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Comparing True Maternal and Paternal Care in Pair-Living, Ex-Situ *Varecia rubra* (Red Variegated Lemurs) Contextualized Among Other Primate Cooperative Breeders

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Comparing True Maternal and Paternal Care in Pair-Living, Ex-Situ *Varecia rubra* (Red Variegated Lemurs) Contextualized Among Other Primate Cooperative Breeders

by

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Thesis Committee:
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Abstract

Observations of variegated lemurs in the wild have revealed a cooperative breeding strategy including extensive male care to young, primarily in the form of infant guarding. This thesis presents an analysis of the first quantitative assessment of true paternal and true maternal care from pair-housed, *ex-situ* red variegated lemurs (*V. rubra*) housed at the Lemur Conservation Foundation's Myakka City Lemur Reserve in western Florida. This study aims to answer specific research questions: How do paternal and maternal care compare when resources are abundant, and paternity is certain? Is male care instinctual? Is it driven by energetic necessity? If male care is instinctual, males can be predicted to offer substantial care to young regardless of whether females experience relatively lower energetic costs due to optimal nutrition and healthcare. If male care is driven by energetic necessity, then when energy is abundant, females can be predicted to offer sufficient care to young in the absence of multiple caregivers. The primary hypothesis therefore is that both males and females will offer substantial care to young in the Reserve setting. The study was conducted in 2007 and 2008 at the Lemur Conservation Foundation's Myakka City Lemur Reserve in western Florida. The study population comprised three litters and their parents over the course of two years. Focal litter and focal caregiver sampling at 5-min time point intervals was used to record litter activity and caregiving behaviors of long duration to determine percentage of time spent on each. All occurrence sampling was used to capture caregiving behaviors of short duration to determine rates of occurrence. The results indicate that mothers offer more care to litters than fathers both in terms of time allocation and frequency of care. In fact, they spend over 40% of their time engaged in caregiving activities, primarily guarding, grooming, and nursing, and to a lesser extent playing, huddling, defense, and infant transport. Fathers spend a considerable 23% of their time engaged in caregiving, primarily guarding, supplemented with grooming, and playing, and with some instances of huddling. The results of this thesis research support the prediction that males and females both provide substantial care to young, even when energetic needs are met by provisioned diet and healthcare. However, males are also apparently adjusting the care they provide as energetic cost to the mother rises (i.e., when mothers reach peak lactation, fathers take on more caregiving activities). Thus, male care is likely both instinctual and modulates in accordance with nursing mothers' energetic demands.

I would like to dedicate this thesis to my beloved son, Theodore. You inspired my interest in studying parenting and you give me a reason to keep working towards my goals every day.

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Chapter 1 Introduction and Background

1.1 Introduction

Ever since variegated lemurs (Genus *Varecia*) were first studied in *ex situ* settings, researchers noted that males offer substantial care to young, primarily in the form of infant guarding (Klopfer & Boskoff 1979, Pereira *et al*. 1987). Female *Varecia* were also observed caring for young who were not their own in these settings. Observations in the wild soon confirmed that *Varecia* males were not the only non-maternal individuals assisting mothers in raising young (Morland 1990). Indeed, extensive and systematic alloparenting documented for *Varecia* led to their eventual designation as cooperative breeders (Vasey 2007).

Care of offspring by males is rare in mammals (Kleiman & Malcolm 1981, Woodroffe & Vincent 1994), though more frequent within the order Primates (Kleiman & Malcolm, 1981). Furthermore, only a small number of mammals exhibit cooperative breeding (Lukas & Clutton-Brock 2017). Among primates, cooperative breeding has evolved only among a few genera including variegated lemurs and humans. In wild *Varecia* specifically, young are raised by multiple non-maternal caregivers (Vasey 2007), who are both kin and non-kin (Baden *et al*. 2013). Surprisingly however, we still lack quantitative data on how much care *Varecia* males provide infants and how levels of male care compare with those of mothers. To address this gap, I present an analysis of the first quantitative assessment of true paternal and true maternal care from pair-housed, *ex-situ* red variegated lemurs (*V. rubra)* housed at the Lemur Conservation Foundation's Myakka City Lemur Reserve in western Florida.

Paternity is very challenging to establish in wild primates. Mating may take place out of view of observers or females may mate with several males, making paternity very difficult to determine accurately without genetic data. However, *ex-situ* pair-housing of lemurs permits observation and documentation not only of male care, but true paternal care (defined in this study as care from males toward their own genetic offspring). Data collected at the LCF Lemur Reserve will permit me to establish facultative levels of maternal and paternal care in the absence of other caregivers (contrasting with the plural breeding pattern documented in the wild). Results of this study will also be of significant comparative value after quantitative data on infant care by males, mothers, and other community members become available from a wild, cooperatively breeding population of *V. rubra* from Masoala National Park, northeastern Madagascar (Vasey in prep.).

1.2 Background

Varecia Reproduction

The primate genus *Varecia* has several unusual and also some highly seasonal reproductive traits governed by photoperiod. *Varecia* mating occurs in an narrow window between May and July (austral winter), during which time animals mate within a one-week span (Morland 1993, 2007). Estrus lasts merely 24-72 hours (*ex situ*: Foerg 1982), and gestation lasts on average 102-109 days (wild: Morland 1993, Vasey 2007), although females during their primiparous estrus cycles generally do not reproduce successfully (Boskoff 1977). The birth season in Madagascar follows between September and November (austral spring), also occurring within a one-week span (Morland 1993, Vasey 2007). Physical adaptations to reproduction in this genus include having a third pair of mammae and strong tendency towards multiple births, most frequently twins or triplets (*ex situ*: Boskoff 1977; wild: Morland 1990, Vasey 2007). Females bear non-clinging young in arboreal nests and stash them in the treetops for several months (Morland 1990, Vasey 2007).

Male and female *Varecia* have sexual cycles. Males experience an increase in testicular size preceding female estrus, reaching maximum size on the day of copulation (Foerg 1982). In females, the vagina is imperforate; three to five days before receptivity the vagina opens to a round pink circle (Foerg 1982). Behavioral changes also occur in males and females during the mating season including courtship displays and aggression (e.g., squeal-approach by males, Morland 1993, Vasey, 2007). Mating is polygamous (multiple mating by both males and females) and likely facilitated by female choice and social dominance, meaning that females may accept, solicit, or reject males for mating purposes through calls, grooming, agonism, and aggression (Morland, 1993).

Varecia Social Organization

Varecia in *ex* situ settings are often housed in female-male pairs or in family groups consisting of a breeding pair and their offspring (Brockman *et al*. 1987, Taylor, pers com.). However, in the wild, *Varecia* live in large multi-male, multi-female communities characterized by fission and fusion (Vasey 2006, Baden *et al*. 2016). A fission-fusion community includes all individuals within a large territory that generally have affiliative interactions and is characterized by perpetual formation and disbanding of subgroups that vary in size, duration, and composition (individual and/or age-sex, Goodall 1986).

In *Varecia*, fission-fusion dynamics occur throughout the year even as social affiliation patterns change seasonally (Vasey 2006). *Varecia* communities are made up of multiple core groups, which are subsets of animals within the community that affiliate with each other more often than they do with members of other such core groups. In the austral summer, core group members fizz and fuse (i.e., form subgroups) with individuals from other core groups as well as with members of their own core group, whereas in the austral winter, core group members fizz and fuse almost exclusively with members of their own core group within geographically distinct parts of the communal home range (known as "core areas"). Larger subgroup sizes appear common in the presence of infants and are attributed to communal infant care which may increase infant survival rates (Holmes *et al*. 2016).

Male Care in Primates and other Mammals

Male care is defined as "any increase in a pre-reproductive mammal's fitness attributable to the presence or action of a male" (Kleiman & Malcolm 1981: 348). Male care is not always indicative of biparental care because often male caregivers may not be the biological sires (Woodroffe & Vincent 1994). In fact, most female mammals (90%) care for their young without male investment (Kleiman & Malcolm 1981, Woodroffe & Vincent 1994). In taxa where male care has evolved, males are more likely to help females rear young when the benefits outweigh the costs, such as when females are scarce and helping to care for young improves chances of future mating (Woodroffe & Vincent 1994), or when helping to care for young improves access to resources in a shared home range or territory (Vasey 2007). Other factors that may predispose male mammals to care for young include social living and paternity certainty (Kleiman & Malcolm 1981). Male parental investment therefore plays a key role in molding social organization (Kleiman & Malcolm 1981). Costs associated with male care include increased risk of predation, reduced mobility and foraging time, loss of body mass and condition, loss of mating opportunities, and possibly reduced survival (West & Capellini 2016).

Most primate species have primarily maternal care, yet they have the highest percentage of male care of any order of mammals (40% of species, Kleiman & Malcolm 1981). In a few New World monkeys - *Callicebus* and *Callithrix* - male care is extensive involving full-time infant carrying, which reduces maternal energetic burden (Wright 1990). These genera are relatively small-bodied (< 1300 g *Callicebus;* < 500 g *Callithrix*) and have relatively large infant-maternal body weight ratios (Table 1). When males carry offspring, birth frequency is often higher, allowing females to invest more energy in milk production and wean earlier (West & Capellini 2016). Indeed, in the entire New World subfamily Callitrichinae, male care is obligate (meaning that young do not survive without non-maternal care), tied to the high maternal energetic costs of gestating while lactating (Erb & Porter 2020, Snowdon & Ziegler 2007, Zahed *et al*. 2010). The extent of male care is also remarkable in the lemur genus *Varecia*, notably in terms of infant guarding. Yet the factors underlying male care must be different because *Varecia* are larger-bodied seasonal breeders and enter reproductive condition only once a year (West & Capellini, 2016). Furthermore, male *Varecia* are not known to carry infants (Pereira *et al*. 1987).

Cooperative Breeding

A breeding system refers to an animal species' strategy for attracting mates, mating behavior, and parental care (Reynolds 1996). Cooperative breeding refers to when individuals other than parents offer parent-like care to young, such as feeding, grooming, or babysitting (Jennions & Macdonald 1994). Among group-living mammals the strategy may be singular, meaning that a single female gives birth and non-breeding individuals contribute to infant care (e.g., provisioning, defense). In this case, caregivers defer breeding and instead assist in infant care meanwhile experiencing the benefits of group living such as future reproduction and protection from predators (Jennions & Macdonald 1994). Alternatively, cooperative breeding may be plural, where multiple adults mate and multiple females give birth. In this case, both breeding and non-breeding group members may help care for young (Lewis & Pusey 1997). Cooperative breeding is known in a small percentage of avian species (3.2% Arnold & Owens 1998; 9% Cockburn 2006), and fewer than 1% of mammalian species, scattered across a small number of genera within the orders Carnivora, Rodentia and Primates (Lukas & Clutton-Brock 2017).

