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Individual and demographic consequences of mass eviction in cooperative banded mongooses

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In animal societies, conflict within groups can result in eviction, where individuals are often permanently expelled from their group. To understand the evolution of eviction and its role in the resolution of within-group conflict requires information on the demographic consequences of eviction for individuals and groups. However, such information is usually difficult to obtain because of the difficulty in tracking and monitoring individuals after they are evicted from their natal groups. Here we used a 15-year data set on life history and demography to investigate the consequences of eviction in a tractable cooperatively breeding mammal, the banded mongoose, *Mungos mungo*. In this species, groups of individuals are periodically evicted en masse and eviction is a primary mechanism by which new groups form in the study population. Following eviction, we found sex differences in dispersal distance: some females established new groups on the study peninsula but males always dispersed away from the study peninsula. Evicted females suffered reduced reproductive success in the year after eviction. For the evicting group, eviction was associated with increased per capita reproductive success for females, suggesting that eviction is successful in reducing reproductive competition. However, eviction was also associated with increased intergroup conflict for the evicting group. Our results suggest that within-group conflict resolution strategies affect group productivity, group interactions and the structure of the population, and hence have fitness impacts that reach beyond the individual evictors and evictees involved in eviction.

Conflict over resources and social status in social groups can be resolved by various means, a conspicuous form of which is eviction or forced expulsion. Eviction, although sometimes temporary, often results in the permanent exclusion of one or more individuals from their group (Balshine-Earn, Neat, Reid, & Taborsky, 1998; Buston, 2003; Clutton-Brock et al., 1998; Kappeler & Fichtel, 2012; Thompson et al., 2016). Eviction may be costly to evictors in the short term (Bell, Nichols, Gilchrist, Cant, & Hodge, 2012; Dubuc et al., 2017), but yield longer term direct fitness benefits by returning groups to optimum size and reducing competition (Stephens, Russell, Young, Sutherland, & Clutton-Brock, 2005; Thompson, Cant, et al., 2017; Young et al., 2006). Its costs and benefits are expected to influence the frequency and pattern of eviction, and have been the focus of recent theoretical research on reproductive skew and cooperation (Buston, Reeve, Cant, Vehrencamp, & Emlen, 2007; Johnstone, 2000; Johnstone & Cant, 1999; Thompson, Cant, et al., 2017). However, these simple models usually focus on two players, an evictor and an evictee, with a fixed fitness consequence to each of eviction and without consideration of potential fitness consequences to other group members or the rest of the population. As shown by recent structured population models, the demographic consequences of social acts are crucial in determining the direction of selection for helping and harming traits (Gardner & West, 2006; Johnstone & Cant, 2008; Lehmann & Rousset, 2010). Theoretical models of eviction would benefit from the addition of demographic information to fully incorporate the costs and benefits of eviction to evictors, evictees, other group members and the wider population. For example, the benefits to evictors of evicting natal individuals depends on the degree to which this alleviates local competition, the success of evictees in forming or joining new groups, and their subsequent reproductive success. Empirical studies can provide much needed detail on these demographic consequences of eviction.

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Eviction is likely to inflict costs on permanently dispersing individuals who are faced with the challenge of living outside their natal group (Bowler & Benton, 2005; Clobert, Baguette, Benton, & Bullock, 2012; Dieckmann, O'Hara, & Weisser, 1999), particularly for social species in which eviction usually involves the expulsion of single individuals (Kappeler & Fichtel, 2012; Ridley, Raihani, & Nelson-Flower, 2008; Young et al., 2006). Evicting multiple individuals at once may improve individual survival or the chances of group formation, but these groups require territory and associated access to food resources to survive and reproduce. In a saturated population where groups form contiguous territories, dispersing evicted cohorts and newly formed groups moving through a mosaic of established groups are likely to trigger intergroup aggression in an attempt to acquire sufficient territory (Bonte et al., 2012; Mech, 1994; Mitani, Watts, & Amsler, 2010; Wilson & Wrangham, 2003). The reproductive success of evicted individuals is dependent on overcoming these obstacles to establish a new group, but little is known about these consequences of eviction because tracking dispersing groups is logistically challenging and the long-term fate of evicted individuals is often unknown.

