Explaining negative kin discrimination in a cooperative mammal society

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Kin selection theory predicts that, where kin discrimination is possible, animals should typically act more favourably towards closer genetic relatives, and direct aggression towards less closely related individuals. Contrary to this prediction, we present data from an 18-year study of wild banded mongooses, Mungos mungo, showing that females that are more closely related to dominant individuals are specifically targeted for forcible eviction from the group, often suffering severe injury, and sometimes death, as a result. This pattern cannot be explained by inbreeding avoidance or as a response to more intense local competition among kin. Instead, we use game theory to show that such negative kin discrimination can be explained by selection for unrelated targets to invest more effort in resisting eviction. Consistent with our model, negative kin discrimination is restricted to eviction attempts of older females capable of resistance; dominants exhibit no kin discrimination when attempting to evict younger females, nor do they discriminate between more closely or less closely related young when carrying out infanticidal attacks on vulnerable infants who cannot defend themselves. We suggest that in contexts where recipients of selfish acts are capable of resistance, the usual prediction of positive kin discrimination can be reversed. Kin selection theory, as an explanation for social behaviour, can benefit from much greater exploration of sequential social interactions.

Kin selection theory aims to understand how selection acts on social traits, such as altruism and selfishness, that affect the fitness of social partners and local group members (1, 2). The theory predicts that where animals can discriminate between more closely and less closely related individuals within their social group, they will preferentially direct altruism towards closer genetic relatives, and aggression towards less closely related targets (1–3). Instances of such positive kin discrimination are taxonomically numerous and widespread (4), while reported examples of negative kin discrimination are rare (5, 6).

Contrary to the predictions of traditional kin selection theory, we show below that banded mongooses exercise negative kin discrimination during attempts at eviction; and that this result is not readily explained by inbreeding avoidance or local kin competition. However, a simple and very general sequential game model of selfish behaviour that takes into account the possibility of active resistance on the part of recipients does provide a potential explanation for negative kin discrimination. We first describe the model, and then test predictions of the model using our data.

Explaining negative kin discrimination: a model

Consider the interaction between two individuals, the first of whom (Player 1) may perform a selfish act at the other’s expense, such as stealing a food item, killing offspring, or, in the case with which we are concerned, evicting the other from the territory or group. We suppose that this act entails some fitness cost to the actor, denoted \( c_1 \), but that the cost is outweighed by the benefit to be gained, \( b_1 > c_1 \). The act, if carried out, also deprives the recipient, Player 2, of a benefit \( b_2 \), that it would otherwise enjoy. If the two individuals are related by a coefficient \( r \), then Hamilton’s rule tells us that the act will be favoured by selection provided that \( b_1 - c_1 - r b_2 > 0 \). Consequently, selfishness will never be directed toward a closer relative where it would not also be directed toward a more distant one.

Suppose, however, that if Player 1 attempts the selfish act, Player 2 may then choose to resist. Resistance ensures that the act will fail; Player 1 will still suffer the cost \( c_1 \) of attempting the act, but will not enjoy the benefit \( b_1 \) of success, nor will Player 2 suffer the consequent loss of benefit \( b_2 \). At the same time, resistance entails a fitness cost to Player 2 of \( b_2 - c_1 - r b_1 \). This situation may be modelled as a two-step, sequential game, as illustrated in Figure 1 (see Supplementary Information for a population genetic formulation of the model).

How does relatedness affect the outcome of this game? Applying Hamilton’s rule once again, if \( c_1 > b_2 - r b_1 \), then the cost of resistance to Player 2 outweighs the benefit of preventing the selfish act. Under these circumstances, Player 2 will submit, and selection once again favours performance of the selfish act provided that \( b_1 - c_1 - r b_2 > 0 \). If, by contrast \( c_1 < b_2 - r b_1 \), then Player 2 will resist, and selection consequently does not favour the selfish act. Since a more closely related recipient of the selfish act may prefer to submit where a more distantly related recipient would resist, it follows that selfishness may be directed toward a closer relative where it would not be directed toward a more distant one. To be precise, if we consider two levels of relatedness, \( r_{\text{high}} \) and \( r_{\text{low}} \) (\( r_{\text{low}} < r_{\text{high}} \)), then provided that

\[
\frac{b_1 - c_1}{b_2} > r_{\text{high}} > \frac{b_2 - c_1}{b_1} \quad \text{or} \quad \frac{b_2 - c_1}{b_1} > r_{\text{low}}
\]

Significance

Kin selection theory predicts that animals will direct altruism towards closer genetic relatives, and aggression towards more distantly related individuals. Our 18-year study of wild banded mongooses reveals that, unusually, dominant individuals target females who are more closely related to them for violent eviction from the group. This puzzling result can be explained by selection for unrelated individuals to resist eviction, and for related individuals to submit more easily. In support of this idea, we show that kin are targeted for aggression only when individuals are capable of resisting. Our results suggest that, where potential victims can oppose aggression, the usual predictions of kin selection theory can be reversed.

