

# Female reproductive competition in *Eulemur rufifrons*: eviction and reproductive restraint in a plurally breeding Malagasy primate

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## Abstract

In mammals with female philopatry, co-resident females inevitably compete with each other for resources or reproductive opportunities, thereby reducing the kin-selected benefits of altruism towards relatives. These counteracting forces of cooperation and competition among kin should be particularly pronounced in plurally breeding species with limited alternative breeding opportunities outside the natal group. However, little is still known about the costs of reproductive competition on females' fitness and the victims' potential counter-strategies. Here we summarize long-term behavioural, demographic and genetic data collected on a plurally breeding primate from Madagascar to illuminate mechanisms and effects of female reproductive competition, focusing on forcible eviction and potential reproductive restraint. The main results of our study indicate that females in groups of redfronted lemurs (*Eulemur rufifrons*) above a critical size suffer from competition from their close relatives: females in larger groups face an increased probability of not giving birth as well as a higher probability of being evicted, especially during the annual mating and birth seasons. Eviction is not predicted by the number of adult females, the number of close female relatives, female age or inter-annual variation in rainfall but only by total group size. Thus, eviction in this species is clearly linked with reproductive competition, it cannot be forestalled by reproductive restraint or having many relatives in the group, and it occurs in the absence of a clear dominance hierarchy. Our study therefore also underscores the notion that potential inclusive fitness benefits from living with relatives may have been generally over-rated and should not be taken for granted.

**Keywords:** altruism, competition, eviction, kinship, primates

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## Introduction

Kin selection theory and Hamilton's rule have played pivotal roles in explaining social behaviour in animals (Hamilton 1963). Accordingly, individuals should behave less competitively and more altruistically towards relatives than non-relatives because they share relatively many alleles that are identical by descent. By facilitating survival and or reproduction of relatives,

copies of these genes are more likely to be passed on to the next generation, thereby enhancing the indirect fitness of altruists. Limited dispersal from the natal group or area tends to increase average dyadic relatedness, and, hence, opportunities for altruism (Hamilton 1964; Perrin & Mazalov 2000; Dobson *et al.* 2012). However, co-resident relatives also compete with each other for resources or reproductive opportunities, thereby reducing the kin-selected benefits of altruism towards relatives (West *et al.* 2002). Whereas Hamilton's rule can be extended to allow for competition among relatives (West *et al.* 2002), empirically estimating the importance

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of competition among kin has turned out to be difficult, and quantitative assessments of these costs exist for only a few mammalian species, including dwarf mon-goose (*Helogale parvula*: Creel & Creel 1991), meerkat (*Suricata suricatta*: Clutton-Brock *et al.* 1999), African wild dog (*Lycaon pycus*: Creel & Creel 2002), striped mice (*Rhabdomys pumilio*: Schradin *et al.* 2010) and some callitrichid primates (reviewed in Silk 2007).

In most mammals, females are the philopatric sex (Greenwood 1980; Waser & Jones 1983). As a result, co-resident females are on average more closely related with each other than other dyads (Storz 1999; Ross 2001; Lukas *et al.* 2005). This pattern is found across mammalian lineages and social systems (e.g. de Ruiter & Geffen 1998; Kappeler *et al.* 2002; Cutrera *et al.* 2005; Dugdale *et al.* 2008; Apio *et al.* 2010; Pérez-España *et al.* 2010; Viblanc *et al.* 2010; Armitage *et al.* 2011; Kerth & van Schaik 2012). The predicted altruistic behaviour towards female relatives has also been documented in different taxa, for example in the form of cooperative and communal breeding, grooming or alarm-calling (e.g. Belding's ground squirrel: Sherman 1977; banded mongoose: Gilchrist *et al.* 2004; primates: Silk 2009; African wild dog: Spiering *et al.* 2010; yellow-bellied marmot: Armitage *et al.* 2011; spotted hyena: Holekamp *et al.* 2012). However, co-resident females also compete with each other for fitness-limiting resources, including mates (Silk 2007; Clutton-Brock 2009; Stockley & Bro-Jørgensen 2010). Female competition in solitary species is typically about access to a territory (Schradin *et al.* 2010), whereas females in group-living species compete for social rank (Sterck *et al.* 1997), which in turn regulates differential access to food and other resources that are important for reproduction. Reproductive success is indeed often rank-dependent under such a competitive regime in species with plural breeding females (e.g. Holekamp *et al.* 1996; Pusey *et al.* 1997; van Noordwijk & van Schaik 1999; Côté & Festa-Bianchet 2001).

Under some conditions, one dominant female prevents all or most other females from breeding, using a combination of behavioural and physiological mechanisms, such as interference with subordinate mating, aggression, reproductive suppression, eviction of rivals and infanticide (Hoogland 1985; Cant *et al.* 2001, 2010; Clutton-Brock 2002, 2007; Clutton-Brock *et al.* 2006; Gilchrist 2006; Kutsukake & Clutton-Brock 2006). Compared to birds, female mammals appear to be less able to prevent subordinate breeding (Raihani & Clutton-Brock 2010), but where it occurs, female age, aggressiveness, individual body condition and demographic factors play important roles in determining and maintaining dominant status (Kutsukake & Clutton-Brock 2006; Hodge *et al.* 2008). Because subordinate

females typically have poor prospects of breeding elsewhere, they can maximize their inclusive fitness by helping related dominants to rear their offspring (Clutton-Brock 2009). Thus, in cooperative breeders the most extreme form of female competition is associated with an extreme form of altruism (Jarvis 1981; Young *et al.* 2006).