Here we investigate the demographic consequences of eviction in banded mongooses, *Mungos mungo*, a highly cooperative species that exhibits conspicuous conflict over reproduction and group membership. Banded mongoose groups contain a cohort of older dominant females (median = 4) that monopolize reproduction and evict younger females (Cant, Nichols, Thompson, & Vitikainen, 2016; Cant, Otali, & Mwanguhya, 2001; Nichols, Amos, Cant, Bell, & Hodge, 2010). Older males monopolize mating with oestrous females through mate guarding (Cant, 2000; Nichols et al., 2010). Evictions of groups of females, sometimes with males, are triggered by intense intrasexual reproductive competition (Cant, Hodge, Bell, Gilchrist, & Nichols, 2010; Gilchrist, 2006; Thompson et al., 2016). Previous research has shown that 53% of these mass eviction events are female-only (median = 6 females evicted, range 1–12); in the remaining 47% of evictions males are also evicted (median = 13 individuals, range 6–26; Thompson et al., 2016). Evictions are almost always of groups of individuals (just three eviction events (6%) were of a single individual; Thompson et al., 2016). Eviction events are either temporary, with all evictees readmitted to the group (47% of all evictions; median time to readmittance = 6 days, range 1–158 days), or permanent, with some or all evictees permanently leaving the group (53% of all evictions; Thompson et al., 2016). Eviction can therefore have important effects on group size and composition, particularly sex ratio. In banded mongooses, males contribute most to babysitting offspring at the den (Cant, 2003; Gilchrist & Russell, 2007; Hodge, 2007) and, during experimental simulated intergroup encounters, exhibit the most aggression towards intruders (Cant, Otali, & Mwanguhya, 2002). Changes in adult sex ratio following eviction could therefore affect the availability of helpers to care for young and defend the group.

Among females, young individuals are more likely to be targeted for eviction than older individuals and there is evidence of negative kin discrimination among older females, with those more closely related to dominants in their group more likely to be evicted and to permanently disperse (Thompson, Cant, et al., 2017). Evicted pregnant females are more likely to regain entry to their group if they abort their litter (Cant et al., 2010; Gilchrist, 2006). Evicting other group members has substantial costs to dominant females: their pups are lighter and fewer survive to independence if dominant females are involved in an eviction (Bell et al., 2012). Voluntary dispersal is not observed in adult females, and is uncommon in males: 70% of individuals that reach 1 year old are born and die in their natal group (Cant et al., 2016; Thompson & Cant, n.d.). Consequently, mass eviction is a primary mechanism by which new groups form in the population (Cant et al., 2016).

Eviction may also have impacts on intergroup relations, which in banded mongooses are particularly frequent and violent (Cant et al., 2002; Nichols, Cant, & Sanderson, 2015; Thompson, Marshall, Vitikainen, & Cant, 2017). Groups actively defend territories and regularly engage in ‘intergroup interactions’ with rivals over food, territory and mates (Thompson, Marshall, et al., 2017). Adult mortality increases in the 3-day period after being involved in an intergroup interaction, and litters are less likely to survive to emergence if their group is involved in an intergroup interaction during the babysitting period (Thompson, Marshall, et al., 2017). In our population, groups live at high density (Cant, Vitikainen, & Nichols, 2013). As such, eviction could have consequences for levels of conflict among established groups, and between established groups and evicted individuals attempting to gain territory and other resources. The costs of such conflict are likely to be particularly high for evicted cohorts.

Below we use our long-term data to examine the predicted consequences of mass eviction for evictees, evictors and the wider population in the banded mongoose system. We first examine the consequences of eviction for dispersal, specifically (1) whether eviction results in dispersal to form new groups in the population. We then consider (2) the reproductive success of evicted females, predicting that permanently evicted females will have lower reproductive success than females that stay in their group (hence the reluctance of females to leave voluntarily). We examine (3) the size and composition, and the litter survival, of evicting groups, predicting that litter survival will increase following an eviction event if eviction is an effective means of reducing reproductive competition. Finally, we investigate (4) patterns of conflict between groups in the study population, before and after an eviction event, predicting that the attempts by evicted cohorts to establish new groups in the population will lead to elevated levels of intergroup conflict following an eviction event.