Cooperative Breeding in Primates

Cooperative breeding is known in only three primate lineages, the Callitrichinae **(**marmosets and tamarin monkeys of Central and South America), *Microcebus* (mouse lemurs), and *Varecia* (red ruffed lemurs). It is also established in human societies (Hrdy 2009).

Callitrichines (*Callithrix, Mico, Cebuella, Saguinus, Leontopithecus*)

Callitrichines were the first nonhuman primates shown to practice cooperative breeding and extensive male care of infants (e.g., Erb & Porter 2020, Saltzman *et al*. 2004, Snowdon and Ziegler 2007, Zahed *et al*. 2010). Many genera in this subfamily (listed above) form extended family groups which produce twins up to twice per year (with the exception of *Callimico* and *Callibella*, which produce singletons). These groups consist of a single breeding female, breeding males, other nonbreeding adults, and mixed age offspring (Zahed *et al*. 2010). The production of twins by Callitrichines is probably driven by heavy predation and their adaptations as colonizing species (Martin 1992). The high energetic expense of gestating twins while lactating requires the help of additional non-maternal caregivers (Erb & Porter 2020, Snowdon & Ziegler 2007, Zahed *et al*. 2010). Among most callitrichines, fathers are the primary caregivers (Erb & Porter 2020, Snowdon & Ziegler 2007, Zahed *et al*. 2010) with older brothers (from prior litters) taking a secondary caregiving role (Zahed *et al*. 2010). However, all members of the social group participate in infant care to varying degrees and will adjust their roles as additional caregivers become available or unavailable (Erb & Porter 2020, Zahed *et al*. 2010).

Caregiving behaviors include carrying young, food provisioning, grooming, and vigilance against predators (Erb & Porter 2020, Snowdon & Ziegler 2007, Zahed *et al*. 2010). Carrying young is extremely important to offset maternal energetic costs because callitrichine infants weigh ~20% of maternal body weight at birth (Table 1), and at 6-10 weeks, up to 50% maternal body weight (Erb & Porter 2020). Additionally, carrying serves several other functions including transportation, protection, and thermoregulation (Zahed *et al*. 2010). Carrying young can be an extremely costly form of care, as fathers have been found to spend 11% less time feeding and 15% more time resting (Erb & Porter 2020), and fathers with no help lose up to 10.8% of body weight while carrying infants (Achenbach & Snowdon 2002). Carrying is the primary caregiving behavior studied in callitrichines because of its high energetic expense, however another significant male caregiving behavior is providing novel food sources for infants, which allows mothers to gradually reduce nursing and wean infants earlier (Snowdon & Ziegler 2007). Cooperative care ultimately relieves mothers from absorbing all reproductive costs and allows them to concentrate energy to produce twins twice a year (Snowdon & Ziegler 2007).

Caregivers also receive benefits from providing care to infants. These include parenting experience, social prestige, enhanced survival, and future reproductive opportunities (Erb & Porter 2020). Older brothers who practiced infant care later show significantly higher rates of carrying and reproductive success as they became fathers (Zahed *et al* 2010). Alloparents also receive more grooming from parents, likely as a reward or incentive for their help (Snowdon & Ziegler 2007).

Though callitrichines are often considered singular cooperative breeders, they have been shown in certain circumstances to practice plural cooperative breeding as well (Saltzman *et al*. 2004). Usually, related females (specifically mothers and daughters) group together with fathers and other offspring. Daughters have never been observed to mate with their own fathers (Saltzman *et al*. 2004). In marmosets (*Callithrix, Mico,* and *Cebuella*), daughters are reproductively suppressed by their mothers, meaning they do not ovulate if they are behaviorally subordinate to their mothers (Saltzman *et al*. 2007). Tamarins (*Saguinas* and *Leontopithecus*) in contrast are reproductively oppressed, meaning daughters are kept from mating through aggressive behaviors from mothers

(Snowdon & Ziegler 2007). However, when the father in a family group is replaced with an unrelated novel male, ovulating daughters have been shown to mate and reproduce successfully, leading to plural cooperative breeding (Saltzman *et al*. 2007).

Mouse Lemurs (*Microcebus)*

Among lemurs, mouse lemurs practice plural cooperative breeding, but not male care. Cooperative care in this genus includes nest sharing (Perret 1998), grooming, allonursing and adopting related infants after the death of their mothers (Eberle & Kappeler 2006). In *Microcebus murinus*, female mouse lemurs spend the austral winter months in a state of torpor in mixed-sex groups with males that remain active (Perret 1998, Eberle & Kappeler 2006). During the breeding season, however, females form single-sex nesting groups of up to four adults (Perret 1998). These nesting groups consist of young plus mother and daughters or sisters (76%), grandmothers and granddaughters, or nieces and aunts (20%), and cousins (4%); they never include males or unrelated females (Eberle & Kappeler 2006). However most of the time only one female is present in the nest, taking on the energetically expensive task of providing all infants with care while the other females forage (Eberle & Kappeler 2006). Interestingly, females transport only their own young, and although they provide care to all offspring, they groom and nurse their own young more often, (Eberle & Kappeler 2006).

Nesting lasts up to 16 weeks employing one or two nests (Eberle & Kappeler 2006). When nests are switched, entire groups move together rather than separating

(Eberle & Kappeler, 2006). Nest sharing, and in turn, alloparenting, has been shown to minimize the energetic cost of infant care by 20% when grouped in pairs, and up to 40% when groups consist of three or more adult females (Perret 1998). Though nest sharing has been shown to increase predation, it is nonetheless a species-specific behavior. This suggests that the energetic benefits outweigh the costs, and that natural selection is likely at play (Perret 1998). Mouse lemurs differ from callitrichines in that mating is seasonal and limited to a four-week period (Eberle & Kappeler 2006), meaning only one litter (1-3 infants) can be produced per female per year. So, they do not benefit from increased reproductive output from cooperative breeding. Instead, it is thought that they benefit from reduced energetic cost during seasonal food shortages (Perret 1998) and reproductive fitness through survival of kin, as kin selection appears to apply to their alloparenting strategy (Eberle & Kappeler 2006).

Variegated lemurs (*Varecia)*

Varecia practice a plural cooperative breeding strategy similar in some ways to each of the above lineages (callitrichines and *Microcebus*), but identical to neither one. Multiple adult females within a social community reproduce and systematically share extensive maternal responsibilities (Baden, 2011, Vasey 2007). In fact, like callitrichines, energetically costly forms of alloparenting are seen in adults and subadults of both sexes (Vasey 2007). Unlike callitrichines however, *Varecia* males are not the primary caregivers, females exclusively carry infants (Pereira *et al.* 1987), and breeding is strictly seasonal (Morland 1993, Vasey 2003). In the lemurs (*Microcebus* and *Varecia*), litter weight as a percentage of maternal weight is typically less than half of that in callitrichines where males routinely carry young (Table 1). Like mouse lemurs, *Varecia* give birth to non-clinging infants, build nests to bear them in, share nests (Baden *et al*. 2011, Baden *et al*. 2013, Baden *et al*. 2019, Vasey 2007), allonurse (Pereira *et al*. 1987, Vasey 2007), and in some cases adopt young (Vasey 2007). Yet, alloparenting is not tied exclusively to kinship; instead, mutualism may play a large role in prompting individuals to care for young who are not their own genetic offspring (Baden *et al*. 2013, Vasey 2007).

Cooperative breeding appears essential to *Varecia* because of the high energetic expense associated with its reproduction. When body size is corrected for allometrically, Young *et al.* (1990) found that among strepsirrhines, *Varecia* produces the heaviest litters relative to maternal body weight. Alongside *Microcebus* and *Cheirogaleus*, *Varecia* also has the highest rate of prenatal maternal investment, comparable to that of haplorrhines (Young *et al*. 1990; see also Table 2). This is because they produce litters of 2-3 offspring over a relatively short gestation, whereas most other primates have singletons. Unlike the vast majority of primate infants, *Varecia* young are unable to cling to their mothers at birth and are instead transported orally. Activity budgets and ranging by *Varecia* females reveal strategies that help conserve and store energy during gestation to make up for the high energy expenditure of lactation and infant care (Vasey 2005, Vasey 2006).

One alloparental behavior that conserves energy in *Varecia* is stashing infants (Baden *et al*. 2011, Baden *et al*. 2013, Baden *et al*. 2019, Vasey 2007). Females select the largest trees in the forest for nesting and stashing young (Vasey *et al*. 2018) in areas with higher densities of feeding trees (Baden *et al*. 2019). As infants grow, mothers begin stashing their non-clinging infants in arboreal sites beyond the natal nest site, often alongside a non-maternal caregiver (Baden *et al*. 2019, Vasey 2007). Communal nesting sometimes occurs and results in lower infant mortality than singular nesting (Baden *et al*. 2011, Baden *et al*. 2013, Baden *et al*. 2019, Vasey 2007), as well as energetic benefits to mothers by allowing them more time for feeding (Baden *et al*. 2011). Communal stashing is not necessarily linked to kinship or female social dominance, but rather a case for mutualism appears integral (Baden *et al*. 2013, Vasey 2007). When other adult caregivers are available, mothers will leave their young alone at a younger age (Morland 1990, Pereira 1987). In one study, about 36% of infants' social time was spent with non-maternal caregivers (Morland 1990).

Another key aspect of *Varecia* alloparenting is male care. While females exclusively allonurse and transport young, reproductive males provide extensive care for infants including guarding, grooming, huddling, coordinated predator defense, and play (Morland 1990, Vasey 2007). During the day, infants may even spend more time in proximity to the likely father than the mother while mothers are foraging, traveling, and engaging in social activities away from the infant (Morland 1990). Males and other members of the mother's coregroup station themselves near (but not in) the nest as early as the second week after birth in the mother's absence (Vasey 2007). Likewise, one *ex-situ* study on free-ranging *Varecia* (Pereira *et al*. 1987) found that mothers kept fathers and unrelated lemurs away from infants during the newborn stage. Two to three weeks later, infants were moved from the natal nests and left alone while the mother foraged.