The ultimate costs and benefits of female reproductive competition in the majority of mammals remain poorly understood, however (Silk 2007), partly because most reproductive skew models have only considered the relationship between a dominant and a single subordinate (but see e.g. Johnstone *et al.* 1999; Reeve & Emlen 2000). However, in the majority of group-living mammals, several females breed, and reproduction is distributed among multiple individuals (Packer *et al.* 2001; Silk 2007). Group size and kinship appear to be important determinants of reproductive skew in plural breeders without helpers, in particular. These two variables apparently have antagonistic effects because group size and the number of kin are not independent, but they affect reproductive skew through different behavioural mechanisms. On the one hand, there is a negative correlation between group size and female fitness because within-group feeding competition increases with group size (Koenig 2002) so that only dominant females enjoy better access to resources, which, in turn, translates into higher reproductive success (e.g. van Noordwijk & van Schaik 1999; review: Pusey *in press*). On the other hand, the presence of kin generally enhances female reproductive success (Silk 2007) because bonding and coalitionary support are much more pronounced and widespread among kin (Silk *et al.* 2003, 2010; Holekamp *et al.* 2012). However, additional analyses at the individual level are required to illuminate under which conditions dominants in plural breeders begin to suffer fitness costs from subordinate breeding (Clutton-Brock *et al.* 2010) and whether a given pattern of reproductive skew among multiple females is the result of concessions or the lack of control by the dominant (Clutton-Brock 1998; Cant *et al.* 2010). The threat of eviction and reproductive restraint are likely to be important variables in this context because external breeding options are minimal in species with female philopatry. Subordinates may therefore be forced to exercise reproductive restraint in order to avoid eviction by the dominant individual (Johnstone & Cant 1999). However, high relatedness and strong ecological constraints are predicted to increase the costs of eviction to the dominant, and, hence, to promote subordinate reproduction (Johnstone & Cant 1999).

Among mammals, the links between female sociality and fitness are relatively well studied in primates (Pusey *in press*) because their diverse social systems

have been subject to many behavioural studies. Among primates, obligate singular breeding with cooperative care of young is restricted to marmosets and tamarins (Abbott 1984; Saltzman *et al.* 2009). In these small New World primates, the dominant female gives birth to twins, which are carried by helpers that may or may not be related to the breeding female (Faulkes *et al.* 2003; Huck *et al.* 2005). Breeding attempts by subordinates are countered by the threat of female infanticide should reproductive suppression fail (Digby 2000; Saltzman *et al.* 2008). However, members of both sexes disperse (Pope 2000a), so that subordinate females can eventually pursue alternative breeding opportunities elsewhere.

Among Old World primates, groups of virtually all species contain multiple females, but variation in female dispersal differentially mitigates the costs of female competition. Variation in female dispersal is strongly related to the type of feeding competition (Sterck *et al.* 1997) and also exhibits a strong phylogenetic signal. There are, of course, exceptions within each of the two major lineages, but it is striking that in many colobines females compete primarily for access to a prime-aged male that provides protection from infanticide by other males, and females are free to disperse among groups (Steenbeek *et al.* 2000; Sterck & Korstjens 2000). Ranks are poorly differentiated, and female reproductive skew is low (Chapman & Pavelka 2005; Borries *et al.* 2008). In most cercopithecines, in contrast, females are strictly philopatric and develop rank hierarchies that are reinforced by coalitionary aggression among the multiple matriline of a group (Walters & Seyfarth 1987). In savannah baboons (*Papio cyanocephalus*), for example, 80% of all observed aggression is coalitionary and benefits close kin (Silk *et al.* 2004). Members of a matriline also form the strongest social bonds among each other, and the strength of social bonds is positively related to infant survival—and, hence, inclusive fitness (Silk *et al.* 2009). Because female dispersal is not an option and group fissioning is rare, members of subordinate matriline have to accept the costs of competition with dominants.

During the evolutionary history of primates, groups with multiple adult females not only evolved once among the ancestors of the Old and New World monkeys, but also twice independently among the primates of Madagascar—the Lemuriformes (Horvath *et al.* 2008; Perelman *et al.* 2011). Previous research has established that lemurs live in much smaller groups than same-sized Old and New World monkeys (Kappeler & Heymann 1991) and that the sexes do not differ in body size (Kappeler 1991) and that females exhibit masculinized genitals (Drea & Weil 2008) as well as social dominance over males (Jolly 1998). Moreover, coalitionary aggression among lemur females is virtually absent (Pereira & Kap-

peler 1997; but see Roeder *et al.* 2002), social ranks are neither stable nor inherited matrilineally (Pereira 1995; Kappeler 1999) and female dispersal is common in some species (Erhart & Overdorff 2008a; Morelli *et al.* 2009; Kappeler & Fichtel 2011), despite a general male bias in dispersal. However, females of a group are all closely related with each other (Wimmer *et al.* 2002; Lawler *et al.* 2003), and some affiliative behaviour is biased towards kin (Kappeler 1993a; Sbeglia *et al.* 2010). In captive groups, reproduction is not restricted to a single female (Kappeler 1989), but in some members of the Lemuridae, relatives are nevertheless episodically targeted for sudden aggression and evicted from their groups (Foerg 1982; Vick & Pereira 1989; Gresse *et al.* 1994), and female infanticide has been observed in the wild (Jolly *et al.* 2000). These observations indicate that female competition might be a salient feature of lemur sociality, and that the fine balance between altruism and competition might be fruitfully studied in this group of primates.