METHODS

Study Population and Data Collection

We studied a population of banded mongooses in 13 groups living on the Mweya Peninsula, Queen Elizabeth National Park, Uganda (0°12′S, 29°54′E), between September 1997 and December 2012. For further details of habitat and climate, see Cant et al. (2013). The Mweya Peninsula is a 4.95 km^2 heart-shaped promontory that projects into Lake Edward and is connected to the mainland by a narrow strip of land, making dispersal routes off and away from the peninsula limited (Fig. 1; Cant et al., 2016, 2013). In our study population, banded mongooses live in groups of approximately 20 adults, plus offspring, and breed continuously throughout the year (Cant et al., 2016, 2013). Groups in which eviction was observed had a mean group size (individuals aged over 6 months) of 26.4 individuals (range 11–43). Birth is highly synchronized within (but not between) groups (Hodge, Bell, & Cant, 2011) and the communal litter is cared for by parents and nonparents of both sexes (Cant, 2003; Gilchrist & Russell, 2007). Groups were located using radiotelemetry (Cant, 2000) and visited every 1–3 days to record group composition, life history and behavioural data, and daily to record the identity of evicted individuals and those that returned to their group (if any). All individuals were uniquely marked by either colour-coded plastic collars or, more recently, shave patterns on their back and were regularly trapped to maintain these markings (see Jordan, Mwanguhya, Kyabulima, Rüedi, and Cant (2010) for further details of the trapping procedure). Individuals were trained to step

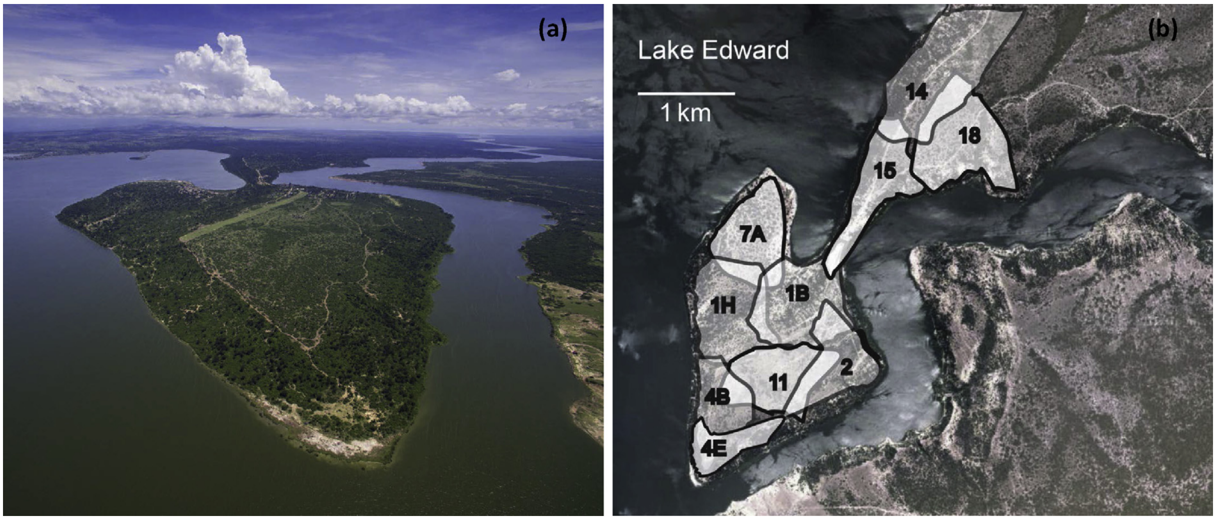

Figure 1. The study peninsula and population. (a) An aerial photograph of the Mweya Peninsula. The peninsula is surrounded by the waters of Lake Edward and the Kasinga Channel and connected to the mainland by a narrow strip of land. For scale, the light green airstrip that runs diagonally across the peninsula is approximately 2 km long. Image courtesy of Feargus Cooney. (b) A satellite image of the Mweya Peninsula with the approximate territories of 10 social groups (as of November 2012). Groups form contiguous territories with extensive areas of overlap meaning there is little vacant area on which evicted cohorts can establish a territory. Reproduced with permission from Cant et al. (2013).

onto portable electronic scales to obtain weight measurements. Rainfall measurements were recorded by our own weather station.

