a fruit-rich diet in captivity, they ingest far more carbohydrates than they would in the wild (Schwitzer et al., 2008). However, according to their website, the American Zoological Association is developing a ruffed lemur care manual that will include a diet specific to the genus to alleviate the health concerns associated with this high-sugar diet.

Activity Patterns

Ruffed lemurs are broadly considered to be diurnal, but some recent studies have presented evidence that they are cathemeral as well. One Duke Lemur Center project that

investigated activity patterns in relation to light found that black and white ruffed lemurs showed activity peaks around dawn and dusk (Rea et al., 2014). The same study also found higher levels of nocturnal activity in *V. variegata* than in some other lemur species that are generally regarded as diurnal, although as the authors noted, this pattern may have been caused by the illuminated parking lot adjacent to the *V. variegata* enclosures (Rea et al., 2014). The red ruffed lemurs, however, did not show significant peaks in activity at dawn and dusk but instead exhibited a consistent pattern throughout the day (Rea et al., 2014). Another study at the Duke Lemur Center yielded similar results, concluding that there is some evidence for cathemeral activity in the ruffed lemurs (Bray et al., 2017). In this case, *V. variegata* and *V. rubra* were considered together, but a peak in activity at dusk was clear and consistent (Bray et al., 2017).

Social Behavior

Although previously thought to live in small, pair-bonded groups, recent studies have shown that ruffed lemurs live in flexible multimale/multifemale groups of up to 30 individuals with a polygynandrous mating system (Vasey, 2007). Like chimpanzees, these larger groups fission and fuse in response to ecological and social variables (Lehmann et al., 2007; Baden et al., 2016). The primary factors influencing group composition are climate, fruit phenology,

female reproductive status, and overall group size. Since ruffed lemurs are primarily frugivorous, fruit seasonality greatly affects grouping patterns.

Ruffed lemurs in different regions of Madagascar respond to changes in fruit availability in different ways. In one study, ruffed lemurs formed larger groups during the rich season when fruit is plentiful and then split off into smaller subgroups during the lean season, associating only with kin (Vasey, 2007; Baden et al., 2016). Madagascar is famous for its intense seasonal shifts, so researchers have proposed that this change in group size is a response to uncertainty in the environment (Vasey, 2007; Baden et al., 2016). However, Holmes et al. (2016) found that during periods of lower food availability, ruffed lemurs formed larger subgroups, contrary to other results (Baden et al., 2016; Baden et al., 2021). Both studies utilized similar methods and had comparable durations, so the primary difference seems to be the characteristics of the study sites. Holmes and colleagues proposed that the formation of large groups when resources are scarce seems counterintuitive at first but may be a response to intergroup competition (Holmes et al., 2016; Baden et al., 2021). With reduced food availability, patches are fewer and more dispersed, so fission can be counterproductive (Baden et al., 2021). If this is the case, maintaining a larger group would be beneficial to monopolize food patches, whereas forming subgroups could prevent lemurs from gaining access to any food (Baden et al., 2021). Due to these unresolved issues, it is evident that the influence of food seasonality on ruffed lemurs warrants further investigation.

Reproduction and Infant Care

Only a handful of primates give birth to litters and construct nests in which to care for their young. Generally, primates that do this are small bodied, nocturnal, and solitary, making ruffed lemurs a distinct exception (Vasey et al., 2018). For strepsirrhines, ruffed lemurs are large, tend to be most active during the day, and are dependent on group living (Vasey et al., 2018). Notably, ruffed lemurs also differ in their use of nests. Other litter-bearing primates will utilize nests throughout the year for raising young and sleeping, but ruffed lemurs are unusual in that they use nests solely for rearing offspring in the first few weeks of life, and then they stash or park their older infants rather than carry them around as they forage (Vasey et al., 2018).

Parking offspring is considered to be an ancestral trait, as other strepsirrhines and tarsiers practice infant parking while anthropoids tend to carry their infants (Ross, 2001). Rarer still, ruffed lemurs defy the assumption that carrying infants is more beneficial for large-bodied primates than parking (Ross, 2001). This may be due to litter size; while large-bodied anthropoids tend to produce single offspring, ruffed lemurs regularly have twins or triplets. While ruffed lemurs are among the largest Lemurids, the production of litters makes traveling with infants energetically costly and risky, so mothers stash them in nests instead. Females may transport their litters from one nest to another, but mothers do not carry infants when they forage (Baden et al., 2016). During the mother's absence, other members of the group sometimes station themselves near but never inside the nest (Vasey, 2007). After approximately two weeks,

mothers remove their infants from the nest and stash them in the canopy in areas where they are protected from the elements and unlikely to fall (Vasey, 2007). Once infants leave the nest, group members interact with them more and contribute to their care and protection (Vasey, 2007). In ruffed lemurs, parking and stashing young is associated with faster infant growth and survival than in other large-bodied lemurs, forming a crucial aspect of the species' life histories (Tecot et al., 2012).

Reproduction also influences group dynamics. Ruffed lemurs are highly synchronous breeders, meaning that females typically produce litters around the same time. When birthing events occur, ruffed lemurs tend to fission into smaller subgroups (Baden et al., 2016). Provisioning for the litter is energetically costly for the mother, so it may benefit her to be surrounded by only a few closely related kin. In the larger group, mothers may have to compete with other individuals in the group for food, causing feeding tension (Baden et al., 2016). However, subgroup sizes during reproduction tend to be larger than subgroup sizes during the lean season, thereby allowing mothers and other individuals to collectively care for infants (Baden et al., 2013; Holmes et al., 2016). Cooperative rearing is beneficial to ruffed lemur mothers as it increases infant survival and allows the mothers to share the energetic burden of infant care with other group members (Baden et al., 2013). The high energetic cost of reproduction in ruffed lemurs is hypothesized to contribute to female leverage in the genus (Vasey, 2007).

Conservation Status

The IUCN classifies both red ruffed lemurs and black and white ruffed lemurs as critically endangered with a decreasing population size (Borgerson et al., 2020; Louis et al., 2020). The primary threats to ruffed lemurs include the expansion of agriculture, timber harvest, local hunting, and habitat disturbance due to cyclones (Borgerson et al., 2020; Louis et al., 2020). As land is continuously turned over for agricultural use, the range of ruffed lemurs is constrained (Baden et al., 2014; Borgerson et al., 2020). Furthermore, ruffed lemurs appear to rely on the largest trees in primary forest which are also the trees targeted by logging, making the genus especially susceptible to selective logging and forest clearing (Hekkala et al., 2007). Moreover, as the largest lemurs, ruffed lemurs are a preferred target for subsistence hunters, and harvest exceeds sustainable levels (Golden, 2009). People also occasionally keep ruffed lemurs as pets locally or sell them internationally via illegal pet trade markets (Reuter and Schaefer, 2017). For both species, these factors are anticipated to cause a population reduction of >80% in the next 25 years, pushing the ruffed lemurs to the brink of extinction (Borgerson et al., 2020; Louis et al., 2020).

Some ruffed lemur reintroduction efforts have been successful (Britt et al., 2004). One study released captive-bred black and white ruffed lemurs into the Betampona Reserve in eastern Madagascar, and although not all individuals survived, nearly half of them bred with wild conspecifics and even integrated into social groups (Britt et al., 2004). Reintroductions can be

challenging, however, as not all captive-bred animals are “behaviorally competent” and viable for release (Britt et al., 2004). Facilities like the Duke Lemur Center offer a semi-free-ranging experience that provides an environment in which captive-bred lemurs have the best chance at becoming successful reintroduction candidates.

In Captivity

Ruffed lemurs are prone to health issues in captivity due to their specific dietary needs. As captive lemurs consume more fruit than wild lemurs, captive lemurs are often obese, which not only decreases animals’ welfare but also reduces their reproductive ability (Goodchild and Schwitzer, 2008). Lemurs also suffer from diabetes in captivity. One study that surveyed AZA institutions found that 30% of zoos that house primates reported at least one diabetic individual (Kuhar et al., 2013). Iron storage disorders are another serious concern in captivity. In the wild, lemurs consume tannins that impede iron absorption. However, zoos do not feed lemurs plant materials that contain tannins, making it is easier for lemurs to overload on iron, which can result in iron deposition in the body tissues (Clauss and Paglia, 2012). Many lemurs, particularly the ruffed lemurs, are sensitive to dietary fiber and can exhibit diarrhea or dehydration symptoms when fed insufficient fiber (ZAA, 2015).

As the ruffed lemurs are critically endangered, there is a growing need for a stable breeding population in captivity (Borgerson et al., 2020; Louis et al., 2020). The Prosimian Taxon Advisory Group (TAG) manages both species of ruffed lemur. This group is led by Christie Eddie from Omaha's Henry Doorly Zoo and Aquarium. Gina Ferrie, from Disney's Animal Kingdom, serves as the TAG's vice program leader, and over 20 additional professionals, including several from the Duke Lemur Center, serve as program advisors. Current population data for the black and white ruffed lemurs was unavailable from TAG, but the AZA reports 187 red ruffed lemur individuals, with a TAG goal of 225.

Research Questions

1. Are intersexual conflicts more likely to be decided than intrasexual conflicts?
(A decided conflict is defined as a conflict in which only one lemur showed unambiguous submissive behavior.)
2. Are females more likely than males to win intersexual conflicts?
(The winner of a conflict is defined as the lemur who received unambiguous submissive behavior.)
3. Is there a significant difference in the outcome of intersexual conflicts between the *V. variegata* and the *V. rubra* groups?

4. Does dominance or leverage appear to be the source of female power in the genus *Varecia*?
5. Is there a significant difference in the source of female power (dominance or leverage) between the *V. variegata* and the *V. rubra* groups?
6. Are males more likely to maintain spatial proximity to females than females are to males?
7. Are males more likely to be near females than they are to be near other males?