Despite several long-term field studies of group-living members of the genera *Lemur*, *Eulemur* and *Propithecus*, the mechanisms and consequences of female competition have not yet been comprehensively investigated in any wild lemur population. Here, we combine demographic and genetic data from a 15-year study of red-fronted lemurs (*Eulemur rufifrons*) to illuminate two aspects of female competition: reproductive restraint and forcible eviction. Redfronted lemurs occur in central western and in southeastern Madagascar, where they live in groups of 5–15 individuals, including multiple adult males and females. Reproduction is highly seasonal, with females producing single infants once a year, after reaching sexual maturity at 2–4 years (Overdorff *et al.* 1999; Ostner & Kappeler 2004). An average of two females reproduced annually in each group, with body size and age influencing reproductive success (Overdorff *et al.* 1999). Newborn individuals of this sexually monomorphic, but sexually dichromatic species initially exhibit the male phenotype and female infants change into the female phenotype around weaning at 3–4 months, suggesting the presence of unique selection on vulnerable female infants (Barthold *et al.* 2009). However, a potential sex difference in infant mortality has not been examined yet. Mating is promiscuous, but male reproductive success is skewed towards one socially powerful male (Kappeler & Port 2008). Redfronted lemurs exhibit high levels of social tolerance and dominance relations are weakly pronounced, but one individual of each sex may be agonistically particularly powerful (Pereira & Kappeler 1997; Ostner & Kappeler 1999). Males disperse voluntarily from their natal group upon reaching sexual maturity and may transfer several more times thereafter (Ostner & Kappeler 2004), but voluntary female dispersal has

not been observed in this species (Pereira & Kappeler 1997; Overdorff *et al.* 1999; Erhart & Overdorff 2008a), and the fate of evicted females remains unstudied. The observation that all female members of a group were related (Wimmer & Kappeler 2002) indicated that evicted females may only rarely join other groups.

Female redfronted lemurs do not interfere with matings of other females and contest competition over food is rare (Pereira & Kappeler 1997; Pereira & McGlynn 1997). Because female infanticide has only rarely been observed (Jolly *et al.* 2000), forcible eviction following sudden bursts of targeted aggression (Vick & Pereira 1989) may therefore be the most effective mechanism for females to reduce competition with other females in the absence of a dominance hierarchy. Because there are no clear rank differences among females, other variables may predict the identity of victims of eviction. Females rarely intervene on behalf of victims of aggression, but the presence of many close kin may thwart the risk of eviction. In addition, females may respond to a threat of eviction by exercising reproductive restraint (cf. Cant *et al.* 2010).

The specific aims of this study were, therefore, to analyse all cases of female eviction in a study population at Kirindy forest, where individuals from several groups have been studied continuously since 1996. Based on the above, we examined evidence for reproductive restraint by identifying factors that predict a failure of adult females to reproduce. To this end, we determined the degree of pre-natal deviation from the maximum reproductive rate as well as post-natal infant survival rates and related them to various potentially explanatory variables. We also tested the predictions that (i) forcible evictions are more likely to occur at a particular group size, (ii) forcible evictions are more likely to occur at a particular female group size, (iii) females with less potential kin support are particularly vulnerable to being forcibly evicted, and (iv) evictions are more likely in ecologically challenging years. The last prediction is based on the established relationship between inter-annual variation in rainfall and primate food availability (van Schaik *et al.* 1993), which translates into varying intensities of food competition (Koenig 2002). With this study, we therefore hope to contribute comparative data on the mechanisms and consequences of female competition in a plurally breeding species without communal infant care.

## Materials and methods

### Study site and population

Kirindy forest is located in central western Madagascar, about 60 km northeast of Morondava. The German Pri-

mate Center has operated a field research station in this dry deciduous forest since 1993 (Kappeler & Fichtel 2011). The area is characterized by pronounced seasonality, with virtually all of the about 900 mm annual precipitation falling between November and March. Beginning in 1996, all members of a local population of redfronted lemurs (*E. rufifrons*, inhabiting a c. 70 ha local study site along the Kirindy river have been regularly captured, marked with individual nylon or radio collars and subjected to regular censuses and behavioural observations (e.g. Ostner & Kappeler 1999, 2004; Fichtel & Kappeler 2002; Wimmer & Kappeler 2002; Port *et al.* 2009; Clough *et al.* 2010). Small ear biopsies from captured and anaesthetized animals have been used to extract DNA for subsequent genetic paternity and pedigree analyses, using mtDNA haplotypes and variation at 11 microsatellite loci (methods described in Wimmer & Kappeler 2002; Kappeler & Port 2008). Pairwise relatedness coefficients were calculated with RELAT-EDNESS 5.0.8 based on a method of Queller & Goodnight (1989). Maternity and matrilineal relationships for all infants born after 1995 were inferred from observed births.

