Causes and consequences of female competition in redfronted lemurs (*Eulemur rufifrons)*

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SUMMARY

Competition among female mammals appears to be much more widespread than previously thought, and it can take on extreme forms, including eviction and even death. Nevertheless, female competition has only recently been acknowledged as a pervasive mechanism of sexual selection and it remains understudied in comparison to male competition, so that its causes, mechanisms, and consequences remain comparatively poorly understood. Although research on female competition in the light of sexual selection has been accumulating over the past years, most studies examine patterns of female competition isolated from other aspects of sociality such as reproductive interests of males or without consideration of multiple causes. Particularly rare and infrequent mechanisms of female competition such as female evictions have so far only been studied in a few species.

In this thesis, I studied causes and consequences of female competition in redfronted lemurs (*Eulemur rufifrons*), a primate species endemic to Madagascar where evictions have been previously documented. I aimed to understand demographic circumstances favouring female-female competition, causes of conflict, trade-offs with kin selection, and interactions with male reproductive strategies. In addition, I examined potential consequences of evictions on social structures of groups. Based on 24 years of demographic data and 6 years of behavioural observation and hormonal data of known individuals, I showed that female redfronted lemurs targeted close female kin for forcible, permanent, and presumably lethal eviction, even though groups contain multiple unrelated males. I identified limited group size as the main driver for departures of individuals of both sexes from groups and showed that male emigrations and female evictions are therefore not independent of each other. While female evictions were more likely at higher numbers of juvenile females, male emigrations were more likely when the proportion of adult males to adult females was increased. In addition, I found that infant survival decreased with number of juvenile females present. I could show that despite increased glucocorticoid levels, agonism levels in both sexes were not related to resource availability or reproductive season. The fact that female competition did not seem to be linked to immediate competition for food resources or access to mates, suggests that the mechanisms of female evictions in redfronted lemurs might be an evolutionary stable strategy that is aimed at longer-term benefits. Beyond this, the social structure of groups seemed to be unaffected by group member loss.

Together, these three chapters create a comprehensive portrait of an extreme case of female competition. They highlight the importance of conducting integrative studies that consider all group members to create a more complete picture of what causes competition in females and how it can form a species' social organization. It further highlights the importance of long-term studies to facilitate the detection and quantification of sporadically occurring mechanisms of female competition.

ZUSAMMENFASSUNG

Weibliche Konkurrenz in Säugetieren scheint weitaus verbreiteter zu sein als ursprünglich angenommen und kann extreme Formen annehmen, einschließlich Ausschluss von Weibchen aus Gruppen und sogar Tod. Dennoch wurde weibliche Konkurrenz erst kürzlich als ein weit verbreiteter Mechanismus der sexuellen Selektion anerkannt und bleibt im Vergleich zum männlichen Wettbewerb wenig erforscht, sodass ihre Ursachen, Mechanismen und Konsequenzen vergleichsweise schlecht verstanden sind. Obwohl in den letzten Jahren vermehrt zu weiblicher Konkurrenz im Kontext der sexuellen Selektion geforscht wurde, untersuchen die meisten Studien die Muster weiblicher Konkurrenz isoliert von anderen Aspekten der Sozialität, wie den reproduktiven Interessen der Männchen oder nicht unter Berücksichtigung mehrerer Ursachen. Besonders seltene und wenig erforschte Mechanismen weiblicher Konkurrenz, wie der Ausschluss von Weibchen aus Gruppen, wurden bisher nur bei wenigen Arten untersucht.

In dieser Dissertation habe ich Ursachen und Konsequenzen weiblicher Konkurrenz bei Rotstirnmakis (*Eulemur rufifrons*) untersucht, einer Primatenart, die endemisch in Madagaskar vorkommt und bei der der Ausschluss von Weibchen aus Gruppen zuvor dokumentiert wurde. Mein Ziel war es, die demografischen Umstände, die weibliche Konkurrenz begünstigen, zu verstehen und Konfliktursachen, den Zusammenhang mit Verwandtenselektion und Interaktionen mit männlichen Fortpflanzungsstrategien zu untersuchen. Darüber hinaus habe ich potenzielle Konsequenzen von Ausschluss von Weibchen aus Gruppen für die sozialen Strukturen von Gruppen untersucht. Basierend auf 24 Jahren demografischer Daten und 6 Jahren Verhaltensbeobachtungen und Hormondaten bekannter Individuen zeige ich, dass weibliche Rotstirnmakis nahe Verwandte dauerhaft und gegen ihren Willen aus Gruppen ausschließen, mit vermutlich tödlichen Konsequenzen hat. Ich zeige, dass begrenzte Gruppengrößen die Hauptursache für das Ausscheiden von Individuen beider Geschlechter aus Gruppen ist und zeige, dass männliche Abwanderungen und weibliche Vertreibungen daher nicht unabhängig voneinander sind. Während weibliche Vertreibungen wahrscheinlicher waren, wenn mehr juvenile Weibchen anwesend waren, waren männliche Abwanderungen wahrscheinlicher, wenn der Anteil erwachsener Männchen zu erwachsenen Weibchen erhöht war. Darüber hinaus konnte ich zeigen, dass

Überlebensraten von Jungtieren mit der Anzahl der vorhandenen juvenilen Weibchen abnahm. Ich konnte zeigen, dass trotz erhöhter Glukokortikoidspiegel, Aggressionsraten in beiden Geschlechtern nicht mit der Ressourcenverfügbarkeit oder der Fortpflanzungssaison zusammenhingen. Die Tatsache, dass weibliche Konkurrenz scheinbar nicht mit unmittelbarem Wettbewerb um Nahrungsressourcen oder den Zugang zu Fortpflanzungspartnern verbunden war, legt nahe, dass der Mechanismus vom Ausschluss von Weibchen aus Gruppen bei Rotstirnmakis eine evolutionär stabile Strategie sein könnte, die auf längerfristige Vorteile abzielt. Darüber hinaus schien die soziale Struktur von Gruppen durch den Verlust von Gruppenmitgliedern nicht beeinflusst zu werden.

Zusammenfassend bieten diese drei Kapitel ein umfassendes Bild eines extremen Falls des weiblichen Wettbewerbs. Sie unterstreichen die Bedeutung von integrativen Studien, die alle Gruppenmitglieder berücksichtigen, um ein vollständigeres Bild davon zu erhalten, was den weibliche Konkurrenz verursacht und wie sie die soziale Organisation einer Art formen kann. Darüber hinaus heben sie die Wichtigkeit langfristiger Studien hervor, um die Entdeckung und Quantifizierung sporadisch auftretender Mechanismen weiblicher Konkurrenz zu erleichtern.

GENERAL INTRODUCTION

Competition among female mammals appears to be much more widespread than previously thought, and it can take on extreme forms, including eviction and even death (Clutton-Brock and Huchard, 2013; Stockley and Campbell, 2013). Nevertheless, female-female competition (in this dissertation referred to as “female competition” for simplicity) has only recently been acknowledged as a pervasive mechanism of sexual selection, and it remains understudied in comparison to male competition, so that its causes, mechanisms, and consequences remain comparatively poorly understood. Unlike males, females experience a greater diversity of causes for intrasexual competition (Clutton-Brock, 2016), and the associated costs and benefits often occur with some time delay. This complexity demands a more nuanced approach to study female competition, as traditional methods used for males may only be partially applicable and may not cover all aspects of competition patterns in females, especially those that defy classical sex roles. As a result, various cases of female intrasexual competition continue to perplex researchers.

Sex roles

Sex roles in sexually-reproducing species describe the differences between males and females in within-sex competition, mating preferences, and parental care (Schärer et al., 2012). Beginning with Darwin (1871), competition and aggression in mammals was attributed mostly to males while females were considered as passive and choosy (Clutton-Brock, 2007; Kappeler, 2017). This dichotomy has been attributed to a fundamental difference in the determinants of reproductive success, with male success constrained by the number of mates and female success depending on access to resources (Bateman, 1948; Trivers, 1972; Williams, 1966). Such differences are linked to anisogamy, wherein female gametes are larger but fewer in number than male gametes, resulting in a steeper increase in male reproductive success with multiple mates, commonly referred to as the 'Bateman gradient' (Bateman, 1948). Consequently, traditional theory suggests that females, due to their limited reproductive opportunities, should exhibit heightened selectivity in partner choice and invest more in parental care while minimizing involvement in intrasexual competition. This original view of “classical” sex roles has been summarised under the Darwin-Bateman paradigm (Dewsbury, 2005). However, not all social systems fit this simple view of sex roles.

The Darwin-Bateman paradigm and its connection to anisogamy-driven sex roles have therefore been subject to criticism in multiple studies (Ah-King, 2013; Pollo and Kasumovic, 2022; Sutherland, 1985). Darwin himself was already contemplating about "reversed" species, where females exhibit higher levels of aggressiveness and competitiveness in mating and courtship, while males invest more in parental care and offspring rearing. However, our understanding has since expanded to encompass a wider range of mating and parental care systems in animal societies (Ah-King and Ahnesjö, 2013; Clutton-Brock, 2021, 2016). More studies have recently invested in the study of female reproductive competition and male mate choice (Puurtinen and Fromhage, 2017) and different expression of sex roles have been linked to aspects of social systems, as for example adult sex ratios or mate encounter rates (Kappeler, 2017; Kappeler et al., 2023; Kokko and Johnstone, 2002). However, we still lack knowledge of those species that fall between classical and reversed sex roles.

Sexual selection

The existence of species outside the Darwin-Bateman paradigm has led to broad discussions on how sex-roles are perceived and how to adjust established frameworks to account for species that do not match this original view (Clutton-Brock, 2009a; Crook, 2017; Roughgarden et al., 2006; Roughgarden and Akçay, 2010; West-Eberhard, 1983, 1979). Early studies of mammalian socio-ecology reinforced the view that a higher concentration of breeding females in group-living species enhances the potential for polygyny, leading to predictable relationships between female group size, male monopolisation potential, and sexual dimorphism in size, strength, and weaponry underlying male competitive ability (Clutton-Brock et al., 1977). Because males either compete directly for mates or social rank, which mediates access to mates (Alberts, 2012), there consensus over the fact that males are more aggressive and competitive and that these traits evolved under sexual selection (Clutton-

Brock, 2017, 2009a). But can this sexual selection framework also explain patterns of female competition, and how can we compare competitiveness between the sexes?

The original definition of sexual selection, as proposed by Charles Darwin proposed in 1859, as “struggle between the males for possession of the females” (Darwin, 1859) applies mostly in cases where individuals directly compete for access to mates. Despite a second, broader definition Darwin proposed in 1871, defining sexual selection as “the advantage which certain individuals have over other individuals of the same sex and species solely in respect of reproduction” (Darwin, 1871), sexual selection as competition for mates seems to prevail until today. However, causes of female competition are much more diverse and might still ultimately impact reproductive success. West-Eberhard (1979) therefore introduced “social selection” as an evolutionary mechanism encompassing all forms of social competition, including access to mates (Lyon and Montgomerie, 2012), but also those that contribute to better survival. This conceptual framework appears promising for explaining many cases of female ornamentation (Tobias et al., 2012) and for integrating sexual selection and kin selection (Rubenstein, 2012). However, its practical usefulness has also been questioned as, ultimately, all components of competition impact lifetime reproductive success – the standard measure of fitness (Clutton-Brock and Huchard, 2013). Hence, social selection is difficult to study empirically, but acknowledging it allows for the appreciation of female competition beyond the immediate mating context and offers a broader perspective than has traditionally been adopted. Simultaneously comparing female and male competition and linking it to reproductive or resource competition could contribute valuable insights to this ongoing discussion.

Overlooked Female Competition

Studies of the causes, consequences, and mechanisms of female competition have long lagged behind those focusing on males for three main reasons. First, in contrast to males, the occurrence of elaborate female ornaments and armaments is not strictly associated with the occurrence of intense female reproductive competition, making any association less obvious (Clutton-Brock, 2007; Tobias et al., 2012). Second, the frequency and intensity of female aggression are often clearly reduced compared to males, presumably because the immediate fitness consequences of winning a particular fight are smaller for females, who do not benefit as much from obtaining an additional mating opportunity that way (Clutton-Brock and Huchard, 2013). For this reason, sexual dimorphism in secondary sexual characters is typically more pronounced in males of polygynous species, and larger males equipped with more elaborate ornaments and weapons have presumably attracted more research interest (Stockley and Campbell, 2013). Third, competition has been studied mostly by male researchers, who were over-represented among early researchers across fields (Risi et al., 2022). This reflects the broader trend of male prevalence in sexual selection research, where research starts with male-centred investigations or explanations and only subsequently considers female-centred equivalents (Ah-King, 2022). Studies on female competition are therefore often based on methods used to study male competition, for example, focussing on more apparent competitive behaviour known from males and trying to link the causes of competition to immediate costs. Even today, studies on male intrasexual competition outnumber studies on female intrasexual competition by a considerable degree (Fromonteil et al., 2023). Consequently, only a limited number of studies attempted to establish a more comprehensive understanding of the causes and consequences of female competition by bridging the gap between female competition, male interests, and the resulting consequences for social organisation and structure of species.

Causes of female competition

Female competition can take many different forms within the animal kingdom and is closely linked to a species reproductive biology. For example, egg-laying species or species with asexual reproduction will face different challenges with regards to division of parental care or mate access. As this dissertation studies a case of female competition in mammals, I will focus on competitive patterns in mammals in the following sections.

Deciphering the underlying causes of competition among females poses challenges and frequently involves multiple interacting factors. While intrasexual competition for mates in the classical sense of sexual selection is prevalent in males, some forms of competition among females can also be explained by intrasexual selection because they directly affect mating success (Clutton-Brock, 2007; Hare and Simmons, 2019). Recent research suggests that sexual selection in females is more widespread than previously assumed and that females typically benefit from multiple mating (Fromonteil et al., 2023). The advancement of molecular paternity analyses in the past few decades has significantly contributed to this finding, revealing extrapair copulations in several species once believed to be monogamous (Taylor et al., 2014). Consequently, we do find competition for mates in females. This cause of competition has been traditionally considered as unlikely for females, as sperm should not be easily depleted and limitation of male mating partners was thus thought to be negligible. However, numerous examples provide evidence that under specific circumstances, for example, when oestrus is synchronised and females engage in multiple mating or when females share preferences towards specific males, sperm becomes limited, and females may respond with increased intrasexual competition (Bebié and McElligott, 2006; Bro-Jørgensen, 2007; Hohmann and Fruth, 2003). A prominent example are saiga antelopes (*Saiga tatarica*), in which female competition for mates had only emerged after the ratio of available males to females significantly decreased due to poaching (Milner-Gulland et al., 2003).

Females engage more frequently in competition for food than for mates, as their energetic demands are often increased due to their reproductive needs, particularly during gestation and lactation (Clutton-Brock et al., 1989; Patterson et al., 2021; Sadleir, 1969; Stockley and Bro-Jørgensen, 2011; Wise and Ferrante, 1982). Alternatively, such resources can be secured through the acquisition and defence of territories, either by females themselves or by competing for males that hold territories (Clutton-Brock and Huchard, 2013; Kaufmann, 1983; Stockley and Bro-Jørgensen, 2011). In species in which females live in groups, feeding competition is frequently observed and the fitness of females may decrease with increasing group size as resources become depleted faster and must be shared with more individuals (Clutton-Brock, 2009b, 2002; Clutton-Brock et al., 2010, 1982; Silk, 2007; Van Schaik et al., 1983). In general, fitness effects of resource competition will have a delayed onset and might only become apparent when examining lifetime reproductive success (Kahlenberg et al., 2008; Pusey et al., 1997; Van Noordwijk and van Schaik, 1999), highlighting the need for long-term studies to establish correlations between the outcomes of such competition and the females' survival or reproductive output.

In group-living species, females may further compete to raise their offspring by increasing survival chances of their own offspring or reducing future competition for them by reducing the number of juveniles within the same cohort. Factors that might increase survival probabilities of own offspring and can be competed for are include paternal care and protection, shelter, social position, or food resources (Clutton-Brock, 1991; Stockley and Bro-Jørgensen, 2011). Some of these aspects are interconnected. For instance, mates could provide both care and shelter, and higher social positions often grant prioritised access to food resources, as seen in maternally inherited ranks in spotted hyenas (*Crocuta Crocuta;* Smale et al., 1993). Alternatively, females can mitigate future competition for their offspring by actively limiting the birth or survival of offspring of other females, achieved through various mechanisms discussed in the next section. Females might therefore not always compete for immediate but rather future access to resources to improve their reproductive output.

Mechanisms of female competition

In contrast to the causes, the main mechanisms of competing with same-sex conspecifics over reproduction have been found to be strikingly similar for both sexes (Clutton-Brock and Huchard, 2013; Stockley and Bro-Jørgensen, 2011; Stockley and Campbell, 2013). However, the effects of female competition in mammals are often delayed and might have more long-term effects. Competitive actions might therefore occur only sporadically rather than to rely on mechanisms and structures that are permanently held in place (Bosch, 2013; Clutton-Brock and Huchard, 2013; Clutton-Brock and Parker, 1995; Kvarnemo and Ahnesjo, 1996; Rosvall, 2013; Stockley et al., 2013). While different mechanisms differ in their relative frequencies in both sexes, they resemble one another in their general form.

First, although more common in males, there are several cases of female ornamentation and weaponry (Tobias et al., 2012). Unlike males, female armaments have likely evolved primarily for competing for food rather than mates (Stankowich and Caro, 2009). The most common examples in mammals are found in ungulates, in which females use antlers or horns to compete for resources or defend their offspring (Robinson and Kruuk, 2007; Stankowich and

Caro, 2009). Ornamentation in females has been primarily described in birds in which it has originally been considered a by-product of male ornamentation, as a consequence of genetic correlation, and was thought to be non-adaptive (Darwin, 1871; Lande, 1980). However, more recent studies suggested that ornamentation is in many cases related to contest competition and maintained by male mate choice and therefore more analogous to ornamentation in males than previously thought (Amundsen, 2000; Tobias et al., 2012).

Second, in species with stable group membership and individual recognition, dominance interactions based on the outcome of recent agonistic interactions lead to a reduction of costly physical fights. While in males dominance is usually established through direct physical contest, female hierarchies are often less linear and can rely on other factors such as social alliances or maternal rank (Smale et al., 1993; Stockley and Campbell, 2013). As mentioned earlier on, this makes the observation of female competition often more complicated, as dominance interactions frequently rely on threats or other social signals (Cant and Young, 2013). As in males (Alberts, 2012), female dominance ranks are proximately based on intrinsic traits, such as size and strength, and higher rank is correlated with several measures of female reproductive success, such as the length of inter-birth intervals and infant survival (Pusey, 2012).

Third, where females compete to raise their offspring and for future reproduction, dominant individuals might suppress subordinate reproduction. This can be achieved through behavioural, pheromonal, or physiological mechanisms (Baniel et al., 2018; Clutton-Brock and Huchard, 2013; Kraus et al., 1999). Physiological and behavioural suppression are often linked, and dominant individuals might interfere with subordinate reproduction by causing chronic stress (Abbott et al., 2003; Bowman et al., 1978; Silk, 2007; Wasser and Barash, 1983; Young, 2009). For example, lighter and low-ranking females were more likely to abort during periods of intense female competition in banded mongooses (*Mungos mungo,* Inzani et al., 2019). Also, reproductive suppression might increase when resources are scarce, as it has been shown in Damaraland mole-rats (*Fukomy damarensis;* Young et al., 2010). However, an alternative interpretation to active suppression by dominants is reproductive restraint by subordinates if costs of reproduction in presence of dominants are too high (Young, 2009).

Frequently, it is difficult to make a clear distinction between both mechanisms and they might not be mutually exclusive.

Fourth, in addition to prenatal down-regulation of rival reproductive success, females commit infanticide of infants in the same cohort (Lukas and Huchard, 2019). This phenomenon is widespread among mammals and occurs in species in which the presence of offspring of other females reduces the survival chances of a given female's offspring. However, an alternative hypothesis to resource competition of offspring suggests that female-led infanticide may be related to resource exploitation by the infanticidal female itself due to increased demand (Digby, 2000). Often, its cause cannot be definitely determined (Walker et al., 2021). Although female infanticide has previously been thought to be modulated by kinship, this has now been questioned (Lukas and Huchard, 2019).

Finally, both sexes might evict same-sex rivals from their territories or groups (Dubuc et al., 2017; Thompson et al., 2017). This form of competition is among the most intense mechanisms of female competition as it is related to extreme costs for individuals of species that are obligatory group-living. In some cases, the consequences of evictions may even be more extreme than physical injury as evicted females are deprived of all benefits of group-living, like protection from predators or access to resources within fended territories. Stress-induced abortion rates, for example, are increased in evicted female banded mongooses (Gilchrist, 2006). Compared to other mechanisms, evictions occur at low frequencies in most cases, which might be the reason why more elaborate descriptions of their causes, mechanisms, and consequences had only been described in a few long-term studies. So far, detailed knowledge of the context of evictions only exists for two species of mongooses.

Modulation of the intensity of female competition

In contrast to males, in which variation in the distribution and synchrony of potential mates determines reproductive tactics (Nunn, 1999), much less is known about the nature and relative importance of factors modulating the intensity of female competition across seasons or years, or among groups, populations, and species. Species in which females provide most of the parental care, as in mammals, they are confronted with higher costs but less immediate benefits during physical fights, which is why conflicts are often more indirect and, for instance, modulated through social relationships. Conflicts in females are therefore more difficult to observe, as instead of observing physical fights, researchers require a thorough understanding of a species' social structure to be able to quantify those more subtle processes. A recent study, for example, has found that in animal societies with prevailing female dominance, submissive signals are used more frequently than physical agonistic interactions to establish dominance hierarchies (Kappeler et al., 2022b). Such signals and their significance must be known to the observer in order to relate them to competitive or dominance interactions.

Relatedness among group members should modulate competition as benefits of competition for the individual should be balanced against costs of reducing inclusive fitness through closely related kin, particularly as female mammals are frequently philopatric (West et al., 2002). In cases in which the costs of competition are high, as in the case of reproductive suppression or eviction, female competition is indeed often modulated by kinship. In fact, females in solitary species compete less with neighbours when they are relatives (Lambin and Yoccoz, 1998), and the intensity of aggression and the risk of eviction decrease with increasing kinship in some group-living species (Clutton-Brock et al., 2010).

In addition, social relationships within groups can modulate individual dispersal decisions or reproductive patterns (Armansin et al., 2020), adjusting within-group competition to variation in group size and resource availability. While smaller groups experience less within-group competition over food, larger groups are more likely to succeed in between-group competition (Koch et al., 2016). Local variation in group size should therefore indicate variation in food availability, but is also related to female reproductive strategies (Markham et al., 2015).

Consequences of female competition and their interplay with male sociality

Understanding the dynamics of female competition can provide valuable insights into the evolutionary processes that shape the social organisation, social structure, and mating system of a species. The intensity of competition influences the number of females within groups and vice versa, and provokes several downstream effects. Early studies of mammalian socio-ecology reinforced the view that the concentration of breeding females in group-living species enhanced the potential for polygyny, leading, for instance, to predictable relationships between female group size and male monopolisation potential (Clutton-Brock et al., 1977). The socio-ecological model predicts that the distribution of females is determined by the distribution of ecological resources and risks in the female environment, while the number of males is ultimately linked to the distribution of females (Crook and Gartlan, 2002; Emlen and Oring, 1977).

As the determinants of distribution differ for both sexes, it is often useful to study patterns of their sociality separately (Clutton-Brock, 2021). However, where both sexes share the same groups, male and female sociality will affect each other, and sexes might face different challenges of reproduction and survival, which could potentially lead to a conflict of interests between males and females (Chapman, 2006). Reproductive tactics are often aligned to avoid inbreeding. In species in which females are philopatric, males disperse at maturation or male tenure is decreased to be shorter than the average female maturation time, which decreases chances of breeding with kin (Clutton-Brock, 2016; Lukas and Clutton-Brock, 2011). In addition, comparing patterns of competition in both sexes might decipher intrasexual competition from intersexual or sex-independent competition. Thus, a holistic approach that embraces the complexities of male-female interactions is essential for a thorough comprehension of the role of competition in shaping the social organisation of species.

Why study female competition?

Apart from fundamentally impacting the social organisation of species, understanding female competition might contribute to explaining phenomena that had previously posed challenges to animal behaviour research. Some sociobiological enigmas have already profited from the increasing awareness of female intrasexual competition in the study of animal behaviour. First, female bird song had originally posed a major unresolved question to behavioural biologists until female competition was considered as its cause and has proven to be a frequent driver of this behaviour (Tobias et al., 2011). Second, female-female competition has been suggested to be a key driver of the evolution of menopause. In social systems in which females do not disperse, menopause appears to be the result of kin selection that reduces intergenerational conflict (Johnstone and Cant, 2019). Third, female competition as the result of unpredictable resources and subsequent maternal stress might be at the very basis of a phenomenon called the “lemur syndrome”, summarising several typical traits of diurnal Lemuridae that diverge from other primate species, including female masculinisation, female dominance, even adult sex ratios and the lack of a sexual size dimorphism (Kappeler and Fichtel, 2015, discussed in more depth in the next section). Increasing our knowledge of the causes and patterns of female competition might therefore help answering yet unresolved questions in the study of animal social systems.

Identifying patterns of female competition in primates can also offer valuable insights into the evolution of female competition in humans. Initially, the underrepresentation of women in higher positions was often attributed to the perception of women as inherently less competitive (Croson and Gneezy, 2009; Gneezy and Rustichini, 2004; Niederle and Vesterlund, 2007). However, more recent studies suggest that willingness of women to enter competition depends to a large extent on the context and setting (Comeig Ramírez et al., 2016; Frick and Moser, 2021; Hanek et al., 2016). In Western societies, corporate hierarchies have primarily been shaped by male competition, making it relatively easier for men to attain leadership roles, while creating more challenges for women in achieving similar positions. In fact, research suggests, that women tend to exhibit overt competition predominantly in high-ranking positions (Benenson, 2013), which could put them at a disadvantage when competing with men for lower-ranking roles. A more complete understanding of how female animals engage in competitive behaviours can thus significantly contribute to enhancing our theoretical knowledge of power structures and potentially aid in dismantling patriarchal norms, thereby fostering progress towards a more equitable and inclusive society.

Lemurs

In order to better understand female competition in mammals, it might be useful to study the contexts in which female competition is most intense. This includes species in which we observe female evictions. Within mammals, evictions can be found in two major groups: the Herpestidae, including meerkats and banded mongooses, and lemurs. Lemurs provide study systems where multiple scenarios of competition seem likely. First, they have to cope with ecosystems that are less productive than other habitats of the same latitude (Dewar and Richard, 2007; Donati et al., 2017; Federman et al., 2017) and which often express pronounced seasonality. Resource limitation might therefore be one reason why lemur groups are often relatively small compared to other primates of similar body size (Kappeler and Heymann, 1996). Second, reproductive season and receptive periods of females are often synchronized, extremely short, and in Lemuridae, for example, often limited to one or two days (Boskoff, 1978; Ostner and Kappeler, 1999; Overdorff et al., 1999), which could increase competition for mates during a short reproductive season. Furthermore, infanticide has been reported in several cases (Hood, 1994; Jolly et al., 2000). Lemurs therefore face challenges related to both resource limitation and reproductive pressure.

In addition, group-living lemurs offer a good opportunity to study the causes and functions of female competition because the social systems of group-living lemurs are characterised by a combination of traits that is unique among mammals (referred to as the lemur syndrome; Kappeler and Fichtel, 2015; Kappeler and Schäffler, 2008). First, lemur sex roles deviate from the typical mammalian pattern in that often all adult females dominate all adult males or in that sex has no consistent effect on dominance relationships. Female dominance is accompanied by a general lack of sexual dimorphism and a masculinisation of female genitals. As groups are relatively small, females within groups tend to be closely related and often belong to a single matriline (Wimmer et al., 2002). In addition, adult sex ratios are usually even or male-biased. Finally, periods of increased aggression towards group members, so called episodic targeting aggression (ETA), is frequent among the Lemuridae. Most aspects of the lemur syndrome can be linked to female competition (Kappeler and Fichtel, 2015).

One of the species in which ETA has been described are redfronted lemurs (*Eulemur rufifrons*). This cat-sized species lives in multi-male, multi-female groups of 5-12 individuals with even or male-biased adult sex ratios (Ostner and Kappeler, 2004). As females are philopatric, most females within a group belong to the same matriline (Wimmer and Kappeler, 2002) and both sexes lack pronounced dominance hierarchies among or between each other (Ostner and Kappeler, 1999). Consequently, social tolerance in feeding context is relatively high (Fichtel et al., 2018a). In addition, rates of decided agonistic interactions are comparatively low in this species and redfronted lemurs show no clear signs of female dominance (Pereira et al., 1990; Pereira and Kappeler, 1997; Seex et al., 2022). Females reach maturity in their third year of life and have the potential to give birth to a single offspring annually (Kappeler et al., 2022c). As the habitat of redfronted lemurs is highly seasonal, reproduction takes place towards the end of a 7-month long cool dry season. Males are the dispersing sex and typically leave their natal groups at the age of three years. Secondary dispersal is common and usually voluntary (Wimmer and Kappeler, 2002). There is no rank-related variation in the levels of testosterone and glucocorticoids in males. Nevertheless, the concentrations of these hormones increase during the mating and birthing seasons (Ostner, Kappeler, & Heistermann, 2008). Redfronted lemurs have a flexible circadian activity pattern ("cathemerality") characterised by irregular bursts of activity around the 24h cycle (Kappeler and Erkert, 2003) during which they forage for fruits, leaves and – opportunistically – for small animal prey in home ranges of about 25 hectares which largely overlap among neighbouring groups (Pyritz et al., 2011). They are themselves prey for large raptors, snakes, and carnivores, and reach a maximum longevity of about 20 years (Kappeler et al., 2022c). Females are the philopatric sex, but they may be evicted from their natal group during the mating or birth season (Kappeler and Fichtel, 2012). Not a single evicted female has been observed to successfully return to its natal group, and only very few managed to establish or join a new group.