Expected Findings

First, I expected to find that in both *V. variegata* and *V. rubra*, intersexual conflicts would be more likely to be decided than intrasexual conflicts. Meyer et al. (1999) found that >90% of intersexual conflicts were decided in captive red ruffed lemurs. Similarly, Raps and White (1995) showed that most intersexual conflicts were decided, but intrasexual conflicts were often ambiguous with no clear winner or loser. This pattern was more pronounced in the black and white ruffed lemurs than the red ruffed lemurs (Raps and White, 1995).

Second, I expected to find that in both *V. variegata* and *V. rubra*, females would be significantly more likely than males to win intersexual conflicts. Previous studies have found striking female bias in ruffed lemur intersexual conflict outcomes, some of which took place at the Duke Lemur Center as well (Kaufman, 1991; Raps and White, 1995; Meyer et al., 1999).

Each of those studies found that >90% of decided intersexual conflicts were won by females (Kaufman, 1991; Raps and White, 1995; Meyer et al., 1999). I expected to find a similar trend in this study, lending evidence to the existence of female power in ruffed lemurs.

Third, I did not expect to find a significant difference in the outcome of intersexual conflicts between the two species. Raps and White (1995) found some evidence that subtle distinctions exist between *V. variegata* and *V. rubra*. They stated that black and white ruffed lemurs had more undecided conflicts as well as more interactions that involved male aggression toward females. From their analysis, >90% of red ruffed lemur intersexual conflicts were decided and won by females, but approximately 75% of black and white ruffed lemur intersexual conflicts were decided, with >90% won by females (Raps and White, 1995). However, these results could reflect individual behavioral variations rather than variations in the species as a whole. I did not anticipate finding a similar trend to Raps and White, but I still analyzed my data for species distinctions.

Fourth, I expected to find that leverage is the primary source of female power in the genus *Varecia*. Since there is no sexual dimorphism in the ruffed lemurs, it is unlikely that females can physically overpower males, exhibiting dominance (Lewis, 2002, 2020; Voyt et al., 2019). Instead, I expected to find that females maintain power via leverage. As such, I anticipated that weight would have little effect on the outcome of intersexual conflicts, but age would (Lewis, 2002, 2020; Voyt et al., 2019).

Fifth, I did not expect to find a significant difference in the source of female power between the two species. Both black and white ruffed lemurs and red ruffed lemurs experience severe reproductive stress that is thought to necessitate female power (Vasey, 2007). Since the

two species are influenced by similar conditions, I expected to find that both species show leverage, rather than dominance, as the source of female power.

Sixth, I expected to find that males would be more likely to maintain spatial proximity to females than females to males. Other studies have shown that males sometimes approach females and behave submissively without provocation from the females (Raps and White 1995; Overdorff et al., 2005). However, females do not commonly approach males (Raps and White 1995; Overdorff et al., 2005). I expected that the lemurs in this study would show a similar pattern in which the males are more responsible for maintaining spatial proximity to females but the females have little responsibility for maintaining proximity to males.

Lastly, I expected to find that males would be more likely to be near females than other males. Dovetailing with the previous hypothesis, if males have greater responsibility for maintaining proximity to females, I anticipated that they would be found near females more often than they would be found near other males. Additionally, if leverage is the source of female power in the ruffed lemurs, there is a social or reproductive incentive for males to associate with females.

CHAPTER 2

METHODS

Study Site

The research was conducted at the Duke Lemur Center (formerly Duke University Primate Center), located at 3705 Erwin Rd, Durham, NC 27705, USA, from May 3rd to July 2nd, 2021. Founded in 1966, the Duke Lemur Center is home to the world's largest and most diverse population of lemurs outside of Madagascar. The Duke Lemur Center covers a land area of 100 acres and houses over 200 animals, with 14 species represented.

The ruffed lemurs at this facility are divided into eight groups (four *V. variegata*, four *V. rubra*), ranging from two to four individuals per group. Some groups live in indoor/outdoor, chain-link fenced enclosures. Other groups range free in large, multispecies enclosures called Natural Habitat Enclosures. One group of *V. rubra* (including three individuals: Minias, Hunter, and Pandora) lives in an outdoor enclosure called “the silos,” which are refurbished grain silos with a chain-link exterior. Appendix B details which individuals live together and in what type of enclosure.

Study Subjects

In total, I observed 16 individuals for this study (*V. variegata* n=5, *V. rubra* n =11). The study subjects consisted of eight males and eight females that varied in age and weight (Table 1). I excluded six lemurs, all *V. variegata*: a female pair that lives in a single-sex group and a group that lacks a mature male and is composed of four highly related individuals. All other lemurs live in mixed-sex groups that ranged in size from two to three mature individuals per group, and these individuals varied in the number of individuals who were kin or potential mates (Table 1). All individuals were sexually mature, with the exception of one *V. variegata* female.

Data Collection

I recorded observations on paper datasheets for 7 hours a day and five days a week (Monday-Friday). I used a combination of continuous focal animal sampling and all occurrence sampling for this study, meaning that I observed a specific individual within a group constantly throughout one day, but also recorded all instances of conflict for that group, even if the focal animal was not involved. I recorded both intersexual and intrasexual conflict, though the primary

Table 1

Demographic data for study subjects. Includes name, species, sex, age in years, weight in grams, group number, potentially reproductive pairs, and related pairs. Potentially reproductive pairs are defined as an intersexual pair that is unrelated. For the related pairs, specific relationships are indicated in parentheses.

Name	Species	Sex	Age	Age Class	Weight (g)	Group	Potentially Reproductive Pairs	Related Pairs
Afo	<i>V. rubra</i>	Male	7.06	Adult	2780	1	Judith & Afo, Mae & Afo	Judith & Mae (sisters)
Judith	<i>V. rubra</i>	Female	3.14	Adult	3400	1		
Mae	<i>V. rubra</i>	Female	3.14	Adult	3500	1		
Kizzy	<i>V. variegata</i>	Female	16.22	Adult	4020	2	Kizzy & Ravo	n/a
Ravo	<i>V. variegata</i>	Male	18.09	Adult	3280	2		
Antika	<i>V. rubra</i>	Female	12.13	Adult	3760	3	Antika & Kalani	n/a
Kalani	<i>V. rubra</i>	Male	5.07	Adult	3940	3		
Hermione II	<i>V. variegata</i>	Female	5.36	Adult	3060	4	Hermione II & Herschel	Hermione II & Ripley (mother) Herschel & Ripley (father)
Herschel	<i>V. variegata</i>	Male	8.12	Adult	3200	4		
Ripley	<i>V. variegata</i>	Female	1.14	Juvenile	3010	4		
Borealis	<i>V. rubra</i>	Male	33.17	Adult	3360	5	Ruby & Borealis, Ruby & Buzz	Borealis & Buzz (father)
Buzz	<i>V. rubra</i>	Male	4.09	Adult	3940	5		
Ruby	<i>V. rubra</i>	Female	3.14	Adult	3420	5		
Hunter	<i>V. rubra</i>	Male	25.14	Adult	3660	6	Pandora & Hunter, Pandora & Minias	Hunter & Minias (brothers)
Minias	<i>V. rubra</i>	Male	27.2	Adult	3140	6		
Pandora	<i>V. rubra</i>	Female	10.15	Adult	4240	6		

interest of this study is conflict between the sexes. I created a randomized schedule to ensure that I observed all groups and individuals equally throughout the course of the study.

This project utilizes specific terminology that may have slightly different definitions outside of the context of conflict behavior. For this reason, Table 2 defines the terms commonly used throughout the methodology.

When a conflict occurred, I first determined whether the conflict was ambiguous or unambiguous. I did not record ambiguous conflicts, in which the recipient of aggressive/submissive behavior was unclear. If the conflict was unambiguous, meaning the recipient was clear, I began recording data. The data on conflicts included five key components. First, I recorded the date and time. Then, I identified the individuals involved in the conflict. The Duke Lemur Center utilizes colored collars and partial tail shaves to mark individuals that are not easily identifiable. The research team and husbandry staff helped me to ensure I identified individuals correctly. Third, I recorded the specific behavior(s) following the Pereira ethogram (Pereira et al., 1988). I also recorded the directionality of the agonistic and/or submissive behavior. Context is an important variable as well, so I noted the predominant activities of the two lemurs in the 10 seconds prior to the conflict. If the two individuals were engaging in separate activities (e.g., focal lemur was resting while the other lemur was traveling), I recorded the context of the focal animal as the behavioral context, but this rarely happened in practice.

Table 2

Behavioral terminology and definitions used in this paper

Term	Definition
Ambiguous Conflict	A conflict in which the observer could not discern a clear target. These conflicts were not recorded.
Unambiguous Conflict	A conflict with a clear target. All unambiguous conflicts were recorded.
Decided	A type of unambiguous conflict in which only one lemur in a conflicting pair showed submissive behavior. Example: Lemur A bites Lemur B and Lemur B flinches. Example: Lemur A chatters at Lemur B, unprompted by aggressive behavior
Undecided	A type of unambiguous conflict in which either both lemurs showed submissive behavior or no lemurs showed submissive behavior. Example: Lemur A chatters at Lemur B and Lemur B chatters back at Lemur A. Example: Lemur A bites Lemur B and Lemur B bites back.
Director	The initiator in a conflict. The director may use aggressive and/or submissive behavior, and may or may not win a conflict.
Recipient	The target in a conflict. The recipient may use aggressive and/or submissive behavior, and may or may not win a conflict.