Malagasy field assistants have documented all births, deaths, immigrations and disappearances in five study groups (A, B, B2, F and J) to within a few days because all groups are being censused several times a week. Females mate repeatedly with several resident adult males during a brief seasonal oestrus in May/June and give birth to a single infant 4 months later (Kappeler & Port 2008). Infants are carried exclusively by their mother for the first 12 weeks following birth (Barthold *et al.* 2009). Because matings occur early in the dry season, we considered the previous rainy season as potentially ecologically relevant determinant of female lemurs' reproductive decisions. We calculated the cumulative rainfall during the preceding wet season for each annual reproductive cycle as a broad predictor of food availability because within years, rainfall is the best predictor of food tree phenology at Kirindy (Sorg & Rohner 1996; see also Lawler *et al.* 2009). We estimated food availability indirectly because phenology data are not available for all years of the study.

The major cause of death in this population is predation. Kirindy forest harbours an intact local predator community, of which Madagascar's largest carnivore, the fossa (*Cryptoprocta ferox*), is the most important member from a redfronted lemur perspective (Rasoloarison *et al.* 1995; Fichtel & Kappeler 2002). Following fossa predation, parts of the body or collars can typically be found within the study area. Other causes of death appear to be rare, as we only discovered one dead animal that was not preyed upon in 15 years. Male infanticide has not been observed, although it



appears to present a latent threat (Ostner & Kappeler 2004; Ostner *et al.* 2008). Female infanticide has never been observed or suspected as a cause of death of young infants, but we found one young infant that was bitten to death by an unknown conspecific.

Most changes in group composition are the result of female eviction and male transfer. Male immigration is often in the form of aggressive take-overs, in most cases by pairs of males (Ostner & Kappeler 2004), which, in turn, typically trigger emigration of previous resident males. Voluntary female dispersal has never been observed; female emigration is always preceded by sudden bursts of unusually extreme aggression (see Vick & Pereira 1989). In cases where individuals disappeared suddenly and no signs of predation were discovered, we distinguished between disappeared and evicted females. Individuals that were never seen again (i.e. that were either killed or emigrated) were classified as 'disappeared'. Chances of re-sighting long-distance emigrants are high because redfronted lemur groups living within several kilometres of the study area come to the only available dry season water holes along the Kirindy river bed, which are located within the study area, during the latter part of the annual dry season (Scholz & Kappeler 2004). Because disappeared females could have been evicted without us noticing the preceding aggression, or they could have been preyed upon without us finding any remains, we included all disappeared females in one set of analyses, assuming that most of them were evicted. For a second set of analyses, we made the more conservative assumption that only females that were seen at least once alive following their disappearance from their natal group were 'evicted'. A third category ('residents') comprised all females that remained and bred in their natal group.

#### *Dependent and independent variables*

For the present analyses, we determined the identity and number of all resident males and females of all age classes (infants: <1 year; juveniles: <2.5 years; adults: >2.5 years) at the end of April of each year when all surviving infants born in the previous year were old enough to be captured for the first time. For repeated sampling of group demography we considered 12 months (i.e. a group year) to be a sufficiently long period for group composition to change. For each disappearance or eviction, we determined the group composition on the day the victims were last seen in the group. From our demographic records, we extracted the month of the eviction, the age of the victim at the time, the number of resident adult females at the time, the number of female maternal relatives (combining categories of kin with  $r = 0.5$  and  $0.25$ ; for females born before

the onset of the study,  $r$  was not always known), total group size, the number of offspring per group born in the current year and the number of infants surviving to independence (>3 months) that year. To test the possibility that females may evade eviction by exhibiting reproductive restraint, we determined for every year the number of potentially reproductive females (i.e. those that were  $\geq 30$  months during the mating season) as well as the number of females actually giving birth.

#### *Analyses of competition and eviction*

To investigate whether females were less likely to breed as the number of females of reproductive age increased, we conducted a GLMM which fitted as binomial response term whether or not each female in the group gave birth during the current breeding attempt. As fixed factors, we included the number of adult females, female age, group size and cumulative rainfall during the corresponding rainy season to control for seasonal variation. Female identity and group identity were included as random factors to control for territory quality. We investigated the influence of the number of adult females on offspring survival, using the proportion of infants surviving to 3 months in a given year as the response term in a GLMM with binomial errors (Crawley 2007). Group size and the cumulative rainfall of the corresponding rainy season were used as fixed factors, and group identity was used as random factor. To investigate the circumstances of an eviction event, we fitted the occurrence of eviction during 53 breeding attempts (total number of adult females observed during a breeding season across the study) in five groups as the binomial response term in a GLMM. Number of adult females, female age, number of offspring born in a given cohort, group size and rainfall were used as fixed factors; female and group identity were again used as random factor. We calculated two models for this analysis: one including all females that disappeared and one including only confirmed evictions. Finally, to characterize evicted females we used the number of adult females in their group, the number of dyadic relationships with close female relatives (i.e. mother, daughters, sisters, grandmother, granddaughter), female age, total group size, number of offspring in the current cohort and rainfall as fixed factors; female identity and group identity were used as random factor.

