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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

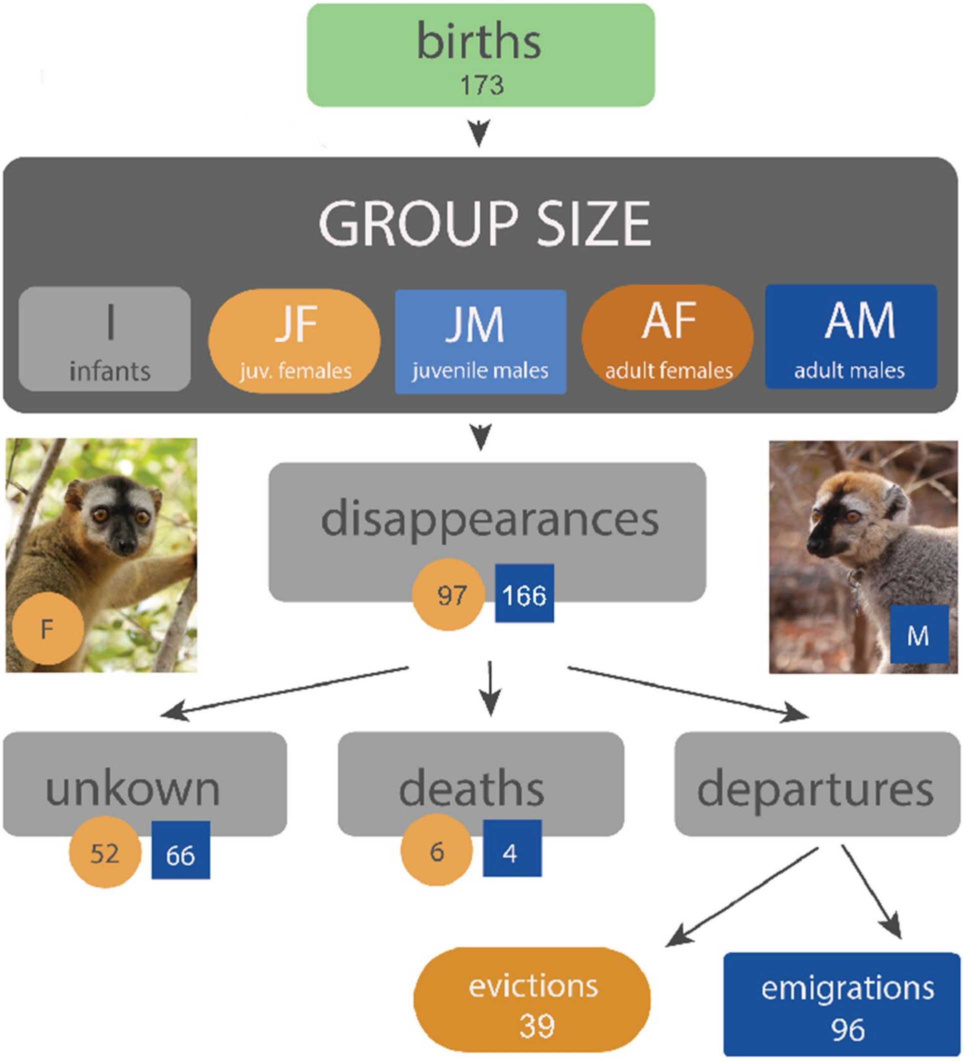

Fig. 1 Summary of redfronted lemur demography. Frequencies of births, deaths, evictions, and emigrations observed in four study groups over 24 years are depicted. Evictions and emigrations are combined into departures and refer to events in which an individual (females: orange; males: blue) was seen 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 = female, 0 = 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 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