Infants were often stashed together and nursed by multiple lactating females. Males guarded nests and became aggressive with other lemurs and humans who came close to them. Lastly, males frequently came into proximity of nests while females were away, and left the area once females returned (Pereira *et al*. 1987).

Humans (*Homo* spp.)

Vasey and Walker (2001) proposed that cooperative breeding first became established ~ 2 MYA in the genus *Homo* and this idea has subsequently taken root in paleoanthropological literature (e.g., van Schaik & Burkart 2010). It is hypothesized that humans developed this type of breeding system due to harsh environmental conditions (Martin *et al*. 2020). This hypothesis is supported by modern studies where cooperative infant care is observed more often in regions where environmental conditions are unpredictable or harsh (Martin *et al*. 2020). However, instances of cooperative infant care are lower in regions where starvation is more prevalent (Martin *et al*. 2020). In these locations, the ultimate benefit of cooperative breeding does not outweigh the risk to personal survival (Martin *et al.* 2020).

Bogin and Varea (2017) have pointed out that humans have evolved a plural cooperative breeding strategy that resembles *Varecia* more closely than any other primate, even compared with our closest relatives, the hominoid apes. The human reproductive strategy includes extensive cooperative care of young and pregnant mothers by all members of the community (Bogin & Varea 2017). This care strategy allows humans to experience the unique life history trait of childhood - the period between 3 and 6 years during which children are no longer nursing but are still reliant on adults for food provisioning and care (Bogin & Varea 2017). In effect, humans wean their infants earlier, return to sexual receptivity quicker, and reproduce more often than other apes (Bogin & Varea 2017). This is interesting because although humans practice cooperative breeding just as do as callitrichids, mouse lemurs and *Varecia*, each lineage has arrived at it by different means.

Some researchers suggest that cooperative breeding is so fundamental to human evolution that it may be the key trait that separates us from the rest of the apes (Burkart *et al*. 2009). Humans and the large apes (i.e., chimps, gorillas, orangutans) share heightened cognitive abilities, yet humans have unique mental capacities. Burkart *et al*. (2009) suggest that cooperative breeding is associated with psychological changes and greater prosociality. They also suggest these prosocial psychological behaviors combined with ape-level cognitive abilities lead to the uniquely human cognitive abilities we possess.

Cooperative breeding is still essential to human survival and wellbeing today, despite many western cultures' shift toward small nuclear families living in single family homes. A study by Sear and Mace (2012) examined the effects of alloparenting in a population in Gambia that has a 50% child mortality rate. They found that mothers were critical for child survival in the first two years; yet between age two and five, care from other community members became a significant predictor of child survival. Furthermore, they found that the person providing care makes a difference. Matrilineal kin were correlated with growth and survival of children, while patrilineal kin were correlated with increased maternal fertility. Another study suggests that mothers with alloparental support are less likely to abandon their infants, immediately impacting their chance of survival (Hrdy, 1999). Additionally, Olds *et al.* (2002) found that even intermittent visits to postpartum mothers by nurses able to provide support improved children's outcomes later in life (cognitive, school, and life choices).

Chapter 2 Methods

2.1 Scope of Study and Predictions

Varecia has many unusual reproductive traits compared with other primates, made more interesting in that some are shared with humans, such as non-clinging neonates and comparatively greater investment by males in the survival of young. These traits co-occur with, and likely mitigate, the very high energetic costs of female reproduction in *Varecia*. At the LCF Myakka City Lemur Reserve where diet and healthcare are optimized and more stable compared with seasonal oscillations experienced in the wild, females may require less care from non-maternal caregivers to raise young. Thus, with the Reserve data I should be able to detect whether one correlate of high female reproductive costs, male care, is instinctual (i.e., under strong genetic control). If so, I would predict males to offer substantial care to young regardless of whether females experience relatively lower energetic costs due to optimal nutrition and healthcare. Likewise, if *Varecia* have evolved a bust and boom reproductive pattern in tandem with stochastic environmental conditions (i.e., yearly variation in the occurrence and severity of extreme weather, including cyclones. Ratsimbazafy 2002, Vasey *et al*. 2022), then I would predict that when energy is abundant (e.g., under Reserve conditions) females are able to offer sufficient care to young in the absence of multiple caregivers. My primary hypothesis therefore is that both males and females will offer substantial care to young in the Reserve setting.

To address this prediction I compare the extent and frequency of different types of maternal and paternal care. Specific research questions include: How do paternal and maternal care compare when resources are abundant and paternity is certain? Is male care instinctual? Is it driven by energetic necessity? The answers to these questions will help shed light on male care within the genus *Varecia*, and by extension, to other cooperatively breeding primates.

2.2 Methods and Data Analysis

Study Site

The study was conducted in 2007 and 2008 at the Lemur Conservation Foundation's Myakka City Lemur Reserve in western Florida. Local vegetation includes pine flatwoods and oak hammocks. Lemur habitats include two separate forest enclosures (one 9 acres and one 13 acres) made up of native Floridian vegetation supplemented with mango, passionfruit, guava, grapes, persimmon, and bamboo. Lemurs are allowed to range freely and forage within these enclosures and are fed a primary diet of primate chow and fresh fruits and vegetables daily. Lemurs have access to indoor shelters and are brought inside during times of physical or environmental stress. They are also housed in shelters (without access to the forest) when anticipating birth of young and during the early months postpartum. *Varecia rubra* breeding pairs have access to nest boxes for infant stashing and care to encourage their natural behaviors.

Study Animals

The study population (Table 3) comprised three litters and their parents over the course of two years. The adult pair Bopp (female) and Tsard (male) produced a litter of three, born on 28 April 2007. These three included a male Orana, a female Kintana who died less than two weeks later on 9 May, and a male Volana who died 8 August. Adult pair Hale (female) and Tsikey (male) produced their first litter on 1 May 2007. Their offspring included two males and one female who died in August 2007. In 2008, Hale and Tsikey produced their second litter together. This all-male litter, born 28 April 2008, included Rivotra, Masoandro, and Volana II.

Data Collection

Data were collected from 19 May until 31 August 2007 and 12 May until 31 July 2008 over the course of a total 327.45 hours (19.3 hours maternal observations, 17.33 hours paternal observations, 290.82 hours litter observations). Data were collected by LCF husbandry staff Monica Mogilewski and Tyann Marsh using a data collection protocol developed by Vasey (2009). Two sampling methods were used to effectively sample target behaviors of both long and short duration (Martin and Bateson 2007). Focal litter and focal caregiver sampling at 5-min time point intervals was used to record litter activity and caregiving behaviors of long duration (i.e., that occur as states) to determine percentage of time spent on each. All occurrence sampling was used to capture caregiving behaviors of short duration (i.e., that occur as events) to determine rates of occurrence. In 2007, data were collected by observing litters (2 focal litters, N = 6 infants), while in 2008, data were collected by observation of both litters and caregivers (one focal litter, N = 3 infants; focal caregivers, N = 2). For litter and caregiver time point samples, observers recorded date, litter identity, litter age in weeks, litter/caregiver activity (feed, rest, move, other, out of sight), type of infant care, caregiver identity, and caregiving related vocalizations (infant squeaks). For litter and caregiver all occurrence samples, observers recorded date, litter identity, litter age in weeks, caregiver identity, type of infant care, and infant squeak vocalizations. Additionally, notes on developmental milestones were made. An ethogram of observed types of infant care can be found in Table 4 with an indication as to whether each behavior is best treated as an event or a state for purposes of statistical analysis and interpretation. Types of infant care include adult-infant play, defense, groom, guard, huddle, infant transport, nurse, and stash. Nursing was the only behavior for which duration was recorded.

Data Analysis

Caregiver Observations

For data analysis, I used R (version 4.1.2 (2021) "Bird Hippie"). Initially, I used the caregiver time point data collected in 2008 to determine activity budgets for the dam and sire (i.e., mother and father). To do this, I totaled the number of time points each parent spent engaged in caregiving, feeding (consuming chow, produce, or foraged foods; does not include nursing), resting (not engaged in movement or other activities, includes huddling for infants), moving (movement that involves the whole body and does not involve play), out of sight, and doing other activities. Next, I calculated the percentage of time points for each activity to illustrate overall activity budgets. Then, I compared the maternal and paternal activity budgets using G tests to determine whether or not there was a significant difference between parents in time spent caregiving, feeding, resting, moving, and in other activities.

Afterward, I examined behaviors within the caregiving category exclusively (Table 4) to determine percentages of caregiving time spent on each type of care. Again, I used G tests (goodness-of-fit tests used to determine whether experimental frequencies fit into the theoretical expectation, in this case whether male care is equivalent to female care) to determine if the mother or father spent more time engaged in particular caregiving behaviors. To supplement this analysis, I used the caregiver all-occurrence data to determine an hourly rate for each caregiving behavior (i.e., how many times, on average, the mother or father initiated each behavior per hour) and ran G tests on those hourly rates as well. The reason both types of data were analyzed in this way is because time point samples provide a measure of how much time is spent on specific behaviors, while all occurrence samples measure how often these behaviors are occurring irrespective of time spent on them. Time point sampling better represents behaviors that last a long time but are less frequent (such as guarding) while all occurrence sampling better represents behaviors that are frequent but may only last seconds or minutes (such as playing or grooming).

Litter-based Observations

` After examining the caregiver-based data, I analyzed the litter-based data from 2007 and 2008. First, I used the all-occurrence data to count how many times each parent (mother or father) was observed providing care and calculated hourly rates for each. Next, I used a G test to determine if there were significant differences in the hourly rates of care between mother and father. Then, I repeated the previous steps, excluding care marked as “nursing” since nursing is biologically limited to females. I also calculated the total amount of time spent nursing, and the mean and median lengths of nursing sessions.

Subsequently, I examined specific care behaviors. Using the time point litter data, I determined the percentage of caregiving time the infants received each type of care. Using the all-occurrence litter data, I determined the frequency (hourly rate) with which infants received each type of care. Then I examined the frequency (hourly rate) with which infants received each type of care from each parent. I ran G tests on these frequencies to determine if infants received certain types of care more often from the mother or father. Finally, I divided observations by infant age (in weeks) and compared frequencies of caregiving behaviors by mothers and fathers on a weekly basis. These data are illustrated in line graphs (Figs. 4-11) and show how caregiving changes as infants grow.