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then the subgame-perfect equilibrium of the game features target-
ging of a selfish act towards a recipient related to the actor by \( r_{high} \), but not towards a recipient related by \( r_{low} \). To illustrate, suppose \( b_1 = b_2 = 1, c_1 = 0.25 \) and \( c_2 = 0.75 \); then the model predicts that a recipient of low relatedness (\( r_{low} < 0.25 \)) would resist a selfish act, and hence should not be targeted, while a recipient of higher relatedness (\( 0.75 > r_{high} > 0.25 \)) will submit, and so should be targeted.

Unrelated recipients are more likely to resist a selfish act, favouring preferential targeting of more closely related victims, when \( c_2 \) (the cost of resistance) is small, and \( b_2 \) (the benefit to be retained) is large. These effects are illustrated in Figure 2. If \( c_2 \) is typically too large, or \( b_2 \) too small, even unrelated recipients are unlikely to resist, favouring indiscriminate selfishness; only for smaller values of \( c_2 \) or larger values of \( b_2 \) is negative kin discrimination predicted.

**Negative kin discrimination in banded mongooses**

We examine kin discrimination in the context of a conspic-
uous form of intragroup aggression in cooperatively breeding
banded mongooses, *Mungos mungo*; the violent eviction of males
and females from the group. Banded mongooses live in highly
cooperative groups with limited dispersal and varying levels of
relatedness between group members (7). In our study population
in Uganda, groups consist of around 20 adults, plus offspring,
and breed on average four times per year (8). Multiple females
give birth synchronously to a communal litter that is cared for
by members of both sexes (typically not the parents) (7). Each
group contains a cohort of multiple dominant females (median =
4) that are older than the other females, breed more regularly
and more successfully, and aggressively evict younger females
(7, 9, 10). Older males monopolise mating with oestrus females
by mate-guarding them and aggressively driving away younger,
subordinate males (10, 11). Previous work shows that both sexes
are capable of kin discrimination in the context of mating, sup-
porting the assumption of our model that such discrimination
is possible in this system (12). Evictions are relatively common,
involve intense, targeted aggression, and result in the forcible
expulsion of males and females older than 3 years (8). Multiple females
give birth when co-breeding with more closely related
versus less closely related females (GLMM, \( b_2 \) = -0.06 ± 0.12, \( \chi^2 = 0.23, p = 0.63 \); Table S5); nor was there a difference in the
proportion of the emergent litter that were assigned maternity
to dominant individuals (GLMM, \( b_2 \) = -0.08 ± 0.14, \( \chi^2 = 0.27, p = 0.60 \); Table S5).

Among males, by contrast with females, there was no effect
of an individual’s mean pairwise relatedness to dominant group
members (males and females older than 3 years) on the proba-
ability of being subject to an eviction attempt (mixed-sex eviction
attempts; GLMM, \( b_2 \) = 0.84 ± 3.08, \( \chi^2 = 0.07, p = 0.79 \); Table S1). We found no evidence of any discrimination as to which
males were targeted for eviction (Table S1). There was also no
discrimination of any kind when we restricted our analysis to cases
where the identity of primary aggressors was known (Table S2),
or when we tested the effect of mean pairwise relatedness to
same-sex and opposite-sex dominants (Table S3). Unlike the case
for female-only eviction attempts, both males and females were
primary aggressors in eviction attempts directed at both sexes
(GLMM, \( b_2 \) = 1.80 ± 0.56, \( \chi^2 = 12.48, p = 0.001 \); Figure 3B; Table S4).