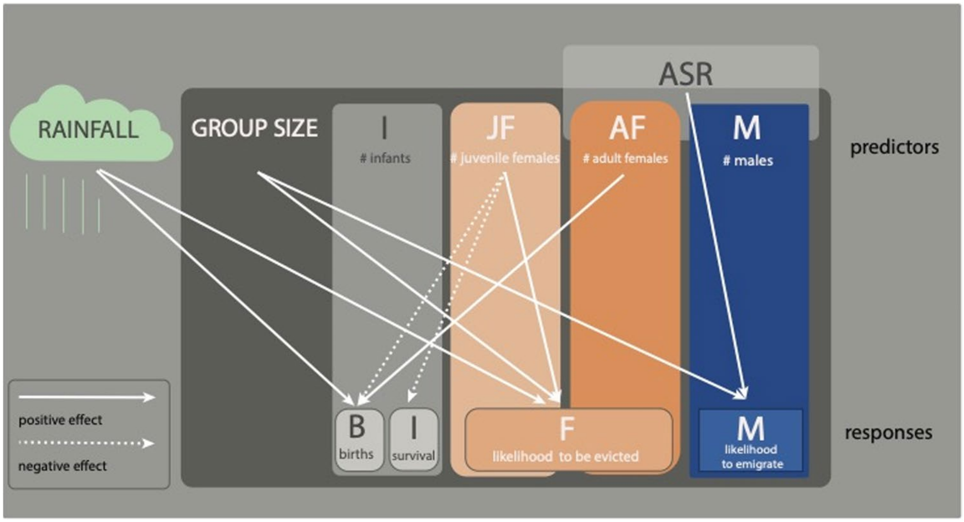

Fig. 2 Overview of positive and negative significant effects of predictors on responses of models 1, 2, 3, 6, and 7. Dashed arrows represent negative effects on responses; non-dashed arrows represent positive effects. We only included results of the main models, omitting results of multi-model inference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

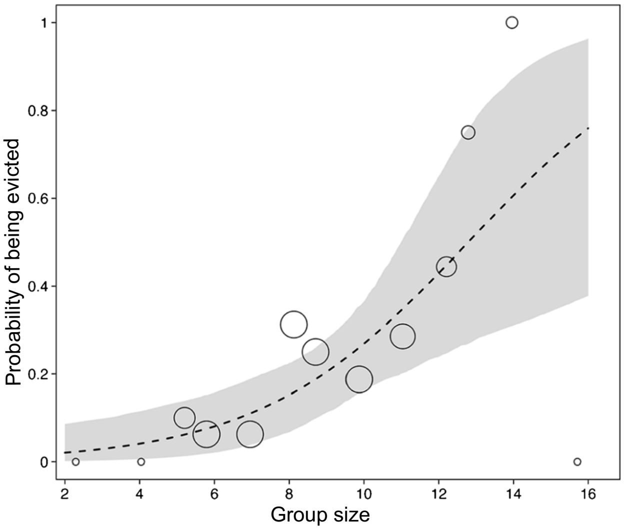

Fig. 4 Probability of female eviction as a function of group size. Dashed line indicates the regression line and polygons the 95% confidence intervals. Point size is relative to number of observations

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).