Generalized linear mixed models using a logit link function were fitted using the R software (R Development Core Team, Vienna, Austria 2010) with the lme4 package (Zuur *et al.* 2009). We entered all predictor variables simultaneously because stepwise procedures lead to inflated Type I error rates (Mundry & Nunn 2009). We used maximum likelihood ratio tests to test

the full model with fixed factors against the null model including only the intercept and random factors (Faraway 2006).

## Results

### *Do females experience reproductive competition?*

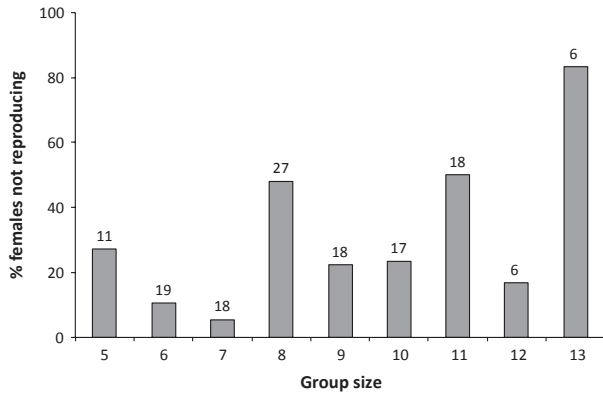
The number of adult females per group varied between 1 and 4 ( $2 \pm 1$ ; mean  $\pm$  SD) across 62 group years. Mean age at first reproduction was 36 months ( $\pm 12$ ; range: 18–54;  $N = 12$ ). Not every adult female reproduced every year, however: on average only  $68 \pm 2\%$  ( $N = 15$  years; range 0–100%) of adult females per group gave birth. In 2005 and 2010, not a single one of 7 and 13 females in the population, respectively, gave birth, but across years birth rate and rainfall were not correlated (Spearman  $r = 0.078$ ,  $N = 15$ ,

NS). Thus, the full reproductive potential was not exploited, suggesting the existence of pre-natal competition, and some years appeared so unfavourable that no one reproduced. The probability that a female did not reproduce was not influenced by the number of adult females, female age or rainfall, but by total group size (Table 1 'Reproductive restraint'; GLMM:  $\chi^2 = 11.49$ ;  $P = 0.022$ ). Thus, females in larger groups were less likely to reproduce than females in smaller groups (Fig. 1).

Competition may also act post-natally by compromising survival of those infants that were born. To test this possibility, we examined whether the number of adult females in a group had an influence on offspring survival (to 3 months). However, offspring survival was neither influenced by the number of adult females, nor by group size or rainfall (Table 1 'Reproductive competition'; GLMM:  $\chi^2 = 0.46$ ;  $P = 0.926$ ).

**Table 1** Parameter estimates for the GLMM

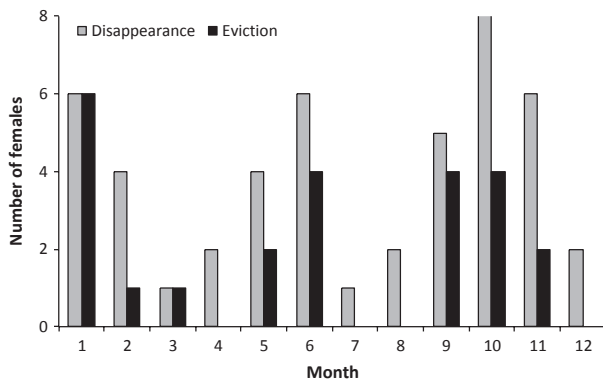
Model	Response variable	Random factors	Fixed factors	Estimate	SE	P-Value
Reproductive restraint	female has given birth ('yes' or 'no' for each individual in each group)	ID nested in group identity	Intercept	4.59	1.26	<0.001
			Number of adult females	-0.42	0.37	0.26
			Female age	0.003	0.005	0.52
			Group size	-0.25	0.1	0.01*
			Rainfall	-0.001	0.0007	0.13
Reproductive competition	Offspring survival (proportion of infants)	Group identity	Intercept	0.04	0.96	0.97
			Number of adult females	0.18	0.29	0.55
			Group size	-0.02	0.08	0.78
			Rainfall	-0.001	0.001	0.71
			Intercept	-7.03	1.45	<0.000
Disappearance All females	Disappearance ('yes' or 'no' for each individual in each group)	ID nested in group identity	Number of adult females	0.26	0.4	0.51
			Female age	-0.01	0.005	0.02
			Number of born offspring in a cohort	0.12	0.2	0.58
			Group size	0.48	0.11	<0.000
			Rainfall	0.001	0.001	0.08
Eviction Confirmed events	Eviction ('yes' or 'no' for each individual in each group)	ID nested in group identity	Intercept	-12.14	2.66	<0.001
			Number of adult females	-0.12	0.66	0.85
			Female age	-0.006	0.007	0.39
			Number of born offspring in a cohort	0.11	0.32	0.73
			Group size	0.89	0.21	<0.001
Factors predicting the target of an eviction	Eviction ('yes' or 'no' (for each individual in each group)	ID nested in group	Rainfall	0.002	0.001	0.1
			Intercept	-13.12	2.93	<0.001
			Number of adult females	-0.19	0.69	0.79
			Number of females ( $r = 0.5$ )	0.43	0.53	0.42
			Number of females ( $r = 0.25$ )	0.11	0.67	0.87
			Number of born offspring in a cohort	0.09	0.33	0.79
			Females age	-0.006	0.008	0.41
			Group size	0.94	0.24	0.001
			Rainfall	0.003	0.002	0.1



**Fig. 1** Results of a GLMM exploring determinants of reproductive constraint. The probability of not giving birth was associated with a significantly higher mean group size, here depicted as the proportion of adult females not reproducing while living in a group with a particular size. For each group size, the number of group years contributing to this analysis is shown.