Evictions were highly conspicuous events because they involved high levels of aggression and violence directed towards evicted individuals (Thompson, Cant, et al., 2017; Thompson et al., 2016). We defined an eviction event to have occurred if one or more individuals left their group for at least 1 day following a period of intense aggression towards themselves or other group members (Cant et al., 2010; Gilchrist, 2006; Thompson, Cant, et al., 2017; Thompson et al., 2016). Rare instances where individuals left their group without any observed aggression towards any group member were defined as voluntary dispersal events and were not considered in our analyses ($N = 37$ adult individuals, all male). We observed the eviction of 431 individuals in 46 eviction events over the course of the study. For convenience we label evicted groups of individuals 'evicted cohorts' (although cohorts in our case are not necessarily composed of individuals of the same age). Following a mixed-sex eviction (where both males and females were evicted), the permanently evicted group split into single-sex cohorts which dispersed separately, either remaining on or dispersing away from the peninsula. Further details on the dispersal fate of permanently evicted cohorts are given in the Results.

Statistical Analyses

Statistical analyses were performed in R 3.3.0 (R Development Core Team, 2016) using generalized linear mixed-effect models (GLMM) in the 'lme4' package (Bates, Mächler, Bolker, & Walker, 2015), using a binomial error structure and a logit link function, or a Poisson error structure and a log link function. Poisson models were checked for overdispersion of the response variable (Bolker et al., 2008). In each analysis, the maximal model was fitted, including all fixed effect terms of interest and biologically relevant interactions. 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 (Bates et al., 2015). We present the parameter estimates and standard errors from the maximal models, due to problems associated with stepwise model reduction (Forstmeier & Schielzeth, 2011; Mundry & Nunn, 2009; Whittingham, Stephens, Bradbury, & Freckleton, 2006). We did, however, remove nonsignificant interactions from our maximal model to test the significance of the main effects (Engqvist, 2005). To determine differences between the reproductive success of females, and of groups, following an eviction event we conducted a post hoc multiple comparison of means using the 'glht' function with Tukey's all-pairwise comparisons in the 'multcomp' package in R (Hothorn, Bretz, & Westfall, 2008; Hothorn et al., 2016).

Consequences of eviction for evictees

To investigate the consequences of eviction for evicted cohorts, we compared the size and sex ratio (individuals aged over 6 months) of the newly formed group with that of the group from which they originated ($N = 6$ new groups formed from female cohorts evicted from three groups).

Reproductive success of evicted females

To investigate whether eviction affected evicted female reproductive success we compared the number of emergent pups (pups that survived at least 30 days after birth; Cant, 2003) born in the 12 months following an eviction event to nonevicted, temporarily evicted and permanently evicted females. We determined maternity from parentage assignments (see Sanderson, Wang, Vitikainen, Cant, and Nichols (2015) for details). We excluded females that dispersed from the study peninsula, for which we did not have posteviction information on births and death. We restricted our analysis to females aged over 10 months (the age at first conception; Cant et al., 2010; Gilchrist, Otali, & Mwanguhya, 2004). To avoid potential compound effects of multiple eviction events, we excluded females that experienced another eviction event in their group in the subsequent 12 months. We fitted the number of emergent pups born to a female in the 12 months after an eviction event in a Poisson GLMM. Eviction category (not evicted, temporarily evicted or permanently evicted), female age (days) and their interaction were included as fixed effects to capture potential differences in the effect of eviction on older versus younger females. Weight (g) and mean monthly rainfall (mm) in the 12 months after the eviction event were fitted as additional fixed effects. To account for differences in females' opportunity to reproduce, we included an offset term of the $\log_e$ of the length of lifetime (days) following an eviction event (up to 12 months) as an additional fixed effect

(Crawley, 2007). We accounted for repeated measures by including group, eviction and female identity as random intercepts and fitted the model to data on 90 females ($N = 53$ not evicted, $N = 23$ temporarily evicted and $N = 14$ permanently evicted) in 15 eviction events in five groups.

We also investigated whether eviction affected a female's reproductive success over her remaining lifetime following an eviction event. We fitted the number of emergent pups born to a female in her remaining lifetime following an eviction event as the response variable. We included female age (days) and weight (g) at the eviction event and an offset term of the $\log_e$ of the female's lifetime (days) following the eviction event as additional fixed effects. We included group identity and eviction event as random intercepts, and an observation level random effect to control for overdispersion of the response variable (Harrison, 2014). We fitted the model to data on 31 females ($N = 9$ not evicted, $N = 15$ temporarily evicted and $N = 7$ permanently evicted) in 12 eviction events in five groups. Analysis of male reproductive success following an eviction event was not possible since no permanently evicted males remained on the study peninsula for longer than 10 months.