Conflicts were marked as “decided” if only one lemur showed submissive behavior as defined in Pereira’s ethogram. I considered the director of the submissive behavior to be the loser of the conflict, and the recipient of the submissive behavior to be the winner. A decided conflict could involve a lemur acting submissively after an agonistic interaction with another lemur or a lemur spontaneously acting submissively to another lemur. If both lemurs showed submissive behavior, I still recorded the conflict, but I marked it as undecided. Additionally, if a lemur acted aggressively toward a groupmate, but that groupmate did not react with submission, I marked the conflict as undecided. This methodology is outlined in Figure 1 below.

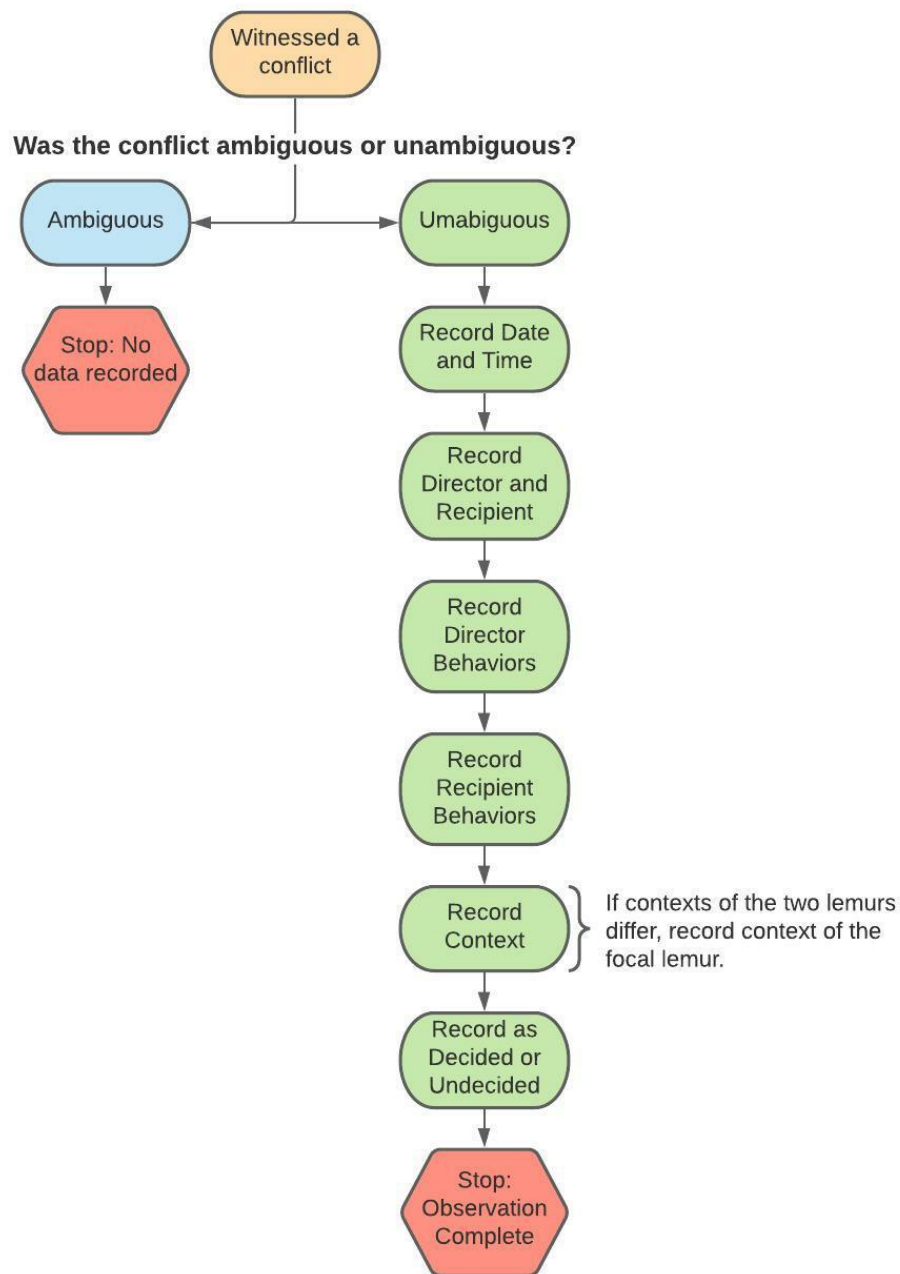


Figure 1. Flow chart depicting the order of observations for conflicts.

Following the focal animal for a given day, I monitored that lemur's movements and how those movements affected their proximity to the other group members. For example, using continuous sampling, I recorded the number of occasions in which the movements of the focal lemur (lemur A) united it with another group member (lemur B) or when lemur A's movements separated it from lemur B. In this project, I considered a pair of lemurs to be united when they were within 1 meter of each other and to be separated when the distance between them was greater than 1 meter (per Dolotovskaya et al., 2020). I used the Hinde index to determine the responsibility of group members in maintaining spatial proximity to each other (Hinde and Atkinson, 1970).

I also recorded spatial data using instantaneous scan sampling. Every 10 minutes, I visually estimated all pairwise spatial distances of the focal animal to its other groupmates to the nearest 0.5 m and recorded them on a datasheet separate from the behavioral observations. On some occasions, one or more lemurs were not visible due to distance or terrain, and I marked this as "not visible" on the datasheet. Similarly, caretakers separated some groups for feeding, and those animals could not access their groupmates. I marked these instances as "not accessible" on the datasheet.

Age and Body Mass Data

I obtained data on age and weight from the Duke Lemur Center's records. The age data serves as a proxy for leverage and weight as a proxy for physical dominance, as in the study by Voyt et al. (2019). I used these two variables in my analyses using generalized linear mixed models to evaluate their influence on the outcome of intersexual conflicts.

Ethogram

Following the example of many other *Varecia* studies (Kaufman, 1991; Raps and White, 1995; Meyer et al., 1999; Overdorff et al., 2005), this project draws on an ethogram from Pereira et al. (1988). This ethogram focuses on ruffed lemur agonistic and submissive behaviors and can be found in Appendix A.

Statistical Analysis

The statistical analysis was completed by the Statistical Consulting Services at Northern Illinois University. They used R Studio and generalized linear mixed models to answer all seven research questions. I recorded time as standard hours and minutes and later organized those time stamps into three categories (morning, midday, and afternoon) for ease of analysis. I show the cutoffs for each time category in Table 3.

Table 3
Range of the three time categories (morning, midday, and afternoon)

	Morning	Midday	Afternoon
Range	8:00-10:59	11:00-13:59	14:00-16:00

The generalized linear mixed model for Research Question 1 used pair ID as a random effect and conflict outcome (decided or not), conflict type (intersexual or intrasexual), species, and time as fixed effects. The model for Research Question 2 used pair ID as a random effect and director victory, director sex, species, and time as fixed effects. Elements of the first two models answered Research Question 3. For Research Questions 4 and 5, the model used pair ID as a random effect and female victory, female weight, female age, male weight, male age, species, and time as fixed effects. The model for Research Question 6 used pair ID as a random effect and united, focal animal sex, species, and time as random effects. Lastly, the model for

Research Question 7 used focal animal and group as random effects and distance, type of pair (intersexual or intrasexual), species, and time as fixed effects. All models used a 5% significance level. The consulting team generated boxplots depicting the influence of weight and age on conflict outcomes using R Studio. I completed basic calculations such as means and frequencies using Microsoft Excel. I created all pie charts, bar graphs, and tables in Microsoft Excel and Microsoft Word.

I used the Hinde index as one of two ways to analyze the spatial proximity data. From the focal animal observations, I calculated and reported Hinde indices for each pair in the group using the following equation (Hinde and Atkinson, 1970):

$$\text{Lemur A's responsibility for proximity to Lemur B} = \frac{U_A}{U_A + U_B} - \frac{S_A}{S_A + S_B}$$

U_A = number of occasions that lemur A's movements united lemur A and B

U_B = number of occasions that lemur B's movements united lemur A and B

S_A = number of occasions that lemur A's movements separated lemur A and B

S_B = number of occasions that lemur B's movements separated lemur A and B

The index ranges from -1 (lemur B is totally responsible for maintaining proximity) to +1 (lemur A is totally responsible for maintaining proximity), and a value of 0 indicates equal responsibility.

CHAPTER 3

RESULTS

Conflict Observations

I recorded observations for approximately 7 hours a day, five days a week during May, June, and the first week of July, for a total of 273 observation hours. During that time, I recorded 196 conflicts between individuals in all six groups of lemurs. Of the 196 total conflicts, 137 conflicts were decided and 59 conflicts were undecided (Table 4). Females won decided conflicts 103 times, whereas males won decided conflicts 34 times (Table 5). A total of 154 conflicts occurred between lemurs of the opposite sex and 42 conflicts were between lemurs of the same sex. Of those 154 intersexual conflicts, 107 were decided and 47 were undecided. Of the 42 intrasexual conflicts, 18 occurred between two males and 24 occurred between two females.

Table 4

Varecia conflicts by category (decided or undecided)

	Decided	Undecided	Total
Number of Conflicts	137	59	196

Table 5

Varecia conflict outcomes by sex and species. Includes all decided intersexual and intrasexual conflicts.

Species	Type	Female Won	Male Won	Total
<i>V. variegata</i>	Intersexual	25	1	26
	Intrasexual	12	0	12
<i>V. rubra</i>	Intersexual	63	18	81
	Intrasexual	3	15	18
Total		103	34	137

The most common context for conflict was feeding. Ninety-two conflicts occurred within the context of feeding, accounting for 46.9% of the total conflicts. Traveling, grooming, and resting were also common contexts for conflict, with similar frequencies at 30, 28, and 27 respectively. Traveling accounted for 15.5% of the conflict contexts. Grooming accounted for 14.3% of the conflict contexts. Resting accounted for 13.9% of the conflict contexts. The least common context was occupation of preferred space, which occurred 19 times, accounting for 9.8% of the conflicts (Figure 2).