#### *Which factors influence female evictions?*

We documented a total of 47 female disappearances over 62 group years in the five study groups. Females disappeared mainly during the mating season, during the birth season and at the time of infant weaning (Fig. 2). The probability that a female disappeared was neither influenced by the number of co-resident adult females in a group, nor by the number of offspring born that year, but rather predicted by her age and total group size (Table 1 'Disappearance all females'; GLMM:  $\chi^2 = 33.31$ ;  $P < 0.001$ ). Specifically, younger females disappeared more often than older females,

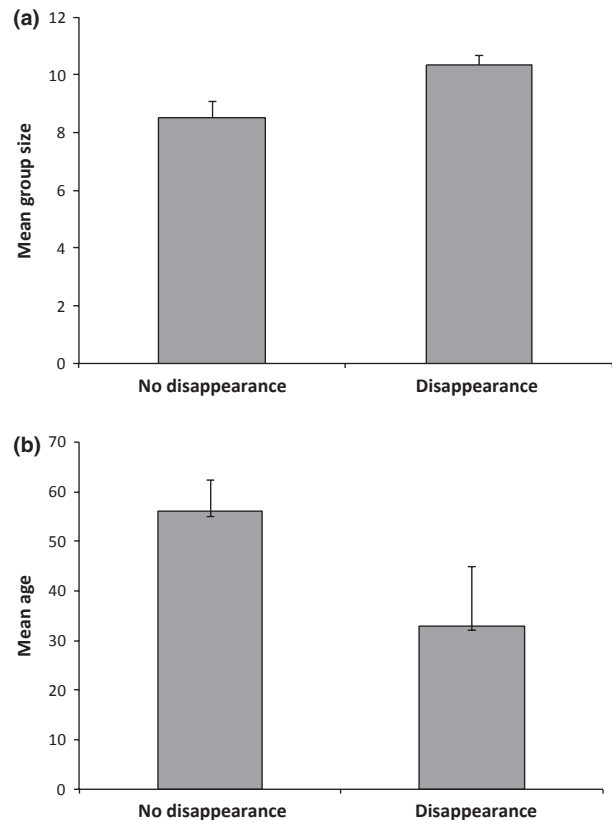


**Fig. 2** Distribution of female disappearances and evictions across the year. Mating takes place in May/June; gestation lasts from June to October; births take place in September/October, and lactation lasts from October to January. Disappeared females include all evicted ones plus all those that were never seen again after leaving their natal group.

and females from larger groups disappeared more often than females from smaller groups (Fig. 3a, b).

Focusing on the 24 confirmed evictions of 22 females (one female was evicted three times), an almost identical pattern emerged. Evictions peaked at the same periods of the annual reproductive cycle as all disappearances (Fig. 2). The probability that a female was evicted was also not influenced by the number of adult females in a group, female age, the number of offspring born or by rainfall, but only by total group size (Table 1 'Eviction confirmed events'; GLMM:  $\chi^2 = 35.48$ ;  $P < 0.001$ ). Thus, females were more likely to be evicted when groups were larger (Fig. 4). In contrast to disappearances, evictions occurred independent of female age (Table 1).

Neither the number of adult females, nor the victim's age, number of offspring born that year or the number of close relatives of evicted females within a group predicted the probability of eviction. Instead, group size emerged again as the only significant factor (Table 1 'Factors predicting the target of an eviction'; GLMM:



**Fig. 3** The probability of female disappearance was predicted by group size and age. (a) The number of disappearances was higher in larger groups (mean  $\pm$  95% CI). (b) Females that disappeared were on average significantly younger than the females in their group that did not disappear.

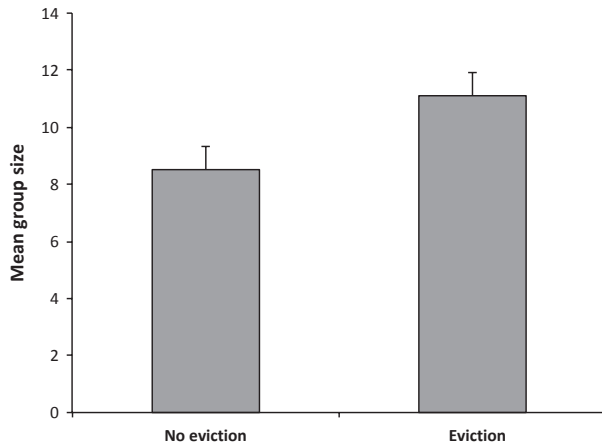


Fig. 4 The probability of female eviction was only predicted by group size. Groups from which females were evicted were on average larger (mean  $\pm$  95% CI).