Litter survival in evicting groups

To examine whether eviction events had an effect on litter survival in the evicting group we compared the number of pups that survived to emergence (per female that gave birth) in litters born following an eviction event to those not born following an eviction event. For litters born following an eviction event, we only considered litters born within 60 days of an eviction event (the approximate length of gestation; Cant, 2000), where there was no eviction event observed in the 60 days after birth to exclude potential effects of a recent eviction on litter survival (e.g. see Bell et al., 2012). For litters born in a period that did not follow an eviction event, we only considered litters where there was no observed eviction event in the 60-day period before, or the 60-day period after, the birth of the litter. We fitted the number of pups that survived to emergence as the response variable in a Poisson GLMM. We fitted whether the litter was born following a temporary eviction (where all evictees return to the evicting group), following a permanent eviction (where some or all evictees permanently leave the evicting group) or not following an eviction as the main term of interest, and included group size at the birth of the litter, and mean rainfall (mm) in the previous 30 days as fixed effects. Since the communal litter is born and kept in the den for the first 30 days after birth, we were unable to determine the number of pups born into the communal litter. We therefore included an offset term of the $\log_e$ of the number of females that gave birth to the communal litter (since this is correlated with the number of pups born in the litter) as an additional fixed effect (Crawley, 2007). We accounted for repeated measures by including group and eviction identity as random intercepts and fitted the model to data on 48 litters ($N = 16$ born following a temporary eviction, $N = 12$ born following a permanent eviction and $N = 20$ not born following an eviction) in seven groups.

Patterns of conflict between groups

To investigate the perturbative effects of eviction on the wider population we examined the frequency of intergroup conflict between groups before and after an eviction event. Intergroup interactions are highly conspicuous events and were recorded ad libitum. Following Thompson, Marshall, et al. (2017) we defined an intergroup interaction as any occasion when two groups sighted each other and responded by screeching, chasing and/or fighting. We fitted the number of intergroup interactions involving the evicting group in a 30-day period as the response variable in a Poisson GLMM. Each 30-day period either came immediately before or immediately after an eviction from the evicting group. We chose a period of 30 days because, as only 55% of evicted individuals remain on the peninsula longer than 30 days after eviction, any effects of dispersing evicted cohorts on the frequency of intergroup conflict are likely to be detectable during this period. We included interactions with evicted cohorts in our analysis. We only used 30-day periods in which there was no other eviction event observed in the 30 days before or after the focal eviction event. We included whether the 30-day period was immediately before or after an eviction event, and the type of eviction event (permanent or temporary) as fixed effects. We included group and eviction identity as random intercepts and fitted the model to data on 78 30-day periods ($N = 39$ periods immediately before an eviction and $N = 39$ periods immediately after an eviction) in eight groups. To investigate the effect on intergroup conflict of the presence of the evicted cohort we repeated this analysis, but excluded any intergroup interactions that involved the evicted cohort.

To investigate the effect of eviction on intergroup conflict in the wider population, we fitted the number of intergroup interactions involving groups other than the evicting group in a 30-day period as the response variable in a Poisson GLMM. We included the same fixed and random effects as those in the analysis of intergroup conflict involving the evicting group and fitted the model to data on 78 30-day periods ($N = 39$ periods immediately before an eviction and $N = 39$ periods immediately after an eviction) in eight groups. We then repeated this analysis, but excluded any intergroup interactions that involved the evicted cohort.

Ethical Note

All research procedures received prior approval from Uganda Wildlife Authority and Uganda National Council for Science and Technology, and adhered to the ASAB/ABS Guidelines for the Treatment of Animals in Behavioural Research and Teaching. All research was approved by the Ethical Review Committee of the University of Exeter.

RESULTS

Consequences of Eviction for Evictees

Over the study period, 66 males were permanently evicted from their group. These males dispersed from the peninsula within 10 months (median time to dispersal from the peninsula = 22 days, range 0−296 days) and were not successful in joining a dispersing cohort of females to form a new group in the study peninsula (but may well have done so outside the study peninsula). By contrast, while the majority of permanently evicted females (68%; total number of permanently evicted females = 91) dispersed away from the peninsula in a similar pattern to males (median time to dispersal from the peninsula = 23 days, range 0−217 days), 32% of permanently evicted females were successful in forming a new group on the peninsula. A total of six new groups were formed by 29 permanently evicted females. They did this either by usurping all females from an established study group ($N = 1$), joining unknown males (males that were immigrants in the population; $N = 2$), joining voluntarily dispersing known males ($N = 1$) or joining both voluntarily dispersing known males and unknown immigrant males ($N = 1$). One cohort of seven females remained on the peninsula for over 2 years without ever permanently joining males. Despite this, all females in this cohort were reproductively successful, mating with males from established groups and giving birth to seven communal litters over the course of their combined lifetime. New groups that were formed on the study peninsula were significantly smaller than the group from which they originated (paired Wilcoxon signed-rank test: $V = 21$, $N = 6$, $P = 0.031$). However, the sex ratio of these newly formed groups was not significantly different to that of the original group (paired Wilcoxon signed-rank test: $V = 11$, $N = 6$, $P = 0.42$).