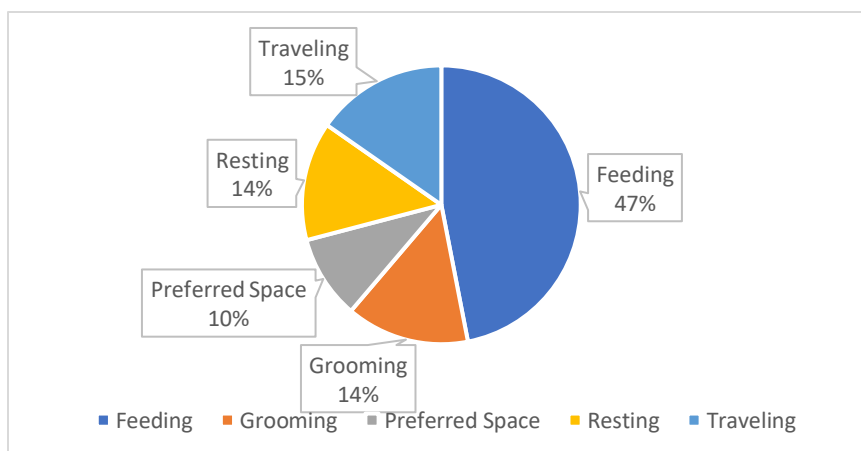


Figure 2. Context (behaviors engaged in immediately prior to the conflict) for all conflicts among the six lemur groups.

V. variegata Conflict Observations

The two *V. variegata* groups were responsible for 63 of the 196 conflicts. Of these conflicts, 38 conflicts were decided and 27 were undecided, females won 37 conflicts and males won 1 conflict, and 49 were intersexual and 14 were intrasexual. Of the 49 intersexual conflicts, 26 were decided and 23 were undecided. Of the 14 intrasexual conflicts, 12 were decided and 2 were undecided (Table 6). The most common context for *V. variegata* conflicts was feeding at 29 occurrences or 46.0%, which coincides with the overall context frequency between both species (Figure 3 and Table 7). The grooming context was recorded 22 times, accounting for 34.9% of conflict contexts, which is much higher than in *V. rubra*. The traveling context was recorded six times, accounting for 9.5% of conflict contexts, which is lower than for *V. rubra*. The resting context was recorded four times, accounting for 6.4% of conflict contexts. The least common context for *V. variegata* conflicts was preferred space at two occurrences or 3.2% of conflict contexts, which is lower than the overall context frequency between both species (Figure 3).

Table 6

Varecia conflicts by species and context frequency

Context	<i>V. variegata</i>	<i>V. rubra</i>
Feeding	29	63
Grooming	22	6
Preferred Space	2	17
Resting	4	23
Traveling	6	24
Total	63	133

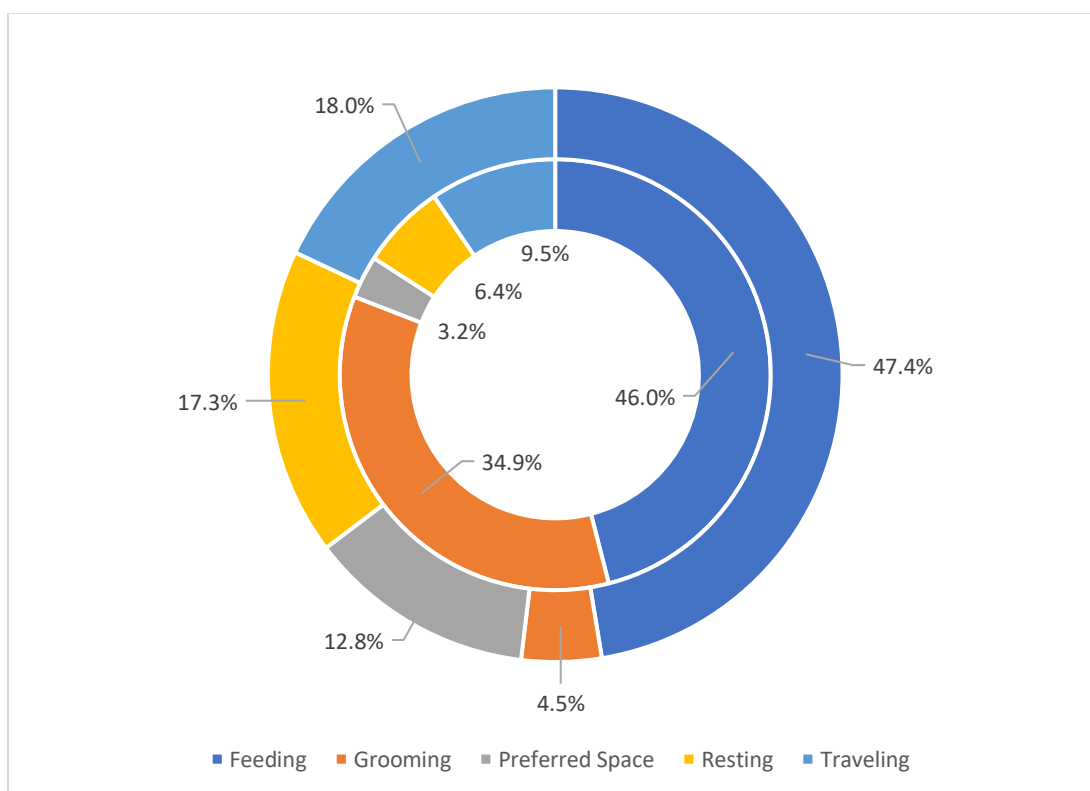


Figure 3. *Varecia* conflicts by species and context proportions. The inner ring represents the *V. variegata* conflicts and the outer ring represents the *V. rubra* conflicts.

Table 7

V. variegata conflict outcomes by type of lemur pair (intersexual or intrasexual)

Intersexual Conflicts	Decided	26
	Undecided	23
	Total	49
Intrasexual Conflicts	Decided	12
	Undecided	2
	Total	14

V. rubra Conflict Observations

The four *V. rubra* groups were responsible for 133 of the 196 conflicts. Of these conflicts, 99 conflicts were decided and 34 were undecided, females won 66 conflicts and males won 33 conflicts, and 105 were intersexual and 28 were intrasexual. Of the 105 intersexual conflicts, 81 were decided and 24 were undecided. Of the 28 intrasexual conflicts, 18 were decided and 10 were undecided (Table 8). The most common context for *V. rubra* conflicts was feeding at 63 occurrences or 47.4%, which coincides with the context frequency for *V. variegata*. The traveling context was recorded 24 times, accounting for 18.1% of conflict contexts. The resting context was recorded 23 times, accounting for 17.3% of conflict contexts. The traveling and resting context frequencies for *V. rubra* conflicts are comparable to those of the *V. variegata*. The preferred space context was recorded 17 times, accounting for 12.8% of conflict contexts, which is higher than the percentage for the *V. variegata*. The least common context for *V. rubra*

conflicts was grooming at six occurrences or 4.5% of conflict contexts, which is lower than the *V. variegata* (Figure 3).

Table 8

V. rubra conflict outcomes by type of lemur pair (intersexual or intrasexual)

Intersexual Conflicts	Decided	81
	Undecided	24
	Total	105
Intrasexual Conflicts	Decided	18
	Undecided	10
	Total	28

Conflict Behaviors

Within the 196 total conflicts between all six groups, I recorded 16 of the 18 unique behaviors identified in Pereira's ethogram. I recorded 233 occurrences of aggressive behaviors and 222 occurrences of submissive behaviors. The most common aggressive behavior was cuff at 152 occurrences or 65.2%. The second most common aggressive behavior was bite at 34 occurrences or 14.6%. I recorded the lunge behavior 18 times and the stare behavior 10 times, each accounting for 7.7% and 4.3% of the aggressive behaviors. I recorded the remaining aggressive behaviors (charge, chase, feint-to-cuff, bipedal hop, pounce on) fewer than 10 times, each accounting for less than 4% of the aggressive behaviors. Together, those five behaviors

accounted for 8.2% of the aggressive behaviors. I did not observe the “push down” behavior. The frequencies of aggressive behaviors can be seen in Figure 4.

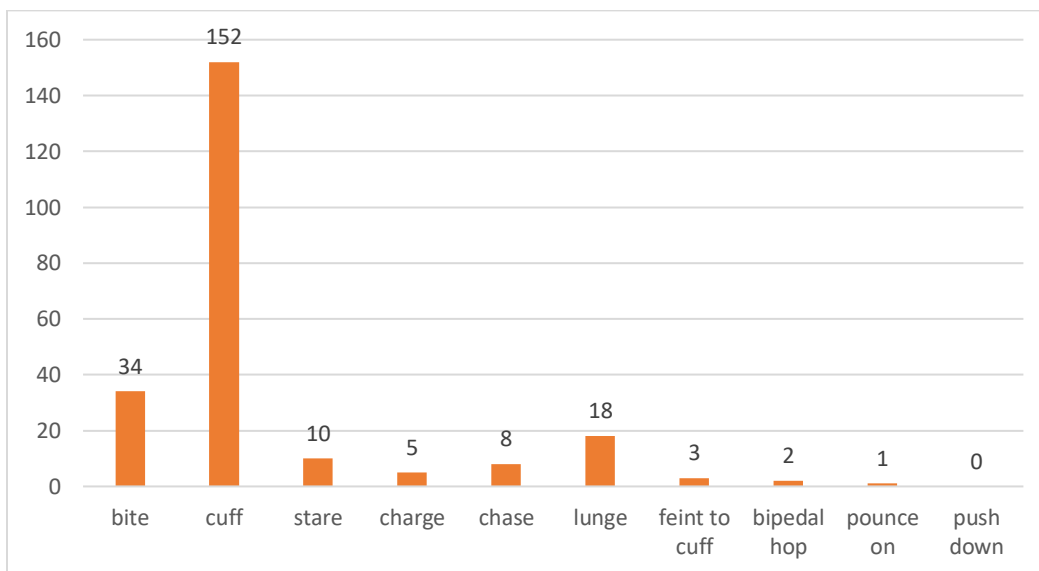


Figure 4. Frequency of aggressive behaviors between the six lemur groups.