$\chi^2 = 36.11$ ;  $P < 0.001$ ). Thus, females were more likely to be evicted when groups were larger, independent of the number of potential kin allies in their group.

Evicted females had poor breeding prospects outside their natal group. Of 22 evicted females, only two returned to her natal group and also reproduced there (one of them was actually evicted three times and returned every time). Seven females were only sighted alone, and they all disappeared from the study area within weeks of the eviction. Another five females were seen with other evicted females, but never with males, before they also disappeared from the study area. One evicted mother and her daughter (two cases) and one evicted mother with two of her daughters successfully attracted adult males; in two out of these three cases they established a new group (including B2 in this study) in the vicinity of the study area. Only one female was seen with a group of unmarked individuals into which she apparently successfully immigrated.

## Discussion

The main results of our study indicate that females in groups of redfronted lemurs above a critical size suffer from competition from their close relatives. Whenever group size exceeds a critical value (of about 10 individuals in this population), females face a reduced probability of giving birth and an increased risk of being evicted from their natal group by their close relatives during the annual mating and birth seasons. Thus, group size acts to limit female reproductive potential both before and after birth, but we are presently unable to determine whether the pre-natal reduction of reproductive rate is the result of restraint or suppression. We therefore focus our discussion on the determinants of group size and composition.

Lemur groups are distinguished from groups of anthropoid primates by two main features: their small size and unusual sex ratio. First, even after controlling for their relatively small body size, which is positively correlated with group size across primates (Clutton-Brock & Harvey 1977), lemur groups are on average smaller (Kappeler & Heymann 1996). This observation has been linked to unique aspects of the ecology of Madagascar. Specifically, it has been suggested that Madagascar is characterized by having smaller feeding trees, relatively low habitat productivity and relatively high climatic unpredictability, compared to habitats of most anthropoid primates (Kay *et al.* 1997; Ganzhorn 1999; Wright 1999; Dewar & Richard 2007). These ecological constraints, presumably mediated by limited food availability during the pronounced lean season, may therefore place a relatively low upper ecological limit on total group size, independent of possible dietary specialization.

The results of this study also indicated that inter-annual variation in food availability does not result in any flexibility in reproductive rates and group size because neither birth nor eviction rates were correlated with current rainfall. While it is clearly desirable to use a more direct measure of food availability, there was also no systematic variation among the five study groups, which experience minor variation in habitat quality and in access to water during the dry season, supporting the notion that social factors act as more immediate constraints on group size than ecological factors. Feeding experiments in captivity suggested a more flexible reproductive strategy because a change from *ad libitum* food to a more restricted diet essentially eliminated twinning in ringtailed lemurs (*Lemur catta*: Pereira & Izard 1989). The complete failure of all females in the study population to reproduce in 2 years, despite observed matings, is also puzzling in this respect, because these were not years with exceptional rainfall, and all females responded in the same way. Thus, some other ecological signal may interact with food availability to affect reproductive decisions. Such population-wide reproductive failure (or anticipation of past years) has also been observed in another redfronted lemur population (Erhart & Overdorff 2008b) as well as in other mammals (e.g. Boutin *et al.* 2006; Ruf *et al.* 2006; White 2007), but more detailed studies of lemur feeding ecologies will be required to unravel the underlying chain of proximate mechanisms triggering these events.

Redfronted lemur group size appears to be controlled within very narrow margins, as indicated by the observation that eviction rates increased with group size. Similarly, in a population of Verreaux's sifakas (*Propithecus verreauxi*) at Kirindy, adult female



group size is 1 or 2. Even in groups containing two females, average individual reproductive success is compromised, and in rare groups with three or four females, reproduction is even further suppressed (Kappeler & Fichtel 2011). Similarly, in ringtailed lemurs, which form the largest groups among lemurs with about 15 members, female stress levels, as measured in faecal glucocorticoid levels, are related to group size in an inverted U-shape (Pride 2005). Females in very small and in large groups experience higher stress levels, and their reduced birth and infant survival rates mirror this pattern (Takahata *et al.* 2006). Thus, also other lemur species appear to experience a narrowly defined optimal group size.

Second, lemur groups exhibit on average even adult sex ratios, with a pronounced trend towards a slight surplus of males (Kappeler 2000). The number of males (and juveniles) is apparently factored into female reproductive decisions, because neither birth nor eviction rates were influenced by the number of adult females alone. This observation raises the question why lemur groups have such an unusually large number of males, and, ultimately, how group composition is controlled (Kappeler *et al.* 2009). The relatively large number of lemur males is puzzling from the perspective of male reproductive competition, and several previous studies have focused on that aspect (Pochron & Wright 2003; Kappeler & Sch  ffler 2008). Previous studies of red-fronted lemurs and modelling of their demography suggested that the tolerance of additional subordinate males may significantly reduce the probability of group take-overs by outside males (Ostner & Kappeler 2004; Port *et al.* 2010).