Reproductive Success of Evicted Females

Reproductive success over the 12 months following an eviction event was significantly lower for permanently and temporarily evicted females than for nonevicted females (Fig. 2, Appendix Tables A1, A2). However, there was no significant difference in the number of emergent pups that nonevicted, temporarily evicted or permanently evicted females had during their remaining lifetime following an eviction event (Appendix Table A1).

Litter Survival in Evicting Groups

Following an eviction event that resulted in the permanent dispersal of some, or all, of the evicted cohort, there was a significant reduction in the size of the evicting group (paired *t* test: $t_{22} = 6.68$, $P < 0.0001$), and a significant increase in the sex ratio of males to females (paired Wilcoxon signed-rank test: $V = 67$, $N = 23$, $P = 0.030$). Litter survival in the evicting group was significantly longer following a permanent eviction than a temporary eviction or no eviction (Fig. 3, Appendix Tables A3, A4).

Patterns of Conflict Between Groups

There were significantly more intergroup interactions involving the evicting group in the 30 days following an eviction event than in the 30 days before one (Fig. 4a, Appendix Table A5). However, once the intergroup interactions involving the evicted cohort were removed from the analysis, there was no difference in the frequency of intergroup conflict in which the evicting group was involved before and after an eviction event (Fig. 4b, Appendix Table A5). To rule out the possibility that observed increases in intergroup interactions involving the evicting group were attributable to increases in observation effort we compared the number of visits to the evicting group before and after an eviction event. We found no significant difference in the number of visits to the evicting group in the 30-day period before and after an eviction event (paired Wilcoxon signed-rank test: $V = 46.5$, $N = 19$, $P = 0.09$). We found no difference in the number of intergroup interactions involving groups in the population other than the evicting group before and after an eviction event, both when including and excluding intergroup interactions involving the evicted cohort (Appendix Table A5). Therefore, eviction events were associated with intergroup conflict involving the evicting group and the evicted cohort.

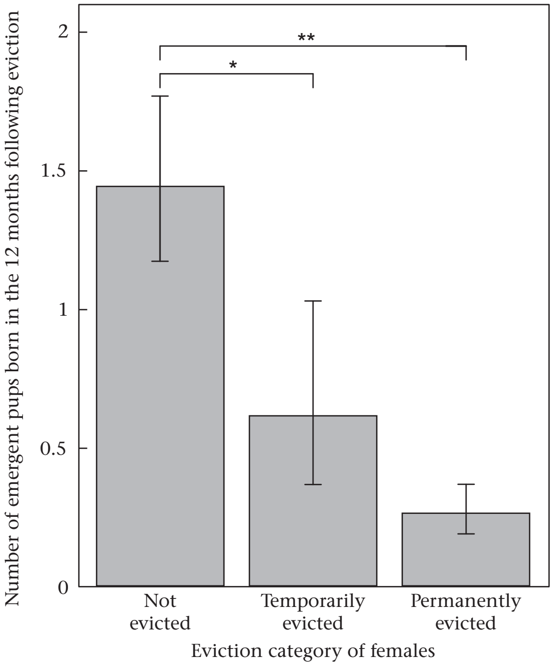

Figure 2. The effect of eviction on the reproductive success of evicted females. The number of emergent pups born in the 12 months following eviction to females that were not evicted, temporarily evicted and permanently evicted ($N = 90$ females ($N = 53$ not evicted, $N = 23$ temporarily evicted and $N = 14$ permanently evicted) in 15 eviction events in five groups). The bars show means from the GLMM ± SE. Asterisks refer to post hoc Tukey's all-pairwise comparison of means across the three categories: $^{*}P < 0.05$; $^{**}P < 0.01$.