The most common submissive behavior was chatter at 73 occurrences or 32.9%. The second most common submissive behavior was displacement at 58 occurrences or 26.1%. The flee behavior was recorded 26 times and the cower/flinch behavior 25 times, each accounting for 11.7% and 11.3% respectively. The jump away behavior was recorded 21 times and the turn head/avert eyes behavior 17 times, each accounting for 9.5% and 7.7% respectively. The grimace behavior was observed only twice, accounting for less than 1%. I did not observe the “back away” behavior. The frequency of submissive behaviors can be seen in Figure 5.

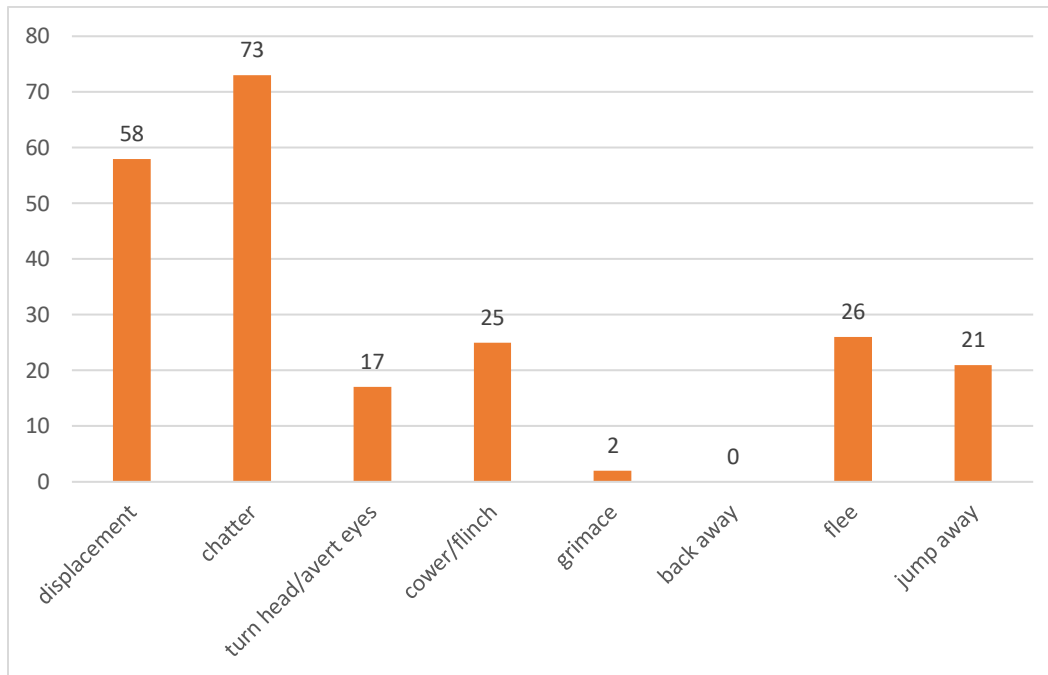


Figure 5. Frequency of submissive behaviors between the six lemur groups.

Research Question 1

Are intersexual conflicts more likely to be decided than intrasexual conflicts?

Statistical analysis of the conflict data showed that intersexual conflicts were not significantly more likely to be decided than intrasexual conflicts ($p=0.563$). However, the odds of an intersexual conflict being decided were 1.89 times (95% CI, 0.218 to 16.390) that of an intrasexual conflict (Table 9).

Table 9

Results of a generalized linear mixed model (binomial, logit: Decided ~ Intersexual + Species + Time + (1 | Pair_ID))

Variable	Estimate	Std. Error	Z-value	p
Intercept	1.951766	1.011991	1.929	0.05378
Intersexual	0.636777	1.102027	0.578	0.56338
Species	-0.008518	1.136131	-0.007	0.99402
Time: Midday	-0.434386	0.535251	-0.812	0.41705
Time: Morning	-1.213061	0.441867	-2.745	0.00605

Unexpectedly, the analysis showed a significant temporal effect. Conflicts that occurred in the morning had significantly lower odds of being decided than conflicts that occurred in the afternoon ($p=0.00604$). The likelihood of a conflict being decided in the morning was 0.297 times (95% CI, 0.125 to 0.707) that of a conflict that occurred in the afternoon. Additionally, conflicts that occurred at midday were less likely to be decided than conflicts that occurred in the afternoon, though not at a significant level ($p=0.417$). The likelihood of a midday conflict being decided was 0.648 times (95% CI, 0.227 to 1.849) that of a conflict in the afternoon. In other words, conflicts are most likely to be decided in the afternoon (Table 10).

Table 10

Conflict outcomes by time

Time	Decided	% Decided	Undecided	% Undecided	Total
Morning	49	35.77%	33	55.93%	82
Midday	35	25.55%	11	18.64%	46
Afternoon	53	38.68%	15	25.43%	68
Total	137	100%	59	100%	196

Research Question 2

Are females more likely than males to win intersexual conflicts?

Females were significantly more likely to win an intersexual conflict than males ($p=2.027e-07$). In fact, females were 239 times (95% CI, 30.323 to 1889.069) more likely to win an intersexual conflict than males (Table 11).

Table 11

Results of a generalized linear mixed model (binomial, logit: Director_Win ~ Director_Sex + Species + Time + (1 | Pair_ID))

Variable	Estimate	Std. Error	Z-value	p
Intercept	-1.1457	0.9097	-1.259	0.208
Director_Sex: Female	5.4779	1.0541	5.197	2.03e-07
Species: V.variegata	-0.3989	1.4197	-0.281	0.779
Time: Midday	-0.9462	1.1094	-0.853	0.394
Time: Morning	-0.5469	0.8325	-0.657	0.511

Research Question 3

Is there a significant difference between the outcome of intersexual conflicts between the *V. variegata* and *V. rubra* groups?

There is no significant difference in the outcome of intersexual conflicts between the *V. variegata* and *V. rubra* groups ($p=0.994$). The odds of a *V. variegata* conflict being decided were 0.992 times (95% CI, 0.107 to 9.191) that of a *V. rubra* conflict (see Table 11). In other words, females of one species are not significantly more likely to win a decided, intersexual conflict than females of the other species.

Research Question 4

Does dominance (weight) or leverage (age) appear to be the source of female power in the genus *Varecia*?

Statistical analysis showed that higher female weight and younger female age are important determinants in intersexual conflicts won by females. In cases where females won, the female tended to be younger and heavier than the male (Figures 6 and 7).

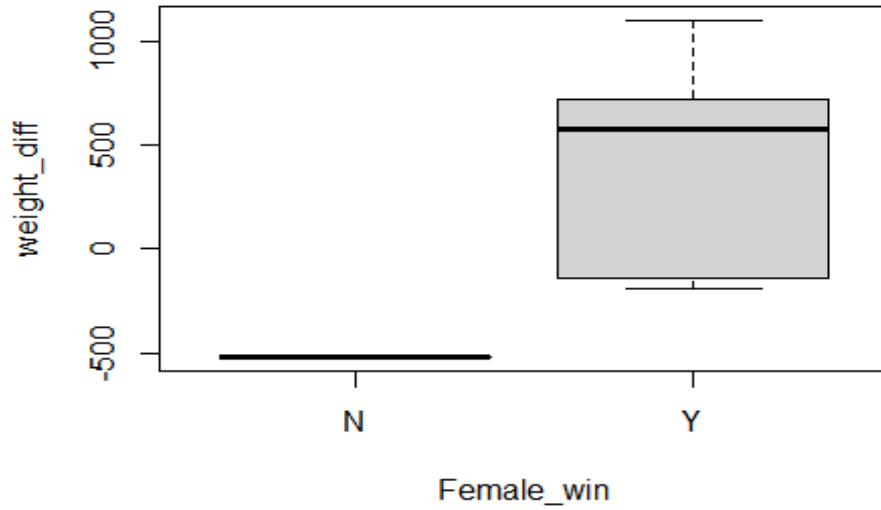


Figure 6. Outcome of conflicts (Female won [Y] or lost [N]) and weight differential (female weight-male weight) for each possible intersexual pair of lemurs.

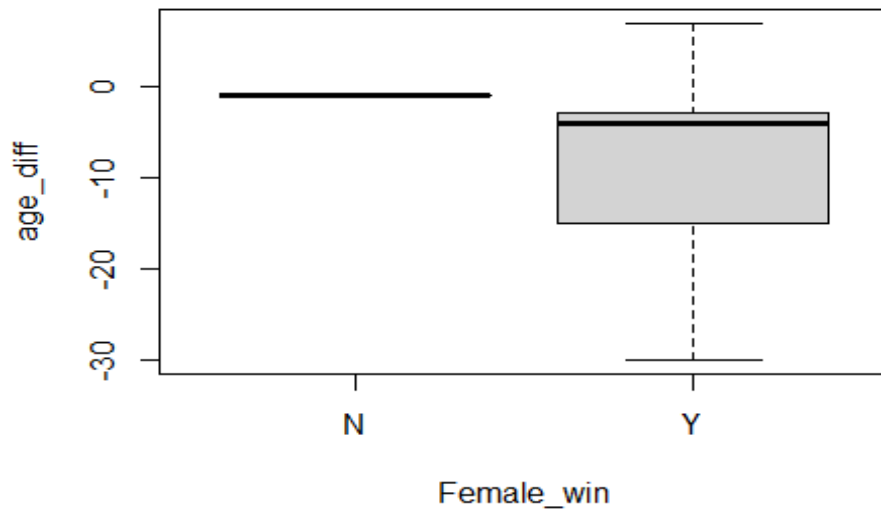


Figure 7. Outcome of conflicts (Female won [Y] or lost [N]) and age differential (female age-male age).