This benefit of the presence of multiple males may be significant for females as well because it reduces the risk of potentially infanticidal take-overs, which is apparently bigger than the costs of evicting female relatives. Thus, the costs of evicting female relatives, which includes foregoing potential inclusive fitness benefits, are either relatively small, or the benefits of tolerating several unrelated males instead are relatively high. As males appear to contribute few other benefits to group augmentation, e.g. in the form of important participation in inter-group defence or anti-predator vigilance (Nunn & Deaner 2004; Kappeler *et al.* 2009), the risk of infanticide may be particularly high in this lineage, despite widespread seasonal reproduction. If this was true, females without infants may pose an infanticide risk as well (see Jolly *et al.* 2000), possibly explaining their evictions during the birth season.

Groups of redfronted lemurs contain a small number of females that are all members of the same matriline (Wimmer & Kappeler 2002). However, female redfronted lemurs were not buffered from the adverse effects of

eviction by having many close relatives in the group. The lack of coalitionary support in polyadic agonistic interactions and low rates of reconciliation following conflicts (Kappeler 1993b) is in contrast to many anthropoids and underscores the interpretation that individuals pursue individualistic fitness maximizing strategies that largely ignore potential inclusive fitness benefits. Experiments with captive ringtailed lemurs also revealed extreme intolerance among unrelated females because members of one matriline invariably evicted all members of another, experimentally added matriline (Pereira & Izard 1989). Moreover, females that were evicted from captive *Lemur* or *Eulemur* groups were not allowed to return (Vick & Pereira 1989). During the 62 group years of our study, only two evicted female returned to their natal group and continued to breed there. This observation provides an interesting contrast with meerkats and banded mongooses, where many evictions are only temporary and the victims return to their natal group after the dominant has given birth (Cant *et al.* 2001, 2010; Kutsukake & Clutton-Brock 2006).

The costs of evictions appear to accrue primarily to the victims because we have no records of injuries in those females that carry out the eviction. Furthermore, only a fraction of evicted redfronted lemur females were subsequently able to establish themselves in the study area by attracting adult males. These new groups were relatively small, and most of them disappeared from the study area altogether after 1 or 2 years (see also Ostner & Kappeler 2004). This cost of eviction also suggests an interesting contrast between the members of the two lemur families in which group-living evolved independently. In the group-living members of the genera *Lemur* and *Eulemur* (Lemuridae) female philopatry constrains alternative breeding opportunities elsewhere. Eviction is therefore the main mechanism of regulating group size. In members of the genus *Propithecus* (Indridae), however, females are much less constrained by philopatry. Multiple dispersals, formation of new groups and successful reproduction by adult females in several different groups have been documented in at least two species (*P. diadema*: Morelli *et al.* 2009; *P. verreauxi*: Kappeler & Fichtel 2011). It is thus tempting to speculate that the members of these two lineages independently evolved different solutions to the problem of female competition, with the '*Propithecus* solution' having striking similarities with the pattern of female dispersal found among many colobines and howler monkeys (Pope 1992, 2000b; Sterck & Korstjens 2000), whereas the '(Eu-)Lemur' solution based on evictions is apparently unique among primates.

The present study is also interesting for future attempts to model the determinants of reproductive

skew because eviction occurs in the absence of a clear dominance hierarchy. Thus, differences in agonistic rank cannot be reliably used to characterize dyadic female relationships in redfronted lemurs. Reproductive concessions and restraint are therefore of limited use for analysing individual strategies. Instead, reduced birth rates and eviction were not independent, as both were dependent on group size, and reproductive restraint (or suppression) was not effective in preventing later eviction (see also Cant *et al.* 2010). Moreover, as in banded mongooses, this constellation of female competition raises interesting questions about optimal individual strategies among multiple players, because a coordination problem similar to the prisoner's dilemma arises among several potential victims of eviction about whether or not to exhibit reproductive restraint, independent of others' decisions (Johnstone & Cant 1999; Cant *et al.* 2010). If reduced birth rates are instead mediated by reproductive suppression, it will be interesting to identify not only the proximate mechanisms underlying this effect, but also the rules structuring it in a rather egalitarian species.

Female competition has been recognized as a pervasive force in mammalian societies (Sterck *et al.* 1997; Clutton-Brock 2007, 2009; Silk 2007). The combination of behavioural (e.g. female dominance), morphological (e.g. lack of sexual dimorphism; genital masculinization) and demographic (small groups with even sex ratios) traits of lemurs suggest that this so-called lemur syndrome may ultimately reflect a set of adaptations to female competition. Lemur females appear to have evolved adaptations to deal with chronic stress in order to secure individual reproduction and survival in small social groups, where potential inclusive fitness benefits are discounted by other selective forces. Similar studies of other lemur species may therefore contribute to a broadening of our understanding of the mechanisms and consequences of competition among kin in species with plural breeders.

General conclusions emerging from this study indicate that even in the absence of clear-cut dominance relations, particular individuals can be evicted from a group. Moreover, potential inclusive fitness benefits from living with relatives may have been generally over-rated because mechanisms invoking substantial fitness costs arising from competition with kin can be firmly established in the behavioural repertoire of a species that lives in tightly knit kin groups. Furthermore, models dealing with competition among multiple players are needed to better predict the reproductive strategies in plurally breeding species. Finally, female competition may take on such dimensions that, over evolutionary times, a whole suite of co-evolved adaptations arises.

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## Data accessibility

Data are available in the Dryad database, doi:10.5061/dryad.5t689.