Evictions

In captive lemurs, evictions peak during the annual mating and birth seasons (Vick and Pereira, 1989), suggesting that they are functionally tied to reproductive competition rather than to feeding competition, but this notion remains untested in the wild. In contrast to other taxa, victims include closely-related group members of the same matriline, which are not allowed to return (Kappeler and Fichtel, 2012). Nonetheless, species with ETA differ markedly in social tolerance (Fichtel et al., 2018b), and it remains intriguing why females evict female relatives rather than unrelated males who are present in higher proportions than in other primate species (Kappeler et al., 2009).

Evictions have so far been described in only a few species. However, compared to other mechanisms of female competition, eviction in mammals appears to have a much stronger phylogenetic signal, because it is relatively common among social carnivores but notably rare among primates (Kappeler and Fichtel, 2012; Pusey, 2012). While in lemurid primates typically single adult females are evicted, in Old World primates mass evictions take place that are better described as group fissioning, as for example in rhesus macaques (*Macaca mulatta*; (Larson et al., 2018). In carnivores, the phenomenon and its underlying social and hormonal processes have been well described for meerkats (*Suricata* suricata; Bell et al., 2014; Young et al., 2006) and banded mongooses (Cant et al., 2010; Thompson et al., 2016). In both species, females may return into their natal group after being evicted. Contrastingly, in primates, evicted females have rarely been observed to return to their natal groups.

While evictions may occur at large group sizes, as in banded mongooses (Gilchrist, 2006), they might not always be ultimately related to resource competition. In meerkats which had been provisioned with food, eviction rates increased rather than decreased (Dubuc et al., 2017), and cases of evictions have been reported in captive redfronted lemurs that were not limited by food (Vick and Pereira, 1989). In mongooses, dominant individuals experience reproductive costs when subordinates breed (Cant et al., 2010). Similarly, dominant female meerkats suffer long-term fitness costs when groups get too large (Stephens et al., 2005). Evictions could therefore be a tactic by dominant females to avoid future reproductive competition as in many cases, victims of evictions are younger females that are subordinate to the evicting individual (Clutton-Brock et al., 1998; Pope, 2000). However, almost nothing is known about what drives evictions in primates such as redfronted lemurs.

Female competition in redfronted lemurs

In my dissertation, I used long-term demographic data, behavioural observations, and hormone samples to examine the causes and consequences of female competition in redfronted lemurs. By expanding analyses to integrate both males and females, I 1.) aim to determine differences and similarities in the causes of competition in females and males, 2.) to better understand the link between female competition and social organisation in redfronted lemur groups, and finally 3.) explore how groups might be affected by the loss of group members as a possible result of competition. An outline of my objectives can be seen in figure 0.1.

With this, I hope to contribute to resolving the perplexing phenomenon of evictions in redfronted lemurs and increase the general knowledge of evictions and female competition in general in mammals. First, I examined the ultimate causes of competition in both sexes to determine the relative impact of feeding and reproductive competition. I first examined the potential causes of conflict by investigating the impact of food availability and reproductive season on cortisol levels and then investigated the influence of food availability and reproductive season on rates, intensity and, decidedness of conflicts. Second, I investigated the proximate drivers of eviction events and compared them to drivers of male emigrations. I then explored the link between female competition and fitness components by relating predictors of eviction to lifetime reproductive success, birth rates, and infant survival. Lastly, I explored the potential effect of competition on the social structure of the remaining individuals by comparing rates of affiliation, aggression, and the diversity of relationships within groups before and after events of group member loss.

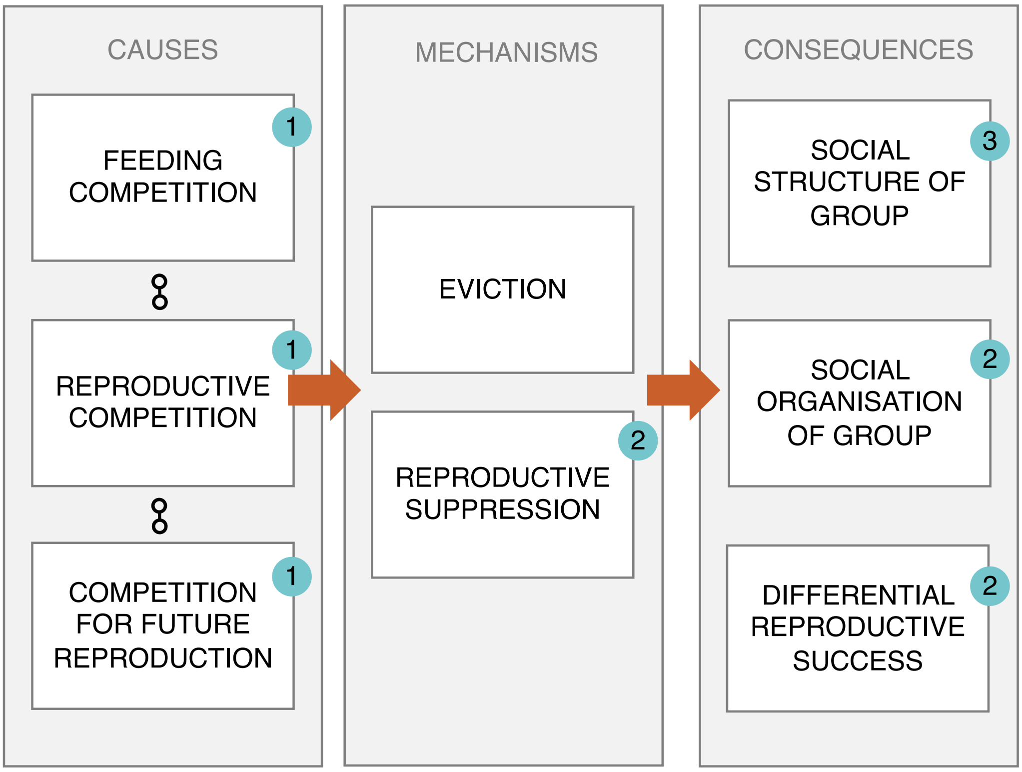

Fig. 0.1: Schematic summary of proposed study. Blue circles refer to the chapters the sections will be addressed in.

CHAPTER I

Seasonal variation in agonism and physiological stress in wild female and male redfronted lemurs (Eulemur rufifrons)

Lea Prox, Michael Heistermann, Claudia Fichtel, Peter M. Kappeler

Abstract

Intraspecific competition with fellow group members represents an unavoidable cost of group living. However, the causes of competition may vary among group members, and ecological and reproductive challenges individuals are confronted with across the year may trigger physical conflicts and or physiological responses. To date, few studies in mammals have described both physiological and behavioral responses to competition simultaneously across the year in both males and females. Such an approach may shed light on ultimate drivers of sex-specific competitive strategies. In this six-year study on multiple groups of wild redfronted lemurs (*Eulemur rufifrons*), a primate species from Madagascar, we intended to identify the relative importance of feeding vs. reproductive competition for both sexes by combining data on fecal glucocorticoid metabolite (FGCM) levels, a proxy for the physiological stress response, with behavioral observations on agonistic interactions during ecologically and socially challenging phases across the year. We found that while FGCM levels increased in both sexes with decreasing fruit consumption, this increase was not accompanied by concomitant changes in agonistic behavior. Female aggression and FGCM levels peaked during the birth season, while for males, aggression remained fairly constant across the year. Our results suggest that redfronted lemurs have mechanisms to avoid direct competition through aggression at times when individuals may need to conserve energy.

Keywords: Competition, lemurs, reproduction, feeding, glucocorticoids, eviction

Introduction

Competition among members of animal societies is a crucial factor shaping the social system of a species, as competition limits group size (Janson and Goldsmith, 1995; Thompson et al., 2017; Wrangham et al., 1993), affects adult sex ratios (Kappeler, 2017; Schacht and Uggla, 2023), triggers dispersal events (Waser, 1985) and defines its competitive regime (Koenig, 2002; Sterck, 1997; Thierry et al., 2021). Thus, competition can substantially influence a population's demographic dynamics and spatial distribution (Hobbs and Munday, 2004). Diverse causes of competition, such as resource limitation or access to mates, may impact the sexes differently, however, because male and female fitness are limited by different factors. Whereas female reproductive success is primarily limited by access to food and other resources, male reproductive success is limited by access to receptive females (Trivers 1972; Clutton-Brock 2017). Yet, it is now also widely acknowledged that female competition may extend into the realm of reproduction (Clutton-Brock 2007; Clutton-Brock and Huchard 2013). Moreover, because drivers of competition vary throughout the year in accordance with ecological and reproductive seasonal cycles for most species, the sexes may also experience seasonal variation in the nature and intensity of competition, raising interesting questions about behavioral and physiological adaptations to deal with these predictable challenges (Helm et al. 2017).

Periods characterized by resource limitation, mating competition or increased energetic demands to meet the costs of reproduction or climatic challenges intensify within-group contest and scramble competition (Isbell 1991; Koenig 2002). In these situations, vertebrates have two non-exclusive options (Honess and Marin 2006). They can mobilize more energy from internal reserves by increasing their glucocorticoid (GC) secretion, and or they can improve their access to contested resources by engaging in agonistic interactions with conspecifics (McEwen and Wingfield, 2003; Sapolsky et al., 2000); Muller et al. 2021). While both responses offer similar benefits, aggression and elevated GC levels have different costs; i.e., short-term increase in the risk of injury (Archie et al. 2014) vs. long-term detrimental effects of chronic stress (Snyder-Mackler et al. 2020). Agonistic interactions can either change in frequency or in intensity, or both. Moreover, the relative frequency of agonistic interactions with members of the same or opposite sex should reflect who competes with whom because males and females compete for different resources. By additionally considering the context or season of these dynamics, it is possible to identify the drivers of competition. The relationship between behavioral and endocrine responses to challenges have been well studied with respect to reproduction and androgens (Goymann et al. 2019; Maney 2020; Moore et al. 2020), but much less is known about the relationship between different behavioral responses (more or less intense aggression) and GC dynamics (Romero 2002; Creel 2005; Summers et al. 2005; Beehner and Bergman 2017; Muller et al. 2021).

A literature search revealed that out of 62 studies on wild mammals, including seasonal and nonseasonal breeders, that investigated differences in GC levels or agonism rates in relation to reproduction or food availability, only 18 studies considered both, variation in reproductive and ecological factors, as potential underlying causes (Table S1). Of those 18 studies, eight considered both males and females separately, and only four of those were able to use data spanning all seasons. Two of those studies were on lemurs, where reproductive periods appeared to have more impact on levels of aggression or glucocorticoid levels than did ecological factors, such as habitat quality or food availability. In Verreaux's sifakas (*Propithecus verreauxi*), GC levels were elevated in females during gestation, but only higher by trend at times of lower food intake (Rudolph et al., 2020). In collared lemurs (*Eulemur collaris*), highest levels of GC were found in females during gestation and in males during the mating season in both degraded and undisturbed habitat (Balestri et al., 2014). In the two other studies, female dugongs (*Dugong dugon*) had elevated GC levels during gestation (Burgess et al., 2013), and in black capuchin monkeys (*Sapajus nigritus*), GC levels were elevated during the breeding season in both sexes and during periods of low food availability in males (Moreira et al., 2016).

Against this background, the competitive regime of redfronted lemurs (*Eulemur rufifrons*), a sexually monomorphic, group-living Malagasy primate, offers an interesting opportunity to study sex-specific responses to seasonal challenges. In Western Madagascar, they live in highly seasonal dry deciduous forests. Their reproduction is limited to a few weeks each year, with matings taking place at the beginning, and births at the end of an 8-month dry season. Their social structure offers a perplexing paradox because high levels of exceptional year-round social tolerance are punctuated by rare episodes of fierce competition, often culminating in permanent and possibly lethal eviction of closely-related female group mates during periods of reproductive activity that may not be directly linked to year-to-year variation in food availability (Fichtel et al., 2018; Kappeler and Fichtel, 2012; Pereira et al., 1990; Prox et al., 2023; Vick and Pereira, 1989). Indeed, in food-provisioned, captive redfronted lemurs, most episodes of targeting aggression also occurred before and during the mating season and birth seasons (Vick and Pereira, 1989), hinting at the importance of reproductive competition as a driver. Long-term demographic analyses over more than 20 years revealed group size and the number of juvenile female group members as the key drivers of evictions (Kappeler and Fichtel, 2012; Prox et al., 2023). Thus, female competition is not about access to mates and unrelated to current food availability, but evictions have the lasting effect of reducing feeding competition.

In contrast to other primate and carnivoran species, in which aggression is linked to an increase in GC levels (Creel, 2005; Fichtel et al., 2007; Muller et al., 2021; Ostner et al., 2008a, but see Girard-Buttoz et al., 2009), increases in GC and androgen levels during the mating and birth season of redfronted lemur males were not strongly linked to corresponding changes in aggression rates (Ostner et al., 2002, 2008). In fact, redfronted lemurs are characterized by high levels of male-male tolerance and male-biased adult sex ratios (Ostner and Kappeler, 2004), but also one of the highest levels of male reproductive skew reported for any primate species (Kappeler and Port, 2008). It has been suggested that GC levels increase in late gestation and early lactation in females and at times of low food availability in both sexes (Defolie, 2022), but these reproductive and ecological factors are likely confounded, and were tested in separate models that did not control for the respective other factor. Increased levels of glucocorticoids during the birth season, for example, coincide with the late dry season and low fruit availability, so that the relative importance of social and environmental stressors is difficult to determine. Thus, while we have characterized several aspects of the social structure of redfronted lemurs, we still lack a comprehensive picture of year-round variation in rates and intensity of agonism among all types of sex dyads (but see Kappeler, 1993 for data from captivity), and how they relate to GC levels and food intake. Here, we present five years of concurrently collected data on agonism, food intake and fecal GC levels of seven wild groups to further illuminate the causes, patterns and correlates of competition in the unusual social structure of this lemur species.

By comparing the behavioral and physiological dynamics between males and females as well as determining reproductive seasons specifically for each year and discriminating between reproducing and non-reproducing females, we aimed to tease apart the costs of reproduction and the challenges created by reduced food availability, as well as the relationship between behavioral and endocrine mechanisms used to cope with these challenges. Because both sexes are exposed to the same seasonal fluctuations in resource availability and competition, we predicted elevated aggression and GC levels during the resource-poor dry season. Furthermore, we predicted the annual mating and birth seasons to have additional and sex-specific effects on the stress response as well as on the intensity of aggression. Specifically, because pregnant and lactating females experience unique energetic demands of reproduction, and because most evictions take place during the birth season, we predicted rates of female agonism and fGC levels to be higher than those of males at this time of the year.

Methods

Study site and subjects

Data for this study are based on animal focal observations and fecal samples of a population of redfronted lemurs inhabiting a local study area of ca. 80 ha in Kirindy Forest, a dry deciduous forest in western Madagascar. Individuals of this population have been regularly captured since 1996, subjected to standard field morphometric measurements and individually marked with RFID-tags and unique nylon collars (Kappeler and Fichtel, 2012). One adult female per group has been equipped with a radio collar to facilitate the location of groups for the near daily focal observations. The regional climate is characterized by a cool dry season between May and September and a hot wet season from October to April. Redfronted lemurs are seasonal breeders, with matings taking place in late May/early June and births in late September/early October. The data for this study were collected from May 2015 to October 2016 and May 2017 to October 2022 on seven groups including a total of 32 females and 46 males. Four females and twelve males did not reach sexual maturity during the study period (@2 years). We did not include these juveniles and infants in this study as we expected competition to occur mainly between adults.

All applicable international, national, and/or institutional guidelines for the care and use of animals were followed. The authors complied with the ARRIVE guidelines100. This study adhered to the Guidelines for the Treatment of Animals in Behavioral Research and Teaching and the legal requirements of Madagascar and has been approved by the Commission Tripartite de la Direction des Eaux et Forêts.

Behavioral data collection

Between May 2015 and October 2022, we carried out 30 minute focal observations on individuals (Altmann 1974) in the morning between 7 and 11 am and in the afternoon between 2 and 5 pm. Numbers and circadian distribution of observations were distributed equally among individuals. Within these constraints, focal individuals were chosen randomly. In total, we collected 5067 h of focal animal data with an average of 53.90 h of observations per individual. We defined interactions as agonistic, if we observed an aggressive act or signal in at least one animal (fight, chase, bite, hit, lunge, displace). These interactions may or may not also include submissive behavior by one or both opponents (Pereia & Kappeler 1997). We classified the intensity of agonistic interactions as follows: Intensity 3: chasing and fighting for > 3 sec, intensity 2: hitting and biting, and intensity 1: displacements and threats. An agonistic interaction was considered as decided if the recipient of aggression departed within seven seconds after the interaction. During focal observations, we also recorded time spent feeding on different food items as fruit, leaves and flowers to assess food consumption.

Hormonal data collection & measurement of fecal glucocorticoid metabolites

To assess individual glucocorticoid profiles, we collected a total of 2436 fecal samples (1 to 5 samples per individual per month from 29 females and 44 males). Samples were collected from the forest floor immediately after defecation between 7:30 and 11 am and a portion of 0.5 – 1.0 g of well mixed fecal material was placed in 5 ml of 80% watery ethanol. As mean FGCM levels did not seem to be affected by the hour of sample collection, we did not control for this variable. We extracted glucocorticoid metabolites (fGCMs) directly at the field site using a validated field extraction method (Shutt et al., 2012; Nugraha et al., 2017) that has been previously applied successfully in this species (Murillo et al., 2022b). Briefly, tubes with feces were vortexed for 2 minutes to homogenize the fecal matter before centrifuging the suspension for 2 minutes with a manually operated centrifuge (Hettich, Tuttlingen, Germany).

1.5 ml of the extracts were transferred into 2 ml polypropylene tubes which were subsequently stored at ambient temperature in the dark for up to 6 months before transport to the endocrinology laboratory of the German Primate Center where they were kept at -20 °C until hormone analysis. A previous study had shown that storage of red-fronted lemur fecal samples in alcohol at ambient temperature for periods of up to 8 months does not affect FGCM concentrations significantly (Ostner et al., 2008).

FGCM concentrations were assessed using a microtiterplate enzymeimmunoassay for immunoreactive 11-oxoetiocholanolone, which provides a group-specific measurement of 5ß-reduced cortisol metabolites (Heistermann et al., 2006) and which has previously been validated and successfully used to track adrenocortical activity in this study species (Ostner et al., 2008; Clough et al., 2010; Murillo et al., 2022). Prior to assay, fecal extracts were diluted 1:200 – 1:2000 (depending on concentration) in assay buffer (0.04 M PBS, pH 7.2) to bring the hormone concentrations into the working range of the assay, and duplicate 50µl aliquots of diluted samples were then measured along with 50µl aliquots of 11-oxoetiocholanolone standard used as reference. The plates were incubated overnight at 4°C. After incubation, the plates were washed four times, 150µl (667 ng) of streptavidin-peroxidase in assay buffer was added to each well and the plates incubated at room temperature (RT) for 1 hour in the dark. Following a second washing step thereafter, 100µl of a TMB substrate solution was added to each well and the plates incubated at RT in the dark for 45 min. The enzymatic reaction was finally stopped by adding 50µl of 2M H_2SO_4 to each well and optical density was measured at 450 nm (reference 630 nm) in a plate reader. Assay sensitivity at 90% binding was 3 pg. Intraassay coefficients of variation (CV) of high- and low-value quality controls were 5.5% (high) and 7.1% (low), while respective figures for inter-assay CVs were 11.7% (high, N=70 assays) and 14.8% (low, N=70 assays). FGCM values are expressed as mass per gram of fecal dry weight (i.e. ng/g), the latter being determined in the field after sun-drying the fecal matter following FGCM extraction.

For the subsequent statistical analyses, we defined other variables as follows:

Reproductive season: as most births within a group occur within a few weeks, we defined a given birth season to start at the date of the first birth and to last for four weeks because the majority of births occurred within four weeks (Kappeler & Fichtel, unpubl. data). We set the time window of the mating season also to four weeks, starting 121 days (the mean gestation length) plus one week prior to the birth season. We did not include gestation as an additional reproductive season to decrease model complexity, as we did not expect it to cause increases in competition. Periods outside the birth and mating season were classified as "none" and were used as the baseline level in the models.

Fruit consumption: The proportion of time a group was observed feeding on fruit over the past 30 days. We used individual focal observations to calculate time spent feeding on fruits as groups are quite cohesive and usually feed together.

Composition change: If an immigration or emigration occurred within the last 30 days prior to the sampling event, composition change took the levels "immigration" or "emigration". If both an immigration and emigration occurred within 31 days prior to the event, we defined composition change as "both".

Temperature: We included minimum temperature in the glucocorticoid model as low temperature is a common stressor in primates (Beehner and McCann, 2008; Charpentier et al., 2018; Chaves et al., 2019). To account for fecal samples being collected early in the morning, we used minimum temperature from the previous day to the collection date of the sample.

Rainfall: We used the cumulative rainfall of the 31 days prior to the day of observation or hormone collection. Rainfall data were retrieved from the CHIRPS data base (Funk et al., 2015).

Reproductive state: For each female, we indicated whether she was pregnant or with a dependent offspring (up to the age of 3 months), as lactating females that carry small infants might experience more stress than mothers of independent offspring.

Statistical analyses

First, we investigated the impact of reproductive and ecological seasons on different aspects on agonistic interactions; specifically agonistic rates, maximal agonistic intensity and decidedness of conflicts. Second, we investigated the impact of reproductive and ecological seasons on fecal glucocorticoid metabolite (FGCM) levels. As a descriptive statistic, we calculated the percentage of females that had an offspring during the birth season and the percentage of conflicts they were involved in relation to females without offspring. We also determined the percentage of conflicts that took place in a feeding context (10 seconds prior or after feeding behavior) for each season per sex.

Intensity of agonism – Model 1

To investigate whether reproductive or resource competition were better predictors of the intensity of agonistic interactions, we constructed an ordinal Generalized Linear Mixed Model (GLMM) using the package “ordinal” (version 2022.11.16; Christensen, 2018). We set maximum agonistic intensity observed during an individual focal observation as the response. In order to compare effects of fruit consumption and reproductive season between the sexes, we included them as interaction terms in the model, as well as reproductive season, and rate of fruit consumption as fixed effects. We included composition change, group size and adult sex ratio (ASR; Ancona et al., 2017) as control variables and individual ID and group ID as random effects and observation time as offset term. As we included interactions in the model, only the effects of the interactions could be considered, as main effects that were included in interactions have limited interpretation. However, this does not impose any limitation, as instead of discussing for example the effect of fruit availability on agonism in redfronted lemurs in general, we can discuss the effect of fruit availability on female and male redfronted lemurs separately. To avoid type I errors, we included all theoretically identifiable random slopes (Barr et al., 2013; Schielzeth and Forstmeier, 2009). Initially, we built a complete model (Barr et al., 2013) that included correlations among random intercepts and slopes. However, as the absolute values of these correlations were estimated to be close to one, indicating a lack of identifiability (Matuschek et al., 2017), we decided to exclude these correlations from the model. We first excluded all correlations in one model and in a subsequent model just correlations within the random factor “group”. We compared fits of all versions of the model and chose the model with some correlations (excluding correlations within group) as it had the best fit (AIC=-3190.56 compared to -3197.37). The sample for this model encompassed a total of 7536 focal observations in 7 groups with 78 individuals.

Agonistic rates – Model 2

To investigate whether reproductive or resource competition better predict agonistic rates per focal observation, we built a negative binomial model using the package “glmmTMB” (version 1.1.7; Brooks *et al.*, 2017). We set counts of agonistic events per focal observation as the response and included reproductive season, rate of fruit consumption and sex of focal individual as fixed effects, as well as the interactions between sex and reproductive season and sex and fruit consumption, respectively, as we expected reproductive or resource competition to differ between the sexes. As we expected composition change (i.e., immigrations or emigrations), group size and ASR to influence intensity of agonism, we included them as control variables. As random intercept effects, we included individual ID and group ID with all theoretically identifiable random slopes. As in the previous model, we found the estimates of the absolute values of these correlations to be approximately equal to one, which is why we did not include them in the final model. The sample for this model encompassed a total of 7536 focal observations in 7 groups with 78 individuals.

Decidedness of conflicts – Model 3

To investigate whether reproductive or resource competition better predicts the likelihood of a conflict to be decided, we fitted a binomial model using the function glmer of the package “lme4” (version 1.1.31; Bates *et al.*, 2014). We fitted decided (yes or no) as the response and included reproductive season, rate of fruit consumption and sex combination (aggressor-victim), as well as the interactions between rate of fruit consumption and sex and reproductive season and sex, respectively, as fixed effects. We included group ID as well as aggressor ID, victim ID and dyad ID as random effects and included all theoretically identifiable random slopes. We constructed a binomial GLMM. Because of extreme values in the random effect structure, which are likely to indicate overparameterization, we first removed correlations close to 1 and then some of the random slopes. The sample for this model encompassed a total of 1299 conflicts in 7 groups of 52 aggressors and 51 victims.

FGCM levels -Models 4a, 4b, 4c, 4d

To investigate whether reproductive or resource competition better predict individual FGCM levels, we constructed a Gaussian GLMM. Prior to fitting the model, we log-transformed the response variable FGCM (ng/g), as it was not normally distributed. We included reproductive season, rate of fruit consumption and the combined variable of sex of focal individual and reproductive state ("sex/female reproductive 2": female with offspring, female pregnant female none, male none) as fixed effects, as well as the interaction of sex/female reproductive state and rate of fruit consumption (female_pregnant: pregnant females, female_with_offspring: lactating females, female_none: females that were neither lactating or pregnant). As control variables, we included composition change, group size, ASR, rain and minimal temperature, and group ID and individual ID as random effects with all theoretically identifiable random slopes. We included reproductive state in this model as FGCM values have been shown to vary across reproductive states of females, with increasing values during gestation and lactation. As we were also interested in the interaction of sex and reproductive season, but a model including female reproductive state would have been rank deficient, we fitted a second and third model where we excluded this variable. In the second model (model 4b) we used the same data as for first model but excluded the variable of female reproductive state. In the third model we created a subset of the data in which we excluded pregnant and lactating females. In both models we used the same random effects again including all theoretically identifiable random slopes. We fitted an additional model (model 4d), where we used the same variables as in the first model but also included agonism rate within the same group over the two weeks prior to the sample. We constructed a Gaussian GLMM. The sample for models 4a, 4b, and 4d encompassed a total of 2436 FGCM data points from 7 groups with 74 individuals, the sample for model 4c encompassed 2006 FGCM data points from 7 groups with 74 individuals.

Implementation

All analyses were conducted using R (version 4.2.2, R Core Team 2022). We used Generalized Linear Mixed Models (GLMM; Baayen, 2008) with binomial error structure and logit link function for all models, except the models with glucocorticoids as the response, for which we used Gaussian error structure and identity link function. To ease model convergence, we centered all quantitative predictors to a mean of zero and a standard deviation of one before including them into the models. We included all theoretically identifiable random slopes to avoid Type I errors (Barr et al., 2013; Queen et al., 2002). P-values of the fixed effects were derived using likelihood ratio tests (Barr et al. 2013; R function drop1 with argument 'test' set to "Chisq") The drop1 function compares between all possible models by dropping a single term at a time. It provides a robust method for estimating p-values by assessing the significance of each predictor in comparison to others. We compared the resulting model to a null model, comprising all random effects, random slopes and control factors included in the full model but lacking the fixed effects with a likelihood ratio test (Schielzeth and Forstmeier, 2009). This full-null model comparison served to avoid 'cryptic multiple testing' (Forstmeier and Schielzeth, 2011). We obtained confidence intervals for all models by means of parametric bootstraps using the function "bootMer" of the package "lme4", applying 1000 parametric bootstraps. We checked for collinearity by determining Variance Inflation Factors (VIF) for a standard linear model without random effects using the package "car" (version 3.0.11; Field, 2005). To estimate model stability, we proceeded by dropping levels of the random effect one at a time from the data set and compared the obtained estimates to the estimates obtained for the full data set. All models exhibited good stability.

Results

About one fifth of all conflicts (N = 1299) occurred in the feeding context. During the mating season, 18.18 % of conflicts involving females and 16.28 % involving males were observed in the feeding context. During the birth season, these proportions changed to 11.54 % (females) and 6.25 % (males), respectively. Most (84%) females involved in conflicts during the birth season had an offspring, even though they only made up 40% of the female population during this period.

Intensity of agonism

We found a significant effect for the interaction between sex and reproductive season (full-null model comparison: χ2=13.02, df =3, P=0.0004). More specifically, we found that females were involved in conflicts with higher intensity of aggression during the birth season, while for males, intensity levels of aggression remained more or less the same across the three seasonal periods (Fig. 1). Fruit consumption did not have a significant effect in interaction with sex (estimate= -0.49, p-value =0.7; Table 1a).

