

Costs and benefits of multi-male associations in redfronted lemurs (*Eulemur fulvus rufus*)

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The evolution of group-living has fascinated but also puzzled researchers from the inception of behavioural ecology. We use a simple optimality approach to examine some of the costs and benefits of group-living in redfronted lemurs (*Eulemur fulvus rufus*). We show that dominant males profit from accepting subordinates within their groups, as the latter significantly decrease the likelihood that the group is taken over by intruders. This benefit is large enough to outweigh the costs of reproductive competition and may constitute the driving force behind the evolution of multi-male associations in this species.

Keywords: group-living; reproductive competition; cooperation; *Eulemur*

1. INTRODUCTION

Living in close association with conspecifics provides benefits through group augmentation, but may also be accompanied by disadvantages such as within-group competition over resources or mating partners (Pulliam & Caraco 1984). In mammals, a male's reproductive success is mainly limited by access to mates (Clutton-Brock & Parker 1992), which in relation to group-living means that males should try to exclude rivals from groups of females. It has therefore been predicted, that where females form groups that are small enough to be defended by a single male, one-male groups should be the predominant form of social organization (Clutton-Brock 1989). However, this prediction overlooks the possibility that males could also benefit from associating with other males (Kappeler 1999), e.g. through coalition formation and joint defence of territories. Where such possible benefits come into play, selection could have favoured increased tolerance among males and, hence the evolution of multi-male groups.

Using long-term demographic data on redfronted lemurs (*Eulemur fulvus rufus*), we aim to estimate the costs and benefits of multi-male associations from a dominant male's perspective. According to theory,

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owing to small female group sizes (one to three adult females), redfronted lemur groups could potentially be monopolized by a single male, yet the number of adult males equals or exceeds the number of females (Kappeler & Port 2008). Among the males, one male is clearly dominant over all others. Subordinates can either be immigrants or natal males, which delayed dispersal beyond sexual maturity. Even though subordinates can get evicted if group size grows extraordinarily large, immigrants often join groups without overt signs of aggression from resident males. Besides that, groups are occasionally subject to forcible takeovers, as a consequence of which resident males are evicted by coalitions of intruders. To counteract takeovers, preliminary evidence suggests that males benefit from jointly defending their territory (Ostner & Kappeler 2004). On the other hand, grouping together with other males is also costly because of reproductive competition (Kappeler & Port 2008).

Here, we ask whether the benefit of joint territory defence outweighs the costs of reproductive competition. We apply a simple optimality approach to define the costs and benefits of multi-male associations for dominant males and use demographic data from a population of redfronted lemurs to estimate the parameters of our model.

2. MATERIAL AND METHODS

(a) *The model*

Let t be the probability that a group of females (or a territory) defended by either a dominant male alone or by a group of males will be taken over by intruders. If a higher number of males are more successful in defending their territory, we should expect the risk of a takeover to decrease as the number of males, n , increases. Thus, we can denote the takeover risk by $t(n)$ and hence, the males' probability of keeping their territory by $1 - t(n)$.

A dominant male that manages to defend its territory without the help of subordinates will experience no reproductive competition from within the group. Thus, if no paternity is lost to extra-group males (which seems to be a realistic assumption for redfronted lemurs (see Kappeler & Port 2008)), the dominant will sire all offspring in its group, which we standardize to 1. In contrast, we assume that a dominant who accepts a subordinate will inevitably lose a share, p , of reproduction to the subordinate. More generally, assuming that the share of reproduction lost to subordinates is a function of male group size, we can denote the fraction of reproduction left to the dominant by $1 - p(n)$. Thus implicitly, we assume dominants that control group membership (Johnstone & Cant 1999), while reproduction is contested among all group members.

The dominant would be better off accepting versus rejecting an (unrelated) subordinate if the benefit the subordinate provides in terms of a reduced takeover risk outweighs the costs of reproductive competition, i.e. if

$$[1 - t(n+1)] \times [1 - p(n+1)] > [1 - t(n)] \times [1 - p(n)]. \quad (2.1)$$

To check whether expression (2.1) holds in redfronted lemurs and, if it does, over which range of group sizes, we will estimate the functions $t(\cdot)$ and $p(\cdot)$ from our demographic dataset.

(b) *Parameter estimation*

The fraction of reproduction that dominants lose to subordinates has been estimated elsewhere (Kappeler & Port 2008). Here, we use demographic data from the population studied by Kappeler and Port to estimate the takeover risk in groups of various sizes. This population consists of five groups living in a 60 ha study area, which is part of the German Primate Centre field site in Kirindy Forest, western Madagascar (see Kappeler & Port 2008 for details).