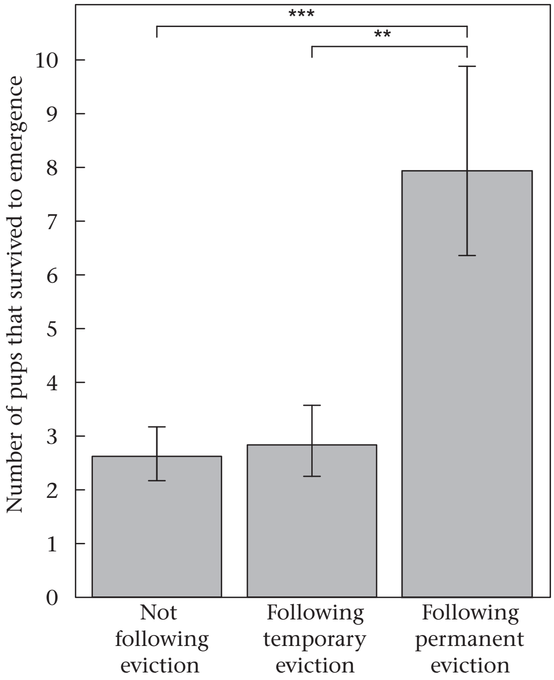

Figure 3. The effect of eviction on litter survival in the evicting group. The number of pups that survived to emergence from litters born following a temporary eviction, a permanent eviction or not born following an eviction event (GLMM, $N = 48$ litters ($N = 16$ born following a temporary eviction, $N = 12$ born following a permanent eviction and $N = 20$ not born following an eviction) in seven groups). The model controlled for the number of females that gave birth to the litter. The bars show means from the GLMM ± SE. Asterisks refer to post hoc Tukey's all-pairwise comparison of means across the three categories: $^{**}P < 0.01$; $^{***}P < 0.001$.

DISCUSSION

Eviction in banded mongooses promoted dispersal and the formation of new groups, and affected the reproductive success of both evictees and members of the evicting group. When eviction resulted in permanent dispersal, cohorts of evicted females occasionally formed new groups in the study peninsula, whereas evicted cohorts of males did not. Eviction was associated with reproductive costs for evicted females through decreased short-term reproductive success. For evicting groups, litter survival improved following a permanent eviction, suggesting that mass

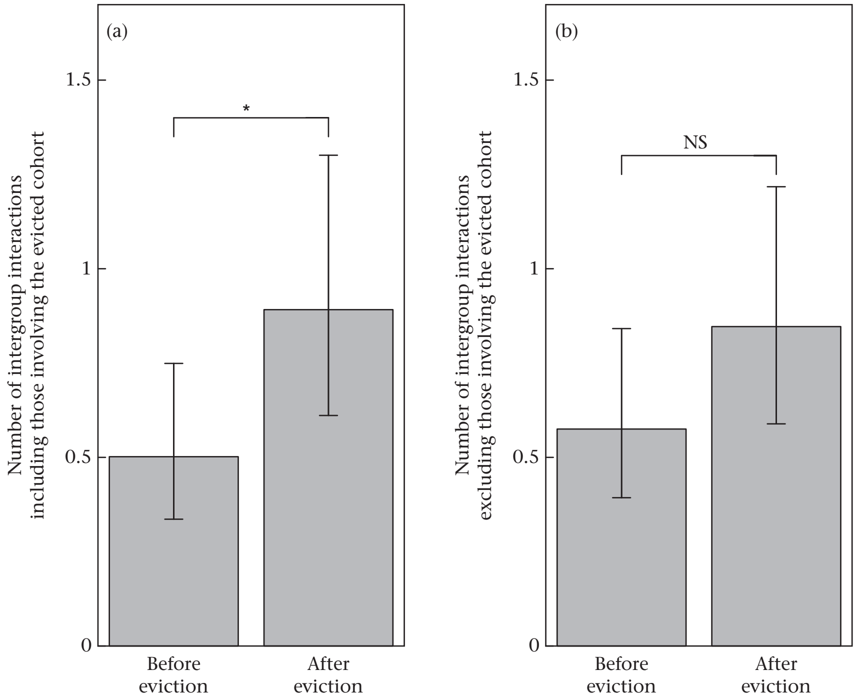

Figure 4. The effect of eviction on intergroup conflict involving the evicting group. (a) The number of intergroup interactions involving the evicting group and including interactions involving the evicted cohort in the 30-day period before and after an eviction event ($N = 78$ periods in eight groups). The bars show means from the GLMM ± SE. (b) The number of intergroup interactions involving the evicting group but excluding interactions involving the evicted cohort in the 30-day period before and after an eviction event ($N = 78$ periods in eight groups). The bars show means from the GLMM ± SE. $^*P < 0.05$.