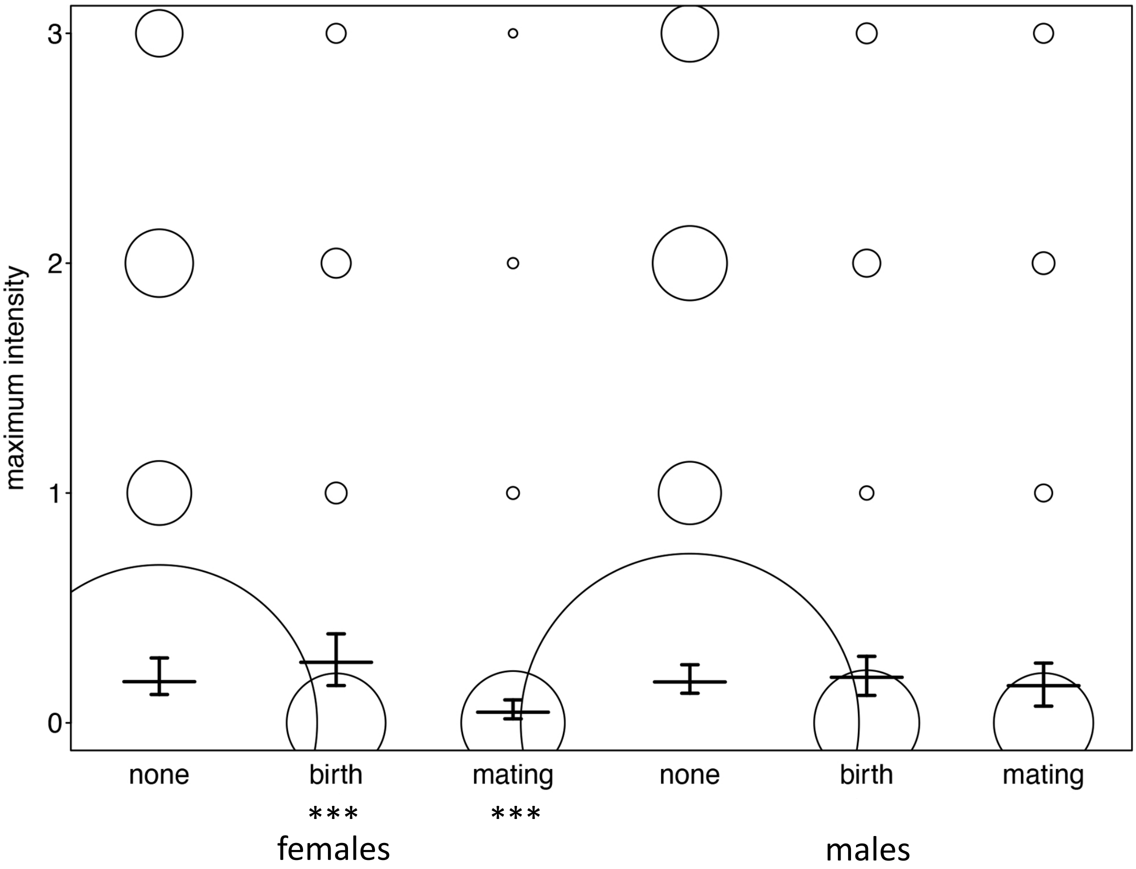

Fig. 1.1: Maximum intensity of agonistic interactions of males and females in different reproductive seasons (model 1). Horizontal lines depict estimates and vertical bars show 95% confidence intervals. Circles show data density for each level.

Agonistic rates

We observed on average 0.29 agonistic interactions per hour. We found the interaction of sex and reproductive season to have a significant effect on agonism rates, with females exhibiting higher agonism rates during the birth season (Fig. 2). Fruit consumption in interaction with sex did not have a significant effect on agonism rates. As the null model for this model did not converge, the results should be treated with care, as we cannot exclude them being due to false positives.

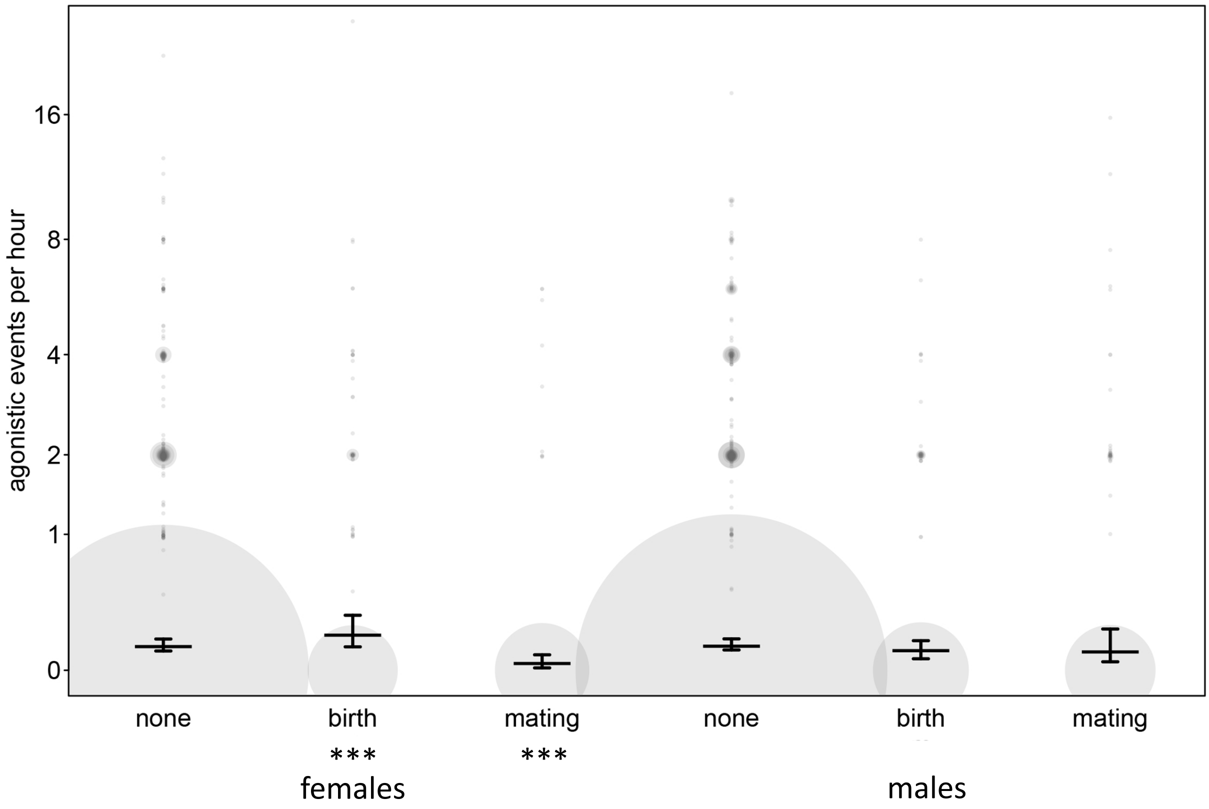

Fig. 1.2: Agonistic rates in males and females in different reproductive seasons (model 2). Horizontal lines depict estimates and vertical bars show 95% confidence intervals. Circles show data density for each level.

Decidedness of conflicts

In total, 45.71 % (N=1299) of all agonistic interactions were decided. 14.77 % of all decided agonistic interactions occurred between females, 62.10 % occurred between females and males, and 23.13 % occurred between males. As the full-null model comparison was not significant, we removed the interaction of reproductive season and sex combination from the full model as it was not significant. The model was overall not significant (full-null model comparison: $\chi2$ = 7.20, df = 9, P= 0.616), which is why we will not further discuss the results (Table 3).

FGCM levels

Overall, full-null model comparisons of all four models were significant (full-null model comparisons: 4a: $\chi2$=29.31, df =9, P<0.001; 4b $\chi2$=25.85, df =7, P<0.001; $\chi2$=25.85, df =7, P<0.001, 4c: $\chi2$=25.85, df =7, P<0.001; $\chi2$=19.92, df =7, P=0.005, 4d: : $\chi2$=25.65, df =10, P=0.004). More specifically, we found that the interaction of the combined variable sex/female reproductive state and rate of fruit consumption was significant, with pregnant and lactating females and males having lower FGCM levels with increasing time spent feeding on fruit (test of the interaction between fruit consumption and sex: χ2=-5.07, df =228.76, P=0.002; Table 4a; Fig. 3a). Reproductive season did not have a significant effect in either sex (Table 4a). In the second model, which excluded female reproductive state from the combined sex variable, we found a significant effect of the interaction between sex and reproductive season with females having elevated FGCM levels during the birth season (*F*=-0.31, df =228.76, P=0.045; Table 4b; Fig. 3b), but no effect of the interaction between sex and fruit consumption. In model 4c, where we fitted a subsample of males and females that were not pregnant or lactating, we found a trend for the interaction between sex and fruit consumption (test of the interaction between fruit consumption and sex: *F*=- 3.01, df 1=0.053, P=0.053; Table 4c) but not for the interaction between sex and reproductive season (Table 4c). Aggression had no significant effect in the model including aggression.

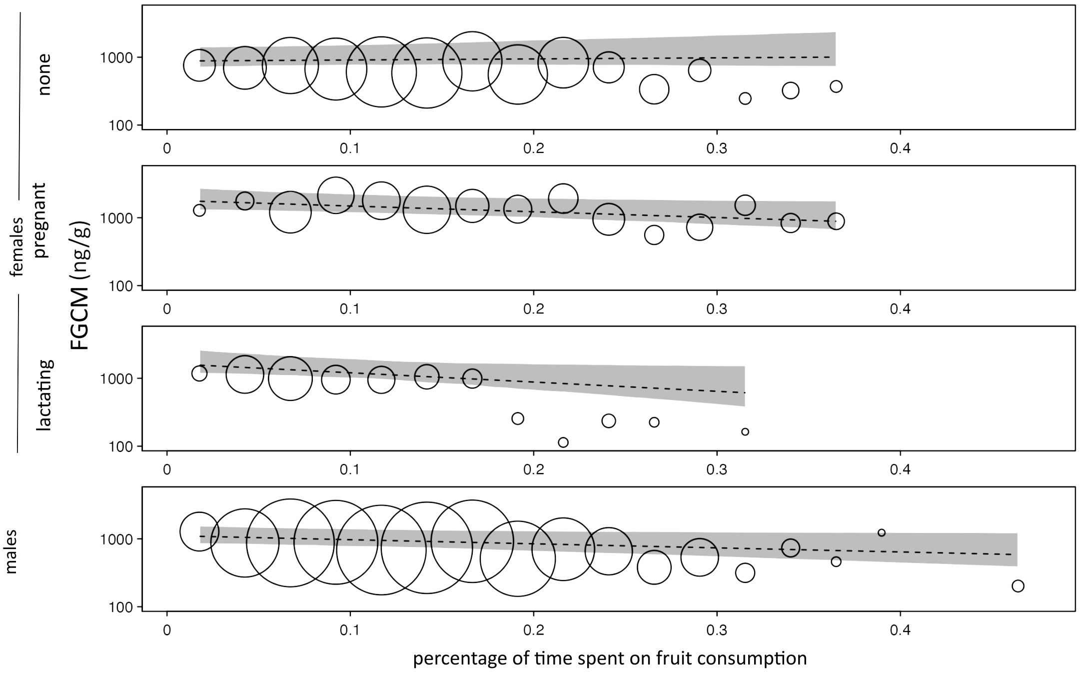

Fig. 1.3a: FGCM levels (ng/g) in relation to time spent on fruit consumption for males and females in different reproductive states (model 4a). Dashed lines indicate the regression lines and polygons the 95% confidence intervals. Point size is relative to number of observations.

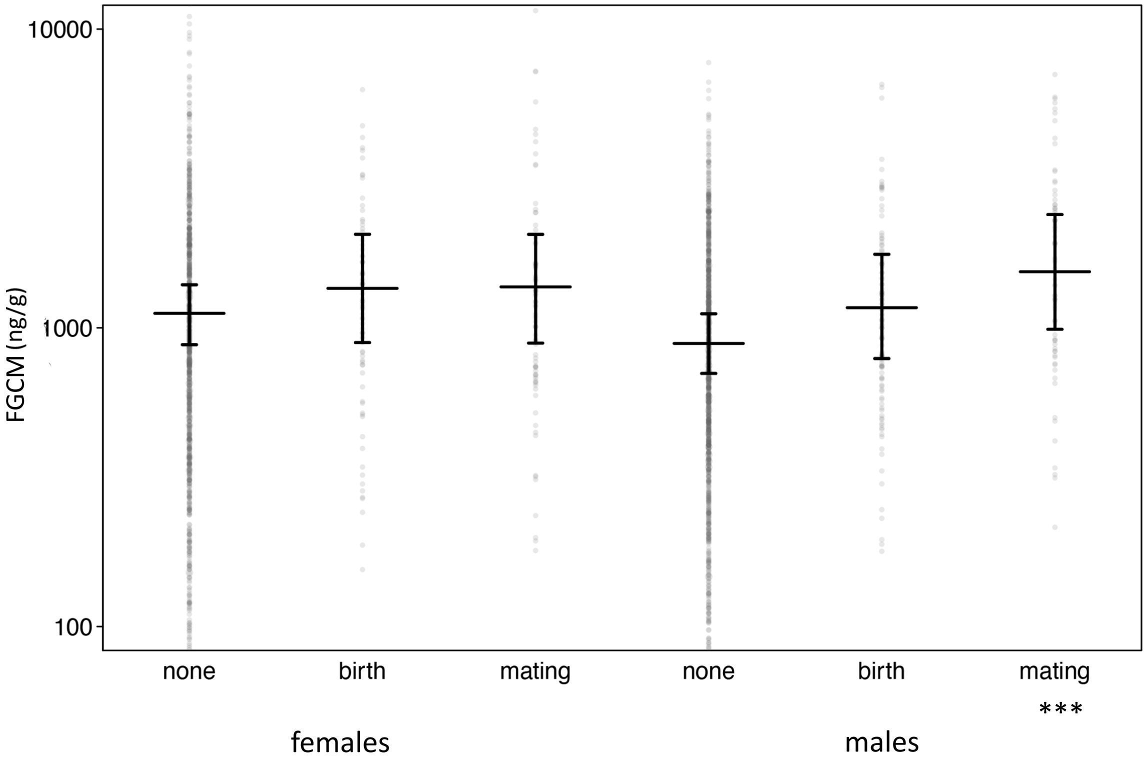

Fig. 1.3b: FGCM levels (ng/g) in relation to reproductive season for males and females (model 4b). Horizontal lines depict estimates and vertical bars show 95% confidence intervals. Circles show data points.

Table 1.1: Results of intensity of agonism model (Model 1)

Term	Estimate	SE	Lower CI	Upper CI	*z* or χ^c	*df*	*P*
Intercept	0.44	0.20					[a]
Composition change (both)	0.00	0.21	-0.37	0.34	1.66		0.465
Conposition change (emigration)	0.03	0.14	-0.38	0.37			
Composition.change (immigration)	0.35	0.17	-0.14	0.76			
Group size[b]	0.11	0.06	-0.18	0.44	1.75	15	0.082
ASR[b]	0.05	0.08	-0.24	0.35	0.66	15	0.429

Rep. season: sex (birth m)	**-0.33**	0.28	-0.99	0.32	8.28		0.008
Rep. season: sex (mate m)	**1.30**	0.48	0.42	0.27			
Fruit cons : sex (m)	-0.49	1.57	-3.06	0.30	-0.62		0.700

[a] not shown because of having a very limited interpretation

[b] z-transformed to mean of zero and a standard deviation of one; mean and standard deviation of the original predictors: group size: mean= 7.70, SD= 2.36; asr: mean= 0.59, SD= 0.10

[c] Chi for interactions, reproductive season and composition change, z-test for everything else.

.

Table 1.2: Results of agonism rate model (Model 2)

Term	**Estimate**	**SE**	**Lower CI**	**Upper CI**	***z* or χ[c]**	***df***	***P***
Intercept	-2.05	0.13	-2.29	-1.81			[a]
Composition change (both)	0.16	0.22	-0.25	0.50	2.47		0.480
Stat change (emigration)	-0.18	0.17	-0.57	0.10			
Stat.change (immigration)	0.20	0.26	-0.37	0.64			
Group size[b]	0.08	0.08	-0.06	0.22	0.54	1	0.345 [d]
ASR[b]	0.08	0.07	-0.05	0.21	1.11	1	0.251
Rep. season: sex (birth m)	**-0.65**	0.30	-1.23	-0.08	7.33		0.026
Rep. season: sex (mate m)	**0.99**	0.48	0.03	2.08			
Fruit cons : sex (m)	-0.05	0.10	-0.26	0.12	NA		0.570 [d]

[a] P-value could not be estimated using the drop1 function (see Methods: Implementation)

[b] z-transformed to mean of zero and a standard deviation of one; mean and standard deviation of the original predictors: group size: mean= 7.70, SD= 2.36; asr: mean= 0.59, SD= 0.10

[c] Chi for interactions, reproductive season and composition change, z-test for everything else.

[d] P-value could not be estimated using the drop1 function (see Methods: Implementation)

Table 1.3: Results of decidedness of conflicts model (Model 3)

Term	Estimate	SE	Lower CI	Upper CI	χ	*df*	*P*
Intercept	-0.54	0.71	-1.99	0.90			[a]
Rep. season: sex (${}_{\text{birth fm}}$)	-0.83	1.34	-3.71	1.81	5.93	0.43	0.431
Rep. season: sex (${}_{\text{mate fm}}$)	-14.15	40.61	- 22.65	-7.73			
Rep. season: sex (${}_{\text{birth mf}}$)	-0.12	0.98	-2.13	1.85			
Rep. season: sex (${}_{\text{mate mf}}$)	-13.77	40.61	-15.68	-9.36			
Rep. season: sex (${}_{\text{birth mm}}$)	-1.60	1.17	-4.52	0.75			
Rep. season: sex (${}_{\text{mate mm}}$)	-14.86	40.61	-16.81	-10.65			
Fruit cons : sex (fm)	4.90	5.72	-6.19	16.77	2.34		0.506
Fruit cons : sex (mf)	2.15	4.82	-6.58	12.38			
Fruit cons : sex (mm)	8.04	5.78	-3.07	20.53			

[a] P-value could not be estimated using the drop1 function (see Methods: Implementation)

Table 1.4: Results of glucocorticoid models (Model 4)

Term	Estimate	SE	Lower CI	Upper CI	*t* or *F*[c]	*df*	*P*
a)							
Intercept	6.81	0.13	6.53	7.09			[a]
Rep. season (birth)	0.21	0.12	-004	0.49	5.61	2.00	0.151

Rep. season (mating)	0.31	0.14	0.10	0.72			
Composition change (both)	0.27	0.18	-0.15	0.68	7.08	2.00	0.435
Stat change (emigration)	-0.03	0.08	-0.21	0.15			
Stat.change (immigration)	0.29	0.18	-0.10	0.71			
Min. temperature	-0.14	0.05	-0.26	0.04	-2.95	2.98	0.163
Group size^b	-0.08	0.13	-0.35	0.20	-0.64	3.04	0.297
Rainfall^b	-0.16	0.13	-0.42	0.09	-1.23	3.18	0.322
Fruit cons : sex con (preg)	**-2.43**	0.79	-3.98	-0.85	5.07	228.76	0.002
Fruit cons : sex con (lact)	**-3.45**	1.34	-6.09	-0.78			
Fruit cons : sex con (m)	-1.86	0.68	-3.22	-0.42			
b)							
Intercept	7.02	0.11	6.80	7.23			^{a}
Composition change (both)	0.25	0.05	0.23	0.62	1.75	3.90	0.298
Stat change (emigration)	-0.06	0.20	-0.06	0.12			
Stat.change (immigration)	0.29	0.18	0.27	0.65			
Min. temperature	**-0.15**	0.05	-0.15	-0.04	-3.00	3.99	0.040
Group size^b	-0.12	0.15	-0.12	0.15	-0.79	3.88	0.475
Rainfall^b	-0.18	0.15	-0.19	0.07	-1.22	3.60	0.296
Rep. season: sex (birth m)	**0.08**	0.13	0.08	0.35	3.10	2148.95	0.045
Rep. season: sex (mate m)	**0.34**	0.14	0.35	0.62			
Fruit cons : sex (m)	-1.01	0.61	-1.04	0.08	2.77	53.21	0.102

c)							
Intercept	6.90	0.15	6.59	7.34			[a]
Composition change (both)	0.24	0.19	-0.18	0.61	1.30	3.44	0.403
Stat change (emigration)	0.01	0.09	-0.22	0.23			
Stat.change (immigration)	-0.36	0.23	-0.14	0.76			
Min. temperature	-0.16	0.05	-0.27	-0.04	-2.88	3.21	0.059
Group size[b]	-0.01	0.17	-0.34	0.30	-0.07	4.27	0.950
Rainfall[b]	-0.16	0.16	-0.47	0.12	-0.98	2.92	0.403
Rep. season: sex (birth m)	0.26	0.20	-0.14	0.68	0.97	264.63	0.382
Rep. season: sex (birth m)	0.11	0.16	-0.22	0.43			
Fruit cons : sex (m)	-1.44	0.73	-3.04	0.02	3.91	58.22	0.053

[a] not shown because of having a very limited interpretation

[b] z-transformed to mean of zero and a standard deviation of one; mean and standard deviation of the original predictors: **Model 4 a,b,d:** rainfall: mean= 0.07; 0.11, SD= 179.23; min. temperature: mean= 21.49, SD= 2.76; group size: mean= 8.46, SD= 2.81; **Model 4c:** rainfall: mean= 0.08; 0.12, SD= 179.23; min. temperature: mean= 21.64, SD= 2.73; group size: mean= 8.50, SD= 2.84.

[c] F-test for interactions, reproductive season and composition change, *t*-test for everything else.

Discussion

We provide one of the first studies simultaneously investigating competitive patterns in relation to feeding and reproductive competition in multiple groups of redfronted lemurs. We investigated these effects on adrenocortical activity in both males and females by monitoring fecal glucocorticoid metabolite levels and agonistic behaviors over a period of five years. We collected data over the course of the ecological and reproductive seasons in order to determine when and why male and female redfronted lemurs experience more or less intense levels of competition across the year, and in whether there are indications for seasonal predictors of competition that may underly female evictions. Although no evictions were observed during the study period, we could identify phases of heightened conflicts for both sexes. While FGCM levels in both sexes appeared to be equally affected by food limitation, only males also had increased FGCM levels during the mating season. Only female, but not male, individuals responded behaviorally with increased aggression to challenges during the birth season. Interestingly, the lack of increased aggression during periods of reduced food availability suggests that fruit consumption does not appear to govern competition in either sex. Redfronted lemurs therefore seem to primarily respond physiologically to periods of potential conflict.

Reproductive Season

During the mating period, agonism rates generally increased among males in many species, but this effect was not consistently found in all species, as for example in ring-tailed lemurs (*Lemur catta*; Gould et al., 2005). Moreover, only a few studies also investigated effects of reproductive activity on female agonism. An increase in agonism rates in female red deer (*Cervus elaphus,* Bebié and McElligott, 2006), and a higher number of injuries in both sexes in Nepalese gray langurs (*Semnopithecus schistaceus*) during the mating season (Feder et al., 2019) suggests heightened female reproductive competition as well. In meerkats, reproductive competition seems to be increased during gestation, and pregnant dominant females have been observed to be more aggressive (Young et al., 2006). In some mammals, females have been observed to be more aggressive during and before lactation. Here, increased aggression could be attributed to lactating redfronted lemurs experiencing heightened resource demands to compensate the energetic burden of lactation (Lee, 1996; Thompson et al., 2012), promoting increased aggression in feeding contexts. Increased agonism rates have been previously described between males and females during the lactation and the weaning periods in ring-tailed lemurs (Sauther, 1993). They have also been linked to heightened resource competition during lactation in other mammals (Clutton-Brock et al., 1989; Patterson et al., 2021; Stockley and Bro-Jørgensen, 2011; Wise and Ferrante, 1982). In addition, maternal aggression has been linked to offspring protection in other mammals, particularly in species where infanticide is common (reviewed in Maestripieri, 1992). Increased aggression in female redfronted lemurs in the birth season might therefore be linked to offspring protection.

Remarkably, in redfronted lemurs male agonism rates exhibited minimal variation throughout the year, a pattern uncommon in studies investigating seasonal variations in male agonistic behavior. This discrepancy could be attributed to the generally low agonism rates exhibited by redfronted lemurs, where effects of seasonal variation may be subtle. However, we found a clear effect of reproductive season on female agonism rates and intensity. However, contrary to our expectations, we observed this increase in aggression during the birth season, rather than the mating season. There are two possible, not mutually exclusive, explanations for this finding: resource competition and offspring protection. Although increased aggression as a result of increased resource demand has been observed in other mammals before, the percentage of conflicts in feeding context did not increase in the birth season in our study population. Alternatively, mothers may be attempting to discourage unwanted handling of their offspring by other group members, a behavior commonly observed in redfronted lemurs, particularly with dependent infants. Notably, a large proportion (84%) of female conflicts during the birth season involved lactating mothers, despite constituting only 40% of the observed female population during this period. Infanticide has been observed in our study population (PMK unpubl. data), and it has been reported for other populations (Jolly et al., 2000). Thus, while we cannot exclude the possibility that peaks in agonism rates and intensity in redfronted lemurs might be driven by heightened resource competition, maternal protection of offspring as a cause of increased aggression seems more likely, considering the lack of effect of the interaction between sex and reproductive season on agonism rates and intensity.

In many mammalian species, including refroned lemurs, males experience higher levels of glucocorticoids during the mating season (Burgess et al., 2013; Fichtel et al., 2007; Girard-Buttoz et al., 2009; Lynch et al., 2002; Montiglio et al., 2015; Mooring et al., 2006; Pereira et al., 2006; Strier et al., 1999; Ventrella et al., 2018, Ostner et al., 2008),. In addition, several previous studies found a positive association between increased male aggression and glucocorticoid levels (Burgess et al., 2013; Mooring et al., 2006). In females, glucocorticoid levels were usually highest during gestation and lactation (Balestri et al., 2014; Burgess et al., 2013; Carnegie et al., 2011; Cizauskas et al., 2015; Montiglio et al., 2015; Rudolph et al., 2020). Elevated glucocorticoid levels may solely be linked to heightened energy demands associated with reproductive competition. For example, in male Southern muriquis (*Brachyteles arachnoides*), a similar pattern had been observed where increased cortisol levels were associated with fat storage in order to prepare males for the upcoming breeding season (Strier et al., 1999). The present results may therefore indicate that reproductive competition among redfronted lemur males primarily evokes a physiological rather than behavioral response.

Food availability

Effects of seasonal food limitation on agonism rates in males and females were more variable across studies. In ring-tailed lemurs, agonism rates were lower than expected for males and higher than expected for females during the season of higher food availability (Sauther and Sussman, 1993). In Apennine chamois (*Rupicapra pyrenaica ornate*), numbers of agonistic encounters were higher during periods of high food availability, whereas the intensity of aggression increased with decreasing food availability (Fattorini et al., 2018). In redfronted lemurs, agonism rates and intensity appeared to be unaffected by this ecological variable.

Previous investigations in other mammalian species, including lemurs, have similarly documented higher glucocorticoid levels at times of low food availability or quality (Brookman et al., 2017; Carnegie et al., 2011; Defolie, 2022; Gesquiere et al., 2008; Gómez-Espinosa et al., 2014; Lewanzik et al., 2012; Moreira et al., 2016; Muller and Wrangham, 2004; Pride, 2005; Rimbach et al., 2013, 2014; Rudolph et al., 2020; Weiß and Foerster, 2013). This is generally interpreted as a mechanism to facilitate the use of internal energy stores to compensate for the reduced energy intake from external resources given that glucocorticoids play a major role in energy metabolism (Sapolsky et al., 2000). Although the interpretation of an evidence for resource-driven physiological stress on energy stores at low food availability is conceivable, it needs to be considered with caution in wild animals where glucocorticoid levels are usually assessed via fecal analyses. This is because there is evidence that seasonal changes in the amount of food consumed as well as the dietary composition can affect gut passage time and the amount of fecal matter produced (Wasser et al., 1993; Dantzer et al., 2011; van der Ohe et al., 2003; Goymann et al., 2006). Because fecal hormone metabolite levels are expressed per unit fecal mass, they may not be directly comparable between seasons under the aforementioned conditions (Wasser et al., 1993; Goymann 2012).

Unfortunately, we had no data on seasonal food consumption rates and diet composition for our study animals. While it might seem possible that food resource dependent seasonal variation in fecal mass produced may have influenced our FGCM results, other studies suggest that hormone metabolite concentration could also decrease during times of food scarcity (e.g. Wasser et al., 1993). A similar effect might be found in redfronted lemurs that increase the proportion of fibrous leaves in their diet in relation to fruit during times of shortages (Murillo et al., 2022a). Future studies incorporating individual nutrient intake and diet mass and composition would therefore provide a more nuanced understanding of the relationship between fruit consumption, physiological stress and competition.

The absence of an effect of fruit consumption on agonism rates appears counterintuitive in a species facing pronounced seasonal resource limitation. While not all studies investigating the impact of food availability on agonism rates have reported increased aggression at lower food availability, few have found no effect at all. These observations were primarily derived from species that inhabit tropical or subtropical rainforests, which are characterized by little seasonal variation in food availability, as for example in spider monkeys (*Ateles geoffroyi;* Asensio et al., 2009), blue monkeys (*Cercopithecus mitis stuhlmanni;* Pazol and Cords, 2005) or black-and-white ruffed lemurs (*Varecia variegata;* Chen, 2020). Despite the elevation of glucocorticoid levels under conditions of reduced food availability, individuals do not appear to respond additionally with more intense intraspecific competition.

A physiological response to food limitation that coincides with the absence of a behavioral response in the form of increased agonism rates appears to be exceptional in animal societies. While the correlation between aggression and glucocorticoid levels has frequently been investigated (Bergman et al., 2005; Fichtel et al., 2007; Mooring et al., 2006; Muller and Wrangham, 2004; Pride, 2005), few studies have simultaneously examined the influence of resource competition on both glucocorticoid levels and agonism rates (Brookman et al., 2017; Burgess et al., 2013; Rimbach et al., 2014). Reducing aggression in times of low food availability may have two advantages: First, physical fighting is risky and costly and by reducing these costs, individuals may improve their fitness. Second, social relationships have been shown to mitigate negative effects of external stressors (Crockford et al., 2018; Snyder-Mackler et al., 2020; Young et al., 2014). However, agonism rates did not seem to be related to glucocorticoid levels in redfronted lemurs (see also Ostner et al., 2008). Reducing rates of conflicts during times of low food availability might therefore be more likely an adaptation to energy conservation in this harsh habitat. However, no effect of food availability on agonism rates could be found in rainforest-dwelling black-and-white ruffed lemurs (Chen, 2020), but female ring-tailed lemurs had higher rates of aggression during low food availability in an even harsher spiny-forest (Sauther, 1993). Thus, the available comparative evidence does not allow any firm conclusions about the behavioral and endocrinological responses to variation in food availability.