**Testing model predictions**

Two specific predictions of the model are: (1) that selfish acts
will be directed preferentially towards closer relatives only when
recipients can resist; and (2) that resistance to selfish acts offered
by recipients should decrease as their relatedness to the actor

![Fig. 1. A sequential model of selfishness and resistance. Player 1 (blue) first chooses whether or not to attempt a selfish act at the expense of Player 2 (red); in the event of such an attempt, Player 2 then chooses whether or not to resist. Direct fitness payoffs to both players are shown in their respective colours.](image-url)
Fig. 2. Impact of model parameters on patterns of kin discrimination. Here we focus on a region of parameter space in which Player 1 should carry out the selfish act when unopposed, but in which Player 2 may do best to resist (i.e. $b_1 - c_1 - r b_2 > 0$). We show the probability that, at equilibrium, the actor attempts a selfish act, as a function of relatedness, when $c_2$ is drawn from a normal distribution with specified mean and standard deviation equal to 0.2. (A) Probability that a selfish act is attempted at equilibrium, assuming that $b_1 = 1$, $c_1 = 0.1$, $b_2 = 0.5$ and mean $c_2$ as specified for the plotted curves. (B) Probability that a selfish act is attempted at equilibrium, assuming that $b_1 = 1$, $c_1 = 0.1$, $c_2 = 0.5$, and $b_2$ is as shown in the plot.

Fig. 3. Negative kin discrimination and sex-specific aggression in banded mongooses. (A) The effect of mean pairwise relatedness to dominants (males and females older than 3 years) on the probability of a female being targeted for eviction ($N=207$ females in 29 eviction attempts in 5 groups). The line shows the prediction from the GLMM (± standard error). (Inset) Eviction attempts are highly aggressive and involve biting, chasing and wrestling (photo courtesy of Dave Seager; see also Video S1). (B) The number of female (grey bars) and male (open bars) primary aggressors in female-only and mixed-sex eviction attempts ($N=29$ eviction attempts in 6 groups). The bars show the predictions from the GLMM (± standard error).

Fig. 4. Patterns of kin discrimination towards recipients capable of offering varying levels of resistance. (A) In eviction attempts, dominants (males and females older than 3 years) exhibit negative kin discrimination only towards older females ($N=207$ females in 29 eviction attempts in 5 groups). The lines show the predictions from the GLMM (± standard error) for younger females (dotted line and light grey shaded area, 25th percentile of age=522 days) and older females (solid line and dark grey shaded area, 75th percentile of age=1636 days). (B) Following an attempt at eviction, older females who were more related to dominants (males and females older than 3 years) were less successful in regaining entry to the group ($N=76$ females in 14 eviction attempts in 4 groups); this pattern was reversed in younger females. The lines show the predictions from the GLMM (± standard error) for younger females (dotted line and light grey shaded area, 25th percentile of age=446 days) and older females (solid line and dark grey shaded area, 75th percentile of age=922 days).

increases. After we had developed the model, we tested these predictions. To test the first prediction, we examined how the effect of relatedness varied with the age and weight of potential evictees. Our reasoning was that younger or lighter females should be less able to resist eviction attempts, and that the pattern of negative kin discrimination should therefore be more pronounced when eviction is directed at older or heavier individuals. We found that older females were indeed more likely to be targeted for eviction when more closely related to dominants, but that no such effect of relatedness was apparent for younger females (interaction between relatedness and age: GLMM, $\beta = 0.008 \pm 0.004$, $\chi^2_1=5.98$, $p=0.014$; Figure 4A; Table S6). The strong overall positive relationship between the probability of being targeted for eviction and relatedness was thus driven almost entirely by the pattern in older females (see Supplementary Information; Figure S2; Figure 4A). A similar interaction was also found between relatedness and weight (GLMM, $\beta = 0.03 \pm 0.02$, $\chi^2_1=5.63$, $p=0.018$; Table S6). Consistent with prediction (1), therefore, negative kin discrimination was restricted to cases in which the
targets of eviction were older or heavier, and potentially more capable of offering resistance. As predicted by our model, we found no discrimination on the basis of relatedness for cases where the target of eviction were younger or lighter, and therefore likely to suffer high costs of resistance (a high value of $C_2$; Figure 2A).

We found no evidence for the alternative hypothesis that the pattern of negative kin discrimination among older females arises because older, more closely related females inflict higher reproductive costs on dominants (number of emergent pups assigned to dominant female: GLMM, interaction between female co-breeder age and relatedness to dominant female, $\beta \pm \text{SE} = -0.0002 \pm 0.0002; \chi^2_1 = 0.07, p = 1.00$; proportion of emergent litter assigned to dominant female: GLMM, interaction between female co-breeder age and relatedness to dominant female, $\beta \pm \text{SE} = -0.00005 \pm 0.0002; \chi^2_1 = 0.08, p = 0.78$; Table S5).