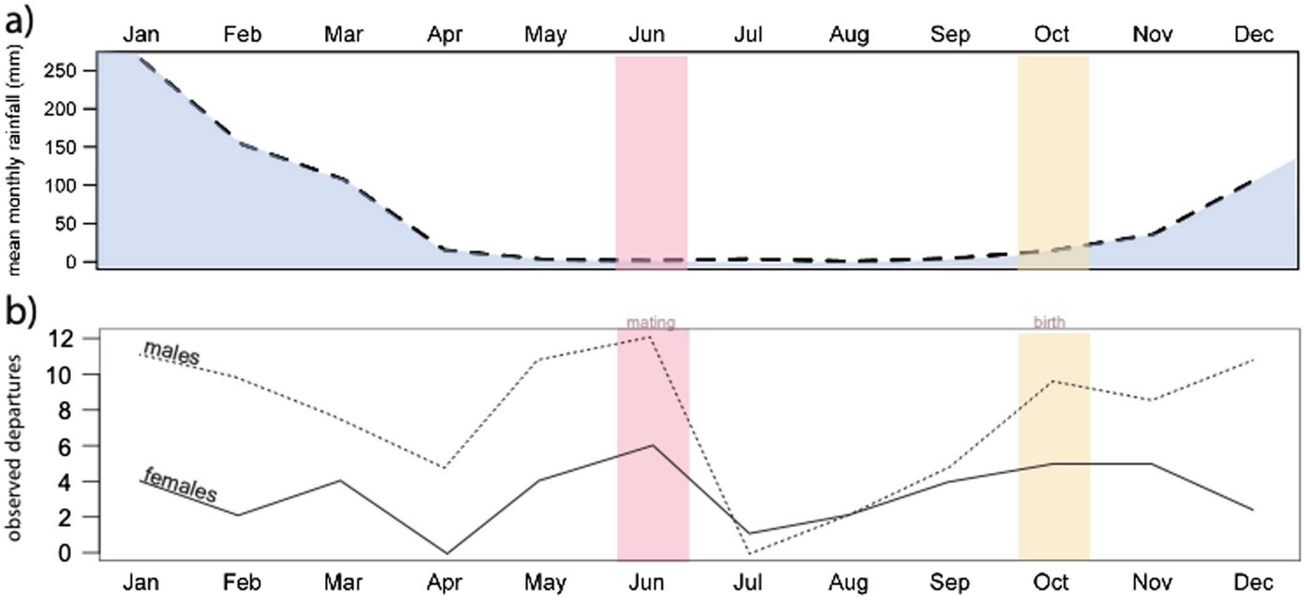

Fig. 3 Annual distribution of rainfall and group departures across the calendar year. a) Average mean monthly rainfall, b) Total number of observed evictions and emigrations in males and females. The timing of the annual mating season is indicated by red bars and the timing of the annual birth season 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)	$\chi^2 = 8.79$,	Intercept	−2.78	1.97	−7.30	1.27	[a]
	df = 2,	Rainfall[b]	**0.52**	0.26	0.06	1.20	**0.049**
	$P = 0.032$	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)	$\chi^2 = 27.97$,	Intercept	−0.39	0.17	−0.75	−0.08	[a]
	df = 3,	Rainfall[b]	0.17	0.17	−0.17	0.52	0.333
	$P < 0.001$	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)	$\chi^2 = 35.56$,	Intercept	−1.40	0.29	−2.55	−0.99	[a]
	df = 3,	Juvenile females[b]	**1.26**	0.27	0.85	2.34	**< 0.001**
	$P < 0.001$	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)	$\chi^2 = 1.12$,	Intercept	−1.06	0.45	−2.38	−0.29	[a]
	df = 2,	Female age[b]	−0.25	0.36	−1.22	0.49	0.492
	$P = 0.553$	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).