Research Question 5

Is there a significant difference in the source of female power (dominance or leverage) between the *V. variegata* and *V. rubra* groups?

There was not enough data to answer this research question with statistical analyses. However, we can see that weights and ages are distributed similarly across the two species (Figures 8 and 9).

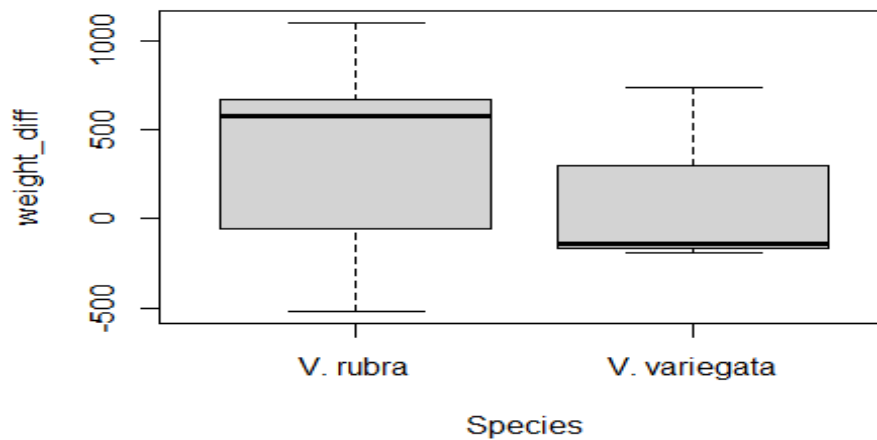


Figure 8. Weight differential (female weight-male weight) by species for each possible intersexual pair.

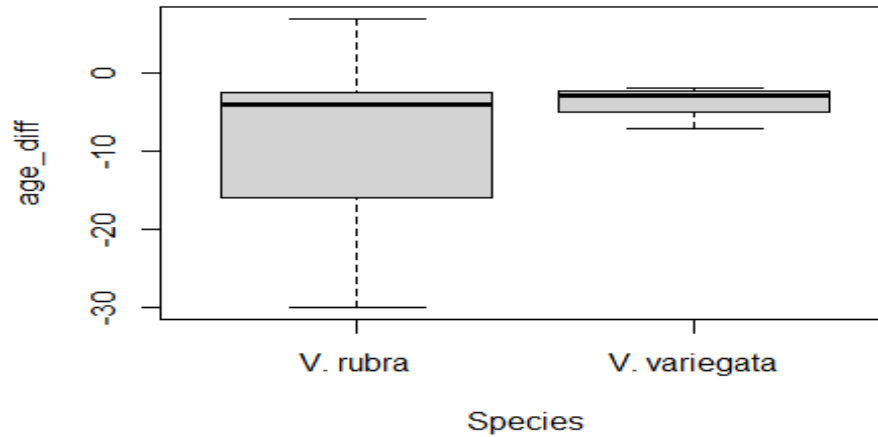


Figure 9. Age differential (female age-male age) by species for each possible intersexual pair.

Movement Observations and Hinde Indices

During the 273 observation hours, I recorded 746 occurrences of lemurs uniting with or separating from a groupmate. Of these 746 observations, 468 occurred within an intersexual pair. Male-male pairs accounted for 37 of these observations and female-female pairs accounted for 241 of these observations.

Research Question 6

Are males more likely to maintain spatial proximity to females than females are to males?

Statistical analysis showed that males were not significantly more likely to unite with females ($p=0.184$) than females were with males. However, males were 1.28 times (95% CI, 0.889 to 1.848) more likely to unite with females than females were with males (Table 12). As spatial proximity did impact conflict resolutions, I also examined the effects of time of day on spatial proximity. Time of day had no significant effect on the spatial proximity of individuals.

Table 12

Results of a generalized linear mixed model (binomial, logit: $\text{United} \sim \text{Focal_Sex} + \text{Species} + \text{Time} + (1 | \text{Pair_ID})$)

Variable	Estimate	Std. Error	Z-value	p
Intercept	-0.17446	0.21716	-0.803	0.422
Focal_Sex: Male	0.24801	0.18679	1.328	0.184
Species: <i>V. variegata</i>	0.23451	0.22256	1.054	0.292
Time: Midday	-0.05523	0.26648	-0.207	0.836
Time: Morning	0.13178	0.22175	0.594	0.552

Using the spatial proximity data and the Hinde index equation, I calculated Hinde indices for all 14 pairs of lemurs. These indices can be found in Table 13. Values between +1 and 0 indicate that the focal lemur (listed first in the pair), showed the greatest responsibility for maintaining spatial proximity to their partner lemur. Values between -1 and 0 indicate that the

partner lemur showed the greatest responsibility for maintaining spatial proximity to the focal animal. Bolded Hinde indices show the intersexual pairs and italicized names indicate male lemurs. In 7 of the 10 intersexual pairs, males had the greatest responsibility for maintaining proximity to females. There are possible confounding factors for the three intersexual pairs that did not have a negative Hinde index. Pair 8 (Hermione and Herschel) is a breeding pair, so the female may have stronger bonds with the male. Similarly, Pair 6 (Ripley and Herschel) is a father and daughter pair. Pair 10 (Ruby and Buzz) included the unusually dominant male and submissive female.

Table 13

Hinde indices for all 14 lemur pairs. Hinde indices were calculated using the spatial movement data and the Hinde index equation. Names in bold are intersexual pairs. Male names are in italics.

Group	Pair ID	Lemur A	Lemur B	Hinde index
1	2	Mae	Judith	0.335
1	11	Mae	<i>Afo</i>	-0.067
1	1	Judith	<i>Afo</i>	-0.083
2	14	Kizzy	<i>Ravo</i>	-0.052
3	13	Antika	<i>Kalani</i>	-0.238
4	7	Hermione	Ripley	-0.137
4	8	Hermione	<i>Herschel</i>	0.6
4	6	Ripley	<i>Herschel</i>	0.056
5	10	Ruby	<i>Buzz</i>	0.064
5	9	Ruby	<i>Borealis</i>	-0.071
5	12	<i>Buzz</i>	<i>Borealis</i>	0.083
6	4	Pandora	<i>Minias</i>	-0.613
6	3	Pandora	<i>Hunter</i>	-0.129
6	5	<i>Minias</i>	<i>Hunter</i>	0.467

Spatial Proximity Observations and Pairwise Distances

During the 273 observations hours, I recorded 2,715 instantaneous scan samples at 10-minute intervals where I approximated the pairwise distances between the focal lemur and its groupmates. Intersexual pairs accounted for 2,030 of the total observations. Male-male pairs made up 325 of the observations and female-female pairs made up 360 of the observations. During my observations, staff occasionally separated the lemurs during feeding, in which case the focal lemur could not access its groupmates. The focal lemur was not accessible 59 times throughout this study. Similarly, lemurs were sometimes not visible due to terrain or physical distance from the focal lemur. Lemurs were not visible 13 times throughout this study.

Research Question 7

Are males more likely to be near females than they are to be near other males?

Males are not significantly more likely to be near females than other males ($p=0.258$). The distance between intersexual pairs was smaller than the distance between intrasexual male pairs, but not on a significant level. Unexpectedly, the statistical analysis showed that female

pairs were significantly nearer than male pairs ($p=0.033$; Table 14). Time of day influenced proximity, with lemurs being significantly closer together at midday. Simple mean distances are displayed in Table 15 for each type of lemur pair. Note that these means differ from the results of the linear mixed model because the model is a more complex form of analysis. The simple means cannot account for the same variables as the model, which controlled for species, time, and unique pair IDs.

Table 14

Results of a linear mixed model fit by REML and t tests using Satterthwaite's method (Distance ~ Type + Species + Time + (1 | Focal:Group))

Variable	Estimate	Std. Error	df	T-value	p
Intercept	5.4275	0.7704	23.1861	7.045	3.38e-07
Type: F-F	-1.2240	0.5744	2385.8421	-2.131	0.03321
Type: M-F	-0.4746	0.4197	2489.4968	-1.131	0.25834
Species: <i>V. variegata</i>	0.6728	1.2120	14.0282	0.555	0.58756
Time: Midday	-0.8113	0.2550	2623.0417	-3.182	0.00148
Time: Morning	-0.3090	0.2485	2643.0925	-1.244	0.21375

Table 15

Simple mean distances (in meters) for male-female pairs, male-male pairs, and female-female pairs

	Male-Female	Male-Male	Female-Female
Mean Distance (m)	4.85	4.59	5.24

CHAPTER 4

DISCUSSION

Conflict Observations

As expected, female ruffed lemurs won significantly more decided, intersexual conflicts than male lemurs. This trend is consistent with the findings of several other ruffed lemur studies (Kauffman, 1991; Raps and White, 1995; Meyer et al., 1999). Previous studies found that females won >90% of intersexual conflicts, but that was not the case in this project (Kauffman, 1991; Raps and White, 1995; Meyer et al., 1999). I found that females won approximately 80% of intersexual conflicts. While this difference in the outcome of intersexual conflicts could be the result of variation among study subjects, environmental conditions, or simply random chance, the difference is large enough to suggest that additional research is needed to explore female power in the genus.