To test further whether negative kin discrimination depends on the capacity of recipients to resist, we examined kin discrimination in cases of infanticide of new born pups. Between one and 12 females reproduce in each breeding attempt (14) and birth is highly synchronised, with pregnant females giving birth on exactly the same morning in 63% of cases (15). Experimental and observational evidence suggest that asynchronous litters are often killed by dominant females (14, 15) and that in asynchronous litters the death of a litter in the first week after birth can be used as a proxy for infanticide (15, 16). In contrast to the pattern of litters the death of a litter in the first week after birth can be killed by dominant females (14, 15), and that in asynchronous exactly the same morning in 63% of cases (15). Experimentally and 12 females reproduce in each breeding attempt (14) and on the capacity of recipients to resist, we examined kin discrimi-...
The way back into the group, and suggests that factors other than strength or the costs of resistance may underlie the pattern by which younger females return to the group. For example, following eviction, dominant males will readily reunite with related, younger females, that would otherwise fare very badly outside the group. The negotiation process by which females regain entry to the group may thus be more complex than the simple two-step sequence of eviction and resistance assumed by our model. While our analysis shows that even a two-step game can yield results that diverge from classical predictions, it is likely that many negotiations in family groups may better be modelled as a sequence of three or more steps, something we have not attempted here.

Negative kin discrimination was evident only in eviction attempts of females: in males we found no relationship between relatedness and the probability of being targeted for eviction. This difference between the sexes could reflect differences in the direct fitness incentive for males and females to retain group membership, which in our model is represented by the parameter \( b_c \) (Figure 1). Females gain greater direct fitness from group membership (i.e. higher \( b_c \)) than males because there is little or no reproductive suppression, and most females breed from the age of 10 months (11, 25). In males, by contrast, most individuals are excluded from mating by the two or three oldest males within the group (10). In our model, low values of \( b_c \) favour little or no kin discrimination (Figure 2B). A relatively low value of \( b_c \) in males compared to females may explain why males sometimes disperse voluntarily as a group, whereas females are invariably forced to leave after being subject to violent attack (7, 13). More generally, our model shows that incorporating even very simple forms of behavioural anticipation can radically change the predictions of kin selection theory. Where such anticipation is possible, higher relatedness can lead to outcomes that are less favourable on average for all those involved, because the threat of resistance or punishment of selfish behaviour is less credible between relatives than between unrelated individuals. Many empirical studies have shown that animals are in fact capable of adjusting their behaviour according to the anticipated responses of their social partners in a range of contexts. Examples include signalling systems (26), negotiation over care of offspring (27), restraint in competitive growth (28), and audience effects (29). However, few have considered the possibility that this kind of anticipation might lead to less cooperative outcomes among closer kin. An example comes from economic studies of kinship behaviour in the context of joint-liability group lending, which have found higher rates of loan default when there are more relatives within a group (30, 31), leading to barring of remaining group members from future borrowing. This pattern has been attributed to the difficulty of group members imposing penalties on relatives to enforce repayment (see 32, 33). Our results suggest that similar patterns might also occur in the behaviour of other species, and that the influence of kinship on aggression and cooperation within animal groups may be considerably more subtle and variable than predicted by classical kin selection theory.

### Methods

#### Study population and data collection

Data were collected from 15 groups of banded mongooses living on the Mweya Peninsula, Queen Elizabeth National Park, Uganda (0°125', 27°54'E), between September 1997 and October 2015. For further details of habitat and climate, see (8). Groups were visited every one to three days to record group composition, life history and behavioural data. Individuals were easily identifiable by unique shave markings on their back, and were regularly trapped to maintain these markings (see (34)). On first capture a 2 mm skin sample was collected from the end of the tail for genetic analyses. For details of genetic analyses and calculating relatedness see Supplementary Information. Individuals were trained to step onto portable electronic scales to obtain weight measurements. The research was conducted with permission from Uganda Wildlife Authority and Uganda National Council for Science and Technology, and all methods approved by the Ethical Review Committee of the University of Exeter.

We observed the attempted eviction of 405 individuals from 8 groups in 44 eviction attempts with evicted individuals excluded from the analysis. To ensure our results were easy to recognise. We defined an eviction attempt to have occurred if one or more individuals left their group for at least one day following a period of intense aggression towards themselves or other group members (13, 35, 36). In 32 out of eviction attempts in 5 groups, 14 of which were in 14 attempts some targeted individuals returned while others did not; and in 9 eviction attempts all targeted individuals dispersed.