Even though peaks of aggression seem to be absent at times of limited resources and do also not seem to be directly linked to reproductive competition, we know that both females and males compete for group membership (Prox et al., 2023). Specifically, we know that overall group size and the number of juvenile females within a group are drivers of female evictions. One of the original aims of this study was to investigate whether this competition for group membership is prompted by limited reproductive opportunities or limited food resources. The results of the present study did not provide definitive support for either explanation. Related to this, studies on captive lemurs have reported evictions despite relaxed feeding competition (Vick and Pereira, 1989). Together, these findings suggest that evictions may be triggered by highly conserved mechanisms that are activated by specific group compositions, regardless of the current situation of food availability. Hence, females may be competing for future rather than for immediate gains. This notion aligns with findings in meerkats (*Suricata suricata*) and banded mongooses (*Mungos mungo*), where large group sizes or the presence of breeding subordinates pose fitness costs to dominant individuals (Cant et al., 2010; Stephens et al., 2005). As in captive lemurs, evictions in meerkats have been observed even when groups were provided with food, contrary to expectations, with higher rates of evictions observed in provisioned groups than in unprovided groups (Dubuc et al., 2017). This could represent an evolutionary stable strategy, as females may experience delayed benefits of competition, such as improved offspring survival, and engaging in competition during periods of resource scarcity could be excessively energetically costly. Further supporting this notion, a previous study revealed a positive correlation between the probability of female evictions in redfronted lemurs and higher mean monthly rainfall (Prox et al., 2023).

Limitations of this study

In this study, we had to rely on rates of fruit consumption per group as a proxy for nutrient intake, as no data were available regarding individual food intake. In addition, it should be noted that no evictions took place during the course of the present focal observations. This could be a possible indication of low levels of competition among females during the course of this study. In subsequent studies focal observations in combination with collection of fecal samples for hormone analyses during eviction events could help to unravel the underlying causes and better understand how these lemurs coexist in groups without engaging in permanent intense competitive behaviors.

Conclusions

Redfronted lemurs are confronted with different challenging phases during the course of a year. These periods of potential conflict appear to vary partially between the sexes and are addressed through different means. Females exhibit a behavioral response during one of these phases, specifically the birth season, characterized by increased aggression. Conversely, males exhibit a physiological response in the form of elevated glucocorticoid levels during the mating season in absence of heightened levels of aggression. A major challenge affecting both sexes is food limitation. In this regard, we observed a physiological response, i.e. an increase in glucocorticoid output during times of limited food availability, but a lack of a behavioral response. Although our findings align with established observations in other mammals, the dissociation between behavioral and physiological responses, particularly in males during the mating season and in response to decreased food availability, has rarely been documented before. However, our study represents one of the first attempts to simultaneously monitor both behavioral and physiological responses during phases of potential conflict. Our findings suggest that factors other than food availability may drive intensive competition in redfronted lemurs, possibly involving competition for future reproduction in females and highly conserved mechanisms triggered by specific group compositions.

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CHAPTER II

Drivers and consequences of female reproductive competition in an egalitarian, sexually monomorphic primate

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ORIGINAL ARTICLE

Drivers and consequences of female reproductive competition in an egalitarian, sexually monomorphic primate

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Abstract

Even after the 150th anniversary of sexual selection theory, the drivers and mechanisms of female sexual selection remain poorly studied. To understand demographic circumstances favoring female-female competition, trade-offs with kin selection and interactions with male reproductive strategies, we investigated female evictions in redfronted lemurs (*Eulemur rufifrons*). Based on 24 years of demographic data of known individuals, we show that female redfronted lemurs target close female kin for forcible, permanent, and presumably lethal eviction, even though groups contain multiple unrelated males whose voluntary emigration actually mitigated the probability of future female evictions. Female eviction and male emigration were predicted by group size, but male emigration was primarily driven by a proportional increase of male rivals. Female evictions were more likely than male emigrations when there were more juvenile females in a group, but the identity of evicted females was not predicted by any intrinsic traits. While birth rates were reduced by the number of juvenile females, they were higher when there were more adult females in a group and in years with more rainfall. Early infant survival was reduced with increasing numbers of juvenile females, but variation in female lifetime reproductive success was not related to any of the predictors examined here. Thus, there seems to be a limit on female group size in this lemur species. More generally, our study demonstrates a balanced interplay between female reproductive competition, competition over group membership between both sexes, and kin selection, contributing new insights into the causes and consequences of female competition in animal societies.

Significance statement

The evolutionary causes of female competition in vertebrate societies remain poorly known. Evictions represent an extreme form of female competition because even close kin are evicted when same-sized unrelated males are theoretically also available as victims. We studied drivers and consequences of evictions in redfronted lemurs (*Eulemur rufifrons*) using 24 years of demographic data from multiple groups. We show that while voluntary male emigration mitigates the probability of future female evictions, females nonetheless appear to accept the fitness costs of evicting female kin. While group size seems to be the main driver of departures by either sex, the number of juvenile females present in groups is the key variable triggering eviction events as well as physiological responses that could be interpreted as female reproductive restraint. Our study therefore revealed that competition does trump cooperation under some circumstances in the intricate interplay between sexual selection and kin selection on females.

Keywords Sexual selection · Kin selection · Female competition · Eviction · Emigration · Lemurs

Introduction

Since Charles Darwin first presented his theory of sexual selection (Darwin 1871), male mammals have long been considered to be the more competitive and aggressive sex, whereas females were portrayed as being more passive and docile (Clutton-Brock 2007; Clutton-Brock and Huchard 2013a). Even though these modal patterns have

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been confirmed in recent meta-analyses (Janicke et al. 2016, 2018), this binary view of "classical" sex roles is now outdated (Schärer et al. 2012; Davidian et al. 2022; Kappeler et al. 2022a; Fromonteil et al. 2023), and the existence of diverse mechanisms of female competition is widely appreciated today (Stockley and Bro-Jørgensen 2011; Tobias et al. 2012; Hare and Simmons 2019). Yet, compared to males, the causes and mechanisms of female intrasexual competition remain understudied.

Existing evidence suggests that the causes of intrasexual competition are more diverse for females. Whereas access to potential mates is the principle cause of male-male competition, and female competition in so-called sex-role reversed species can also directly affect mating success (Clutton-Brock 2007), females may also compete for paternal care, breeding territories, or food during the non-reproductive season. The immediate fitness consequences of winning a particular agonistic interaction are smaller for females because they do not benefit as much from obtaining an additional mating opportunity that way (Clutton-Brock et al. 2006; Clutton-Brock and Huchard 2013b). Yet, the main mechanisms of competing with same-sex conspecific over reproduction have been found to be strikingly similar for both sexes (Clutton-Brock et al. 2006; Pusey 2012; Stockley and Campbell 2013). Specifically, there are numerous examples of behavioral, pheromonal, or physiological suppression of reproductive function in same-sex rivals (West-Eberhard 1979; Clutton-Brock et al. 2008; Bell et al. 2012, 2014; French et al. 2013), and androgenic steroid hormones exhibit effects on aggressive behavior and reproductive suppression in both sexes (French et al. 2013). Moreover, male and female infanticide of unrelated infants has been interpreted as a mechanism that increases the relative reproductive success of the proponents (Lukas and Huchard 2014). Finally, members of both sexes in both singular and plural breeders may evict adolescent or subordinate rivals from their territories or groups (Cant et al. 2010; Dubuc et al. 2017; Thompson et al. 2017). The frequency of eviction is usually higher among members of the philopatric sex because natal individuals of the dispersing sex pose less of a reproductive threat. As a consequence, the intensity of competition is typically higher among members of the philopatric sex because leaving or being evicted is much more costly for them (Mattison et al. 2019).

Compared to the other competitive mechanisms, eviction appears to have a strong phylogenetic signal in mammals, because it is relatively common among social herpestids, including singular breeding meerkats (Young et al. 2006; Bell et al. 2014) and plurally breeding banded mongooses (Cant et al. 2010; Thompson et al. 2016), but notably rare among primates (Kappeler and Fichtel 2012; Baniel et al. 2018). In these mongooses, evicted females or entire matrilines may return into their natal group after being evicted. This does not seem to be the case in primates, where evicted females have rarely been observed to return to their natal groups, as also indicated by the corresponding genetic signatures (Parga et al. 2015). In lemurid primates, typically an adult female (sometimes together with her juvenile offspring) is evicted (Vick and Pereira 1989), whereas the occasional mass evictions observed in some Old World primates are better described as group fissioning (Larson et al. 2018), and many evicted juvenile howler monkeys appear to leave their natal group voluntarily (Crockett and Pope 1993). In lemurs, philopatric females evict close relatives, who are typically unable to join foreign groups and rarely manage to establish a new group, presumably making evictions of female kin often fatal and therefore a key problem in sociobiology because such costly aggression toward kin is not predicted by classic kin selection theory (Hamilton 1964; West and Gardner 2010; Abbot et al. 2011).

Specifically, this theory predicts that kinship should have a modulating effect on the intensity of female competition among group members. The individual benefits of competition among females must be balanced against the inclusive fitness costs of competing with relatives, which are inevitable because of widespread female philopatry among mammals (Clutton-Brock 2021). In cases where the costs of competition are high, females compete indeed less with neighbors when they are relatives (Lambin and Yoccoz 1998), and the intensity of aggression and risk of eviction decrease with increasing kinship in some group-living species (Clutton-Brock et al. 2010).

In addition, social relationships in an established social landscape can modulate individual's dispersal or reproductive patterns (Armansin et al. 2020), leading to an adaptation of costly competition to local variation in group size and resource availability. In smaller groups, within-group feeding competition may be reduced, but group size can also be a key determinant of success in between-group competition (Lemoine et al. 2020), so that dominants should have a selfish interest in retaining a certain number of subordinates (Kappeler et al. 2009). Thus, local variation in group size is expected to reflect variation in food availability, but also the outcome of rank-dependent female reproductive strategies (Markham et al. 2015).

Finally, in species where female dispersal is not an option, low-ranking females may improve their chances of successful reproduction by mobilizing additional energy through increased glucocorticoid secretion (Beehner and Bergman 2017), and they may reduce the risk of eviction by obtaining higher social tolerance through appeasing dominants through increased grooming (Clutton-Brock et al. 2006; Kutsukake and Clutton-Brock 2006) or by foregoing reproduction (Inzani et al. 2019).

The group-living primates of Madagascar (Lemuriformes) hold great promise for insightful comparative studies on the causes, mechanisms, and functions of female competition because they exhibit widespread female dominance and genital masculinization in combination with a lack of sexual dimorphism, indicating adaptations to female competition (Kappeler and Fichtel 2015; Davidian et al. 2022). Moreover, lemur groups are relatively small, promoting high average relatedness among the members of a single matriline (Wimmer and Kappeler 2002), and characterized by male-biased adult sex ratios (Kappeler 2017). Finally, episodic targeting aggression of group members leading to severe wounding and/or eviction is common among the Lemuridae. It also occurs in captive groups and peaks during the annual mating and birth seasons (Vick and Pereira 1989), suggesting that it is functionally tied to reproductive competition rather than to feeding competition, but this notion remains untested in the wild. Victims include closely related members of the same matriline, which are not allowed to return (Vick and Pereira 1989), and it remains unresolved why females evict female kin rather than unrelated males, who are present in much higher proportions than in other primate species (Kappeler 2000; Kappeler et al. 2009).

We studied competition and dispersal in redfronted lemurs (*Eulemur rufifrons*), a cat-sized species living in groups of 5–12 individuals, including multiple males and females, with a male-biased adult sex ratio (Ostner and Kappeler 2004). The females of a group belong to one philopatric matriline (Wimmer and Kappeler 2002) and neither develop pronounced dominance relationships among themselves nor with males (Ostner and Kappeler 1999). As a result, social tolerance in competitive feeding situations is relatively high (Fichtel et al. 2018). Females begin reproducing in their third year of life and give birth to a single infant — potentially every year (Kappeler et al. 2022b). Reproductive activity is tightly adjusted to pronounced predictable ecological seasonality so that infants are being born near the end of a 7-month long cool dry season. In our study population, only four evicted females have been able to successfully return to their natal group in 24 study years, and only two other individuals have been observed to establish or join a new group, suggesting that it is very unlikely for an evicted female to be accepted into a non-natal group. Males do not exhibit rank-related variation in testosterone and glucocorticoid levels, but concentrations of these hormones increase during the mating and birth seasons (Ostner et al. 2008). Thus, redfronted lemurs offer a study system characterized by a perplexing combination of high general social tolerance and relaxed feeding competition with extreme bursts of potentially lethal aggression among closely related females co-residing with multiple males.

Here, we investigated patterns and drivers of female evictions and male dispersal, using demographic data collected over 24 years. Since group size was the best predictor of female evictions in a preliminary study covering only 10 years of demographic data (Kappeler and Fichtel 2012), we were specifically interested in the interplay between female evictions and male emigrations. We investigated which aspects of group composition favor female evictions over male dispersals, whether male dispersals may buffer female evictions, and which traits characterize victims of evictions. In addition, we investigated whether proxies of female competition (number of adult and juvenile females) result in reproductive restraint and consequent fitness consequences of an eviction by investigating which characteristics predict females' birth rates, early infant survival, and lifetime reproductive success.

Methods

Study site and species

Data for this study are based on long-term census observations of a population of redfronted lemurs inhabiting a local study area of ca. 80 ha in Kirindy Forest, western Madagascar. From 1995 onwards, redfronted lemurs of up to 6 adjacent groups have been captured, subjected to standard field morphometric measurements and individually marked with microtransponders and unique nylon collars (Kappeler and Fichtel 2012). In each group, one adult female has been equipped with a radio collar to facilitate near daily censuses, during which the location, activity, and composition of each group are recorded. Both immigrations and births were usually detected within a day. In the case an individual went absent and was not seen in the group for at least the following 4 weeks, we counted this event as a "disappearance." It was not possible to record data blind because our study involved focal animals in the field.

Disappearances can occur for one of two reasons: death or "departure." We distinguished between departures by females ("evictions") and those by males ("emigrations") because the former are virtually always the result of aggression, whereas the latter are typically voluntary. Departures could be confirmed by re-sightings, as for example during the dry season, when groups from outside the study area gather at waterholes within the study area that represent the only bodies of water within several kilometers (Amoroso et al. 2019). Death could be confirmed when the remains of individuals were found following predation by fosas (*Cryptoprocta ferox*), the main predator of lemurs in this area. Individuals that were never re-sighted were included in the counts for "unknown." For this analysis, we used data collected between 1996 and 2020, comprising 1069 group months from 4 main study groups with a total of 257 individuals (75 females, 168 males, 14 infants disappeared before they could be sexed). Over 24 years, we recorded 173 births, 263 events of disappearances, of which 39 were confirmed evictions, and 96 confirmed emigrations, 10 deaths and 118 "unknown disappearances" (Fig. 1). In some cases, more than one individual disappeared at the same time, which led to a discrepancy between the number of events (evictions: $N = 29$; emigrations: $N = 69$) and disappeared individuals (evictions: $N = 39$; emigrations: $N = 96$).

To estimate the effects of age and group composition on departures, we extracted relevant information from censuses of months in which departures occurred, i.e., the month when individuals were last seen in a group and compared them to months without departures. For the latter, we used data from the April census or the one closest to April because offspring from the previous year or immigrant males were individually marked at this time. For each event, we determined group size, numbers of adult (> 36 months) and juvenile (6–36 months) females, adult and juvenile males, the age of individuals, and cumulative rainfall of the natural year (from July of the preceding year to June of the following year) as a proxy for habitat productivity and, hence, subsequent food availability. Because climatic data were not collected regularly during the early years of the study, we used published rainfall data from the CHIRPS data base. To estimate mean relatedness among females of a group, we calculated coefficients of maternal relatedness (assuming that sisters were sired by different fathers) based on lineages for all possible female dyads.

Statistical analyses

Patterns of female evictions and male emigrations and their interplay

First, we investigated the impact of group size and composition, age, and cumulative rainfall on the likelihood for a female to be evicted from her natal group. To this end, we compared for each year adult sex ratio, group size, group composition, and rainfall in months with evictions to a month without evictions. Second, because male emigration

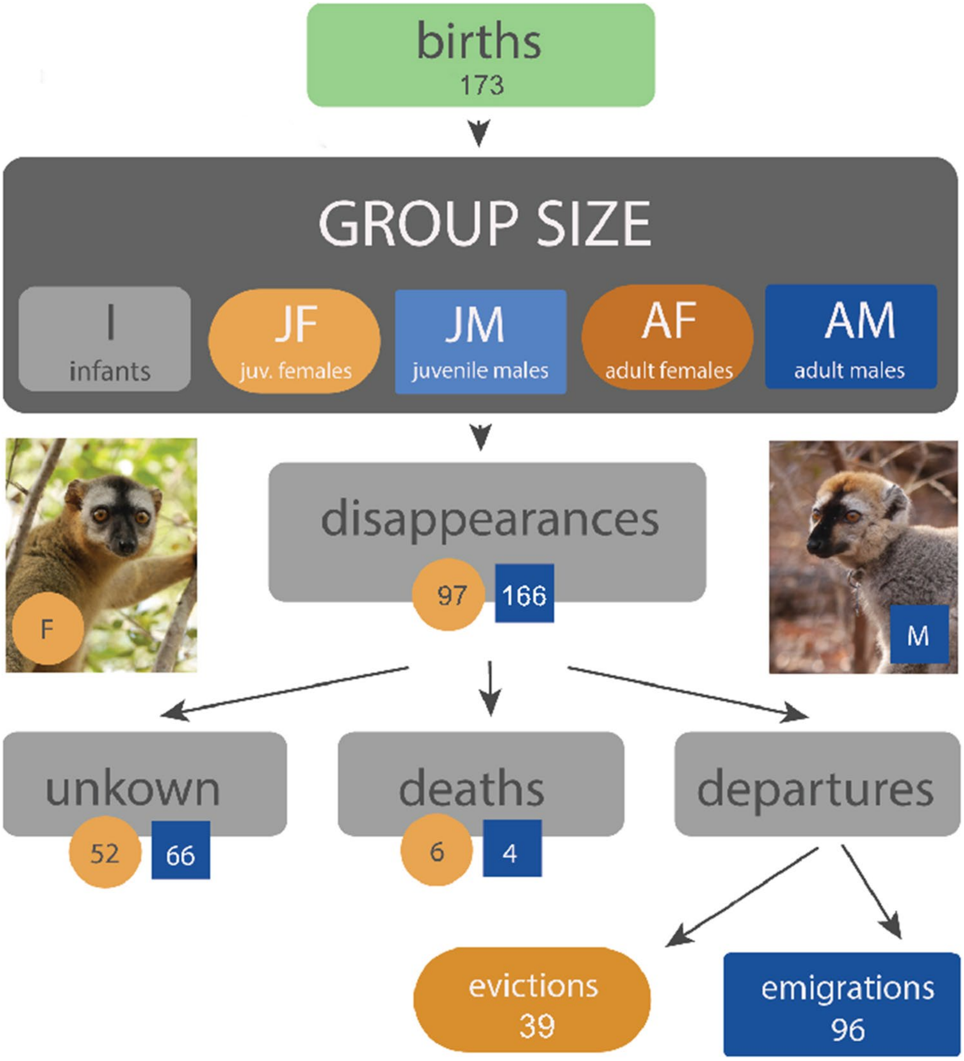

Fig. 1 Summary of redfronted lemur demography. Frequencies of births, deaths, evictions, and emigrations observed in four study groups over 24 years are depicted. Evictions and emigrations are combined into departures and refer to events in which an individual (females: orange; males: blue) was seen at least once alive after leaving a group. Deaths are confirmed events (remains found) and unknown includes individuals that disappeared and were not seen again

may reduce pressures to evict related females, we repeated this analysis for male emigrations. Third, we examined which factors predict whether a female or a male left the group. Fourth, we also investigated which individual traits predict female evictions, and, fifth, whether male emigrations buffer female evictions.

Reproductive restraint and fitness consequences of evictions

We additionally investigated whether female competition manifests itself in reproductive restraint such as (6) birth rates, (7) early infant survival, and (8) life-time reproductive success. We also investigated fitness consequences of evictions by estimating whether an eviction that occurred in a given year before the birth season impacted on the probability of giving birth and whether an eviction that occurred before the birth season and 3 months after births, respectively, impacted early infant survival during the first 3 months postnatally.

Model structure

Predictors of female evictions (model 1)

To estimate the probability of female evictions, we fitted a binomial GLMM with a logit link. We set the occurrence of evictions (yes, no) as the response and included rainfall, adult sex ratio (ASR; i.e., adult sex ratio measured as proportion of adult males of all adult individuals), and group size as fixed effects, and group identity as random effect with rainfall, group size, and ASR as random slopes (Barr et al. 2013). The sample for this model encompassed 123 group-level data points including 29 events of evictions involving 39 females.

As group size had a significant effect, we conducted an exploratory analysis to determine which components of group size caused the observed effect by applying multi-model inference (Barton 2018). We used this method to deal with problems of overfitting the model by including too many predictors for the given small sample size ($N = 29$). We created a set of 15 models containing the cumulative amount of rainfall per year together with combinations of the fixed effects of number of adult females and males as well as the number of juvenile females and males. In all models, we included group identity as random effect and rainfall within group as random slope, even if more random slopes would have been theoretically identifiable for individual models, as rain was the only variable present in all models. This approach is not ideal, but to our knowledge the question of how many degrees of freedom are absorbed by random slopes is still open (Bolker et al. 2009). Hence, this is the only option, since otherwise a joined conclusion based on AICc would not be valid. To additionally control for potential collinearity, we corrected estimates by standardizing them based on partial standard deviations (Cade 2015). For each model we determined Akaike's Information Criterion, corrected for small sample size (AICc; Queen et al. 2002). For comparisons among models, we additionally determined AIC weights for each model and averaged the estimated coefficients and their standard errors using the zero method (Nakagawa and Hauber 2011; ESM Table S1, S2, Fig. S1).

Moreover, since the model compared census data of months with and without evictions, it seemed possible that the estimate for the effect of group size and ASR was biased because of the nature of data created by limiting entries of non-eviction events to 1 month of the year, i.e., April. We therefore conducted a sensitivity analysis. To this end we randomly replaced the group size or ASR obtained for a given group in a given year by a randomly selected group size or ASR value from the same group and year and a month in which no eviction event happened. We repeated this procedure 1000 times, each time fitting the full and the null model as described above, and determined the significance and also the estimate of group size. For the other fixed effect predictor (rainfall), a corresponding assessment was not required as it was constant for a given year and group. We then compared the original estimate and *P*-value for the effect of group size with the distribution of the respective estimates obtained from the repeated random selections. This revealed the estimate of group size to be slightly biased and the significance to remain essentially unaffected (ESM Fig. S2, S3).

Predictors of male emigrations (model 2)

For male emigrations, we fitted two binomial GLMMs with a logit link. Similar to the model on female evictions, we fitted one model with male emigration (yes, no) as the response, including group size, adult sex ratio, and annual rainfall as fixed effects, and group identity as random effect including rainfall within group identity as random slope. As the sample size was larger for male emigrations ($N = 69$) than for female evictions ($N = 29$), we did not use a multi-model inference approach to assess which characteristics of group composition predict male emigrations because we could fit all predictors in the same model. Hence, we fitted a second model with male emigration (yes/no) as the response, number of adult and juvenile females as well as number of adult and juvenile males, and rainfall as fixed effects. As random effect, we included group identity with rainfall as random slope. For model comparison, we used the AICc criterion, considering the model with a delta AIC < -2 as the one with a better fit (ESM Table S3). Since the first model including ASR revealed a better fit, we present this model in the main text. This data set encompassed a sample size of 164 group-level census data points including 69 dispersal events, comprising 96 male dispersals.

When are female evictions more likely than male emigrations? (Model 3)

To investigate under which circumstances the departing individual was more likely to be a female or a male, we included those variables that predicted female evictions and male emigrations by including all variables that had a mean weighted estimate larger than zero in the multi-model inference in the female model (model 1) or a significant effect in the male model (model 2), i.e., rainfall, group size, ASR, number of juvenile females and adult males. Since the number of adult males correlated positively with group size (Pearson correlation: $N = 135$, $r = 0.63$, $P < 0.001$) and ASR (Pearson correlation: $N = 135$, $r = 0.67$, $P < 0.001$), we did not include the number of adult males in this model. We constructed a binomial GLMM including confirmed female evictions and male emigrations by setting sex ($1 = \text{female}$, $0 = \text{male}$) as the response and rainfall, group size, ASR, and number of juvenile females as fixed effects. We included group identity as random effect and included ASR and rainfall as random slopes. The sample for this model encompassed a total of 135 departures with four out of 33 females being evicted between two and four times and 13 out of 68 males emigrating between two and six times.

Individual traits favoring female eviction (model 4)

To estimate intrinsic factors affecting the likelihood to be evicted, we included individual characteristics of all females present during eviction events with a female being evicted or not as response and female age and presence of the mother as fixed effects, and group ID, individual ID, and event ID as random effects with female age within group as random slopes. This data set included only females that were born in the population since 1996 with 111 data points of 31 census entries and 43 individuals.

Are female evictions less likely after male emigrations? (5 permutation test)

To test whether the occurrence of a male emigration event subsequently reduced the probability of a female eviction, we used a permutation test (Adams and Anthony 1996; Manly 1997) that compared the time intervals between an emigration and a subsequent eviction. To this end, we first determined for each female eviction the time lag between the last male emigration event and the eviction. We then determined the mean time lag per group and averaged it across groups. We chose this value as a test statistic.

We then permuted, separately for each group, the temporal distributions of female evictions or male emigrations, depending on which event was more common. The permutation consisted of shuffling the time lags between events. That is, the timing of the first and last event per group remained unchanged, but the intervals between them were permuted. Consequently, the principal distribution of the time lags between consecutive events remained unchanged. We conducted a total of 10,000 permutations, each time conducting the test as described above. If female evictions were less likely after male emigrations, then the majority of permuted data sets should reveal a test statistic smaller than that of the original data. Hence, we determined the *P*-value as the proportion of permutations revealing a test statistic at least as large as that of the original data. To avoid a *P*-value being exactly 0, we included the original data as one of the permutations.

Predictors of birth rates (model 6)

To examine whether female competition resulted in reproductive restraint, we constructed two GLMMs. We fitted one model examining whether a female gave birth (yes, no) as response, female age and longevity, number of co-resident adult and juvenile females in the month of birth, annual rainfall and whether an eviction occurred in the 12 months prior to the birth (yes, no) as fixed effects and female's and group identity as random effect. We included the number of adult females, female's age and longevity as well as rainfall within group and the number of adult and juvenile females, female age, rainfall and whether an eviction occurred within female's identity as random slopes without correlations between random slopes and intercept. We included females' longevity as a control factor in the model because longer-lived females might be more likely to give birth (van de Pol and Verhulst 2006; Nussey et al. 2008; Kappeler et al. 2022b). Since birth rates among primates are predicted by an inverted U-shape of both the number of adult females and females' age (Dunbar and Shultz 2021), we fitted a second model by including female age, the number of adult and juvenile females as linear and squared terms as well as longevity and rainfall as control variables (ESM Table S4). For model comparison, we used the AICc criterion, considering the model with a delta $\text{AICc} < -2$ as the one with a better fit. This model encompassed 218 data points for 34 females from four groups giving birth to a total of 173 infants.

Predictors of infant survival (model 7)

Because infant mortality is highest early in life, we investigated whether the likelihood of an offspring to survive until 3 months of age was influenced by our proxies of female competition. To this end, we fitted a binomial GLMM on whether an infant survived to 3 months (yes, no) as the response variable. We included female age and longevity, number of co-resident adult and juvenile females, annual rainfall and whether an eviction occurred before or 3 months after birth (yes, no) as fixed effects. We included the number of adult females, female age and longevity as well as rainfall within group and the number of adult and juvenile females, female age, rainfall and whether an eviction occurred within female identity as random slopes without correlations between random slopes and intercept. This model encompassed 34 females from four groups giving birth to a total of 173 infants.

Predictors of female lifetime reproductive success (model 8)

To estimate the effects of factors related to evictions on lifetime reproductive success, we fitted another GLMM with the number of offspring born by a female over her lifetime (regardless of how long they survived) as the response and included the mean relatedness to co-resident adult females over her lifetime, mean total number of females present in the group and longevity as predictors. We included group identity as a random effect. This model was slightly overdispersed (1.26). The model comprised 26 females. We restricted our data set to females of known birth and disappearance date.

Implementation

All analyses were conducted using R (version 4.1.0, R Core Team 2019), applying the function glmer from the package "lme4" (version 1.1–21, Bates et al. 2015). We used Generalized Linear Mixed Models (GLMMs; Baayen 2008) with binomial error structure and logit link function. To ease model convergence, we centered all quantitative predictors to a mean of zero and a standard deviation of one before including them into the models. We included all theoretically identifiable random slopes to avoid type I errors (Queen et al. 2002; Barr et al. 2013) except where we applied model comparisons based on AICc. We compared the resulting model to a null model, comprising all random effects and control factors included in the full model but lacking the fixed effects with a likelihood ratio test (Schielzeth and Forstmeier 2009). This full-null model serves to avoid "cryptic multiple testing" (Forstmeier and Schielzeth 2011). We obtained confidence intervals for all models by means of parametric bootstraps using the function "bootMer" of the package "lme4," applying 1000 parametric bootstraps. We checked for collinearity by determining Variance Inflation Factors (VIF, 95) for a standard linear model without random effects using the package "car" (version 3.0.11, Field 2005). To estimate model stability, we proceeded by dropping levels of the random effect one at a time from the data set and compared the obtained estimates to the estimates obtained for the full data set. All models exhibited good stability.

Results

Figure 2 presents a graphical overview of the main outcomes of the models.