Chapter 3 Results

3.1 Caregiver Observations: Overall Activity Budgets, Caregiving Time Budgets, and Hourly Rates of Care

The mother spent 41.37% of time points engaged in infant caregiving behaviors, followed by 39.36% resting, 6.43% feeding, 5.22% moving, and 6.83% in other activities; she was out of sight just 0.8% of the time (Fig. 1). The father spent 57.75% of his time resting, 23.00% on infant care, 6.57% feeding, 5.63% moving, and 7.04% in other activities (Fig. 1). There is a significant difference in time spent caregiving (G = 5.316, X-squared df = 1, p-value = 0.02113) with females spending more time on care. Time spent resting approaches significance with males resting more (G = 3.5037, X-squared df = 1, p-value = 0.06123). However, there is no significant difference in time spent feeding (G = 0.0015077, X-squared df = 1, p-value = 0.969), moving (0.015497, X-squared df = 1, p-value = 0.9009), or in other activities (0.0031796, X-squared df = 1, p-value = 0.955).

When caregiving time was examined exclusively, the mother spent nearly half her time guarding infants (48.54%), followed by nursing (36.89%), grooming while nursing (9.71%), grooming alone (0.97%), and infant transport (0.97%) (Fig. 2). The father spent the vast majority of his caregiving time guarding infants (95.91%), followed by grooming (2.04%) and playing (2.04%) (Fig. 2). The father spent more time guarding infants than the mother, a highly significant result (G = 15.825, X-squared df = 1, p-value = 6.947e-05), whereas the mother groomed young significantly more than the father when behaviors scored as “grooming while nursing” were included (G = 6.4326, X-squared df

= 1, p-value = 0.0112). Time point sampling did not capture the mother playing with the infants, nor the sire transporting or huddling with them. All-occurrence sampling, on the other hand, picked up some of these short-duration or less frequent behaviors. For example, the mother played with infants at a rate of 0.88 occurrences per hour, while the father huddled with infants at a rate of 0.17 occurrences per hour (Table 5).

Hourly rates for each infant care behavior calculated from all occurrence samples demonstrate that the mother frequently groomed young (4.56/hr.), followed by guarding (2.02/hr.), nursing (1.35/hr.), playing (0.88/hr.), huddling (0.73/hr.), defense (0.47/hr.), and infant transport (0.31/hr.). The father more frequently guarded (2.19/hr.), groomed (1.79/hr.), and played (1.56/hr.) with young compared with huddling them (0.17/hr.), and was never observed transporting or defending them (Table 5). G tests indicate no significant differences between mother and father in the frequency of caregiving behaviors they performed in common: guarding (G = 0.0068665, X-squared df = 1, p-value = 0.934), grooming (G = 1.2499, X-squared df = 1, p-value = 0.2636), huddling (G = 0.37537, X-squared df = 1, p-value = 0.5401), and playing (G = 0.19204, X-squared df = 1, p-value = 0.6612). However as discussed in the Methods, behaviors of long duration, such as guarding and nursing, are more appropriately measured and analyzed in terms of time spent, not frequency.

3.2 Litter-based Observations: Time Allocation, Hourly Rates, and Ontogeny of Care Received by Infants

Litter time point data reveal the percentage of time points infants received each type of care combining care from both mothers and fathers (Fig. 3). Most of the time infants were guarded (49.16%), followed by being nursed (23.27%), huddled (6.76%), groomed (1.58%), transported (0.81%), played with (0.11%), and defended (0.05%). Additionally, 17.33% of the time, infants were stashed (i.e., left alone). They were out of sight just 0.93% of observations. Whereas guarding takes up the largest amount of time, all occurrence data (also combining care from both mothers and fathers) reveal high frequencies of several short duration behaviors such as grooming (8.11 occurrences per hour) and play (2.53/hr.) (Table 6). Nursing is both frequent (2.58/hr.) and of long duration (see below). Infant transport is less frequent having the second lowest hourly rate (0.91/hr.) but lasts long enough to be captured in time point samples (Fig. 3), whereas infant defense is both infrequent (0.62/hr.) and of short duration.

Litter-based all-occurrence samples were further used to calculate hourly rates of maternal and paternal care received by young irrespective of type of care. Fathers provided care at a rate of 3.21 occurrences per hour, whereas mothers provided care at a rate of 13.35 occurrences per hour. When nursing is excluded, the maternal rate drops to 10.77 occurrences per hour. With (G = 6.6705, X-squared df = 1, p-value = 0.009802) or without nursing (G = 4.3153, X-squared df = 1, p-value = 0.03777) included, mothers have significantly higher hourly rates of care. However as previously indicated, hourly rates are biased toward short-duration behaviors and therefore do not effectively represent long-duration behaviors like guarding, the predominant type of paternal care. A total of 385 nursing sessions were recorded through the observation periods with 296 (76.88%) having recorded bout durations. These 296 nursing sessions included 36.72 hours of nursing. The mean time per nursing session was 7.44 minutes, and the median was 3.33 minutes.

Considering hourly rates of care received by infants from mothers and fathers separately (Table 6), both parents groomed infants with the highest frequency (6.82/hr. for mothers and 1.28/hr. for fathers), followed by nursing (2.58/hr. mothers), and playing (1.28/hr. for mothers and 1.23/hr. for fathers). Both parents had similarly low rates of defense (0.31/hr. for mothers and 0.33/hr. for fathers) and guarding (0.47/hr. for mothers and 0.34/hr. for fathers), whereas infants huddled more often with mothers than fathers (0.98/hr. for mothers and 0.03/hr. for fathers). Males were not observed transporting infants. As with caregiver-based hourly rates, keeping in mind the methodological pitfalls of comparing short and long-duration behaviors side by side, there were no significant differences in hourly rates of infant care received from mothers versus fathers in terms of defense (G = 0.0006251, X-squared df = 1, p-value = 0.9801), guarding (G = 0.020955, X-squared df = 1, p-value = 0.8849), huddling (G = 1.1301, X-squared df = 1, p-value = 0.2878), or play (G = 0.0014287, X-squared df = 1, p-value = 0.9698). However, there was a significant difference in grooming (G = 4.1596, X-squared df = 1, p-value = 0.0414).

The frequency of parenting behavior was then compared on a weekly basis over the first 15 weeks of the infants' lives to see if maternal and paternal parenting behaviors changed based on the age of their young. In both parents, defense appears to spike before five weeks and drop to very low rates afterward (Fig. 4). Both parents follow a similar pattern in terms of infant guarding as well with steadily declining rates over the course of infancy (Fig. 5). Mothers groomed young more than fathers but decreased their frequency of grooming as the infants matured (Fig. 6). Although fathers did not groom as much as mothers, fathers showed an inversed trend; as infants grew, the frequency of grooming by fathers slightly increased (Fig. 6). Huddling did not appear to have a discernable pattern, though mothers had higher frequencies throughout the 15 weeks (Fig. 7). Infant transport, only observed in mothers, showed a clear pattern of decreasing frequency as infants aged and gained competency in locomotion (Fig. 8).

Perhaps the most interesting pattern is the relationship between nursing and play. In the early weeks, mothers participated in play at higher rates which steadily declined as infants aged (Fig. 9). Inversely, fathers had lower rates of play in early infancy, with rates increasing as infants aged (Fig. 9). Paternal and maternal rates of play mirror each other, intersecting just past 10 weeks. Nursing follows the same pattern as paternal play, starting low and increasing as infants age (Fig. 10). When nursing and play are graphed together (Fig. 11), a clear pattern emerges of fathers taking over play duties at the same time that nursing peaks when mothers reduce their participation in play.

Chapter 4 Discussion and Future Research

4.1 Discussion

The results indicate that mothers offer more care to litters than fathers both in terms of time allocation and frequency of care. In fact, they spend over 40% of their time engaged in caregiving activities. Fathers spend the most time resting, but with a considerable 23% of their time engaged in caregiving. This finding suggests that males contribute substantially to rearing their litters despite not carrying infants nor feeding them. Aside from caregiving, the activity budgets of fathers and mothers did not differ significantly. There was no significant difference between the amount of time spent feeding, moving, or doing other activities, although time spent resting was nearly significantly different (G = 3.5037, X-squared df = 1, p-value = 0.06123). It appears then that *ex-situ Varecia* mothers carve out caregiving time at the expense of rest. How this finding may compare to females experiencing the demands of food acquisition in the wild (i.e., foraging) has yet to be examined.

In congruence with wild data (Vasey 2005), mothers and fathers in this study spent similar amounts of time traveling. However, wild *Varecia* mothers, in every reproductive stage besides gestation, feed more and rest less than males due to the high energetic expense of reproduction (Vasey, 2005). *Varecia* at the LCF Reserve their allocate time differently, given that there is no significant difference between the father and mother in time spent feeding or resting. Similar time allocation for feeding and resting may be expected in this setting because energetic needs are met by provisioning, supplemented by foraging on local resources within the forest habitats.

The effect of food provisioning is apparent in comparisons of *in-situ* and *ex-situ* activity budgets. In the wild, *Varecia* mothers spend about 30% of their time feeding (regardless of season or reproductive stage), whereas males spend about 20% of their time feeding during female lactation (Vasey 2005). In contrast, observations of father and mother with human provisioning show that they spend less than 7% of their time feeding. *Ex-situ* lemurs also spent less than 7% of their time travelling compared to 24.8% for mothers and 26.8% for males during female lactation (Vasey 2005). These percentages do not compensate for reduced ranging possibilities.

When individual caregiving behaviors were analyzed, there were some clear patterns. Mothers are occupied with guarding, grooming, and nursing, and to a lesser extent playing, huddling, defense, and infant transport. Meanwhile, paternal caregiving focusses primarily on guarding, supplemented with grooming, and playing, and with some instances of huddling. These findings are consistent with observations in Madagascar (Morland 1990, Vasey 2007) where male caregivers have been observed guarding and grooming infants and playing with older offspring. In both this study and all wild studies to date, females move infants between nests by mouth carrying. No males have been observed transporting infants in any setting.