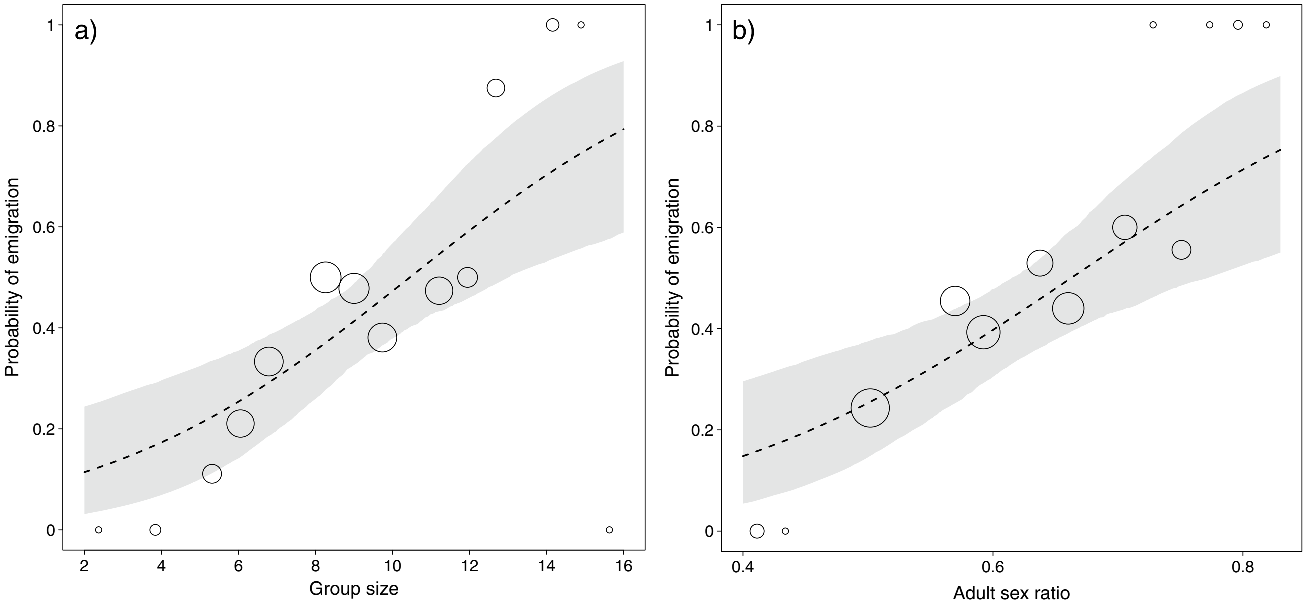

Fig. 5 Probability of male emigration as a function of a) group size and b) adult sex ratio**.** Dashed lines indicate the regression lines and polygons the 95% confidence intervals. Point size is relative to number of observations

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.

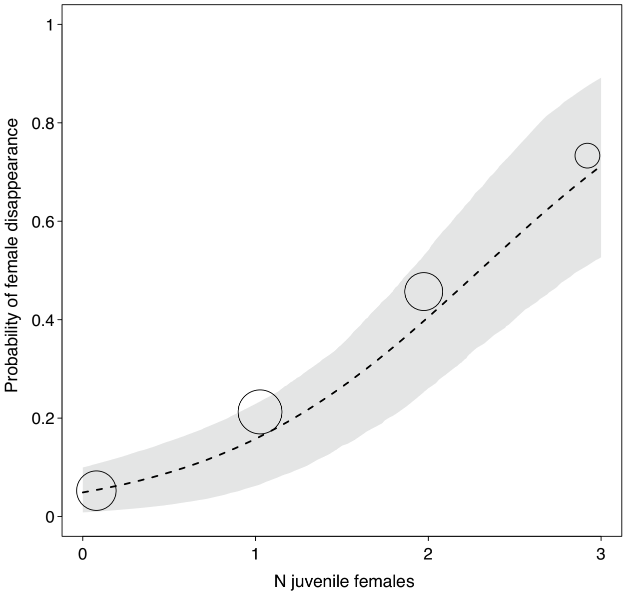

Fig. 6 Probability of the sex of the departing individual to be female as a function of the number of juvenile females. Dashed lines indicate the regression lines and polygons the 95% confidence intervals. Point size is relative to number of observations