Patterns of female evictions and male emigrations and their interplay

Predictors of female evictions (model 1)

In total, we have evidence of 29 eviction events involving 39 females. Evictions occurred throughout the year, but they

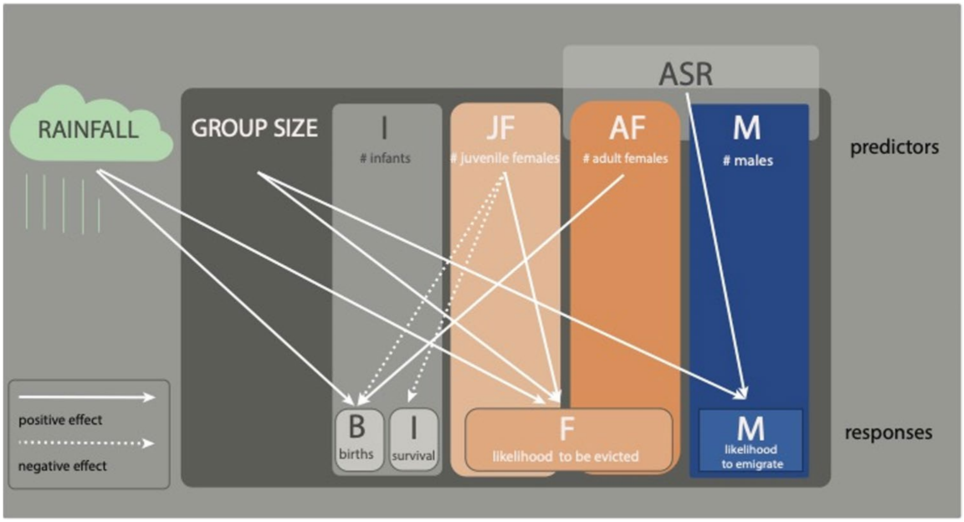

Fig. 2 Overview of positive and negative significant effects of predictors on responses of models 1, 2, 3, 6, and 7. Dashed arrows represent negative effects on responses; non-dashed arrows represent positive effects. We only included results of the main models, omitting results of multi-model inference approach

peaked around the brief annual mating and birth seasons (Fig. 3). The model including the baseline predictors (group size, ASR, rainfall) was overall significant (full-null model comparison: $\chi^2 = 8.79$, df = 3, $P = 0.032$). The probability of an eviction was higher in larger groups and in years with higher rainfall, but ASR did not predict evictions (Fig. 4, Table 1a).

As group size had a significant effect, we additionally applied a multi-model inference approach based on weighted AIC weights to determine which age/sex category drove this effect. These models ($N = 15$) included the number of adult females and males, juvenile females and males, and cumulative rainfall. There was one model that clearly stood out with an AIC weight of 0.57 that included the number of juvenile females, adult males and rainfall as predictors (ESM Table S2, Fig S1, N juvenile females: mean weighted estimate = 0.88, SE = 0.26, number of adult males: mean weighted estimate = 0.67, SE = 0.25, rainfall: mean weighted estimate = 0.48, SE = 0.27). The number of adult females and juvenile males seemed to have no impact on female evictions (N adult females: mean weighted estimate = 0.02, SE = 0.06, N juvenile males: mean weighted estimate = − 0.00, SE = 0.05). Hence, group size best predicted evictions according to our baseline model, and this effect was driven by the number of juvenile females and the number of adult males. Since the number of adult males correlates positively with group size (Pearson correlation: $N = 135$, $r = 0.63$, $P < 0.001$), group size seems to predict evictions better than the number of adult males.

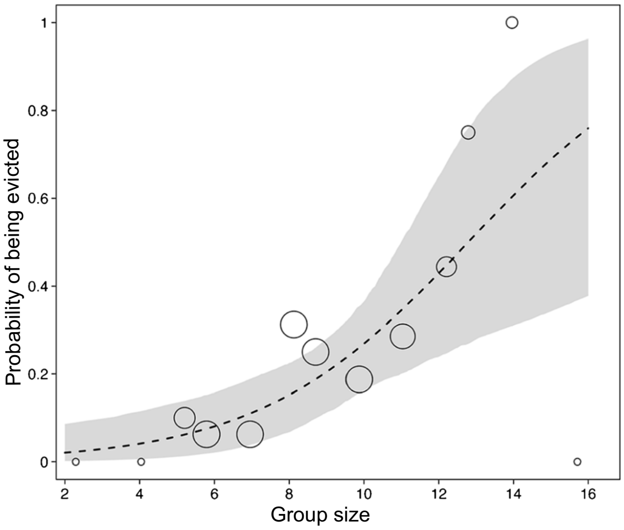

Fig. 4 Probability of female eviction as a function of group size. Dashed line indicates the regression line and polygons the 95% confidence intervals. Point size is relative to number of observations

Predictors of male emigration (model 2)

We observed 69 dispersal events, comprising 96 male emigrations. Emigrations occurred throughout the year with a slight increase during the mating season (Fig. 3b). Male dispersals were best predicted by group size and ASR, but not by annual rainfall (full-null model comparison: $\chi^2 = 27.98$, df = 3, $P < 0.001$). Males were more likely to disperse from larger groups and when the ASR was more strongly male-biased (Table 1b, Fig. 5a, b).

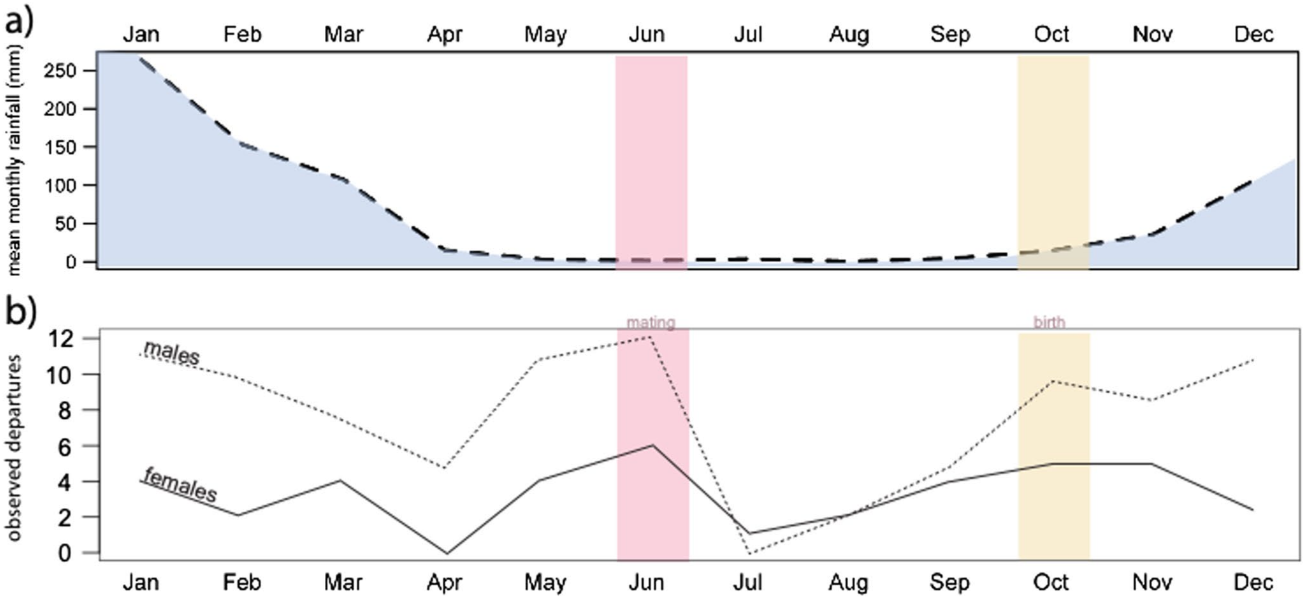

Fig. 3 Annual distribution of rainfall and group departures across the calendar year. a) Average mean monthly rainfall, b) Total number of observed evictions and emigrations in males and females. The timing of the annual mating season is indicated by red bars and the timing of the annual birth season is indicated by yellow bars

Table 1 Results of the models estimating drivers of female evictions and male emigrations and their interplay

Model		Term	Estimate	SE	Lower CI	Upper CI	*P*
a) Female eviction (model 1)	$\chi^2=8.79$, df = 2, $P=0.032$	Intercept	− 2.78	1.97	− 7.30	1.27	[a]
		Rainfall[b]	**0.52**	0.26	0.06	1.20	**0.049**
		Group size[b]	**0.91**	0.33	0.37	1.75	**0.026**
		ASR	2.23	3.29	− 4.88	9.44	0.497
b) Male emigration (model 2)	$\chi^2=27.97$, df = 3, $P<0.001$	Intercept	− 0.39	0.17	− 0.75	− 0.08	[a]
		Rainfall[b]	0.17	0.17	− 0.17	0.52	0.333
		Group size[b]	**0.61**	0.19	0.26	1.07	**< 0.001**
		ASR[b]	**0.60**	0.19	0.24	1.05	**0.001**
c) When are F evictions more likely than M emigrations? (Model 3)	$\chi^2=35.56$, df = 3, $P<0.001$	Intercept	− 1.40	0.29	− 2.55	− 0.99	[a]
		Juvenile females[b]	**1.26**	0.27	0.85	2.34	**< 0.001**
		ASR	− 0.68	0.31	− 1.63	− 0.13	0.080
		Group size[b]	0.47	0.27	− 0.04	1.27	0.071
		Rainfall[b]	0.54	0.30	0.01	1.50	0.070
d) Individual predictors of female eviction (model 4)	$\chi^2=1.12$, df = 2, $P=0.553$	Intercept	− 1.06	0.45	− 2.38	− 0.29	[a]
		Female age[b]	− 0.25	0.36	− 1.22	0.49	0.492
		Presence of mother	0.14	0.68	− 1.21	1.64	0.834

[a] Not shown because of having a very limited interpretation

[b] z-transformed to mean of zero and a standard deviation of 1; mean and standard deviation of the original predictors: **model 1**: rainfall: mean = 888.72, SD = 176.16, group size: mean = 8.68, SD = 2.54; **model 2:** rainfall: mean = 875.59, SD = 177.53, group size: mean = 8.83, SD = 2.53; **model 3**: JF: mean = 1.20, SD = 0.98, group size: mean = 9.93, SD = 2.29; rainfall: mean = 906.34, SD = 162.79; **model 4**: female age: mean = 80.03, SD = 67.17

When are female evictions more likely than male emigrations? (Model 3)

Females were more likely than males to leave a group when there were more juvenile females (full-null model comparison: $\chi^2=35.56$, df = 3, $P<0.001$; Table 1c, Fig. 6). ASR and rainfall predicted only by trend whether females were more likely to depart than males, with females being more likely to depart when the ASR was female-biased and when there was more rain (Table 1c, Fig. 6b). Group size had no effect on female departures (Table 1c).

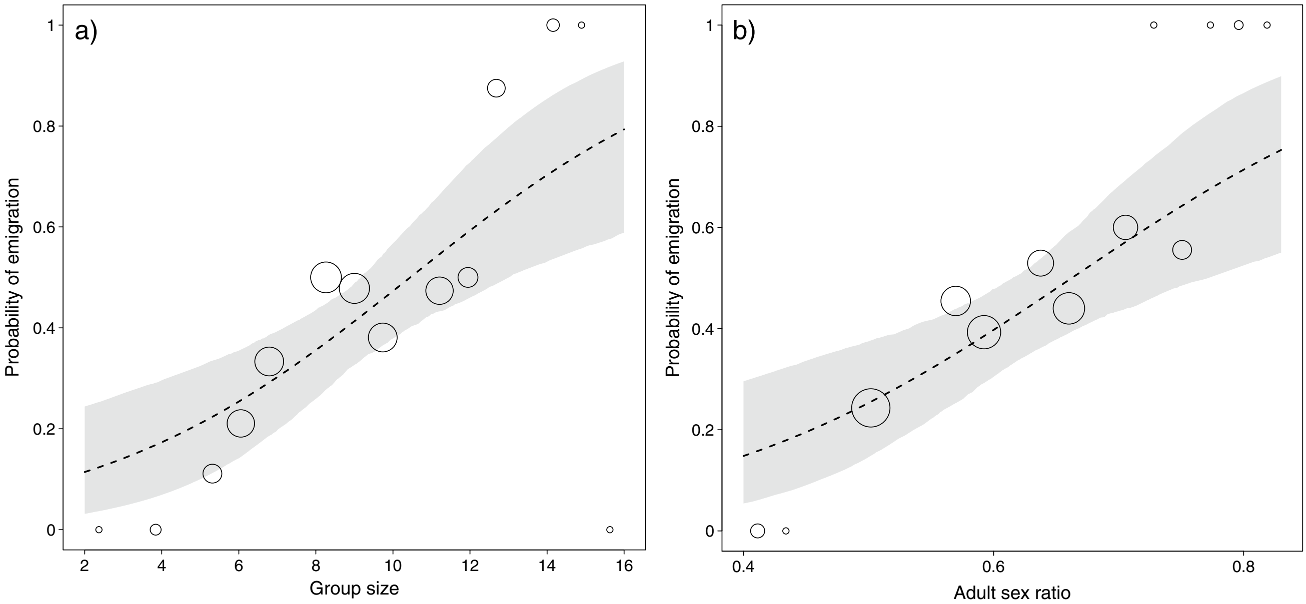

Fig. 5 Probability of male emigration as a function of a) group size and b) adult sex ratio**.** Dashed lines indicate the regression lines and polygons the 95% confidence intervals. Point size is relative to number of observations

Individual traits favoring female eviction (model 4)

The model examining the effect of individual traits on the probability of female eviction was overall not significant (full-null model comparison: $\chi^2 = 1.18$, df = 2, $P = 0.553$, Table 1d). Female age and presence of mother did not predict which female was evicted.

Are female evictions less likely after male emigrations? (Permutation test 5)

The permutation test revealed an effect for the time interval between a male emigration and a subsequent female eviction to be longer than expected by chance ($P = 0.049$), suggesting that male emigrations buffer the occurrence of future eviction events.

Reproductive restraint and fitness consequences of female evictions

Predictors of birth rates (model 6)

The model estimating the probability of giving birth as a function of female age and longevity, number of adult and juvenile females present, rainfall, and whether an eviction occurred before the birth season was overall significant (full-null model comparison: $\chi^2 = 12.39$, df = 3, $P = 0.006$). We found a positive effect of the number of adult females, and rainfall on the probability of giving birth (Fig. 7a, c; Table 2a). We also found a negative effect of the number of juvenile females (Fig. 7b), but no effect of female age and longevity or whether an eviction occurred before the birth season on the probability of giving birth. Hence, females were more likely to give birth when there was more rainfall and when there were more adult females, but less likely when there were more juvenile females.

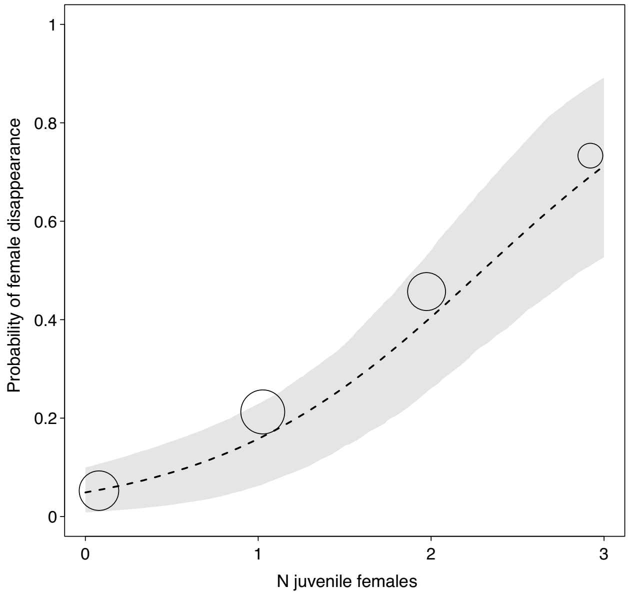

Fig. 6 Probability of the sex of the departing individual to be female as a function of the number of juvenile females. Dashed lines indicate the regression lines and polygons the 95% confidence intervals. Point size is relative to number of observations

Predictors of infant survival (model 7)

The model estimating variation in the proportion of offspring surviving to the age of 3 months as a function of female age and longevity, number of adult and juvenile females, rainfall, and whether an eviction occurred before or 3 months or after birth was overall significant (full-null model comparison: $\chi^2 = 10.15$, df = 2, $P = 0.006$). We found a significant negative effect of the number of juvenile females and by trend ($P = 0.050$) also a negative effect of the number of adult females on early infant survival (Table 2b, Fig. 8a, b). We did not find an effect of rainfall, female age and longevity, and whether an eviction occurred before the birth season or 3 months after birth on early infant survival.

Predictors of female lifetime reproductive success (model 8)

Longevity had a positive effect, whereas the mean relatedness to adult females and the mean number of adult females had no significant individual effects on females' lifetime reproductive success (Table 2c). Since the full-null model comparison was not significant (likelihood ratio test comparing full and null model: $\chi^2 = 1.47$, df = 2, $P = 0.477$), individual effects will therefore not be discussed further.

Discussion

Our analyses revealed that the intensity of female competition in redfronted lemurs was modulated by group size and particularly by the number of juvenile females in a group (model 1, 3, 6, 7), and that both males and females competed for membership in groups with apparently limited size (model 2, permutation 5). The combination of a group size of about 10 individuals (Figs. 4 and 5) and years with higher rainfall made departures from a group more likely. Who actually left was influenced by the number of resident juvenile females, with female evictions being more likely than male emigrations when there were more juvenile females in a group (model 3). The identity of evicted females was not predicted by any of their intrinsic traits, however (model 4). The likelihood of a male emigration was also predicted by group size as well as by a proportional increase of male rivals (model 2), and

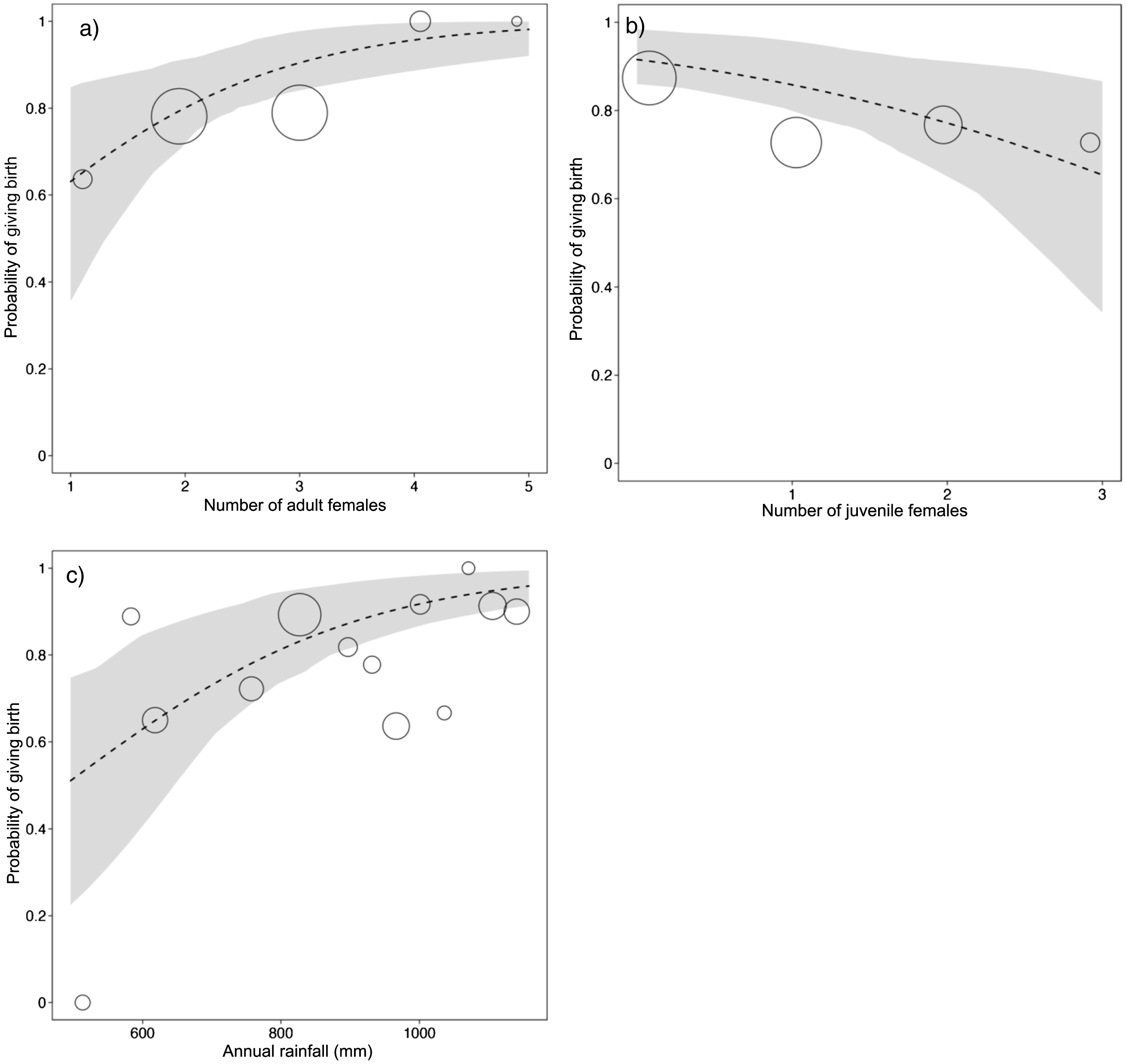

Fig. 7 Probability for any adult female to give birth as a function of a) the number of adult and b) juvenile females as well as c) annual rainfall. Dashed lines indicate the regression lines and polygons the 95% confidence intervals. Point size is relative to number of observations

male emigrations buffered future female evictions (permutation test 5). Female reproductive restraint manifested in reduced birth rates when the number of juvenile females was high, but an eviction before the birth season did not reduce subsequent birth rates (model 6). Birth rates were higher when there were more adult females in a group and also in years with higher rainfall. Early infant survival in turn was lower when there were more juvenile and by trend adult females in the group (model 7). Finally, variation in lifetime reproductive success was not related to any of the predictors examined here (model 8).

Hence, redfronted lemurs are clearly limited in group size and have to balance the costs and benefits of an optimal group size against the additional indirect fitness costs of evicting related females. Our study revealed a corresponding finely balanced interplay between reproductive competition among females and competition over group membership among both sexes. Hence, this is one of the first studies to reveal the importance of considering all group members when investigating causes and mechanisms of competition in one sex. Unfortunately, because evictions are so short and unpredictable events, we lack quantitative behavioral data

Table 2 Results of the models assessing female reproductive restraint

Model		Term	Estimate	SE	Lower CI	Upper CI	*P*
a) Birth rates (model 6)	$\chi^2 = 12.39$, df = 3, $P = 0.006$	Intercept	1.98	0.34	1.53	3.46	[a]
		Rainfall[b]	**0.84**	0.24	0.38	1.84	**0.009**
		Female age[b]	−0.38	0.27	−1.23	0.26	0.168
		Eviction (yes)	−0.53	0.69	−1.91	1.21	0.465
		Adult females[b]	**0.63**	0.25	0.07	1.29	**0.012**
		Juvenile females[b]	**−0.52**	0.24	−1.17	−0.20	**0.021**
		Longevity[b]	0.28	0.30	−0.22	1.16	0.332
b) Infant survival (model 7)	$\chi^2 = 10.15$, df = 2, $P = 0.006$	Intercept	1.57	0.31	1.21	7.74	[a]
		Rainfall[b]	0.15	0.23	−0.43	0.82	0.500
		Female age	−0.39	0.30	−0.39	0.36	0.191
		Eviction (yes)	0.69	0.55	0.69	3.85	0.197
		Adult females[b]	−0.65	0.22	−1.95	-0.21	0.050
		Juvenile females[b]	**−0.66**	0.33	−2.62	-0.24	**0.015**
		Longevity	0.32	0.55	−0.52	1.35	0.197
c) Lifetime reproductive success (model 8)	$\chi^2 = 1.47$, df = 2, $P = 0.477$	Intercept	1.23	0.30	0.64	1.64	[a]
		Mean R to ad. females[b]	0.14	1.14	−0.13	0.44	0.313
		Mean adult females[b]	0.05	0.14	−0.21	0.35	0.742
		Longevity	0.52	0.11	0.33	0.77	0.000

[a] Not shown because of having a very limited interpretation

[b] z-transformed to mean of zero and a standard deviation of one; mean and standard deviation of the original predictors: **model 6:** rainfall: mean = 882.79, SD = 179.23; female age: mean = 7.99, SD = 4.31; AF: mean = 2.55, SD = 0.74, longevity: mean = 13.07, SD = 5.71; **model 7:** longevity: mean = 10.36, SD = 4.65; mean AF: mean = 2.75, SD = 0.46, mean R to AF: mean = 0.23, SD = 0.13; **model 8**: rainfall: mean = 878.40, SD = 182.08; AF: mean2.41, SD = 0.74, JF: mean = 0.91, SD = 0.90

to analyze the associated patterns and dynamics that would reveal the initiators of aggression, the identity of group members that join in on the aggression, as well as general traits these individuals may share. In the present study, we were therefore limited to analyzing the demographic causes and consequences of this type of competition.

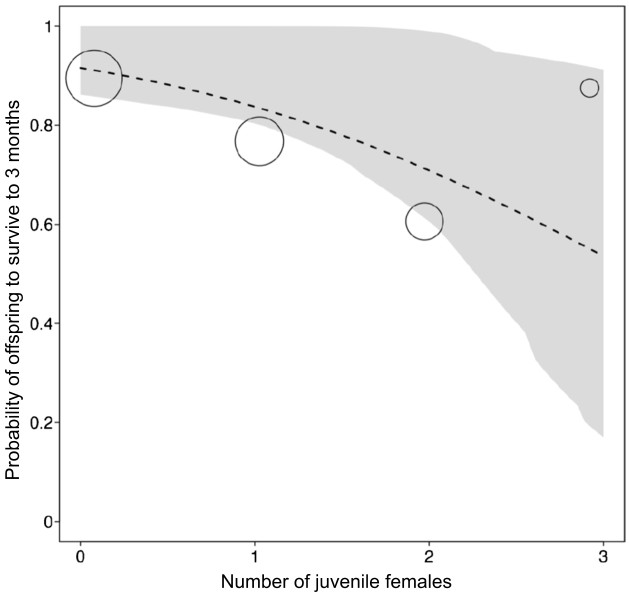

Fig. 8 Probability of an infant surviving to the age of three months as a function of the number of juvenile females. Dashed lines indicate the regression lines and polygons the 95% confidence intervals. Point size is relative to number of observations

Group size and competition for group membership

The prevailing form of competition within groups of red-fronted lemurs is competition for group membership (models 1, 2). Our main model revealed that group size is the best predictor of the departure of an individual of either sex. Importantly, effects of changes in group size occur already at small absolute differences. In contrast to many other primate species, one or two individuals joining or leaving a group can therefore cause fundamental changes in the competitive regime. Variables shaping optimal group size continue to be in the focus of recent studies in behavioral ecology (Majolo et al. 2008; Markham et al. 2015; Rudolph et al. 2019). In general, members of larger groups enjoy benefits in terms of reduced predation risk and enhanced competitiveness toward neighboring groups, but they suffer costs from greater feeding competition, consensus costs during group coordination, travel costs and parasite risk.

Lemurs live in significantly smaller groups than anthropoid primates of the same body size (Kappeler and Heymann 1996), indicating that Malagasy ecosystems are less productive than other tropical primate habitats (Dewar and Richard 2007). In fact, fruit trees in Malagasy forests tend to be smaller and less abundant and carry less nitrogen and fruit than in African forests at similar latitudes (Donati et al. 2017; Federman et al. 2017). Pronounced seasonality, relatively low food availability, and year-to-year unpredictability in rainfall may therefore be the ultimate drivers of the competitive regime to which redfronted and other group-living lemurs have responded with a unique set of adaptations (Kappeler and Fichtel 2015).

Drivers of female evictions

If a group reached a critical size, the likelihood that either a female or a male redfronted lemur departed increased. In case of evictions, this effect was best predicted by the number of juvenile females (model 1), whereas the number of adult males, which was also inferred as a significant factor by the multi-modal inference approach, co-varied with group size in this species with male-biased adult sex ratios. We therefore assume that group size is more likely to explain evictions, but we cannot exclude the possibility that the number of males also has an impact on the likelihood of female evictions. In addition, if there were more than two juvenile females in a group, the likelihood that a female was evicted was higher than the probability that a male emigrated. There was also a tendency that female evictions were more likely than male emigrations when the ASR was more female-biased (model 3). Male emigrations, in turn, seemed to buffer the probability of future female evictions (permutation 5). Hence, female evictions are a result of a fine-grained interplay between group size and composition. The fact that the number of juvenile females best predicted evictions may indicate that adult females may take future reproductive competition into consideration, but the relative importance of behavioral and physiological mechanisms mediating this response remains obscure.

The finding that higher rainfall was positively associated with evictions appears at first glance to contradict the notion that pronounced seasonality, relatively low food availability, and year-to-year unpredictability in rainfall are ultimate drivers of the competitive regime of redfronted lemurs. However, this result indicates that evictions do not seem to be proximately triggered by acute feeding competition, as fruit availability should be positively correlated with cumulative rainfall (Dunham et al. 2018), and fruit consumption correlated positively with rainfall in sympatric Verreaux' sifakas (*Propithecus verreauxi*) at this study site (Koch et al. 2017). Support for this assumption can also be gleaned from the fact that evictions are common in several species of provisioned captive lemur populations (Vick and Pereira 1989; Gresse et al. 1994; Digby 1999). In fact, in one group of captive redfronted lemurs, 18 evictions occurred in just 3 years (Vick and Pereira 1989), which is a much greater rate than observed in any of our wild study groups, even when counting all disappearances as evictions.