Statistical analyses were performed in R 3.3.0 (37). We used generalised linear mixed effect models (GLMM) with a binomial error structure using a logit link function, or a Poisson error structure using a log link function, in the `lme4` package (38). Poisson models were checked for overdispersion (39) and for underdispersion (40). In all analyses, we assessed the significance of each fixed effect by comparing the likelihood ratio of the maximal model to that of the model without the fixed effect (23). We present parameter estimates and standard errors from maximal models, rather than removing non-significant fixed effects due to problems associated with stepwise model reduction (40). We did, however, test for interactions to allow the significance of the main effects to be tested (41).

(i) Negative kin discrimination in banded mongooses

Models were fitted to male and female data separately because not all evicted individuals return. The sample was collected from the end of the tail for genetic analyses. For details of analyses of negative kin discrimination (27), restraint in competitive growth (28), and audience effects (29), see Supplementary Information for details of analyses of negative kin discrimination ([ii]) T esting model prediction (1): the selfish act will be directed preferentially towards closer relatives only when recipients can resist by primary aggressors, to avoid inbreeding, or as a response to reproductive competition among individuals involved. We considered adult males over 1 year old, since females younger than 10 months are unlikely to be regular breeders and are rarely evicted (7, 11, 25). We fitted models that considered the likelihood ratio of the maximal model to that of the model without the fixed effect (23). We present parameter estimates and standard errors from maximal models, rather than removing non-significant fixed effects due to problems associated with stepwise model reduction (40). We did, however, test for interactions to allow the significance of the main effects to be tested (41).

(ii) Testing model prediction (1): the selfish act will be directed preferentially towards closer relatives only when recipients can resist

We repeated the original analysis investigating negative kin discrimination among females in eviction attempts, but included two-way interactions between female relatedness to dominants and age (days), and female relatedness to weight (g). Other fixed and random effects were as in the original analysis. We included group identity and eviction attempt as random effects to model group membership, life history and behavioural data. Individuals were easily identifiable by unique shave markings on their back, and were regularly trapped to maintain these markings (see (34)). On first capture a 2 mm skin sample was collected from the end of the tail for genetic analyses. For details of genetic analyses and calculating relatedness see Supplementary Information. Individuals were trained to step onto portable electronic scales to obtain weight measurements. The research was conducted with permission from Uganda Wildlife Authority and Uganda National Council for Science and Technology, and all methods approved by the Ethical Review Committee of the University of Exeter.
she gave birth first, middle or last) and whether or not each female pups survived the first week after birth. We included the mother in the group, we fitted whether or not each female subject to an infanticidal attack. To test whether pups are more likely to have survived the first week after birth if there were still babysitters being left 7 days after birth, or if she was retrospectively assigned maternity to at least one other pup, we fitted a mixed-effects model with a binomial litters in 23 groups.

We observed 166 females that fitted the criteria outlined above, who gave birth to 120 asynchronous litters in 15 groups. Where none of the female's pups survived the first week after birth, they were assumed to be subject to an infantastic attack. To test whether pups are more likely to be targeted for infanticide when mothers are less related to female dominants in the group, we fitted whether or not each female's pups survived the first week after birth as the binomial response variable. We included the mother's mean pairwise relatedness to female dominants older than 3 years of age, mother's age (days), group size and rainfall (mm) in the 30 days before birth as fixed effects. We controlled for repeated measures of mothers, litters and groups by including these terms as random intercepts, and fitted the model to data on 59 females giving birth to 52 communal litters in 12 groups.

(iii) Testing model prediction (2): resistance to the selfish act offered by recipients should decrease as their relatedness to the actor increases

We fitted whether or not a female over 10 months old that was targeted for eviction overcame efforts to permanently exclude herself from the group as the binomial response variable. We only considered eviction attempts where some evictees were allowed to return and others were not due to problems with fitting a binomial model to outcomes that are exclusively successes or failures. We included mean pairwise relatedness to dominants in the group, age (days), and the interaction between these two variables as fixed effects. We included additional fixed effects in the model due to problems with model convergence. We controlled for repeated measures of individuals, eviction attempts and groups by including these terms as random intercepts, and fitted the model to data on 46 females in 14 eviction attempts in 4 groups.

Author contributions


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