The study groups have been subjected to at least weekly demographic censuses by local field assistants; three groups since 1996, one group since 1997 (this group dissolved in 2002) and one group since 1999. The following analysis is based on the demographic dataset from 1996 to 2007 which, thus, consisted of 45 group-years. For a given group, a group-year was defined as the time period from the mating season in June to May of the following

Table 1. Results of the final GLMM. β_0 and β_1 are the intercept and the slope, respectively, of the linear component of the model, relating the risk of a group takeover to the number of males present in the group.

	estimate	s.e.	z	p -value	-95% CI	+95% CI
β_0	3.23	1.55	2.08	0.037	0.19	6.27
β_1	-1.84	0.64	-2.87	0.004	-3.09	-0.59

year. A detailed table of group compositions is available in the electronic supplementary material.

In order to test whether the number of adult males present has an impact on the takeover risk of a group, we fitted a generalized linear mixed model (GLMM). For each group-year, the occurrence or absence of a takeover was regressed against the minimum number of adult males present in the respective group-year or against the number of adult males present during a takeover, if a takeover occurred. To check whether the number of females affects the takeover risk as well, we included the number of adult females (present during a takeover or which prevailed over most time of the group-year) as a second fixed effect. Finally, to control for possible non-independence of data points, group identity was incorporated as a random effect. The GLMM was carried out in R using the LME4 package.

We started by fitting the maximal model and subsequently removed all non-significant terms. In this way we obtained a final model from which we could estimate the takeover risk, $t(n)$, by back-transforming the linear predictor using the logistic link function (e.g. Collett 2003):

$$t(n) = \frac{e^{\mathbf{x}\beta+v}}{1 + e^{\mathbf{x}\beta+v}}, \quad (2.2)$$

in which \mathbf{x} is the vector of predictors, β is the vector of coefficients and v is the random effect.

3. RESULTS

(a) Reproductive competition

From 1996 to 2004, 29 per cent of the infants born in the study population were sired by subordinate males, but the number of subordinates had no impact on the fraction of reproduction dominants lose (Kappeler & Port 2008). In other words, dominant males lost reproduction to subordinates as soon as there was a competitor in the group, but the share of reproduction they lost did not increase as the number of competitors increased. For the present analysis, we therefore considered the share of reproduction lost to subordinates, $p(n)$, as constant with $p(n) = 0.29$, whenever $n > 1$.

(b) Takeovers and takeover risk

Over the 45 group-years analysed in the present study, 9 takeovers occurred, six of which were reported earlier by Ostner & Kappeler (2004). The GLMM revealed that the risk of a group takeover decreased as the number of adult males present in the group increased ($\beta = -1.84$, $z = -2.87$, $p = 0.004$). A model that also included the number of adult females as a second predictor did not have a significantly superior fit ($\chi^2 = 0.06$, d.f. = 1, $p = 0.8$), indicating that the number of females in a group had no effect on the probability of a takeover. Thus, the linear predictor of our final model included the number of adult males as the sole fixed effect (table 1). We could now use expression (2.2) to calculate the takeover risk in groups of various sizes (figure 1).

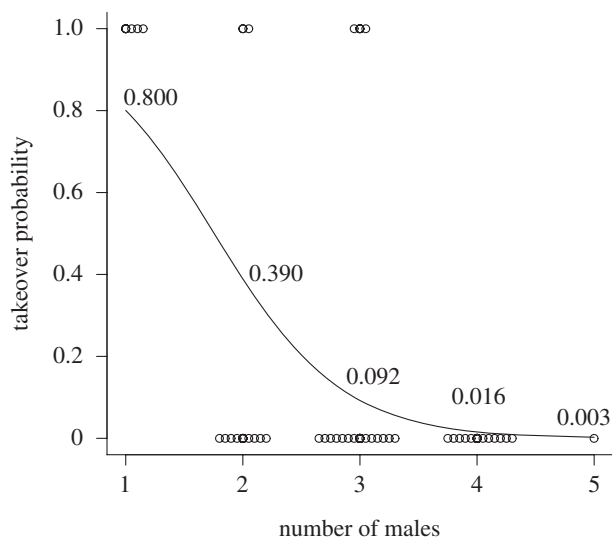


Figure 1. Estimated takeover risks in groups of various sizes.

If groups are defended only by the dominant, the takeover risk is high ($t(1) = 0.8$), but it strongly decreases to $t(2) = 0.39$ if groups contain one and to $t(3) = 0.092$ if groups contain two subordinates, respectively. Eventually, an asymptote is reached where the contribution of further subordinates is only marginal ($t(4) = 0.016$, $t(5) = 0.003$).