Moreover, evictions could even be more likely when evicting females are in relatively good physical condition, i.e., in years with high cumulative rainfall and more available food resources, as the process might be costly for both aggressor and victim. In captivity, where targets of aggression have limited options to escape their predominantly female aggressors, severe wounding and even cases of death have been recorded (Vick and Pereira 1989; Gresse et al. 1994), suggesting high costs for both parties. In the wild, redfronted lemurs exhibit pronounced year-to-year variation in parasite infection intensity (Clough et al. 2010), which might be associated with variation in body condition. Hence, more fine-grained data on the links between rainfall, fruit availability and body condition, as well as on the magnitude of their temporal delays will be required to formally test this postulated link between body condition and female evictions.

Kin selection theory predicts that kinship should have a modulating effect on the intensity of female competition among group members. At large group sizes, evictions in redfronted lemurs were specifically driven by the number of juvenile females in a group, suggesting that factors intrinsically related to females are also relevant for predicting mechanisms of female competition. As the number of juvenile females increases, adult females might want to reserve limited breeding positions for their own daughters, making more distantly related females targets of eviction (Soma and Koyama 2013). However, presence of the mother did not predict which female was targeted for an eviction (model 4). Banded mongooses, in contrast, discriminate negatively against closer kin when it comes to evictions (Thompson et al. 2017). The effect of the number of juvenile females on increased female competition possibly also manifests in the form of sexual mimicry of female infants in redfronted lemurs. They change from a coloration typical for adult males to a female coloration at the age of 3 to 4 months which may protect infant females from female aggression, including female infanticide (Jolly et al. 2000; Barthold et al. 2009). Hence, evictions may serve to reduce both, immediate and future reproductive competition for perpetrators and their female offspring, respectively.

Female reproductive restraint and fitness consequences of evictions

Female competition may also manifest itself by reducing other females' birth rates or offspring survival. As the numbers of females increase, their cumulative reproductive potential also increases. Assuming that feeding competition is most intense among mothers, one might expect them to prevent others from reproducing and any resulting offspring to be less likely to survive in larger groups. However, the number of adult females in a group and higher rainfall actually had a positive effect on birth rates (model 6). The occurrence of an eviction before the birth season did not impact birth rates. In contrast, but similar to evictions themselves, the number of juvenile females in a group promoted a response of adult females that could be interpreted as reproductive restraint (model 6). Since we considered here only birth rates but not aborted pregnancies or still births, the mechanisms underlying reproductive restraint have to be investigated in future physiological studies. Nevertheless, our results indicate that female reproductive competition in redfronted lemur seems to be also implemented via prenatal mechanisms and is driven by the number of juvenile but not adult females.

Similarly, early infant survival was negatively affected by the number of juvenile (and by trend adult) females (model 7). In contrast, in banded mongooses the number of surviving offspring until weaning declined beyond a critical number of adult breeding females (Cant et al. 2013). Those results suggest that female competition also impacts population growth in some species. Independent of the number of competitors, inducing abortions and committing infanticide represent alternative mechanisms of social control over reproduction (Gilchrist 2006), and female infanticide is indeed known from group-living lemurs (Jolly et al. 2000). Thus, female competition seems to have an impact on reproductive output, also via early infant survival.

In contrast to an earlier study on reproductive senescence in this study population (Kappeler et al. 2022b), we did not find that older females were less likely to give birth, whereas female longevity did not influence birth rates in both studies. Since we included only groups for which we had at least 20 years of demographic data in this study, the contrasting results might be due to different sample sizes. Early infant survival was also not predicted by female age or longevity, suggesting that female age and longevity as potential proxies for female condition did not impact early infant survival. Interestingly, females were more likely to give birth in years with higher rainfall, but it did not predict early infant survival. Hence, future studies are required to examine how food intake by mothers may impact infant survival.

Male emigrations

Our study makes a new contribution toward a more comprehensive understanding of social competition by also considering the drivers and effects of male emigration. Male emigration also reduces group size and alleviates pressures on females to evict close kin. Male emigration was predicted by the proportion of adult males to adult females in the group (model 2). While the total number of reproducing females seems to be limited, the number of males seems to be associated with the number of mating opportunities. Both sexes most likely benefit from reducing male emigration because they are either related to the male or because the number of males in the group reduces the take-over risk by foreign males (Port et al. 2010; Port and Cant 2014). This effect may also explain their unusually high levels of social tolerance (Fichtel et al. 2018), both compared to females, but also to most anthropoid primate species (Pereira 1995). Future research should now examine the behavioral mechanisms accompanying male emigration and immigration for a more complete understanding of the proximate control of group size.

In conclusion, female competition is sensitive to demographic and ecological cues, but not to inclusive fitness costs. In contrast to an earlier analysis (Kappeler and Fichtel 2012), including males in the analyses refined our understanding of the drivers of female eviction by identifying the number of juvenile females as an important specific predictor and male emigrations as a buffer of female evictions. In addition, this approach allowed us to investigate the fine-tuned interplay between competition and kin selection.

Supplementary information The online version contains supplementary material available at https://doi.org/10.1007/s00265-023-03330-w.

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Author contribution Conceptualization: LP, CF, PMK Methodology: LP, CF, PMK Investigation: CF, PMK Visualization: LP Supervision: CF, PMK Writing—original draft: LP, PMK Writing—review and editing: LP, CF, PMK.

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Data availability All data are available on figshare: https://doi.org/10.6084/m9.figshare.22673398.

Declarations

Ethical approval This study adhered to the Guidelines for the Treatment of Animals in Behavioural Research and Teaching (Animal Behaviour 2020) and the legal requirements of the country (Madagascar) in which the work was carried out. The protocol for this research was approved by the Malagasy Ministry of the Environment, Water, and Forests (066, 202/15/MEEMF/SG/DGF/DAPT/SCBT; 90, 234/16/MEEMF/SG/DGF/DAPT/SCBT.Re; 47, 215/18/MEEMF/SG/DGF/DAPT/SCBT.Re; 052/19/MEDD/SG/DGF/DSAP/SCB.Re).

Conflict of interest The authors declare no competing interests.

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Supplementary

Overview model outcomes

Tab. S2.1 Overview of model outcomes for multi-model inference for female evictions (Model 1). All predictors were centered. Random slopes were included in models but are not listed here for better readability.

Model	Predictors	Mean weighted estimates	SE
Model 1: Predictors of female eviction (multi-model inference) Weighted means of estimates	Intercept	-1.55	0.29
	Rainfall	0.48	0.27
	N juvenile males	-0.00	0.05
	N adult males	0.67	0.25
	N juvenile females	0.88	0.26
	N adult females	-0.02	0.06

[2] z-transformed to mean of zero and a standard deviation of one; mean and standard deviation of the original: rainfall: mean= 888.72. sd= 176.16. n adult females: mean= 2.52. sd= 0.66. n juvenile females: mean= 1.2. sd= 0.97; n adult males: mean= 3.70, sd= 1.26. n juvenile males: mean= 1.12. sd= 1.16)

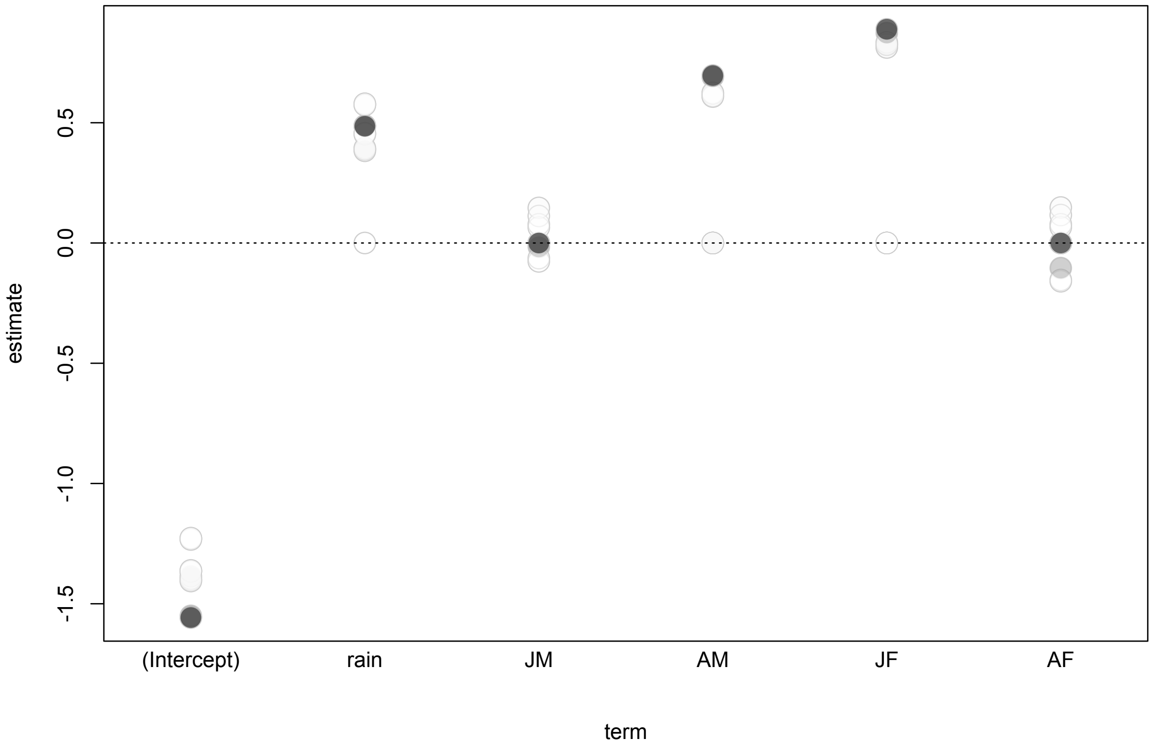

Fig. S2.1. Estimates of predictors for female evictions from multi-model inference (Model 1). Each point represents an estimate from one of 8 models. the shade of gray refers to the AIC weight. with more likely estimates being of darker color. (ASR: adult sex ratio; JM: juvenile males; AM: adult males; JF: juvenile females; AF: adult females)

Tab. S2.2 Single model outcomes for all 15 models of the multi-model inference approach for female evictions (Model 1).

model	AICc	k	w	estimates
1+n juv F+n ad M+rain	123.34	5	0.57	-1.55(0.287) + 0.485(0.267)*rain + 0.696(0.252)*n ad M + 0.889(0.26)*n juv F
1+n ad F+n juv F+n ad M+rain	125.36	6	0.21	-1.55(0.286) + 0.488(0.268)*rain + 0.692(0.27)*n ad M + 0.873(0.26)*n juv F + -0.104(0.267)*n ad F
1+n juv F+n ad M+n juv M+rain	125.53	6	0.19	-1.557(0.287) + 0.487(0.267)*rain + -0.016(0.248)*n juv M + 0.692(0.256)*n ad M + 0.888(0.261)*n juv F
1+n juv F+rain	130.11	4	0.02	-1.386(0.252) + 0.383(0.25)*rain + 0.813(0.241)*n juv F
1+n ad F+n juv F+rain	131.89	5	0.01	-1.402(0.256) + 0.389(0.25)*rain + 0.826(0.246)*n juv F + 0.148(0.239)*n ad F
1+n juv F+n juv M+rain	131.91	5	0.01	-1.395(0.254) + 0.39(0.251)*rain + 0.146(0.238)*n juv M + 0.824(0.243)*n juv F
1+n ad F+n juv F+n juv M+rain	133.86	6	<0.01	-1.406(0.257) + 0.395(0.251)*rain + 0.112(0.245)*n juv M + 0.834(0.246)*n juv F + 0.116(0.248)*n ad F
1+n ad M+rain	135.08	4	<0.01	-1.363(0.29) + 0.574(0.282)*rain + 0.609(0.232)*n ad M
1+n ad F+n ad M+rain	136.77	5	<0.01	-1.361(0.286) + 0.574(0.278)*rain + 0.621(0.251)*n ad M + -0.159(0.25)*n ad F
1+n ad M+n juv M+rain	137.13	5	<0.01	-1.366(0.294) + 0.579(0.283)*rain + -0.076(0.24)*n juv M + 0.612(0.237)*n ad M
1+n ad F+n ad M+n juv M+rain	138.88	6	<0.01	-1.364(0.289) + 0.579(0.28)*rain + -0.063(0.242)*n juv M + 0.625(0.254)*n ad M + -0.154(0.251)*n ad F
1+rain	140.63	3	<0.01	-1.227(0.222)
1+n ad F+rain	142.62	4	<0.01	-1.228(0.222) + 0.452(0.234)*rain + 0.078(0.218)*n ad F
1+n juv M+rain	142.62	4	<0.01	-1.233(0.244) + 0.456(0.25)*rain + 0.078(0.221)*n juv M
1+n ad F+n juv M+rain	144.68	5	<0.01	-1.23(0.223) + 0.456(0.234)*rain + 0.065(0.223)*n juv M + 0.066(0.222)*n ad F
1+n juv F+n ad M+rain	123.34	5	<0.01	-1.558(0.287) + 0.485(0.267)*rain + 0.696(0.252)*n ad M + 0.889(0.26)*n juv F

Tab. S2.3 Model outcomes for alternative models (Models 2 and 6).

Model	Term	Estimate	SE	Lower CI	Upper CI	*P*
Male emigration **χ2 = 21.71,** **df =5,** **P< 0.001**	Intercept	-0.35	0.17	-0.73	-0.03	a
	Rainfall[b]	0.20	0.17	-0.16	0.57	0.238
	Adult females[b]	-0.39	0.19	-0.78	-0.06	0.033
	Adult males[b]	0.77	0.21	0.42	1.28	<0.001
	Juvenile females[b]	-0.10	0.17	-0.47	0.25	0.548
	Juvenile males[b]	0.27	0.18	-0.07	0.65	0.126

[a] not shown because of having a very limited interpretation

[b] z-transformed to mean of zero and a standard deviation of one; mean and standard deviation of the original predictors:: rainfall: mean=875.59, SD=177.53, group size: mean=8.83, SD=2.53;

Model	Term	Estimate	SE	Lower CI	Upper CI	P
Birth rates **χ2=15.94** **df=5** **P=0.007**	Intercept	0.32	0.70	-1.11	1.90	A
	Rainfall[b]	0.69	0.21	0.35	1.31	0.008
	Female age[b]	-0.63	0.35	-1.56	0.03	0.060
	Female age^{2} [b]	0.13	0.15	-0.20	0.53	0.353
	Adult females[b]	0.69	0.26	0.38	0.13	0.002
	Adult females^{2} [b]	0.11	0.19	-0.19	0.69	0.543

Juvenile females[b]	-0.54	0.25	-1.22	-0.05	0.019
Juvenile females^2 [b]	0.32	0.18	0.01	0.76	0.064
Longevity[b]	0.06	0.05	-0.04	0.17	0.191

[a] not shown because of having a very limited interpretation

[b] z-transformed to mean of zero and a standard deviation of one; mean and standard deviation of the original predictors: rainfall: mean= 882.79, SD= 179.23; female age: mean= 7.99, SD= 4.31; AF: mean= 2.55, SD= 0.74, longevity: mean=13.07, SD=5.71 ;

Data structure validation

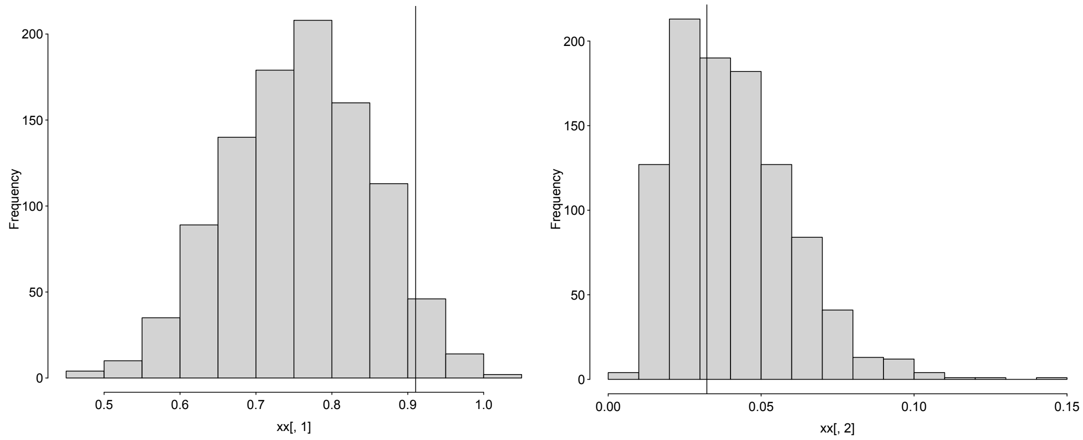

Fig. S2.2 Distribution of estimates and significance for group size obtained by data structure based on different months as non-eviction entries in females (Model 1). The vertical line represents the estimate obtained with using April as the reference month containing no evictions. Note that the estimate obtained with April as the month containing no evictions was slightly biased upwards as compared to randomly selecting various months without evictions from the same group and year. Note also that despite this bias. the test of significance was not obviously biased.

CHAPTER III

Who cares? Behavioural consequences of social disruptions in redfronted lemurs, Eulemur rufifrons

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Who cares? Behavioural consequences of social disruptions in redfronted lemurs, *Eulemur rufifrons*

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Animal groups regularly lose group members as a result of death and dispersal, but the consequences of such a loss on the social relationships among the remaining group members remain generally understudied. Moreover, some of the few studies on this topic reported destabilizing effects of group member loss in some species, whereas in other species individuals apparently compensated for lost partners by strengthening remaining relationships. However, it remains unknown what may drive these contrasting effects in different species. Here, we investigated the impact of the loss of an individual on subsequent social patterns in a basal group-living primate, the redfronted lemur. Using focal animal observation data surrounding 16 disappearance events (five dispersals and 11 predation events) in four groups of wild redfronted lemurs, we tested for changes in the coefficient of variation of relationship strength in affiliative interaction networks, as well as for changes in affiliative and agonistic interaction rates. We found no evidence for significant changes in any of the three measures, indicating that the disappearance of a group member is not reflected by a change in social interactions among redfronted lemurs. Yet, the fact that rates of social interactions did not change significantly indicates that they compensated for the loss of a group member by redistributing their social behaviour towards other individuals. Our study therefore indicates that redfronted lemurs' social interactions are resilient to group member loss. Alternatively, the number of unpredictable disappearance events in our retrospective study may have been too small to detect any effects, underscoring the need for additional comparative research on this topic to determine whether methodological constraints or particular coping mechanisms underly this apparent contrast with anthropoid primates.

In group-living animals, group composition changes regularly, with individuals entering or leaving a group, due to birth, death or dispersal. As losing a group member implies losing a potential social partner for the remaining individuals, every departure has down-stream effects on social structure (Shizuka & Johnson, 2020), which describes the pattern of social relationships that emerges from repeated social interactions (Kappeler, 2019). Studying the effects of group member loss can therefore be important for understanding how the social structure of groups changes over time, as well as the causes of social instability (Beisner et al., 2015), which has been defined as a change in social structure associated with a decreased level of social order (Flack et al., 2006). Social instability refers to a commonly employed experimental design (otherwise individually housed animals spend some time with a randomly selected number and identity of conspecifics each day and are compared with animals that always meet the same partners for equivalent amounts of time) in biomedical studies investigating endocrine, immune and health outcomes of social change (e.g. Capitanio & Cole, 2015). Social order is defined as the way in which various components of a society work together to maintain stability and the status quo and is a key concept in sociological research on human societies (Cooley, 2017; Elster, 1989). Thus, a change in group composition is one way in which social order can change and lead to social instability. Social structure may vary naturally, for example over short timescales due to individual movement or over longer timescales due to seasonal fluctuation (Henzi et al., 2009). Because stable social relationships can provide fitness benefits, such as increased reproductive success (Schülke et al., 2010) or longevity (Silk et al., 2010), and because social instability can negatively impact fitness by compromising within-group coordination (Maldonado-Chaparro et al., 2018), identifying the mechanisms behind network resilience, which can counterbalance

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destabilizing effects, can yield a better understanding of how stable social groups are maintained (see also Goldenberg et al., 2016).

The social processes connected to the loss of a group member have been investigated in various experimental (i.e. removal of an individual from a group) and simulated (i.e. removal of an individual in data) studies in the past, but only few empirical studies on free-ranging animals have been published on this topic (Barrett et al., 2012; Firth et al., 2017; Franz et al., 2015; Goldenberg et al., 2016). These studies revealed that the loss of a group member can impact social structure in several ways. First, a node loss in a social network might destabilize social structure, as network connections are lost. This instability is often measured in terms of increased clustering or decreased degree or strength (Flack et al., 2006; Franz et al., 2015; Maldonado-Chaparro et al., 2018). Second, edge rewiring might occur, as individuals compensate for the loss by directing their social behaviour towards the remaining individuals (Evans et al., 2020; Firth et al., 2017; Shizuka & Johnson, 2020). Third, after the loss of a group member, individuals might also interact more with the remaining group members to compensate for their lost relationship (Firth et al., 2017). This compensation can cause observable changes at both the individual and the group level. Individuals that had been strongly connected to the lost individual might be especially likely to form new relationships or to strengthen remaining ones. For example, Engh et al. (2006) found that female chacma baboons, *Papio hamadryas ursinus*, that lost a close relative increased their grooming rate as well as the number of grooming partners. Similarly, in eastern grey kangaroos, *Macropus giganteus*, a group level increase in mean association strength was found after the loss of several group members due to predation (Carter et al., 2009).

Loss of group members can lead to instability in social structure (Barrett et al., 2012; Flack et al., 2006; Franz et al., 2015; Maldonado-Chaparro et al., 2018), but this effect was often only found after the loss of keystone individuals, that is, those that are highly socially connected or perform a specific function. Flack et al. (2006) found that the experimental removal of policing males in pigtailed macaque, *Macaca nemestrina*, groups resulted in changes in the social networks that they associated with instability, such as a reduced mean degree and increased clustering. In contrast, following the natural loss of alpha and beta baboon males, only a small decrease in mean degree was found, which rebounded after 1 month (Franz et al., 2015). Simulation studies showed that the loss of highly central individuals, but not the loss of random individuals, can destabilize a group's social structure (Lusseau, 2003; Manno, 2008). Indeed, Barrett et al. (2012) reported that the disappearance of a dominant female had a stronger impact on the group's social structure than the disappearance of a low-ranking female.

The intensity of destabilizing effects of group member loss might also vary among taxa, as some species might generally be more resilient towards changing group membership or have mechanisms to maintain stable social structure when certain individuals disappear. For example, the social structure of some macaques and baboons has been found to be destabilized by the loss of group members (Barrett et al., 2012; Flack et al., 2006; Franz et al., 2015), whereas ants, mice, *Mus musculus*, and great tits, *Parus major*, were found to maintain a stable social structure, or even increased their connectivity when losing group members (Annagiri et al., 2017; Evans et al., 2020; Firth et al., 2017). However, it is still unknown which factors may explain this interspecific variation in resilience after group member loss.

Group member loss may also affect social structure differently depending on aspects of the event itself. The unexpected loss of a group member due to predation might have a different effect than the much more predictable dispersal of maturing offspring (Shizuka & Johnson, 2020). Group member loss due to social causes, such as dispersal or eviction, might occur more gradually than the unpredictable loss due to predation. Therefore, the death of an individual might have stronger effects on the remaining group members than a predictable dispersal event. As typically only members of one sex disperse, and are therefore more likely to disappear, the effect of a loss might also vary as a function of the sex. Individuals of the philopatric sex often also have a more central role in the group, as they have more time to develop strong relationships (Matsuda et al., 2012; Sosa, 2016). Therefore, the disappearance of individuals of the philopatric sex might affect a group's social structure more strongly. This might also depend on the frequency of dispersal and the difference in the social positions between females and males in a particular species. However, differences in the effect of group member loss depending on the sex of the lost individual have not been explicitly examined in previous studies.

To examine how group member loss affects the social structure of the remaining group members in a basal group-living primate, we analysed the social behaviour of redfronted lemurs before and after various disappearance events. Redfronted lemurs represent an ancestral lineage that evolved group living independently from other primates (Kappeler, 1997). They live in small multimale, multifemale groups of approximately 5–15 individuals with even or male-biased adult sex ratios (Ostner & Kappeler, 1999; Overdorff et al., 1999). Redfronted lemurs are characterized by a lack of clear dominance hierarchies between and within the sexes (Pereira & Kappeler, 1997) and they exhibit high social tolerance in combination with low rates of agonistic interactions (Fichtel et al., 2018). Males are the dispersing sex and usually leave their natal groups upon reaching sexual maturity; secondary dispersal is also common (Wimmer & Kappeler, 2002). Females are the philopatric sex and do not leave their groups voluntarily, but are occasionally forcefully evicted from their natal group by other females (Kappeler & Fichtel, 2012).

In this first study on the effects of social disruption on social structure in a strepsirrhine primate, we provide one of the first empirical assessments of the effects of the loss of both male and female group members on social structure using a long-term data set. In contrast to previous studies on this topic, we use a broader time window to examine impacts on social structure that last beyond immediate effects within hours or days. We hypothesized that the loss of a group member may either destabilize social structure, or that individuals adapt their social behaviour to compensate for the lost partner. We therefore predicted that (1) as a direct consequence of a group member loss social differentiation would increase (i.e. an increase in variation in affiliation strength) as an effect of destabilization, (2) the rate of agonism increases in the process of redistributing social positions within the group, (3) as an indirect consequence of a group member loss, individuals increase the time spent socializing with remaining group members to compensate for their lost social partner, (4) the loss of females has a stronger impact on changes in social structure than the loss of males, as females are the philopatric sex in this species, and (5) changes in social patterns differ between disappearance caused by either predation or dispersal.

METHODS

Data Collection

This study was conducted with four groups of redfronted lemurs at the Kirindy Forest Research Station of the German Primate Center in western Madagascar. All individuals had been previously marked with unique nylon collars (Kappeler & Fichtel, 2012) for individual identification. One adult female of each group was equipped with a radiocollar to facilitate the relocation of groups for behavioural observations. Based on multiple weekly census counts and observations, immigrations, births and disappearances were detected within 1–2 days. Focal observations of social behaviour were performed multiple times a week and based on an established ethogram (Pereira & Kappeler, 1997). For all events involving more than the focal animal, the identity of all individuals involved was recorded. Furthermore, all individuals within a 1 m radius of the focal animal were noted every 15 min.

Overall, 55 individuals were observed for a total of 2802 h and a total of 28 individuals disappeared from their groups during the study period between 2015 and 2021 (Appendix Table A1). We excluded events where two individuals disappeared in quick succession (within 1 month) of each other, as this confounding aspect of multiple disappearances would have further complicated our models. Therefore, we only analysed a total of 16 disappearance events, including 11 cases of predation (six males and five females) and five dispersals (all males). As the only female eviction in our data set included two individuals, we did not analyse any events of a female disappearance due to social causes.

Analyses

We calculated social network statistics for each group for three consecutive 1-month periods before and after the loss of a group member, including all group members present in the respective periods. For the edge weights of the networks, we used the dyadic composite sociality index (DSI) based on all occurrences of affiliative behaviours (grooming and body contact). The DSI represents the dyadic version of the composite sociality index (CSI; Silk et al., 2013) and is strongly correlated with other measures of social relationships (Schülke et al., 2022). It combines multiple correlated behaviours into one measure by calculating the relative proportion of time each dyad spent exhibiting a certain behaviour compared to the mean of all dyads of the group. Then the mean of these measures for the different behaviours is calculated. This process is described by the formula $\mathrm{DSI}_{xy} = \frac{\sum_{i=1}^{d} \frac{f_{ixy}}{f_i}}{d}$, where d = number of different behaviours, i = a specific behaviour, f = frequency of the behaviour and xy = a specific dyad.

We calculated three measures to assess a change in structure after loss events: social differentiation, agonistic rates and affiliative rates. We measured social differentiation as the coefficient of variation (CV) of dyadic affiliation strengths within each network, as we expected less homogeneous networks, i.e. more variation in edge weight due to the loss of an individual. As social differentiation is correlated with network density but also captures the distribution of weak and strong relationships instead of just the percentage of realized relationships, which are rare in small groups, we used it as a measure of social instability. Potential social instability after group member loss events might also result in higher aggression rates, because new social positions within the group need to be established between individuals. We calculated group level rates of agonistic interactions by using counts (total number) of agonistic interactions and including observation time as an offset term to control for variation in observation time. Types of aggression included biting, hitting, chasing and threats (Pereira & Kappeler, 1997). We also calculated the rate of affiliation for each individual that was present in the before and after time frames ($N = 43$), by dividing the total time spent in affiliation by all group members by their observation time. This measure could be either an indicator of instability, as it is correlated with mean strength and degree of affiliation within groups, which has been shown to be related to instability, or an indicator of compensation of the loss.

To estimate the extent to which the occurrence of a loss event was followed by a change in aggression, social differentiation or affiliation, we fitted three different models. For estimating the effect of a group member loss on social differentiation, we built a linear mixed model (LMM), for estimating the effect on agonism a generalized linear mixed model (GLMM) with Gaussian error structure and logit link function, and for estimating the effect on changes in affiliation, we built a GLMM with negative binomial error structure and logit link function. All models included in the fixed-effect structure the cause of the loss event (predation/social), the sex of the individual being lost, the observation period (before/after) and the month. As we assumed that the difference between before and after periods could be affected by sex or cause of the group member loss, we included interaction terms between period and sex as well as period and cause. Because we expected a month-to-month difference after the loss events in addition to the difference in the period before and after, we included three-way interactions (sex ∗ month ∗ period and cause ∗ month ∗ period). We included group size as a control variable and added individual and group ID as random effects. In the data we coded the 3 months prior to the loss event as −2 to 0 and the 3 months after the loss event as 1–3. We reasoned that a loss event with a social cause, but not those caused by predation, could be preceded by aggression increasing before the loss event. We also reasoned that changes in aggression frequency over time could differ between females and males. We therefore included several interactions in the fixed effects of the model. However, because aggression frequency can be reasonably assumed to be unchanged in the 3 months preceding loss events caused by predation, we did not include a main effect of month in the model. Hence, with regard to the fixed effects of cause, sex, period and month, we used the following model structure:

Cause + sex + period_after + group size

Sex ∗ period_after + cause ∗ month + cause ∗ period_after + period_after ∗ month + cause ∗ period_after ∗ month + sex ∗ period_after ∗ month

where cause is a dummy variable, being 1 for a social cause, sex is a dummy variable, being 1 for a male, period after is a dummy variable, being 1 after the event, and a colon represents an estimate associated with a product of predictors. We used dummy variables because this is the default behaviour of the model-fitting function we used and because dummy coding provides easy interpretable estimates.