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

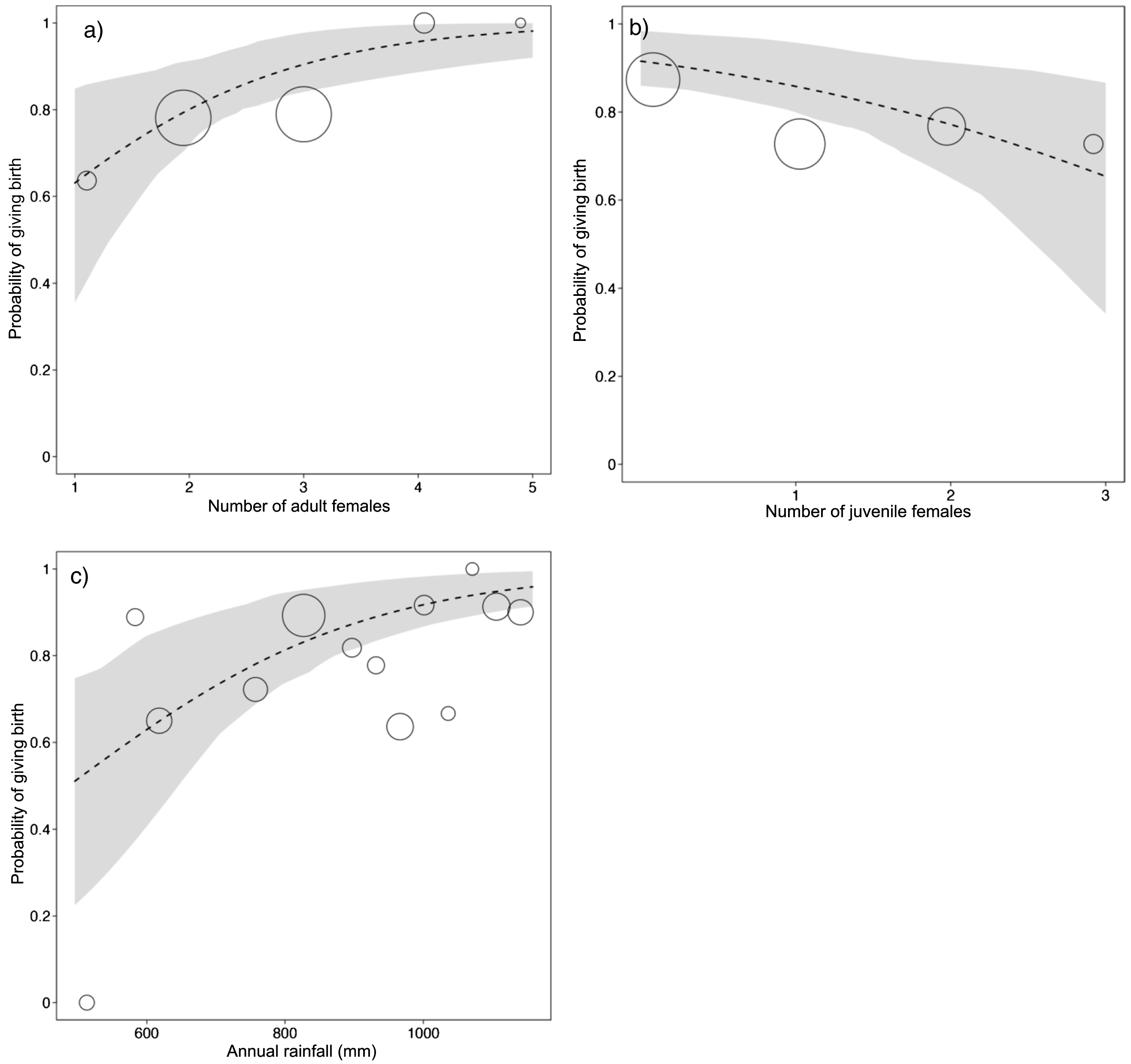

Fig. 7 Probability for any adult female to give birth as a function of a) the number of adult and b) juvenile females as well as c) annual rainfall. Dashed lines indicate the regression lines and polygons the 95% confidence intervals. Point size is relative to number of observations

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.

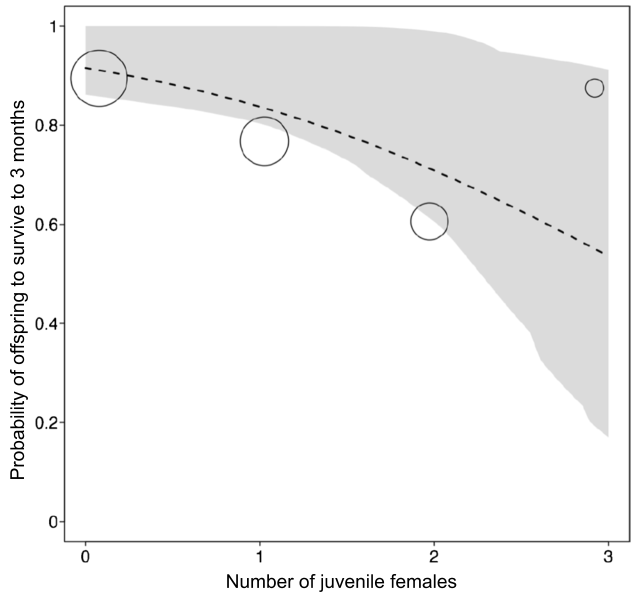

Fig. 8 Probability of an infant surviving to the age of three months as a function of the number of juvenile females. Dashed lines indicate the regression lines and polygons the 95% confidence intervals. Point size is relative to number of observations

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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