One explanation for male care in primates (deriving from callitrichines) is that males transport infants to reduce energetic costs to lactating mothers. In *Varecia*, it appears that maternal nursing peaks just after 10 weeks by which time infant transport has markedly decreased and when, in the wild, infants travel independently for hours at a time but are still stashed for part of the day (Vasey 2007). Since they are mobile, the demand for guarding also decreases. Thus, at the time of peak nursing, the main paternal caregiving behaviors are grooming, playing, and huddling. Male care increases as time spent nursing decreases, according to the data I analyzed. Males do become more involved in care. Males appear to engage in playing with the offspring as they become more coordinated and are spending more time outside of stash sites. Active chase and contact play with multiple offspring can be energetically expensive. Male infant grooming also increases slightly at this time which may involve social bonding between individuals as the offspring mature, although this aspect of male involvement has yet to be studied across a larger study population.

These results align with wild studies reporting that male *Varecia* are key players within their cooperative breeding system and contribute a substantial amount of their time and energy to infant care (Vasey 2007). In fact, in this study, where other potential care givers were not present, fathers played a statistically significant role in survival of their own offspring, contributing nearly one quarter of their time to caring for young. One finding from this study which deviates from wild studies is that defense behaviors are observed much less often in both males and females. This difference is likely due to the difference in predator pressures.

The results of my thesis research support the prediction that males and females both provide substantial care to young, even when energetic needs are met by provisioned diet and healthcare. Despite females at LCF likely having a lower energetic cost than their wild conspecifics, males continue to help, suggesting that male care is instinctual (under strong genetic control) in male *Varecia*. It may be that when given a choice, females would prefer to mate with males who demonstrate a willingness to participate in infant care and show skill when doing so. A learning component is likely for these behaviors and would support the view that non-parental nest helpers are "learning" to parent in the wild. No such non-reproductive individuals were present during the times when data were collected, so it is not possible to predict how much fine-tuning of parenting skills occurs. Males are apparently adjusting the care they provide as energetic cost to the mother rises (i.e., when mothers reach peak lactation, fathers take on more caregiving activities). Thus, male care is likely both instinctual and modulates in accordance with nursing mothers' energetic demands.

4.2 Future Research

This research should be complimented by wild data collected in the same manner. It will be possible to compare whether the patterns in male and female caregiving behaviors noted in this pilot study hold true. This information will give us further insight into the evolutionary advantages of male care in *Varecia rubra*.

Additionally, I hope to use this research as the beginning for future study. Some questions for consideration include: How is male parenting behavior linked to reproductive success in male strepsirrhines, including those taxa who nest and those which do not? How do interaction patterns in subadult males compare to other male primates which exhibit parenting behaviors? How do males learn to parent?

All of these questions have the potential to give us deeper insights into the evolutionary basis of male parenting in *Varecia,* as well as in our own species. As genetic data make it possible to positively identify paternity, it should then be possible to expand our understanding of what fathering is like across the Order.

Table 1. Litter to maternal weight ratios for cooperatively breeding primates[1]

Species[2]	Litter Weight (Average infant weight x number of infants)	Maternal Weight (x)	Litter to Maternal Weight
Callithrix jacchus	64.2g (32g x 2.1)	320g	20.06%
Mico[3]	70.2g (35.1g x 2)	360g	19.5%
Callimico goeldii	50.6g	468g	10.81%
Cebuella pygmaea	33.6g (16g x 2.1)	122g	27.54%
Saguinas[4]	87.25g (43.63g x 2)	484.5g	18 %
Leontopithecus rosalia	25.22g (14.17g x 1.78)	598g	4.22%
Microcebus murinus	6.75g (3.55g x 1.9)	63g	10.7%
Varecia variegata	218g (87.2 x 2.5)	3510g (3.5kg)	6.21%
Homo sapiens	3.375kg	54.8kg	6.16%

[1] Values for litter weight and maternal weight drawn from Lindenfors 2002

[2] Representative species were selected based on completeness of available data

[3] Previously referred to as *Callithrix argentata*

[4] Genus level averages were represented by species for which complete data are available: *Saguinus midas, Saguinus oedipus, Saguinus imperator, Saguinus nigricollis*

Table 2. Maternal investment (litter weight/days gestation) in cooperatively breeding primates.[1]

Species[2]	Litter Weight (Average infant weight x number of infants)	Days Gestation	Maternal Investment (Litter weight/ Days gestation)
Callithrix jacchus	64g (32g x 2)	148 days	0.43g/day
Mico[3]	70.2g (35.1g x 2)	144 days	0.49g/day
Callimico goeldii	50.6	151.5 days	0.33g/day
Cebuella pygmaea	32g (16g x 2)	131 days	0.24g/day
Saguinas[4]	80g (40g x 2)	166 days	0.48g/day
Leontopithecus rosalia	25.22g (14.17g x 1.78)	128.6 days	0.20g/day
Microcebus murinus	7.1g (3.55g x 2)	62 days	0.11g/day
Varecia variegata	174.4-261.6g (87.2g x 2 or 3)	102 days	1.71-2.56g/day
Homo sapiens	3.375kg	269 days	12.55g/day

[1] Values for litter weight and maternal weight drawn from Lindenfors 2002

[2] Representative species were selected based on completeness of available data

[3] Previously referred to as *Callithrix argentata*

[4] Genus level averages were represented by species for which complete data are available: *Saguinus midas, Saguinus oedipus, Saguinus imperator, Saguinus nigricollis*

Table 3. Description of study animals and relationships.

Name	Sex	Relationship	Birth	Death
Bopp	F	Mate to Tsard	-	N/A
Tsard	M	Mate to Bopp	-	2007
Hale	F	Mate to Tsikey	-	N/A
Tsikey	M	Mate to Hale	-	N/A
Orana	M	Infant to B&T	28 April 2007	9 May 2007
Kintana	F	Infant to B&T	28 April 2007	9 May 2007
Volana	M	Infant to B&T	28 April 2007	8 August 2007
Unnamed 1	M	Infant to H&T	1 May 2007	August 2007
Unnamed 2	M	Infant to H&T	1 May 2007	August 2007
Unnamed 3	F	Infant to H&T	1 May 2007	August 2007
Rivotra	M	Infant to H&T	28 April 2008	N/A
Masoandro	M	Infant to H&T	28 April 2008	N/A
Volana II	M	Infant to H&T	28 April 2008	N/A

Table 4. Types and definitions of infant care observed in *ex-situ Varecia rubra*[1]

Type of Care	Definition	Event or State?
Adult-Infant Play	Adults engage in play with infants	Event
Defense	Adults show aggressive behavior to perceived threat	Event
Groom	Caregiver grooms infant(s); may simultaneously huddle with infant(s)	Bout
Guard	Remaining near young (1-2 m) and not primarily engaged in any other activities	State
Huddle	In body contact with young, presumably providing warmth/protection; not simultaneously grooming or nursing	State
Infant Transport	Adult moves infant via oral transport	State
Nurse	Allowing young to suckle; frequently combined with huddling	State
Other	Any activity not listed	NA
Out of sight	Not seen	State
Stash	Leaving offspring alone in a location other than the nest while primarily engaged in another activity	State

[1] Definitions drawn from Vasey 2007 and Vasey 2009

Table 5. Hourly rates of maternal and paternal caregiving behaviors (number of occurrences per hour) based on focal caregiver sampling.

Caregiving Behavior	Dam	Sire
Defense	0.47	0
Groom	4.56	1.79
Guard	2.02	2.19
Huddle	0.73	0.17
Infant Transport	0.31	0
Nurse	1.35	NA
Play	0.88	1.56

Table 6. Hourly rates of care received by infants from mothers, fathers, and both parents combined (number of occurrences per hour) based on focal litter sampling.

Caregiving Behavior	Both	Dam	Sire
Defense	0.62	0.31	0.33
Groom	8.11	6.82	1.28
Guard	1.00	0.47	0.34
Huddle	1.00	0.98	0.03
Infant Transport	0.91	0.91	0
Nurse	2.58	2.58	NA
Play	2.53	1.28	1.23