In the model, sex ∗ period_after estimates how much the sex difference depended on the period, cause(social) ∗ month estimates the effect of month for socially caused loss events, cause(social) ∗ period_after estimates the effect of period for socially caused loss events, period_after ∗ month estimates how much the effect of month differed between the periods, cause(social) ∗ period_after ∗ month estimates how much the effect of month differed between the periods for a socially caused loss event and a predation loss event, and sex ∗ period_after ∗ month estimates how much the sex-dependent difference between month effects depends on the period (each time assuming that the respective other predictors have a value of 0).

We conducted all analyses using R (version 4.1.0, R Core Team 2019), applying the functions str_detect (network construction) from the package stringr (version 1.4.0), glmer.nb (agonsim) and lmer (social differentiation) from the package ‘lme4’ (version 1.1–21, Bates, Mächler, et al., 2015) and glmmTMB (affiliation) from the package ‘glmmTMB’ (version 1.1.2.3, Magnusson et al., 2017). We centred all quantitative predictors to a mean of zero and a standard deviation of 1 before including them in the models to ease model convergence, and we included all theoretically identifiable random slopes to avoid Type I errors, namely group size within group and individual (Barr et al., 2013). For the affiliation model, we manually excluded all random slopes where correlations were essentially 0 (Matuschek et al., 2017). We compared resulting models to a null model, comprising all random effects included in full models but lacking all fixed effects except for group size, with a likelihood ratio test (Schielzeth & Forstmeier, 2009). The purpose of the full–null model comparison is to avoid 'cryptic multiple testing' (Forstmeier & Schielzeth, 2011). We obtained confidence intervals for all models by means of parametric bootstraps using the function 'bootMer' of the package 'lme4', applying 1000 parametric bootstraps. We checked for collinearity by determining variance inflation factors (VIF, Dobson & Barnett, 2018) for a standard linear model without random effects using the package 'car' (version 3.0.11, Field, 2005). This revealed VIF values that were smaller than 1.892 in all cases. Although our models include numerous variables and might seem complex for a limited number of data points (Appendix Table A2), we do not expect them to be overfitted as a large proportion of model complexity results from random effects and random slopes, the presence of which should not have a large effect on the variability of fixed-effect estimates (Bates, Kliegl, et al., 2015). To estimate model stability and avoid overfitting, we proceeded by dropping levels of the random effect one at a time from the data set and compared the estimates obtained to those obtained for the full data set. While the model on social differentiation appeared to be rather unstable (Figs A1, A2), the agonism model exhibited moderate stability (Fig. A3) and the affiliation model exhibited good stability (Fig. A4). Results should therefore be treated with caution in this case.

Ethical Note

This study adhered to the ASAB/ABS Guidelines for the Treatment of Animals in Behavioural Research and Teaching and the legal requirements of the country (Madagascar) in which the work was carried out. The protocol for this research was approved by the Malagasy Ministry of the Environment, Water, and Forests (066, 202/15/MEEMF/SG/DGF/DAPT/SCBT; 90, 234/16/MEEMF/SG/DGF/DAPT/SCBT.Re; 47, 215/18/MEEMF/SG/DGF/DAPT/SCBT.Re; 052/19/MEDD/SG/DGF/DSAP/SCB.Re).

RESULTS

All models below encompassed 16 disappearance events, including 11 cases of predation (six males and five female) and five dispersals (all males).

Social Differentiation

Contrary to our prediction, we did not find a change in social differentiation (i.e. in affiliation strength) after loss events (interaction between cause and period and between sex and period, Table 1, Fig. 1). However, we found an unpredicted effect of the control variable group size (Table 1), with a higher degree of social differentiation in larger groups. In addition, the full model compared to the null model was overall not significant (likelihood

Table 1
Summary of the model statistics

Model	LRT	Term	Estimate	SE	Lower CI	Upper CI	*P*
Change in CV of affiliation strength	$\chi^2_9 = 7.071$	Intercept	217.65	25.45	166.04	267.431	—
		Cause (social)[a]	52.50	44.10	−33.90	138.590	—
		Sex (male)[a]	−15.09	29.07	−74.11	45.574	—
	$P = 0.630$	Period (after)[a]	29.67	43.34	−119.31	58.939	—
		Group size[b]	73.24	14.55	31.34	111.177	0.001
		Sex (male)∗period (after)	40.15	56.30	−76.84	147.08	—
		Cause (social)∗month[b]	25.11	37.08	−49.05	95.78	—
		Cause (social^3)∗period (after)	−78.71	65.11	−207.80	52.86	—
		Period (after)∗month	23.44	39.39	−52.21	96.91	—
		Cause (s)∗period (after)∗month	−8.69	62.42	−134.68	107.92	0.493
		Sex (male)∗period (after)∗month	8.22	51.92	−92.69	110.33	0.814
Change in rate of agonism	$\chi^2_9 = 16.018$	Intercept	−2.32	0.35	−3.34	−1.72	—
		Cause (social)[a]	−1.30	0.80	−3.26	−0.10	—
		Sex (male)[a]	1.11	0.42	0.24	2.13	—
	$P = 0.067$	Period (after)[a]	0.57	0.65	−0.95	1.77	—
		Group size[b]	−0.44	0.13	−0.71	−0.19	0.001
		Sex (male)∗period (after)	−0.58	0.84	−2.34	1.17	—
		Cause (social)∗month[b]	−0.17	0.73	−1.50	1.13	—
		Cause (social)∗period (after)	1.41	1.03	−0.41	3.67	—
		Period (after)∗month	−0.16	0.60	−1.44	0.96	—
		Cause (s)∗period (after)∗month	0.38	1.05	−1.85	2.71	0.716
		Sex (male)∗period (after)∗month	−0.83	0.81	−2.51	0.80	0.306
Change in affiliation rate		Intercept	−2.20	0.14	−2.46	−1.94	—
		Cause (social)[a]	−0.11	0.25	−0.58	0.41	—
		Sex (male)[a]	0.01	0.26	−0.30	0.32	—
		period (after)[a]	0.02	0.22	−0.43	0.45	—
		Group size[b]	−0.19	0.06	−0.32	−0.06	0.002
		Sex (male)∗period (after)	0.07	0.30	−0.53	0.66	—
		Cause (social)∗month[b]	−0.16	0.21	−0.55	0.27	—
		Cause (social)∗period (after)	0.01	0.36	−0.71	0.69	—
		Period (after)∗month	−0.22	0.20	−0.61	0.17	—
		Cause (s)∗period (after)∗month	0.23	0.35	−0.50	0.88	0.504
		Sex (male)∗period (after)∗month	0.12	0.27	−0.38	0.62	0.663

CV: coefficient of variation; LRT: likelihood ratio test; CI: confidence interval. A dash in the last column indicates that no value is shown because of limited interpretation.

[a] Manually dummy coded with 'predation' (cause), 'female' (sex) and 'before' (period) being the reference.

[b] z-transformed to mean of 0 and a standard deviation of 1; mean and standard deviation of the original predictors: group size: 7.63; month: 0.61.

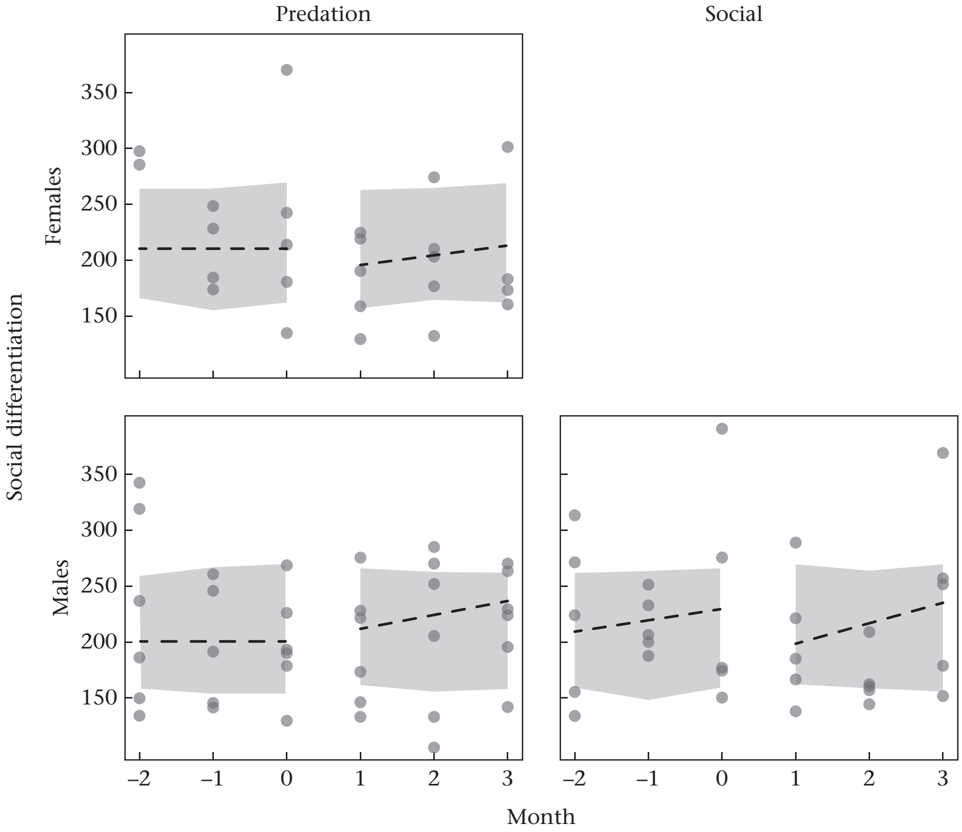

Figure 1. Coefficients of variation in affiliation strength (social differentiation) per group and month (with 0 being the month directly before the loss event occurs) separated by the sex of the individual lost (male/female) and cause (predation/social) for 16 loss events. Dashed lines represent the regression lines, grey polygons represent the 95% confidence intervals and dots represent the individual observations. Note that no female losses due to social reasons were part of the analyses.

ratio test comparing full and null model, Table 1). As this model exhibited a relatively low model stability and confidence intervals were very large (Fig. 1), these results should be treated with caution.

Agonism

In contrast to our second prediction, we found that the rate of agonism was low before and after disappearances (interaction between cause and period and between sex and period, Table 1, Fig. 2). As in the previous model, the full–null model comparison was not significant (likelihood ratio test comparing full and null model, Table 1). Similar to the model on social differentiation, agonism covaried with the control variable group size (Table 1), with lower agonistic rates in larger groups. The lack of detected effects or significant full models seemed not to be caused by unpredictability because of large confidence intervals (Fig. 2).

Affiliation

In further contrast to our predictions, we did not find evidence for this effect, and affiliation rates remained fairly stable over time (interaction between cause and period and between sex and period, Table 1, Fig. 3). As in the previous models, we found a negative effect of the control variable group size (Table 1) with lower affiliation rates in larger groups. The lack of effects seemed not to be caused by large confident intervals (Fig. 3). We were not able to perform a full–null model comparison on the model on affiliation rates, as in this case the null model did not converge.

Sex and Cause

Finally, we also found no effect of sex or of cause of the loss event on any of the response variables (Table 1, Figs 1–3).

DISCUSSION

In this study, we examined the effects of group member loss on social structure in a representative of basal primates that evolved group living independently from other primates (Kappeler & Pozzi, 2019). Contrary to our predictions, we did not find any indications of instability after group member loss, as there was no increase in social differentiation, and aggression rates did not increase either. We also found no evidence for an increase in affiliative interaction rates, which would have been expected if social networks were rewired. However, as the time spent affiliating did not decrease, redfronted lemurs redistributed this time to the remaining group members. Additionally, we did not find any indication that the sex of the lost individual or the cause of the group member loss had an influence on its effects. Thus, these basal primates appear to possess the cognitive abilities to perceive and respond to the loss of a group mate, but they may lack physiological mechanisms that may trigger group level behavioural responses involving increased levels of affiliation or agonism.

There was no increase in affiliation rates after the loss of a group member, suggesting that individuals did not overcompensate for a lost group member by increasing their interactions to build or strengthen connections to other group members. However, the loss of one individual in a group of six, for example, would result in an expected decrease in affiliation rates by 16.7% if the remaining

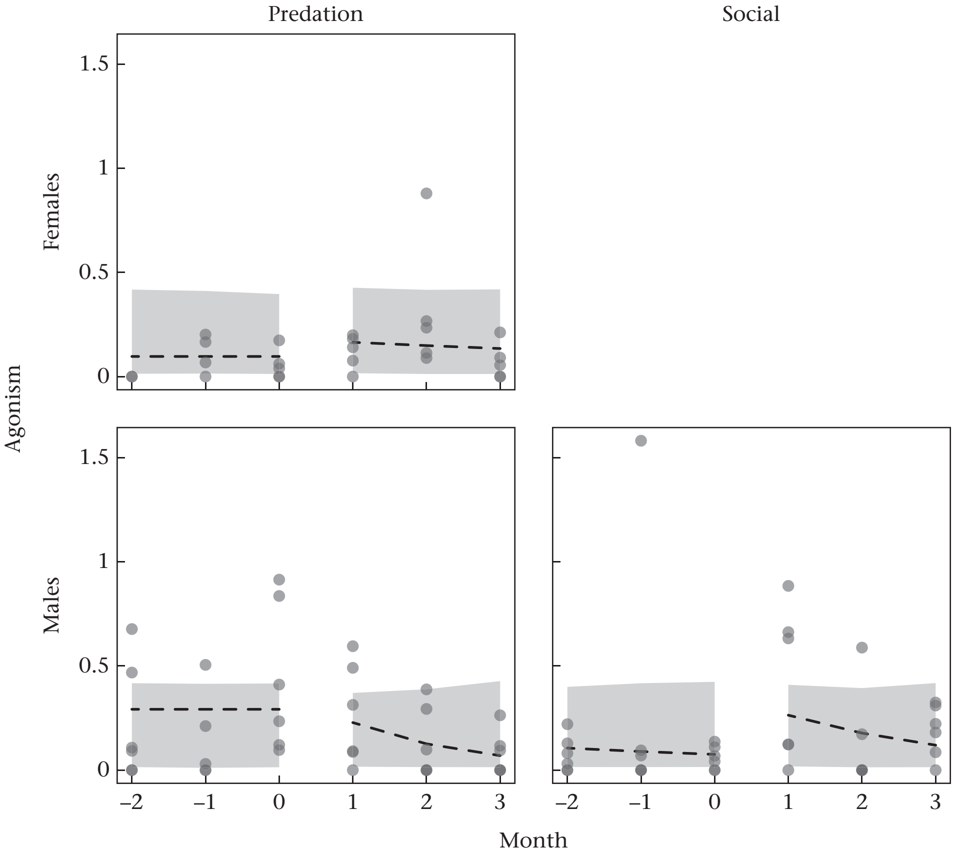

Figure 2. Group agonism rates per month (with 0 being the month directly before the loss event occurs) separated by the sex of the individual lost (male/female) and cause (predation/social) in 16 loss events. Dashed lines represent the regression lines, grey polygons represent the 95% confidence intervals and dots represent the individual observations. Note that no female losses due to social reasons were part of the analyses.

group members continued to interact with each other at unchanged rates. Therefore, the observed lack of change in affiliation rates indicates that individuals perceived the social disruption and responded to it by redistributing their affiliative behaviour among the remaining group members. In other words, they compensated for the loss of a previous potential social partner by increasing average affiliation rates with the remaining group members because they did not exhibit a significant decline in affiliation, which might have been expected in small groups. Alternatively, individuals may have simply continued to spend the same total amount of time on affiliative interactions rather than actively compensating for their loss.

In other primate species, the loss of a group mate has mostly been associated with destabilizing effects, with individuals interacting with fewer group members or networks becoming more clustered. In pigtailed macaques, the removal of policing males resulted in a decrease in mean degree of grooming and play networks, as well as an increase in clustering of proximity networks (Flack et al., 2006). Similarly, the natural loss of high-ranking males caused a decrease in mean degree of grooming networks in yellow baboons, *Papio cynocephalus*; however, this change rebounded after 1 month (Franz et al., 2015). Barrett et al. (2012) found that in chacma baboons the clustering in proximity networks increased in a 6-month period after the loss of a dominant female, but not a low-ranking female, suggesting that such destabilizing effects may only occur when high-ranking individuals are lost.

Furthermore, we did not observe any effects of the sex of the disappeared individual, the nature of the disappearance (predation versus social) and the length of the time window before and after a disappearance (immediate versus long-term effects) on overall interaction rates, indicating a subtle increase in per capita interaction rates among the remaining group members. Predation on males and females creates unpredictable losses, so that a sex-specific response is not expected. However, dispersal is both predictable and male biased, so that a difference in the response to these two types of losses could be expected if predictability mattered. It is possible that the sample size of anchor events could have been too small, even though we combined data from four groups over 6 years, or the rate of interactions was too low, even though we amassed more than 2000 h of focal observations. In addition, the observed confidence intervals do not indicate the presence of any effect that might have gone unnoticed. A more detailed look at the relationships of specific individuals before and after disappearance events may reveal more about how remaining group members compensate for experienced changes. However, potentially only individuals with a strong social relationship may respond behaviourally and physiologically to the loss of a previous group mate. This additional information could help to identify mechanisms developed to increase network resilience and increase our knowledge of how long-term social structure is upheld.

The lack of change in social networks after loss events of group members may indicate that interactions among group members in redfronted lemurs are unstructured and therefore indifferent to perturbation. However, this does not seem to be the case as previous studies show (Pereira & McGlynn, 1997). Interactions between males and females, in particular, seem to be nonrandom and females seem to prefer to associate with the same male (Ostner & Kappeler, 1999). Furthermore, related individuals have been

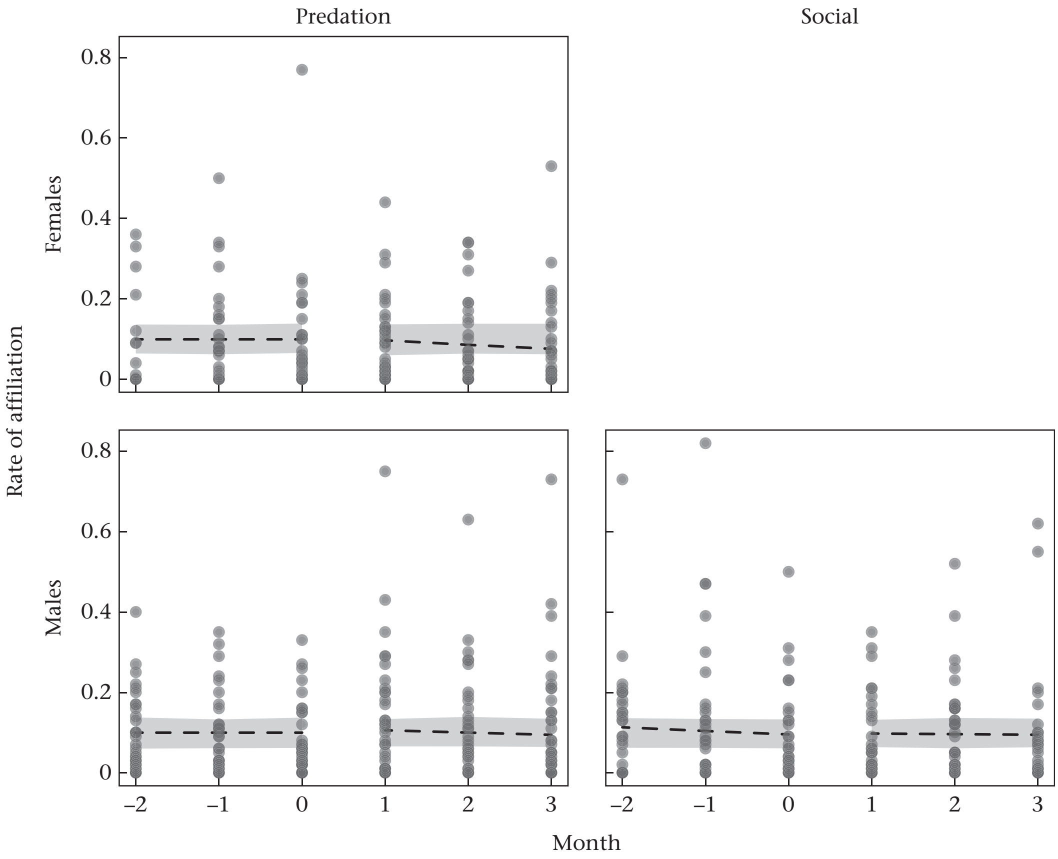

Figure 3. Individual affiliation rates of 43 individuals per month (with 0 being the month directly before the loss event occurs) separated by the sex of the individual lost (male/female) and cause (predation/social) in 16 loss events. Dashed lines represent the regression lines, grey polygons represent the 95% confidence intervals and dots represent the individual observations. Note that no female losses due to social reasons were part of the analyses.

observed to be more likely to show reconciliation with related individuals after agonistic interactions (Kappeler, 1993). Although social causes of loss events might be preceded by a decrease in relationship strength to the individuals concerned, loss events due to predation should include individuals with stronger relationships to group members. The fact that we did not find any change in social structure in either scenario might suggest that social partners can be easily replaced within a short time frame and individuals redistribute their affiliation time among the remaining group members. Since redfronted lemurs exhibit high social tolerance levels and no clear dominance relationships (Fichtel el al. 2018), all group members might be equally important, which is reflected in the fact that no destabilizing or network rewiring effects have been found. This resilience to change in group composition might also be beneficial in groups where individuals frequently enter and leave otherwise stable groups.

In contrast to our findings in redfronted lemurs, destabilizing effects of group member loss have been found in several other primate species (Barrett et al., 2012; Flack et al., 2006; Franz et al., 2015), as well as in zebra finches, *Taeniopygia guttata* (Maldonado-Chaparro et al., 2018). However, other species, including ants, mice and great tits did not exhibit signs of instability, but instead showed signs of network rewiring, such as increased affiliation rates or network connectivity (Annagiri et al., 2017; Evans et al., 2020; Firth et al., 2017). This variation among taxa may be based on differences in cognitive and emotional abilities that may proximately underly the behavioural responses to the loss of a group member. Some taxa, notably some primates, exhibit individual responses towards dead conspecifics that are suggestive of grief or related emotional responses (Anderson, 2020; Gonçalves & Carvalho, 2019) that may be absent in other taxa. The basal phylogenetic position of redfronted lemurs provides an opportunity to assess the baseline condition for primates (Fichtel & Kappeler, 2010). However, different coping mechanisms may have evolved in the Lemuridae and anthropoid primates, which have evolved group living independently. Similar studies in representatives of the Indriidae should therefore be informative because they evolved group living independently from the other two lineages (Kappeler & Pozzi, 2019). At present, comparisons between species are complicated by the different methods of previous studies, as they varied in the time frames and network measures as well as the nature of the group member loss (experimental or natural).

Destabilizing effects of group member loss may only last for a short period of time. Some of the studies only examined changes over multiple hours or days (Flack et al., 2006; Maldonado-Chaparro et al., 2018) and the effects found by Franz et al. (2015) only lasted 1 month. Therefore, short-term destabilizing effects might still have taken place in redfronted lemurs, but we could not detect them even during the first month after the disappearance event. This might indicate that redfronted lemur groups are either resilient to the loss of group members, or that a finer resolution of observational schedules might reveal at least short-term responses. Because the social disruptions on which the present analyses were mainly based are unpredictable to human observers, our study is retrospective and has some inherent limitations associated with this approach. Future studies in this and other species could help to distinguish between these three possibilities by flexibly adapting observation schedules and by combining long-term regular collection of glucocorticoid data (see e.g. Campos et al., 2021) with parallel increases in sampling of all group members following social disruptions to be able to also assess physiological responses. More generally, more comparative studies are required to enhance our understanding of the processes of social network resilience, which may contribute to long-term social stability.

Author Contributions

Amrei Pfaff: Conceptualization, Methodology, Validation, Formal analysis, Writing – Original Draft, Visualization. **Peter M. Kappeler:** Conceptualization, Methodology, Project administration, Supervision, Writing–Review & Editing. **Claudia Fichtel:** Conceptualization, Methodology, Validation, Data Curation, Writing–Review & Editing. **Lea Prox:** Conceptualization, Methodology, Supervision, Writing–Review & Editing.

Data Availability

Data are available at figshare https://doi.org/10.6084/m9.figshare.16896490.v4 ([]). See Pfaff et al. (2021).

Declaration of Interest

None.

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Appendix

Table A1
Disappearance events

Individual	Sex	Cause	Group	Date	Included in analyses
Pia	Female	Predation	A	12 Jul 2015	Yes
Goz	Male	Dispersal	A	30 Sep 2015	Yes
Tri	Male	Predation	A	30 Apr 2016	Yes
Par	Male	Predation	A	23 Mar 2019	Yes
Amo	Male	Dispersal	A	28 Aug 2019	Yes
Bur	Male	Dispersal	B	08 Dec 2018	No
Til	Male	Dispersal	B	10 Dec 2018	No
Rin	Female	Eviction	B	01 Feb 2019	No
Ado	Female	Eviction	B	09 Feb 2019	No
Bor	Female	Predation	B	25 Mar 2019	Yes
Jac	Male	Dispersal	B	26 Jun 2019	Yes
Alo	Female	Predation	B	20 Sep 2020	No
Ban	Male	Predation	B	20 Sep 2020	No
Oma	Male	Predation	B	13 Jan 2021	Yes
Goz	Male	Predation	F	25 Jul 2018	Yes
Tortuga	Female	Predation	F	05 Sep 2019	Yes
Aba	Male	Predation	F	04 Nov 2019	No
May	Female	Predation	F	12 Nov 2019	No
Geo	Female	Predation	J	18 Jun 2015	Yes
Mal	Female	Predation	J	09 May 2016	No
Oma	Male	Dispersal	J	09 May 2016	No
Arm	Female	Predation	J	21 Aug 2019	Yes
Kas	Male	Predation	J	18 Oct 2019	Yes
Kuw	Male	Predation	J	26 Nov 2019	Yes
Mon	Male	Dispersal	J	27 Mar 2020	Yes
Afganistan	Male	Dispersal	J	23 Jun 2020	Yes
Pak	Male	Predation	J	18 Sep 2020	No
Col	Female	Predation	J	21 Sep 2020	No

Table A2
Overview of model complexity

Model	No. of model estimates	No. of data points
Social differentiation	11	90
Agonism	11	91
Affiliation	3	575

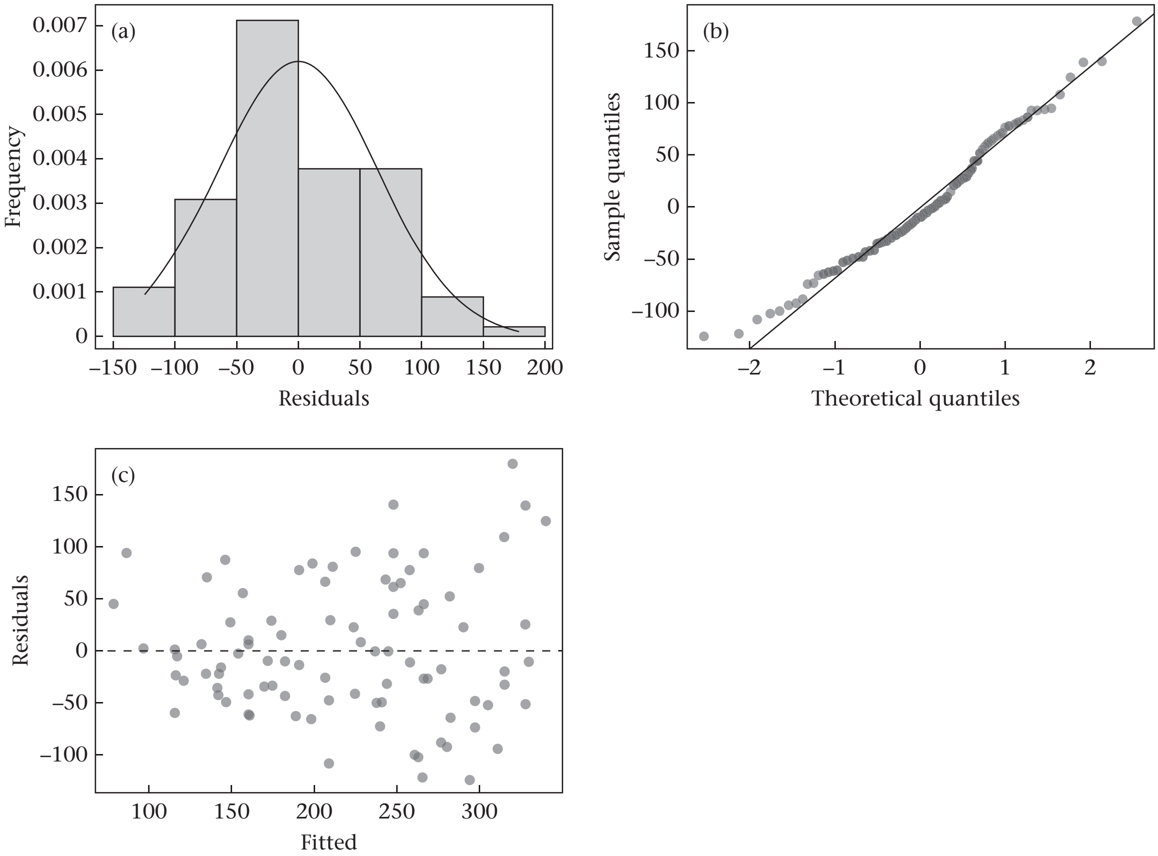

Figure A1. Diagnostic plots of the social differentiation model. Diagnostic plots of the affiliation model and agonism model are not shown here as only Gaussian models assume equal distribution of residuals. (a) Histogram of residuals, (b) qq-plot of residuals and (c) residuals against fitted values.