Other studies have referred to female power in *Varecia* as “striking” and “unambiguous” and considered ruffed lemurs to be similar in power dynamics to ring-tailed lemurs (Kauffman 1991; Raps and White, 1995; Meyer et al., 1999). After conducting my own observations, I disagree with both the description of ruffed lemur power and the comparison to ring-tailed lemurs. Though not recorded as part of my data, I witnessed many ambiguous conflicts in which

I could not discern a clear target. Furthermore, I found that power dynamics were neither predictable nor homogeneous across the groups in my study. For example, one *V. rubra* group (two males, one female) had a young male that frequently acted aggressively toward a female. Sometimes, this female would reciprocate with aggression, but often she responded with submissive behavior instead; thus, she did not consistently hold the most power in the group. In another group, I witnessed frequent aggression between a sister pair rather than between those females and their unrelated male groupmate. Again, I expected to see that these sisters would direct most of their aggression toward the only male in the group. Instead, they seemed to vie for the position of power between themselves while only sporadically fighting with the male. Out of the six groups observed, only three groups (2, 3, and 6) exhibited what I would call “striking, unambiguous” female power (these females always won conflicts with males).

I expected to find that intersexual conflicts were significantly more likely to be decided than intrasexual conflicts, but that did not prove to be true. While intersexual conflicts were nearly twice as likely to be decided than intrasexual conflicts, the difference was not significant. During my observations, I was surprised by how many intrasexual conflicts I observed overall but also by how many of those conflicts were decided. However, there may have been some individuals that affected the results. Two sibling pairs (Mae/Judith, Minias/Hunter) often instigated minor conflicts, but one sibling in each pair typically won the conflicts. It is possible that those sibling pairs biased the ratio of decided and undecided intrasexual conflicts.

As expected, I found no significant difference between the outcomes of *V. variegata* conflicts and *V. rubra* conflicts. The likelihood of a *V. variegata* conflict being decided was nearly identical to that of a *V. rubra* conflict, which lends strength to the assumption that these

two species can be grouped together in behavioral research and captive animal management. Most previous research on female power in *Varecia* has not compared the two species. However, Raps and White (1995) found some evidence that subtle distinctions exist between *V. variegata* and *V. rubra*. They stated that *V. variegata* had more undecided conflicts as well as more interactions that involved male aggression toward females. From their analysis, >90% of *V. rubra* conflicts were decided and won by females, but approximately 75% of *V. variegata* conflicts were decided, with >90% won by females (Raps and White, 1995). These results could reflect individual behavioral variations rather than variations in the species as a whole, but they are worth noting. As a comparison, I found that approximately 78% of *V. rubra* conflicts were decided and won by females while 60% of *V. variegata* conflicts were decided and 66% were won by females.

Unexpectedly, I found more evidence for dominance than leverage in my analysis of female power. Higher female weight was an important determinant in the outcome of intersexual conflicts. In this study, I used weight as a proxy for dominance based on the assumption that larger females are better able to threaten or physically overpower males, thereby achieving dominance in the word's literal sense (Lewis, 2002, 2020). As *Varecia* are not known to be sexually dimorphic, I was not expecting to find much variation in weight, let alone any evidence that weight was an important source of female power (Lewis, 2002, 2020; Voyt et al., 2019). I predicted that my results would show evidence for leverage as the source of female power since ruffed lemurs face extreme reproductive stress in the wild. Females, then, should hold power over males due to their control of a key resource that cannot be taken by force: reproduction. However, my results appear to challenge that assumption.

The ecological and/or evolutionary basis for female dominance in *Varecia* is not entirely clear, so I think it is possible that physical dominance may be unique to the captive setting. In fact, the captive setting may facilitate dominance over leverage. Resources in captivity are more easily monopolized and controlled than in the wild. Food is distributed in clumps throughout the enclosures, making it possible for a single lemur to take food by force and gain more than their fair share of the diet for that day. Dominant females could consistently consume slightly more food than males, gradually increasing in weight and giving them greater means by which to control food in the future. At the Duke Lemur Center, some, but not all, *Varecia* were separated for feeding to avoid this problem. The difference between this study and wild studies could be due to subtle sexual dimorphism in captivity. Baden et al. (2008) reported average body mass for wild *V. variegata*. Females averaged 3.7 kg and males averaged 3.6 kg. The captive *Varecia* in my study were comparable in body mass, with females averaging 3.6 kg and males averaging 3.4 kg. Based on these two datasets, there may be a slight discrepancy in body mass between wild and captive *Varecia*, but future research should investigate this further.

My dataset was too small to fully determine if there was a significant difference in the source of female power between the *V. variegata* and *V. rubra* groups. However, since there was no significant difference in the outcome of intersexual conflicts between the two species, and weight and age were distributed similarly across the groups, it is reasonable to predict that there would not be a significant difference in the source of female power between the two species, even if I had collected more data.

Additionally, it is possible that *Varecia* do not neatly conform to the dichotomy of dominance or leverage. In particular, alloparental care may affect the dynamics of female power

in the species. Males play a significant role in the care of offspring within a group, assisting mothers in supervising and protecting offspring (Vasey, 2007). This may create an incentive for females to maintain good relationships with males so that females may elicit the help of males in the future. In other species, females have little use for the males outside of breeding contexts, so female lemurs in other species may display greater power differentials over males. As discussed previously, males also have an incentive to maintain good relationships with females so that they may breed with the females, increasing their reproductive output. The cooperative nature of ruffed lemurs could facilitate the flexible, somewhat ambiguous female power dynamics that I observed in this study.

Fission-fusion dynamics may also affect female power in *Varecia*. As previous research has shown, ruffed lemur groups are flexible in the wild, varying with seasons and fruit availability (Vasey, 2007; Baden et al., 2016; Holmes et al., 2016). As group size and structure changes, the mechanisms and basis for female power may also change. In small, related groups, females may have less need to assert dominance over males by using force. However, in larger groups with multiple families, females have unrelated males to contend with, possibly leading to an increase in aggressive behavior.

Movement Observations and Hinde Indices

I expected to find that male lemurs were significantly more likely to unite with females than females were to unite with males, but the statistical analysis showed no significant trend. My initial prediction was based on the reasoning that it would be in the males' best interest to associate with the females. Since the females hold power in the species, males may benefit from forming bonds with the females. Conversely, females stand to gain little by associating with the males outside of the breeding season. Therefore, I expected the males to be primarily responsible for maintaining their social affiliations with females, whereas females would be indifferent to males. Without a statistically significant result, I cannot confirm or deny this prediction. However, previous research has found a similar trend where males often approach females, but females seldom approach males (Raps and White, 1995; Overdorff et al., 2005). With an extended time frame for this study, I believe the data would have provided stronger evidence toward this claim. On the other hand, it is possible the weight differential between males and females discourages males from approaching larger females.

The Hinde indices show that in 70% of the intersexual pairs the males showed the greatest responsibility for maintaining social affiliations. I expected to find that a greater proportion of the Hinde indices indicated heightened male responsibility. It is worth noting that three of the females in this study behaved unusually, approaching males far more than any other females. Two of these females were part of the *V. variegata* family group. The high genetic

relatedness in that group likely influenced the females' behavior; they may have approached related males more frequently than females in groups with no genetic relatives. The third female was in the group with the unusually dominant male, whom she often approached. I believe that this male's aggressive behavior affected the Hinde index for the pair. That same female also had a Hinde index biased toward the other male in the group, which provides evidence that she did hold some power.

It is important to consider the fact that many of the Hinde indices, though skewed toward the males, were close to zero. This means that males and females had roughly equivalent roles in maintaining proximity to one another. Again, more data would be beneficial to elucidate the responsibility of males and females for maintaining social bonds.

Spatial Proximity Observations and Pairwise Distances

The average distance between males and females was not significantly smaller than the distance between males and other males. I predicted that the distance between males and females would be smaller than the distance in intrasexual pairs. Dovetailing on the previous prediction, I reasoned that if males have the greatest responsibility for maintaining proximity to females, they will also be found near females more often than they are found near other males. However, this was not evident in my data. In fact, I found that the distance between female pairs was

significantly smaller than the distance between male pairs. This result may have implications within the framework of female power. If female *Varecia* maintain close spatial proximity to each other, strengthening the bonds among females, it may also strengthen the females' position within a group. This subject would be most effectively studied in large groups with multiple males and females, but this is challenging in captivity. Still, the bonds among females and the ways in which those bonds influence female power is an important topic to understand.

Upon reflection, I do not believe that my methods of instantaneous sampling were the most effective. I reasoned that 10-minute intervals between samples was a safe choice. It allowed me ample time to find and identify individual lemurs and estimate pairwise distances. However, I believe that same process could be completed in 5-minute intervals as well, allowing for twice the data points and a more robust analysis. Additionally, I would recommend collecting basic behavioral states during these instantaneous samples. That data could then be used to create a crude activity budget, furthering our knowledge of captive lemur behavior.

Limitations, Delimitations, and Assumptions

One of the primary limitations of this study was the time frame. Without sufficient funds, I could not stay at the Duke Lemur Center for more than two months, whereas a longer study would have been ideal. Additionally, during my two months on site, the Duke Lemur Center

closed on either a Monday or Friday for two holidays, which prevented me from collecting data on those days. I also caught a cold for two days and as per Duke University's Covid-19 protocol, I was not allowed to research. Finally, due to a family emergency, I had fly back to Illinois, which caused me to miss three research days. Given the resources, I would have stayed in North Carolina to make up for the lost time but was not financially able to do so. In any case, it would be best to conduct a study such as this one over the course of a year to capture any seasonal variation in behavior.