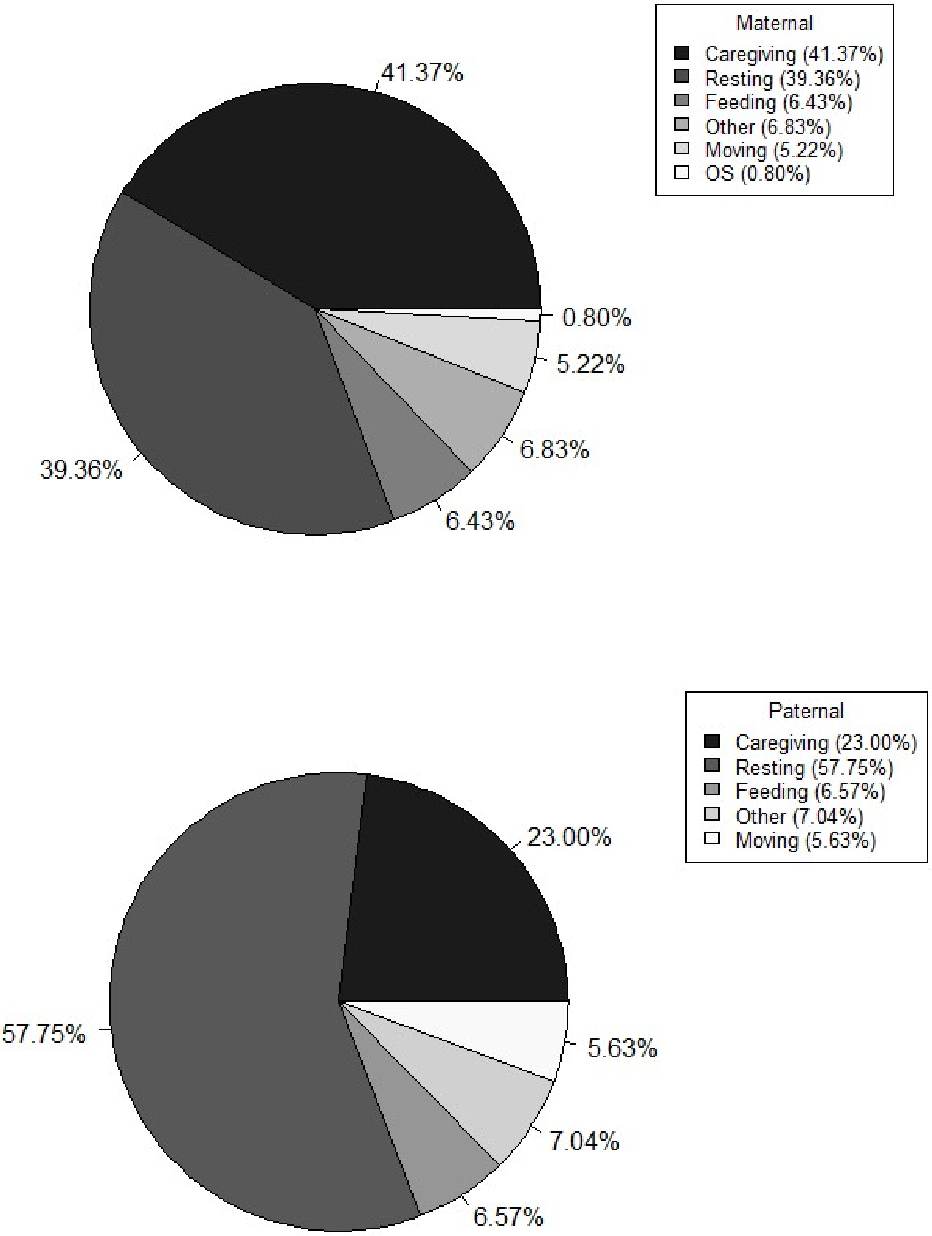

Figure 1. *Varecia rubra* Maternal and Paternal Activity Budgets. Calculated from focal caregiver time points. Top: Maternal activity budget (N = 249 samples). Bottom: Paternal activity budget (N = 213 samples). OS = out of sight.

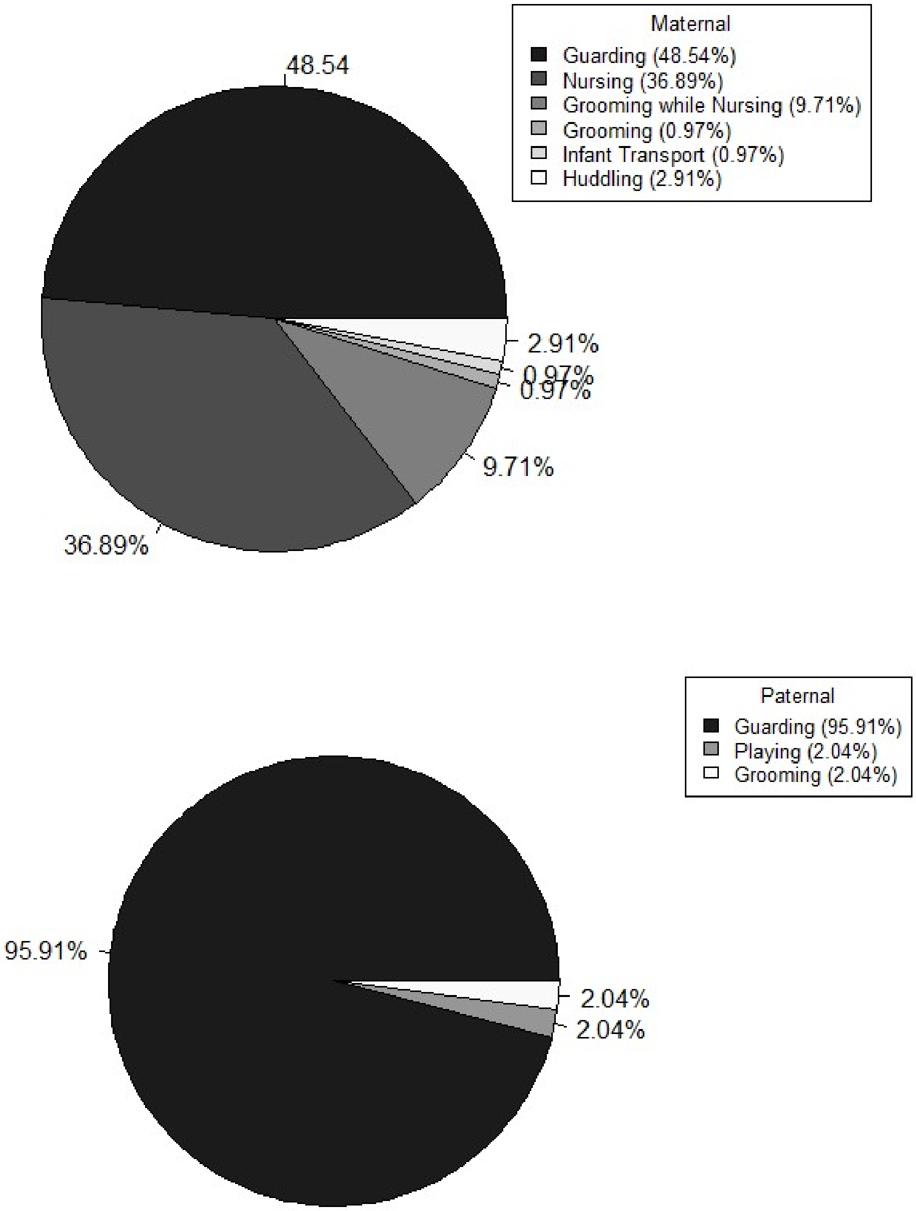

Figure 2. *Varecia rubra* Maternal and Paternal Caregiving Time Budgets. Calculated from focal caregiver time points. Top: Maternal caregiving behaviors (N = 103 samples). Bottom: Paternal caregiving behaviors (N = 49 samples).

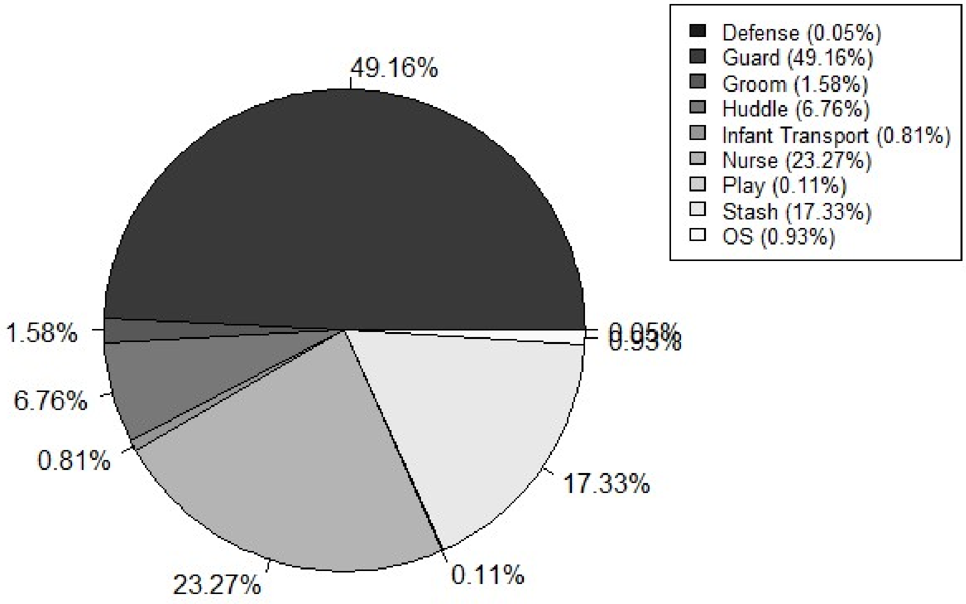

Figure 3. Care Received by *Varecia rubra* Infants from Mothers and Fathers Combined. Based on focal litter time points (N = 1835) OS = out of sight.

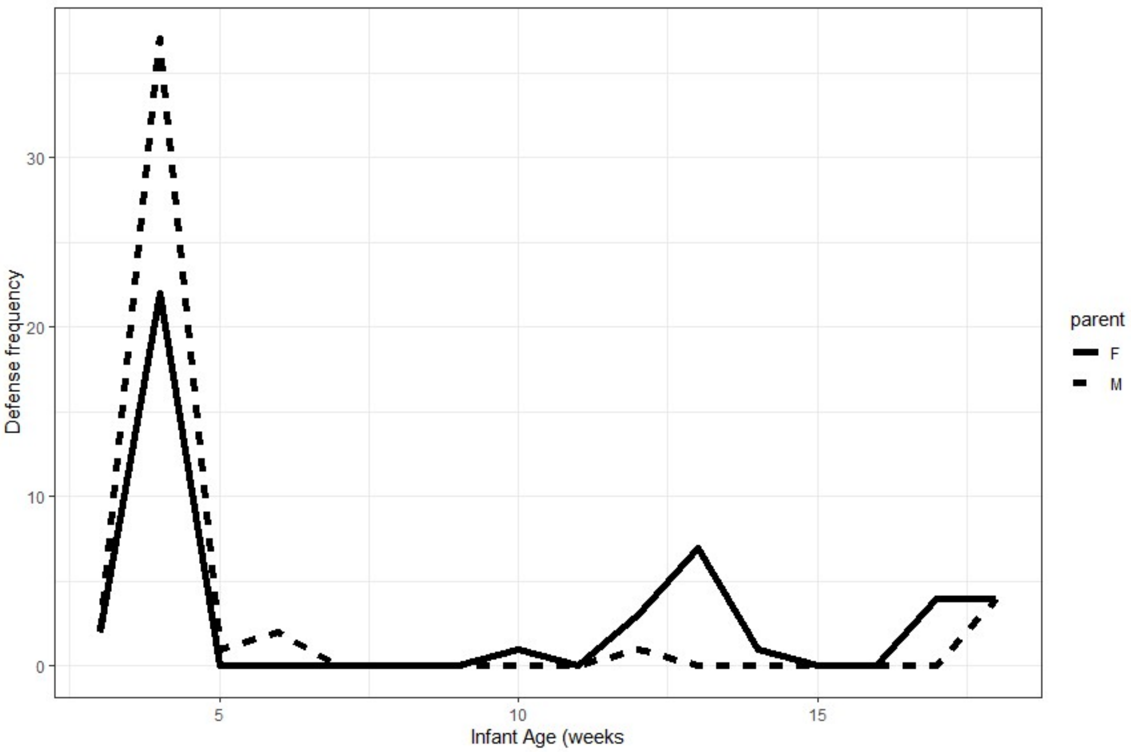

Figure 4. Frequency of defending infants by *Varecia rubra* mothers and fathers over the first 15 weeks of life. Based on focal litter all-occurrence samples (N = 2438 observations).