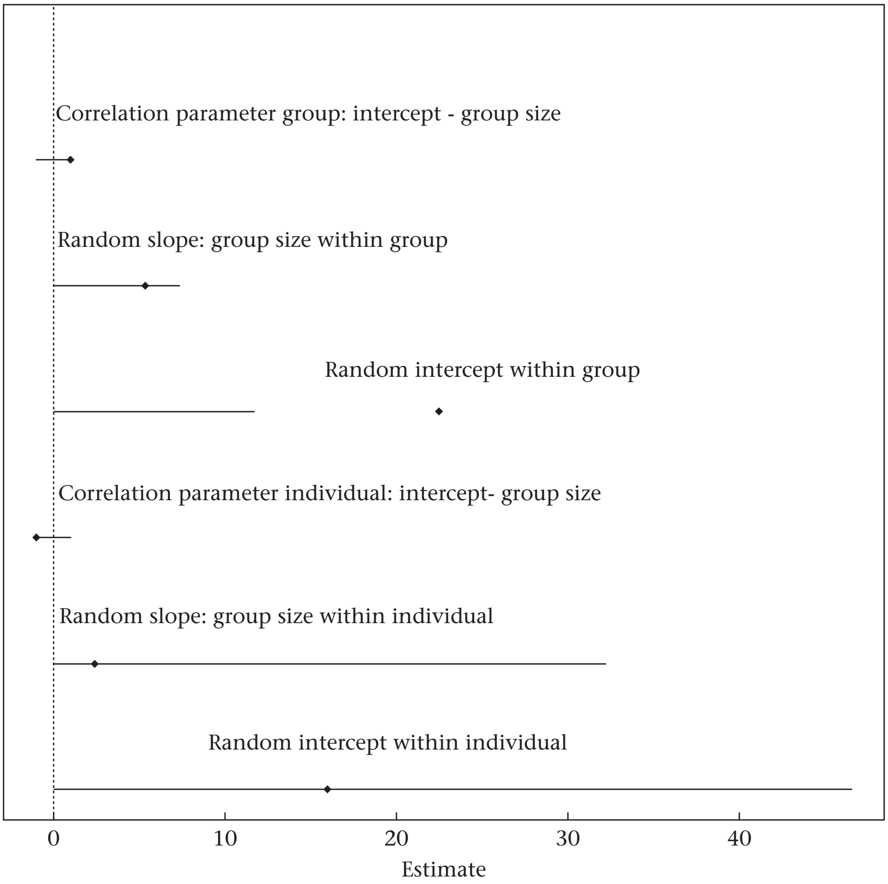

Figure A2. Model stability of the social differentiation model. Model stability is calculated by excluding levels of random effects, one at a time. Diamonds show actual estimates of models and lines represent the range of reduced models with removed levels of random effects.

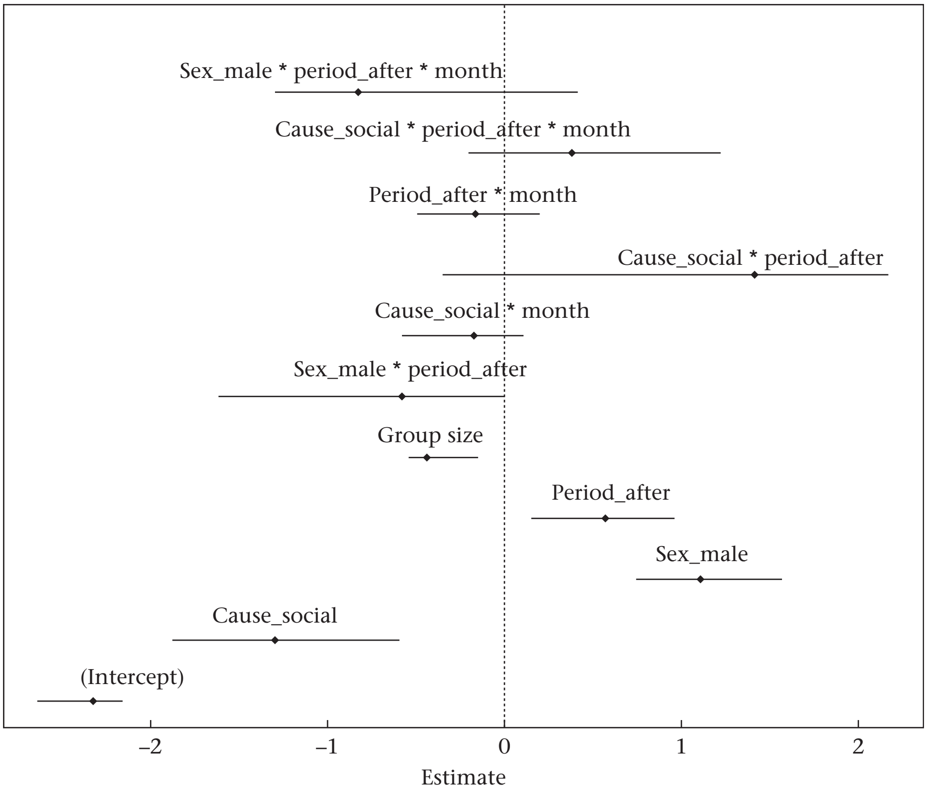

Figure A3. Model stability of the agonism model. Model stability is calculated by excluding levels of random effects, one at a time. Diamonds show actual estimates of models and lines represent the range of reduced models with removed levels of random effects.

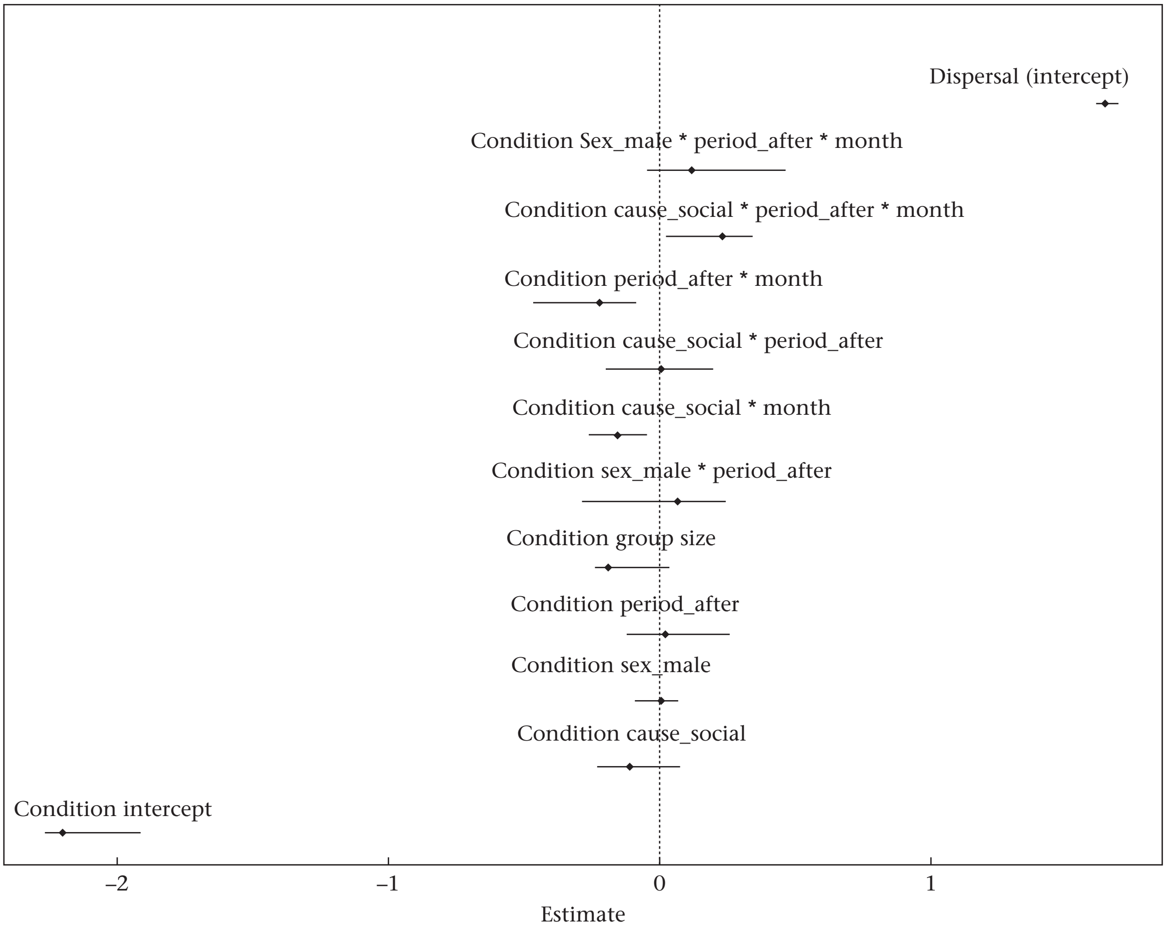

Figure A4. Model stability of the affiliation model. Model stability is calculated by excluding levels of random effects, one at a time. Diamonds show actual estimates of models and lines represent the range of reduced models with removed levels of random effects.

GENERAL DISCUSSION

Female evictions in redfronted lemurs constitute one of the most extreme cases of female-female competition in mammals. As females in this species are philopatric and eviction events have originally been related to a reduction of group size, the question why females choose to evict closely related kin instead of unrelated males in a species with even or male-biased sex ratios has posed an unresolved question in sociobiology. My project was motivated by the fact that even today, research on female competition is - to a large extent - influenced by a classical view of sex roles. Strikingly, female and male competition have rarely been studied simultaneously in the same species. While it is true that female and male sociality is in most cases at least partly determined by different factors, they are not independent and will likely affect each other in sexually reproducing species. In this dissertation, I aimed to investigate the causes and consequences of female competition in redfronted lemurs with the aim to better understand the causes and consequences of evictions. Firstly, I aimed to determine the relative impact of feeding or reproductive competition on glucocorticoid levels and aggression in both males and females in this species. (Chapter I). Secondly, I aimed to investigate the individual, social, and ecological drivers of evictions and how evictions are linked to male competition (Chapter II). Further, I aimed to determine whether evictions are linked to benefits in life-time reproductive success and whether females would express reproductive restraint in order to forego eviction (Chapter II). I lastly aimed to determine the consequences of group member loss on the social structure of redfronted lemurs (Chapter III). In the following sections, I will discuss the specifics of my findings regarding evictions and how they relate to the generally low rates of aggression in this species. I will discuss how my findings contribute to the general knowledge about evictions and compare them to findings made for other species. I will elaborate on the difficulties of studying mechanisms related to competition for future reproduction and discuss how my findings may contribute to the way we study and think about female competition in general.

Patterns of competition in lemurs

Female eviction in redfronted lemurs is one of the most extreme cases of female competition in mammals and its intensity stands in contrast to the overall low aggression rates and high social tolerance in this species. My results showed that redfronted lemurs express low rates and intensity of aggression that neither relate to physiological responses to challenges nor precede or follow demographic changes such as group member loss. This aligns with other studies in several lemur species for which aggression rates have been reported to be low (Chen, 2020; Pochron et al., 2003; Seex et al., 2022) or the observed low intensity of aggression rarely results in physical injuries (Roeder et al., 2002). Beyond decreased rates of agonism, dominant males of captive brown lemurs (*Eulemur fulvus fulvus*) have been observed to intervene in conflicts without the expression of aggression that usually ended conflicts and was followed by affiliative behaviour between opponents (Roeder et al., 2002). The pattern of low aggression rates also holds when comparing lemurs to other primate species (Sussman et al., 2005).

Low aggression rates in lemurs might be explained as an adaptation to conserve energy in the harsh and unpredictable climate of Madagascar. The energy frugality hypothesis, proposed by Wright (1999), suggests that traits summarised under the lemur syndrome, a set of traits in lemurs that differ from typical patterns in mammals (Kappeler and Fichtel, 2015; Kappeler and Schäffler, 2008), are adaptations to either conserve energy or to increase the benefits gained from scarce resources. Several of those traits link to agonism. First, it has been suggested that sperm competition should be energetically less expensive than physical fights for access to mates in males (Wright, 1999). This finds support in several lemur species that increase their testicular size to up to five times during mating (summarised in Wright, 1999) and fits with my finding of unchanged aggression rates in the mating season in male redfronted lemurs in combination with increased glucocorticoid levels. Second, female dominance and the lack of a sexual size dimorphism might have evolved in order to allow for the realisation of feeding priority in females that are under high energetic stress (Wright, 1999). Indeed female-male aggression seems to be higher in species or populations that experience more resource limitation (Kubzdela et al., 1992; Pereira and Kappeler, 1997) Richard, 1985). Female dominance is further likely to lead to generally less aggressive societies (Kappeler et al., 2022b). Third, small group sizes decrease within-group competition. My results show that both female evictions and male emigrations follow intense competition for limited group membership and the finding that male emigration is able to buffer female evictions further supports this assumption. As females have increased energetic demands, the number of females present in a social group might be limited more than the number of males. If larger groups were more likely to win intergroup encounters in redfronted lemurs, the trade-off of larger groups that are more successful in intergroup competition but also might have higher within-group competition, might be achieved by limiting the number of more energy demanding adult females and could explain the unusual even or male-biased adult sex ratios in this species. As data on intergroup encounters have not yet been analysed, this hypothesis could point towards a future study. Lastly, infrequent evictions might be a way to avoid more permanent competition that comes with higher aggression rates. It has been suggested that evictions in lemurs are timed in a way that avoids intense aggression in the dry season, when energy conservation is of particular importance (Pereira, 1993). This aligns with my finding that high monthly rainfall as a proxy for resource abundance positively impacts the likelihood of eviction events. Patterns of aggression in lemurs therefore might be ultimately related to unpredictable and limited resources and support the energy frugality hypothesis.

Patterns of competition in lemurs might be further put into context by considering the historic conditions under which mechanisms of competition might have evolved. A perplexing aspect of evictions in redfronted lemurs is, for example, the possibility of lethal consequences for close kin which could decrease inclusive fitness of evicting females. Historically, this pattern could have been different. Forests in Madagascar are currently shrinking at a rapid rate, and the habitat of redfronted lemurs has significantly decreased in the last decades (Harper et al., 2007). In original forests with less restrained territories, evicted females might have more frequently been able to establish new territories and groups. The evolutionary disequilibrium hypothesis suggests that lemurs are able to adapt to changing environmental conditions, as they might have recently shifted to a diurnal lifestyle as a response to the extinction of large raptors. This hypothesis explains the unusual cathemeral activity observed in some lemur species (van Schaik and Kappeler, 1996). However, current habitat loss and climate change proceed at a much faster rate. Understanding the limits or constraints of behavioural responses to changing conditions is therefore one of the major challenges of current behavioural and conservation biology (Beever et al., 2017; Buchholz et al., 2019). Given the rapid change of the world's climate and ongoing habitat loss, the mechanisms of female competition that aim at long-term reproductive advantages could lose efficiency. When studying the causes and mechanisms of female competition, it is therefore necessary to consider the original conditions under which they might have evolved and their potential recent changes.

Evictions

Among all mechanisms of competition in females, we know least about the evolution of evictions and my dissertation substantially contributes to understanding this form of competition on a broader level. Most of my results align with findings of studies on evictions in meerkats and banded mongooses. First, evictions in meerkats, banded mongooses, and redfronted lemurs seem to predominantly occur at large group sizes and have been related to group size regulation (Stephens et al., 2005; Thompson et al., 2016). Second, (future) reproductive competition seems to be the prevailing cause of evictions. Conversely, immediate food resources did not seem to have an effect, as evictions peaked in reproductive seasons but did show no a relationship to food availability (Dubuc et al., 2017; Thompson et al., 2016). This seems to be related to infant survival being negatively impacted by the number of females (Cant et al., 2010; Hodge et al., 2008), suggesting that the number of offspring that can successfully be raised to independence is limited. This result is more difficult to interpret in redfronted lemurs than in meerkats or banded mongooses, as other than in these two carnivores, infant care is almost exclusively carried out by mothers and not shared communally or cooperatively. However, some aspects of evictions seem to differ in redfronted lemurs compared to other species.

Different to what has been found in mongooses or meerkats, the number of juvenile, non-reproductive females predicted the occurrence of evictions in redfronted lemurs. In banded mongooses the critical group component to increase the likelihood of evictions was the number of reproducing females present at group oestrus (Gilchrist, 2006), and in meerkats the targets of evictions were mostly subordinate females with which conflict was most likely (Young et al., 2006). Although I could not make any assumptions about the age of victims, the fact that the number of juvenile females and not adult females was driving evictions might suggest that in addition to more immediate competition over raising offspring, evictions in redfronted lemurs might be driven by future reproductive success.

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Another difference that has been previously noted is the intensity of competition in species for which female evictions have been reported. Unlike meerkats and banded mongooses, victims of evictions in redfronted lemurs are not allowed to return to the group from which they were evicted. In captivity, where females are not able to leave groups, severe wounding has been observed which in a few cases has even led to the death of the evicted individual (Vick and Pereira, 1989). As evicted females are rarely able to join or found new groups, the effect of evictions in redfronted lemurs might still be fatal for the victim, even if it is able to leave the group unharmed. As mentioned before, historically, evictions might have had fewer fatal consequences. An evolutionary stable strategy model, based on data of evictions in meerkats suggested that eviction as a mechanism of competition was most likely to be stable if survival rate of evicted individuals was between 0.3 and 0.4 (Stephens et al., 2005). However, adaptive forced dispersal as a function of evictions has not been shown in mammals so far and at least in mongooses seemed to be an unlikely explanation for evictions (Thompson et al., 2016). The likely fatal outcome of evictions in redfronted lemurs makes evictions in this species, to my knowledge, the most extreme example of evictions in mammals.

A pattern that is inconsistent among evictions in mammals is the role of kin. While banded mongooses seem to discriminate against kin (Thompson et al., 2017), meerkats predominantly evict more distantly related individuals (Clutton-Brock et al., 1998). Similarly, most cases of evictions that have been reported in ring-tailed lemurs have occurred between less related matrilines (Soma and Koyama, 2013). Although we could neither confirm an effect of relatedness nor presence of mother in wild redfronted lemurs, evictions in captive groups of redfronted lemurs have shown that actors of evictions were usually closely related when acting together against victims that were less related to them (Vick and Pereira, 1989). However, the same study observed cases of mothers evicting daughters, and similarly other studies on captive lemur species observed the same number of evictions of kin as non-kin (Digby, 1999). My results might be further limited as no behavioural data were available on eviction events, and I can draw no conclusions about whether evictions were primarily initiated by less related females. As behavioural data collection continues, future studies will hopefully be able to identify initiators and victims. On the one hand, I cannot rule out that the lack of effect is due to the limited sample size of my study. On the other hand, the few females in wild redfronted lemur groups are usually all closely related, such that evicting kin can often be hardly avoided. As evictions in mammals have only been found in species where females are philopatric, discrimination against kin and a reduction of the actors' inclusive fitness is likely to be a cost that this mechanism of competition has in common across species.

Female philopatry is one of several aspects that is common to the mammal species in which we observe evictions. Finding similarities and differences among these species can help to understand, in which cases this extreme form of competition is an evolutionary stable mechanism. Banded mongooses, meerkats, and lemur species in which evictions have been observed all inhabit highly seasonal and strongly food-limited environments. Limited group size consequently seems to be a strong factor affecting the occurrence of evictions. Reproductive positions seem to be limited not only in females but also in males. In banded mongooses, few males share the paternity of the majority of offspring (Cant et al., 2013), and reproduction in meerkats is usually limited to one reproducing pair. Although redfronted lemur groups are usually composed of multiple males, reproduction in males is highly skewed (Kappeler and Port, 2008). Interestingly, although common in mammals, males are not dominant over females in species in which female evictions have been reported, and in several of these species females even dominate males. In addition, evictions seem to be a mechanism employed when prepartum reproductive suppression is not an option or not successful. While dominant meerkat females usually suppress reproduction of subordinates, subordinates regularly attempt to breed, which, in turn, frequently leads to evictions. This synthesis of common patterns among species that exhibit female evictions could help as a foundation for future studies exploring more global patterns of the occurrence of this mechanism of competition.

Alternatives to evictions

Another way to better understand when and why evictions occur, is to ask why other mechanisms that are linked to competition for immediate or future reproduction and survival of offspring are not in place. Other forms of reproductive suppression, such as the behavioural or physiological suppression of reproduction, require longer-term investment of competitors. Particularly in societies with dominance hierarchies, for instance, few individuals permanently suppress reproduction of others, for example, by exerting frequent aggressions towards victims (Young, 2009). My finding that the number of adult females increases the likelihood for a female to give birth suggests the absence of other forms of reproductive suppression in redfronted lemurs. In groups with a limited number of females, temporarily limited episodes of targeting aggression might be more efficient as they potentially can permanently impede the reproduction of a competitor. Additionally, such temporarily limited episodes of targeting aggression allow for high tolerance and low aggression rates. For meerkats it has been suggested that evictions occur in a way that minimises unnecessary persecution (Young et al., 2006). As elaborated above, in redfronted lemurs, aggression rates in both sexes are generally low, despite increased glucocorticoid levels in seasons of potential conflict. This could suggest the necessity of a strategy that minimises energetic expenses in a habitat with phases of unpredictable and limited resources.

Presumably, infanticide by females is a mechanism to reduce the competition for own offspring within the same cohort, as observed in litter bearing species like mongooses and meerkats (Gilchrist, 2006; Young et al., 2006). Infanticide directed towards female infants, could be an effective and unexplored tactic, in species where females are competing for future reproduction. The only study that investigated sex bias in victims of infanticide comes from bonnet macaques (*Macaca radiata*) where females bias infanticide towards female infants (Silk et al., 1981). Infanticide of daughters has further been reported in multiple human societies. However sociological factors might also impact such patterns (Beltrán Tapia and Marco-Gracia, 2022; George et al., 1992; Miller, 1987). In redfronted lemurs, female infanticide might be avoided by an interesting phenomenon of infant development. Although redfronted lemurs are dichromatic and females and males can easily be distinguished by their coat, infants all share the same fur pattern typical for males up to the age of three months. It has been proposed that this might be a mechanism that had evolved to avoid aggression towards infant females (Barthold et al., 2009). If future studies in Lemuridae achieve to accumulate enough data on the relative rate of infanticides against female and male infants, this could nurture this discussion. So far, few cases have been observed and dead infants are only rarely obtained after infanticidal events so that sexing happens only in exceptions. However, a method developed in lemurs allows sexing of embryos prior to birth by hormonal fecal essays (Gerber et al., 2004; Ostner and Heistermann, 2003). This method is likely to be applicable to more lemur species and could be very valuable to studies of this kind.

How does this dissertation contribute to the study of female competition?

In mammal species with long life spans and thus decreased mortality females frequently compete for future reproductive success and such cases form one of the key differences to male competition that usually aims at immediate resources. This can be related to the relative investment into raising offspring which is usually higher for females than for males. As in females, causes and benefits of competition are often detached from competitive actions in time, it has been more difficult to contextualise competition. In redfronted lemurs, for example, evictions of close kin originally were thought to be primarily caused by large group sizes. However, if the primary objective was a reduction of group size, this strategy seems counterintuitive, as multiple unrelated males could usually be excluded instead of closely related kin (Kappeler and Fichtel, 2012). In banded mongooses, individuals that participate in evictions might even experience costs in reproduction such as the loss of their litter in the process (Bell et al., 2012). In such cases, long-term data is necessary to understand the drivers and consequences of female competition. Competition for future reproduction and survival of offspring might in both cases explain costs that at first glance seem out of proportion but will in many cases remain undetected if groups are not observed for multiple years. One of the limitations of my study was that within 24 years, only a small number of evictions was observed (29 events in four groups) which might explain why I was not able to relate evictions to consequences such as differences in life-time reproductive success. As only two evictions occurred during the sample period of behavioural and hormonal data, I could not explore the costs evictions might imply for the evicting females. To fully understand selective processes shaping specific mechanisms, it is however essential to explore both costs and benefits they might have on the individuals involved (Cain and Rosvall, 2014). Only when long-term data are available, we might be able to fully understand patterns of female competition.

My findings emphasise the limitations of current definitions of sexual selection. Current research still frequently uses Darwin's first definition of sexual selection as a consequence of intrasexual competition for mates (Darwin, 1859), even though a later definition by Darwin defines it as selection driven by advantages some individuals of the same sex might have over others in the context of reproduction (Darwin, 1871). This broader definition could include cases such as female evictions in redfronted lemurs, in which females compete for future reproduction. Alternatively, female evictions could be filed under the framework of social selection, which summarizes any kind of social competition resulting in increased survival or reproductive success.

My finding that female redfronted lemurs compete for future resources and the notion that this might be a frequent cause of competition in female mammals in general raises the question whether this is also a pattern relevant for competition in humans. Women might differ from men in their willingness to enter competition, depending on the nature of the longer-term benefits that are at stake as for example the duration of fixed-term contracts. To my knowledge, this hypothesis has not been tested yet, but might explain patterns of competition in women. In politics, for instance, term limits originally had been predicted to increase female representation in seats as they create more entry opportunities, but to the surprise of researchers resulted in a decrease in representation of women (Carroll and Jenkins, 2001; Bernstein and Chadha, 2003). Another example for this are career paths in academia. As most research positions for young researchers are limited to a few years, motivation to compete for them might be lower in women than in men. This is not at last related to female reproductive biology, as women who plan to have children might perceive the risk of financial insecurity associated with a potential dead end of the academic career path as much higher than men would (O'Brien, 2012). Short research positions might contribute to the so called phenomenon of the "leaky pipeline", the increasing gender gap at higher stages in academia. Continuing the study of female competition in mammals might spark new ideas on how to interpret and study the causes that lead to underrepresentation of women in several types of institutions.

While it is more common to compare male-male and female-female competition in human sociology, this is not common practice yet in animal studies. My results provide an example, why it can be important to consider all participants in social dynamics rather than investigating one sex in isolation. As general competition for group membership among all individuals is intense in redfronted lemurs, a previous study relating environmental and demographic circumstances to the likelihood of evictions found that group size but not the number of females predicted events of evictions (Kappeler and Fichtel, 2012). This paradox was resolved in my study when comparing the circumstances under which female evictions were more likely than male emigrations and disentangling competition among all group members from intrasexual competition. In addition, I showed that female evictions can even be buffered by male emigrations as both limit group size. As drivers of dispersal also differed between sexes, and males were less likely to leave groups if proportionally more females were available, this suggests the presence of a conflict between sexes which could be studied in the future. Linking male and female competition and describing which selective pressures are similar or differ between the sexes has received relatively little attention in the past but could improve the field and the perception of female competition.

Outlook

Although this dissertation has contributed new insights into drivers of evictions, some aspects remain unexplored and new questions have arisen. This concerns both studies in lemurs and on female competition in general. Regarding lemurs, in line with the energy frugality hypothesis explaining the lemur syndrome, I found that female evictions likely aim at avoiding future reproductive competition. However, this hypothesis is based on the unpredictability of food resources as the ultimate cause of lemur social organisation. While this cause seems logical, I did not find any indication of resource limitations affecting the occurrence of evictions or aggression in redfronted lemurs. The fact that individuals experienced increased glucocorticoid levels under a limitation of resources might be interpreted as a potential cause of increased competition. However, limited resource availability did not result in immediate changes in eviction behaviour. Moreover, the number of offspring in each cohort seems to be limited although infant survival did not seem to be related to available resources. Food limitation might therefore have led to evolutionary stable strategies that are detached from immediate shortages of resources. To explore this hypothesis, I propose to construct an evolutionary stable strategy model, similar to what has been tested in meerkats before, to explore the environmental conditions under which this mechanism could have evolved.

When exploring under which circumstances evictions will be adaptive, it is crucial to have knowledge about the costs evictions might have on evicting individuals. While in general, costs of competition are often left unexplored (Cain and Rosvall, 2014), our understanding of costs for actors related to evictions is particularly limited. In mongooses we know that actors are often wounded in the process and in some cases have lost their offspring. By continuously collecting behavioural and hormonal data along with physiological data such as body weight in redfronted lemurs, costs like increased likelihood of abortions or decreased maternal care could be explored in more depth. While I did not find an effect on the likelihood to bear an offspring in the year following an eviction, abortion rates related to evictions have not yet been explored. However, it is possible to detect pregnancies based on fecal samples in this species which could contribute to answering this question (Ostner and Heistermann, 2003). Beyond this, physiological measures such as body weight and glucocorticoid levels could be measured for the actors of evictions in behavioural observations.

The biggest remaining question however is, when and why we find this extreme form of competition between females in some species, but not in others. Although I have highlighted some patterns that are common to the species that exhibit evictions, this observation is qualitative and leaves questions open to speculation, as for instance the link between female dominance and the occurrence of evictions. In order to better understand under which circumstances female evictions evolved, it will be useful to compare species with female eviction to other group-living sympatric species. This could inspire more studies on the relationships between environmental circumstances, social organisation, and the types and mechanisms of female competition, links currently almost unexplored.

General Conclusions

My dissertation contributes to our understanding of the causes and consequences of female competition in general and female evictions in redfronted lemurs in particular. I describe one of the most extreme cases of female competition in mammals that contrasts with generally low aggression rates in this species and shows that patterns of competition in both sexes are likely to be linked to the unique conditions on Madagascar. It is an example in which female competition is mostly caused by competition for future reproduction and is based upon mechanisms that are probably triggered by demographic cues but not related to inclusive fitness. I have shown that to study female competition, it can be helpful to integrate and compare the same patterns in males to get a more complete picture and discern drivers of general competition from intrasexual competition.

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