(c) Should a dominant accept subordinates?

A solitary dominant does better to accept a subordinate than to reject it and to defend its territory on its own since

$$(1 - 0.39) \times (1 - 0.29) > (1 - 0.8) \times 1.$$

Likewise, a dominant living in a two-male association is still better off accepting a third male than defending the territory with only one helper, since

$$(1 - 0.092) \times (1 - 0.29) > (1 - 0.39) \times (1 - 0.29).$$

More generally, because the loss of reproduction to subordinates is constant whenever $n > 1$, while the takeover risk continues to decline as male group size increases, a dominant should always accept an additional subordinate even if the benefit the latter provides is only marginal. As a consequence, there is no upper limit on male group size. However, since the benefit a subordinate provides decreases as the number of subordinates increases (figure 1), the payoff of accepting an additional subordinate will also decrease rapidly and approaches the payoff of rejecting it (figure 2).

4. DISCUSSION

Because of a high takeover risk, one-male groups are highly unstable in redfronted lemurs. Thus, dominant males benefit from accepting a subordinate within their territory, as the latter greatly reduces the takeover risk. This benefit is large enough to outweigh the costs of reproductive competition imposed by the subordinate. Moreover, as additional subordinates further decrease the takeover risk, while the dominant's loss of reproduction remains the same irrespective of the number

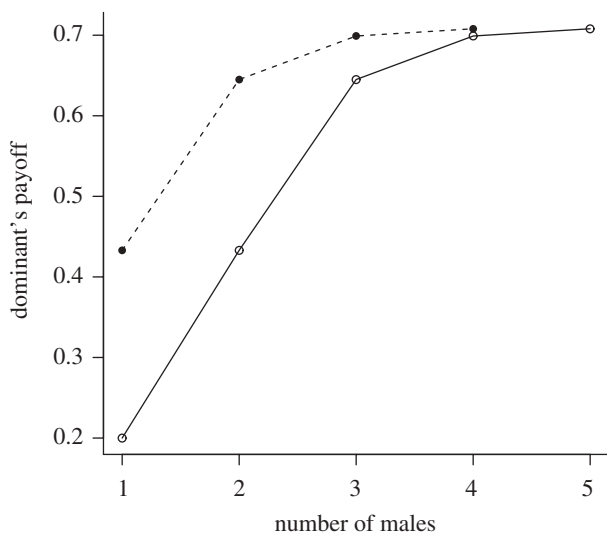


Figure 2. A dominant's payoff in groups of various sizes. The solid line indicates a dominant's payoff if it rejects a subordinate at a given group size, whereas the dashed line indicates a dominant's payoff if it accepts a subordinate (and thereby increases the size of its group by one).

of competitors (Kappeler & Port 2008), our model predicts male group size to increase steadily. However, as male group size rises to four, the payoff of a dominant living in a four-male group becomes almost indistinguishable from that of a dominant living in a five-male group. Thus, as soon as there are further costs of subordinates which add to the loss of reproduction, dominants would do better rejecting an additional male if its contribution to group defence is only marginal, i.e. at a male group size of about four to five individuals. Likewise, if the loss of reproduction were not constant (as estimated by Kappeler & Port 2008) but increased with a higher number of competitors, our model would predict smaller male group sizes (see electronic supplementary material).

Even though our study certainly contributes to an understanding of the evolution of multi-male associations in redfronted lemurs it cannot solve this puzzle completely. We merely focused on a dominant's decision over accepting or rejecting a subordinate willing to join its territory but we did not ask why a subordinate should want to join. Thus, future research should take into account the subordinate's decisions as well. It would have to ask whether it really pays the subordinate to join an established dominant or whether the subordinate would do better trying to take over a group or to establish an own territory.

Over the last two decades, theoretical work has mainly focused on the improvement of group productivity (i.e. the number of offspring raised) as a major benefit of group-living (reviewed in Port &

Kappeler in press). While this appears to be a significant benefit in species that reproduce at relatively high rates (e.g. Langer *et al.* 2004), it does not seem to play a role in redfronted lemurs (P. M. Kappeler 2008, unpublished data). However, our study has shown that cooperative forces other than the improvement of group productivity may constitute a driving force behind the evolution of multi-male associations in this species. More generally, putting more emphasis on the communal defence of territories as a so far often neglected benefit of grouping could help to shed light on the evolution of group-living in other species with similar life histories and social organizations.

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