Another limitation was the lack of diversity in age classes among the Duke Lemur Center's ruffed lemurs. Initially, I had planned to use reproductive maturity as a second proxy for leverage. This variable would have been included in the statistical analysis for Research Questions 4 and 5. However, there were only four immature *Varecia* on-site at the time and only one of those immature individuals was included in this study. The other three juveniles were part of a family group with their mother. This group was excluded due to high genetic relatedness of group members and the lack of a mature male. Additionally, all four juveniles were *V. variegata*, so any comparison between the two lemur species would have been impossible.

Additionally, age is not an ideal proxy for leverage. While it loosely functions as an estimator for reproductive maturity, which is a superior proxy, age may not accurately predict leverage. The primary issue with using age is that its effect on reproduction is not entirely known. For this project, I assumed that reproductive potential increased with age. Once females reach reproductive maturity at approximately 2 years of age, I predicted that older, more mature females would be more successful at birthing and rearing offspring, thereby increasing their

reproductive potential. However, it is possible that ruffed lemurs experience a reproductive peak at some point early in their lives. Perhaps females that have newly reached maturity are more fertile than older females. Without further research, I cannot determine the extent to which age influences reproductive potential, but I recognize that using age as a proxy for leverage may be a significant flaw in my study.

A third limitation in this study was genetic relatedness. Only two of the six lemur groups had entirely unrelated individuals. Three groups had a pair of related individuals that included a pair of sisters, a pair of brothers, and a father and offspring pair. The last group was comprised of a breeding pair and their immature offspring. It is entirely possible that genetic relatedness complicates power dynamics. Ideally, a female power study like this one would include an even mix of related and unrelated groups, but for this project, it was impossible to avoid genetic relatedness while maintaining an adequate sample size. However, I recognize that relatedness may have confounded my results.

A fourth limitation was the small number of study groups. Before arriving at the Duke Lemur Center, I decided to exclude two *V. variegata* groups because they both had high genetic relatedness and lacked a mature male. This choice decreased my sample size by six and skewed the study groups toward the *V. rubra* species. Including those groups would have created an even distribution between the two species, making the comparison between them more accurate. However, I determined that the lack of a mature male was too great a confounder for a study on female power.

Another choice I made regarding the structure of this project was to ignore the difference in housing type among the groups. To be clear, I did not assume that housing type had no influence on the lemurs' behavior. In fact, I think it is a strong possibility that housing type had an effect on their behavior, and initially, I planned to analyze my data accordingly. After arriving at the Duke Lemur Center, I learned that housing arrangements are not static and can be subject to change. I experienced this with one *V. rubra* group that was shifted halfway through my project to an outdoor tour path exhibit. Additionally, two groups that were not free ranging in May started to range free by the start of June. These groups did not consistently range freely, however, and their housing type depended on weather, keeper availability, and the lemurs' cooperation. Another group that originally ranged freely every day was transitioned to free ranging only on certain days because this group did not get along with another species in the enclosure. Only two groups, those kept entirely indoors, did not change housing type during my observations, but even one of those groups changed enclosures within the same building. Since housing arrangements shifted so much over the course of my study, I determined that I could not reasonably include the housing type variable in my analysis.

This study was conducted under the assumption that the genus *Varecia* exhibits female power, either in the form of true dominance or leverage. The available literature on this topic suggests this assumption to be true, and the quantitative studies that have attempted to document female power in the genus corroborate that assumption (Pereira et al., 1988; Kauffman, 1991; Raps and White, 1995; Meyer et al., 1999; Overdorff et al., 2005). Additionally, this study, like many others, assumed that the two species, *V. variegata* and *V. rubra*, are similar enough in their behavior and ecology that conclusions drawn for one species can safely apply to both species.

Future Study Directions and Recommendations

While I purposefully avoided groups with only related individuals, I think that future research should tackle the issue of how genetic relatedness affects female power. In captivity, staff commonly keep ruffed lemurs in family groups, so understanding how relatedness affects power dynamics and conflict interactions is critical. With an increased knowledge of genetic relatedness, managers can adjust group arrangements to minimize conflicts and improve animal welfare. Considering the importance of infants and juveniles for contributing to their species' survival both in the wild and in captivity, this research is urgently needed.

Additionally, I observed intriguing social dynamics from the one family group included in my study (Group 4: Hermione, Herschel, Ripley). This group consisted of a breeding pair and their female offspring who was approximately one year old. More than once, I observed a conflict between the female offspring and the adult male that was interrupted by the adult female. After breaking up such conflicts, the adult female often directed aggressive behavior toward the adult male, seemingly defending her offspring. I did not observe this type of conflict intervention in any other group, and I think that the effect of the presence of a dependent offspring on group relationships is a topic worth investigating. I also observed the same juvenile female interrupting grooming sessions between her parents, which often resulted in conflict between her and her father, but I did not see such behavior in any other group. This group's unique behavior prompted me to ask three questions. 1) As young females mature and encounter conflict with their fathers, at what point do they assert dominance? 2) In what contexts do they assert their

dominance? 3) What role do their mothers play in the process? I hope to see future projects address questions like these in order to shed light on the family group dynamics of captive *Varecia*.

Future research at the Duke Lemur Center or similar institutions should evaluate the effect of housing type on behavior in general but also specifically on female power and conflict interactions. I predict that when lemurs range freely, conflicts are reduced simply by the increase in available space. If lemurs are less likely to encounter each other, they may also be less likely to encounter conflict. I also think that their social affiliations would be looser in natural habitat enclosures where they can spread out more. I observed this briefly in one group (Group 4) that stayed in close proximity while kept indoors but dispersed while free ranging.

It would also be useful to study behavioral changes in the lemurs exposed to the tour path. The zoo-visitor effect has been observed in many captive species, particularly primate species (Hosey, 2005; Mallapur et al., 2005; Cooke and Schillaci, 2007; Todd et al., 2007). How does the presence of visitors affect *Varecia*? In other species, the presence of noisy and/or numerous visitors increased vigilance behaviors and, in some cases, abnormal behaviors (stereotypies; Birke, 2002; Hosey, 2005; Mallapur et al., 2005; Todd et al., 2007). If that is the case with captive *Varecia*, managers can use that knowledge to adjust housing arrangements and potentially improve animal welfare.

Finally, a clear and necessary future direction for female power research is to apply this framework to a wild setting. Most research on the subject has taken place at the Duke Lemur Center or similar facilities. This trend is understandable as these methods translate easily to

captive animal research where subjects can be more closely and consistently observed. However, the value of wild lemur research cannot be overstated. Not only would this research contribute to conservation efforts, but it would also elucidate the ways in which lemur behavior varies between captivity and the wild. Long-term research in both settings is required to fully understand the intricacies of lemur behavior.

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APPENDIX A

PEREIRA ET AL. (1988) RUFFED LEMUR BEHAVIORAL ETHOGRAM

Behavior	Description
<i>Aggressive</i>	
Stare	protracted gaze directed at another with widening of eyes
Charge	direct run toward while staring at a stationary group member
Chase	sprinting pursuit of another ruffed lemur
Lunge	thrusting of upper or whole body toward opponent
Cuff	striking gesture with hand, from a tripod or bipedal position
Feint-to-cuff	rapid raising of hand without cuffing motion
Bipedal hop	hopping maneuvers around opponent preparatory to and during cuffs
Pounce on	jumping upon opponent
Push down	manual seizure of opponent's shoulders, forcing them down to the substrate
Bite	oral seizure of pelage or limbs
<i>Submissive</i>	
Displacement	abandonment of location by one animal due to approach by another
Chatter	high-pitched, rapid, staccato 'ik-ik-ik' vocalization directed toward a dominant opponent
Turn head/ avert eyes	looking away from a threatening individual
Cower/flinch	adduction of the limbs and pulling the body away from an aggressor
Grimace	drawing back the lips, exposing the teeth, keeping mouth fairly closed
Back away	walking backwards, away from but facing opponent
Flee	rapid locomotion away from opponent
Jump away	single jump away from opponent

APPENDIX B

DUKE LEMUR CENTER HOUSING ARRANGEMENTS BY GROUP

Species	Group	Sex	Name	DOB	Age	Dam	Sire	Free-ranging?	Weight	Breeding status
Varecia rubra	1	F	Mae	05/14/18	3.14	6995	6206	NHE3	3500	B
Varecia rubra	1	F	Judith	05/14/18	3.14	6995	6206	NHE3	3400	B
Varecia rubra	1	M	Afo	06/13/14	7.06	oi_100089	oi_100019	NHE3	2780	b
Varecia variegata	2	F	Kizzy	04/17/05	16.22	oi_9759	oi_9760	n	4020	I-18
Varecia variegata	2	M	Ravo	06/05/03	18.09	oi_103260	oi_103259	n	3280	b
Varecia rubra	3	M	Kalani	06/08/16	5.07	6995	6206	n	3940	b
Varecia rubra	3	F	Antika	05/17/09	12.13	oi_200393	oi_900081	n	3760	B
Varecia variegata	4	M	Herschel	05/21/13	8.12	6918	6950	NHE8	3200	b
Varecia variegata	4	F	Hermione II	02/21/16	5.36	oi_104855	oi_104405	NHE8	3060	NB
Varecia variegata	4	F	Ripley	05/12/20	1.14	7287	7155	NHE8	3010	IJ
Varecia rubra	5	M	Borealis	04/30/88	33.17	5587	5768	NHE9	3360	b
Varecia rubra	5	F	Ruby	05/13/18	3.14	-	-	NHE9	3420	-
Varecia rubra	5	M	Buzz	05/30/17	4.09	6633	6240	NHE9	3940	b
Varecia rubra	6	M	Minias	04/26/94	27.20	6203	6241	n	3140	nb
Varecia rubra	6	M	Hunter	05/17/96	25.14	6203	6241	n	3660	nb
Varecia rubra	6	F	Pandora	05/10/11	10.15	6838	6310	n	4240	NB