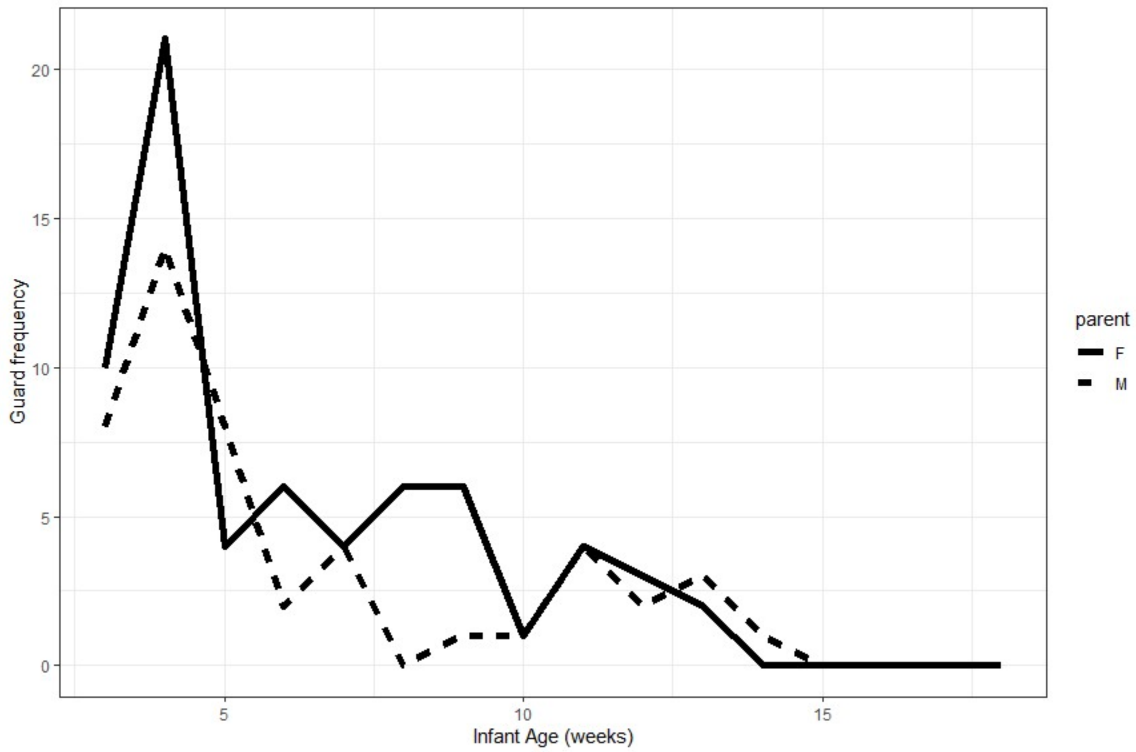

Figure 5. Frequency of guarding infants by *Varecia rubra* mothers and fathers over the first 15 weeks of life. Based on focal litter all-occurrence samples (N = 2438 observations).

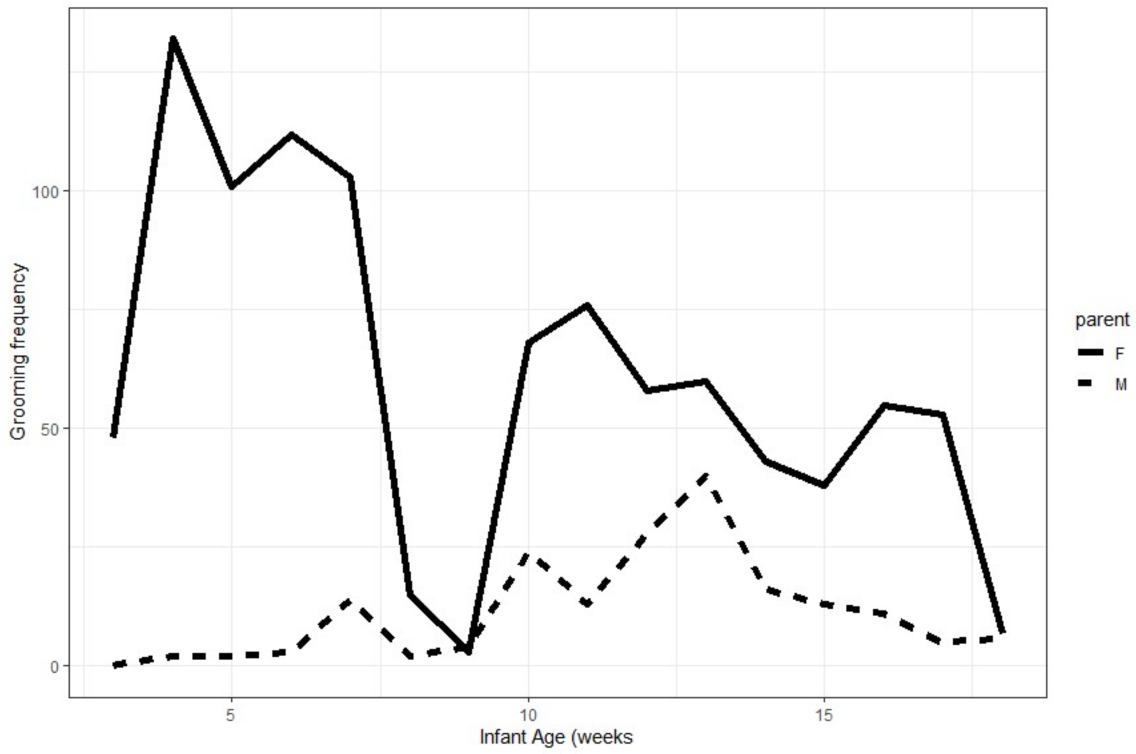

Figure 6. Frequency of infant grooming by *Varecia rubra* mothers and fathers over the first 15 weeks of life. Based on focal litter all-occurrence samples (N = 2438 observations).

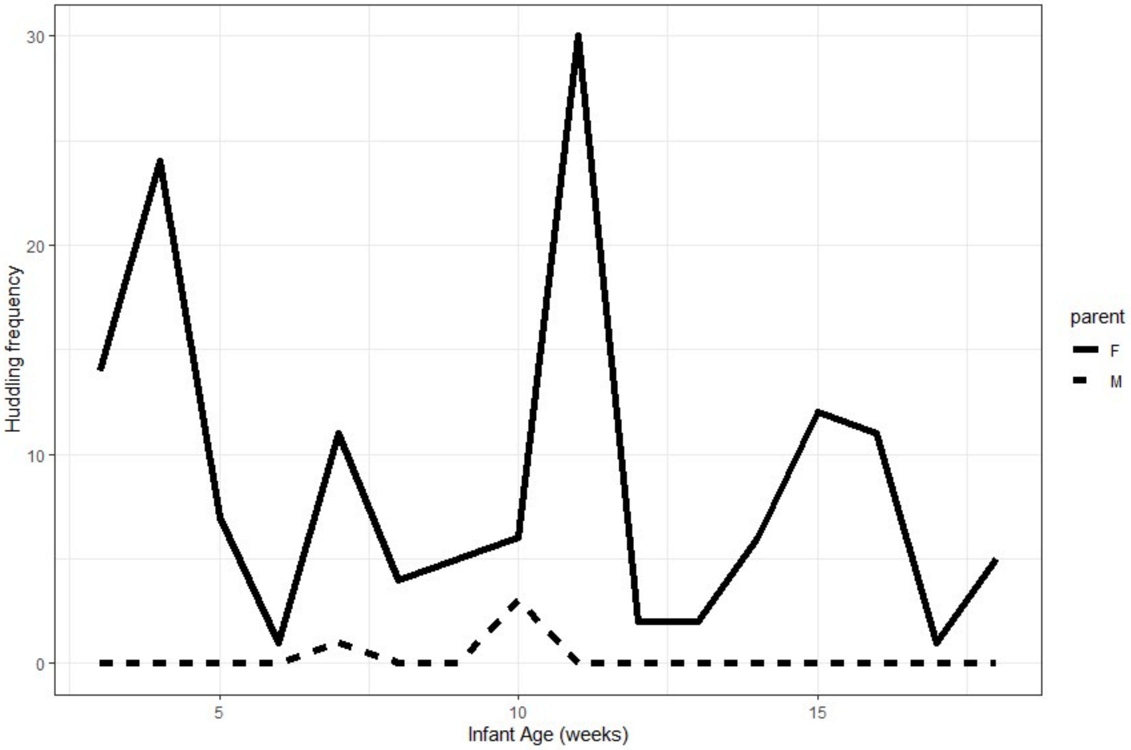

Figure 7. Frequency of huddling with infants by *Varecia rubra* mothers and fathers over the first 15 weeks of life. Based on focal litter all-occurrence samples (N = 2438 observations).

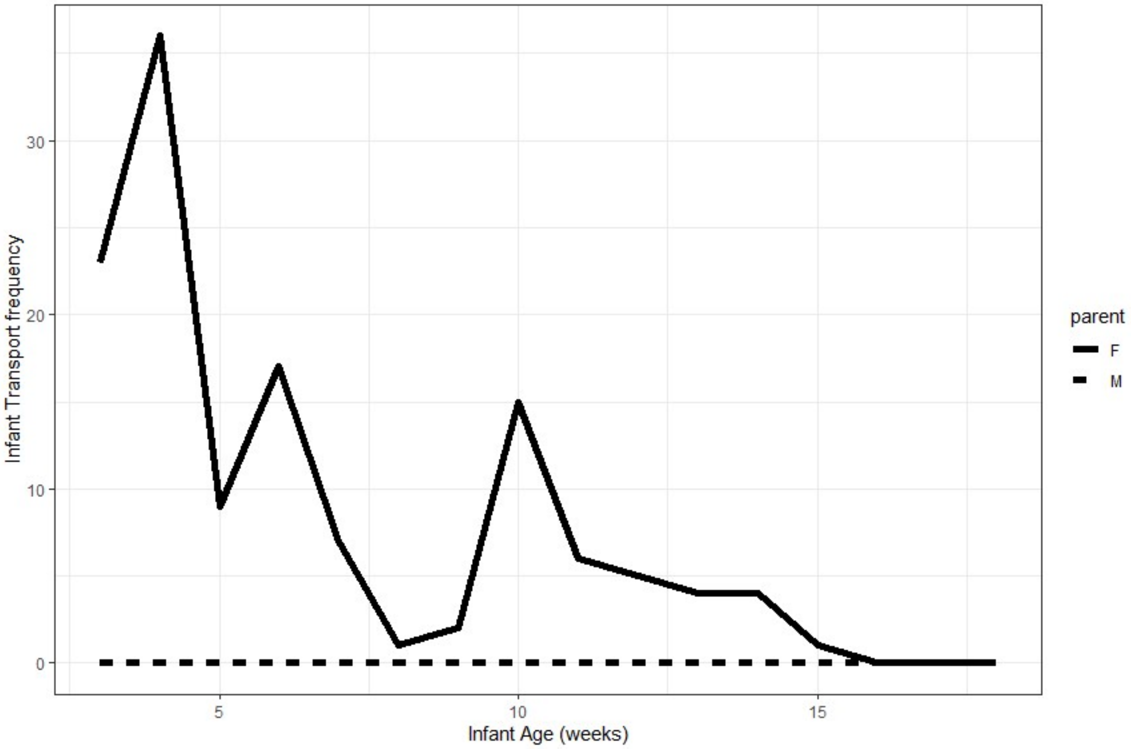

Figure 8. Frequency of infant transport by *Varecia rubra* mothers over the first 15 weeks of life. Based on focal litter all-occurrence samples (N = 2438 observations).

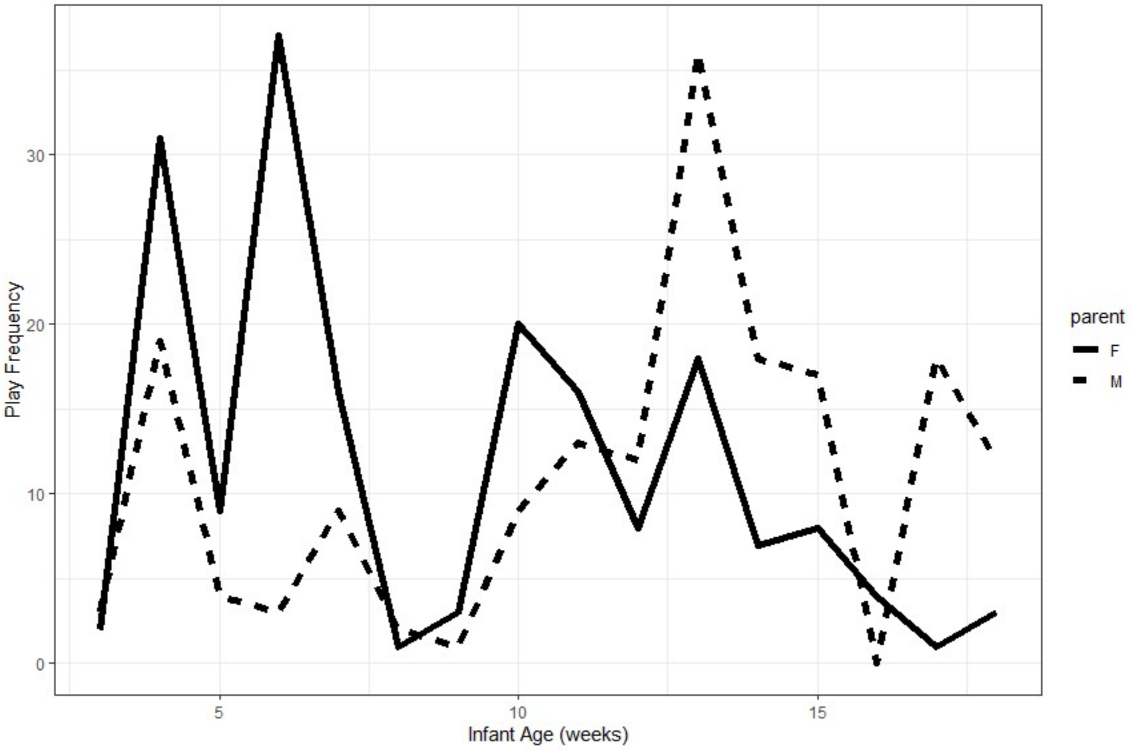

Figure 9. Frequency of adult-infant play in *Varecia rubra* mothers and fathers over the first 15 weeks of life. Based on focal litter all-occurrence samples (N = 2438 observations).

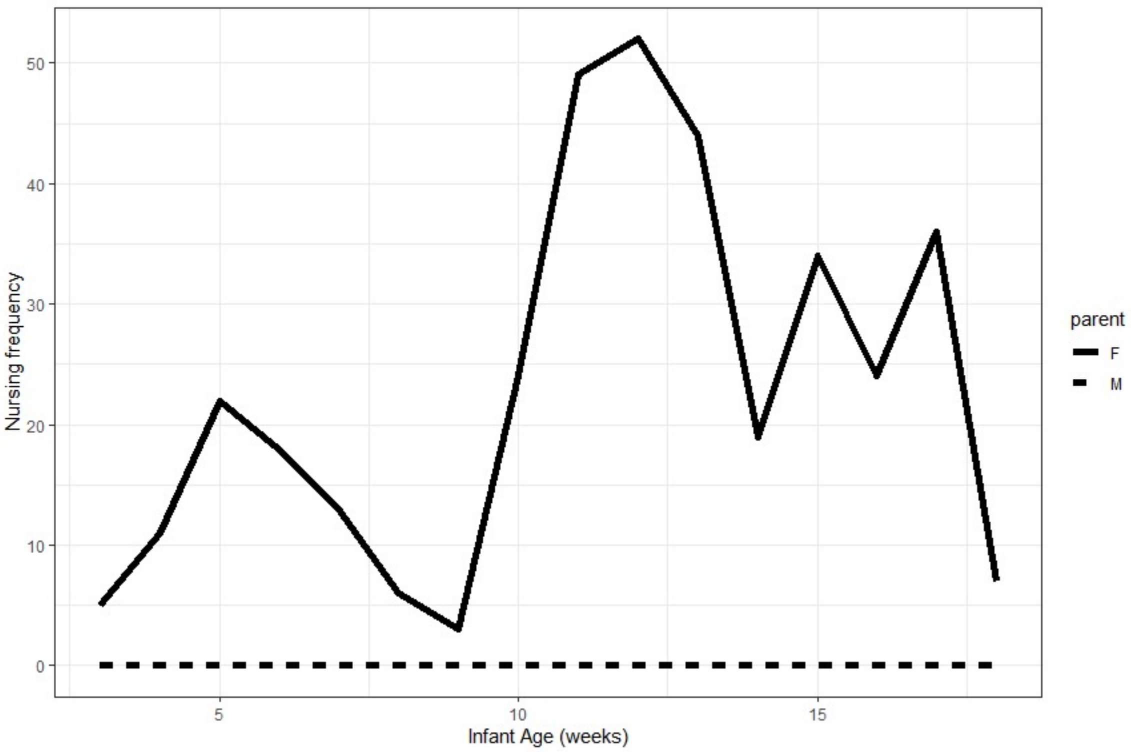

Figure 10. Frequency of nursing in *Varecia rubra* mothers over the first 15 weeks of life. Based on focal litter all-occurrence samples (N = 2438 observations).

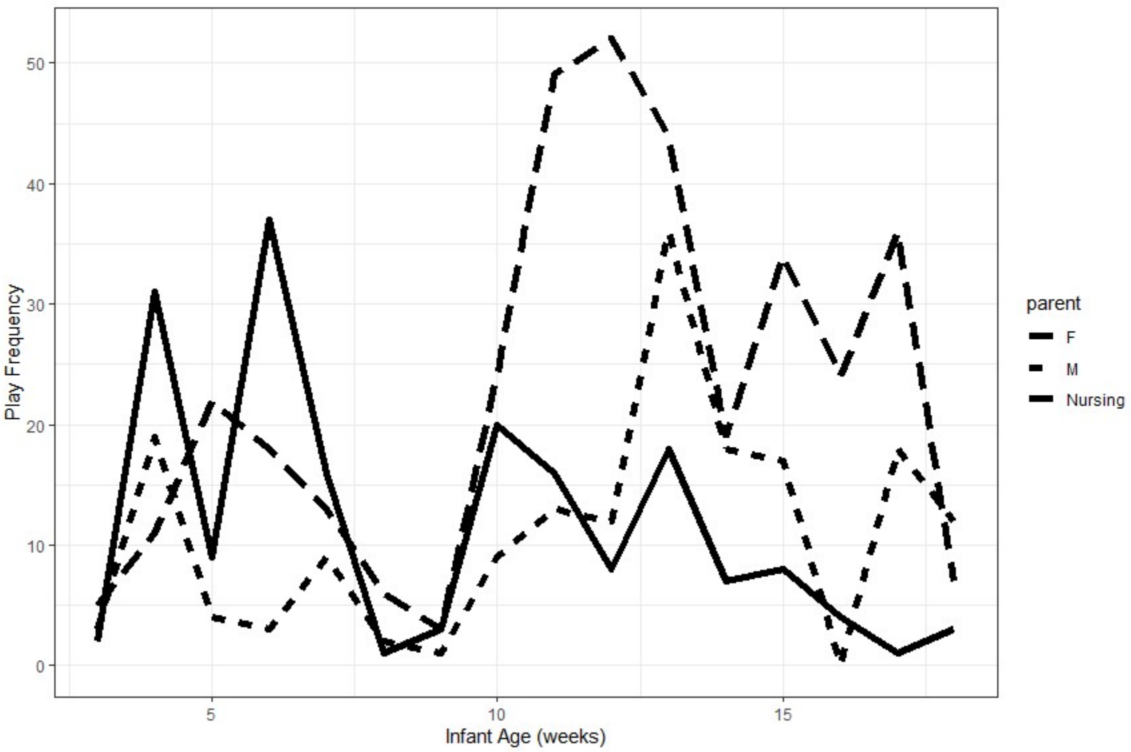

Figure 11. Frequency of nursing and adult-infant play by *Varecia rubra* mothers and fathers over the first 15 weeks of life. Based on focal litter all-occurrence samples (N = 2438 observations).

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