eviction is an effective method of reducing reproductive competition. Eviction was also associated with an increase in intergroup interactions as a result of conflict between the evicting group and the evicted cohort. These results suggest that eviction can have significant consequences for the demography of cooperative species and that these effects can occur at an individual level (through effects on individual reproductive success), group level (through changes in group size and composition, and intergroup conflict) and population level (through dispersal and new group formation).

In our population, mass eviction is the main mechanism by which individuals leave their natal group and is, therefore, a primary route to the formation of new groups (Cant et al., 2016). Seven evicted female cohorts, but no evicted male cohorts, were successful in forming a new group on the study peninsula. Whether this means that females are more successful dispersers overall, or that males simply travel longer distances before forming groups, requires further study. Sex differences in the direct costs and benefits of helping can arise from sex differences in dispersal (Clutton-Brock et al., 2002; Cockburn, 1998; Young, Carlson, & Clutton-Brock, 2005), and theory suggests that sex differences in dispersal can affect selection for helping and harming behaviours in structured populations (Johnstone & Cant, 2008), due to effects on local competition and the genetic structure of the population (Gardner, 2010). In general, these models predict that selection will favour helping among members of the more philopatric sex, and harming among members of the dispersing sex (Johnstone & Cant, 2008). However, these models assume individuals disperse independently, and define sex differences in philopatry in terms of the probability of dispersal (to a far-distant patch), not the distance that dispersers move from their natal patch. Eviction of groups of same-sex individuals, as occurs in banded mongooses and other cooperative vertebrates (Koenig & Dickinson, 2016), may influence selection for helping and harming in ways that have yet to be explored theoretically. For example, simple haploid, asexual models suggest that dispersal of groups of relatives (budding dispersal; Gardner & West, 2006) may promote altruism within groups (Gardner & West, 2006), but these effects have not been investigated in sexual systems.

Eviction resulted in significant changes in the size and composition of groups to which individuals belonged. Permanently evicted females formed smaller groups following dispersal than the group from which they originated, although with a similar sex ratio. These group size changes have major ramifications for reproductive success because, as in other cooperative breeders (Courchamp, 1999; Courchamp, Clutton-Brock, & Grenfell, 1999; Kokko, Johnstone, & Clutton-Brock, 2001), banded mongooses are subject to strong Allee effects since larger groups can leave more babysitters to guard pups at the den (Cant, 2003; Marshall et al., 2016), This may, in part, explain why permanently evicted females suffered lower reproductive success in the 12 months after eviction. In addition, eviction in this species, and in meerkats, *Suricata suricatta*, has been shown to reduce the reproductive success of temporary evictees through spontaneous abortion (Cant et al., 2010; Gilchrist, 2006; Young et al., 2006). When considering lifetime reproductive success, permanently evicted females did no worse than females that remained behind in their natal group. This result raises the intriguing possibility that the short-term costs of being evicted are compensated by improved success later in life, for example, via an escape from local competition. However, we were only able to monitor the reproductive success of a small subset of permanently evicted females that remained on the study peninsula and, as such, there is potential for bias in our results. Individuals in our population live at much higher density than in other areas (Cant et al., 2013), and so dispersing away from the study peninsula could provide evicted individuals with more available territory and lower competition for food resources. The development of GPS technology deployed on evicted individuals that allows dispersers to be tracked over longer distances will be integral in determining the success of local versus distant dispersers.

Previous work in this species, and other cooperatively breeding mammals, has shown that eviction is a strategy employed to reduce levels of intrasexual reproductive competition (Cant et al., 2010; Clutton-Brock et al., 1998; Kappeler & Fichtel, 2012; Thompson et al., 2016). Our result that litter survival improved following a permanent eviction provides evidence that permanent mass eviction is successful in alleviating the level of competition among pups, and that benefits to evictors (and their close kin) could be high enough to offset the immediate costs of the eviction process (Bell et al., 2012). The benefits of permanent eviction are not completely attributable to the reduction in reproductive competition via a reduction in group size, or in the number of breeding females (since both variables were controlled for in our analysis). Instead, eviction was associated with increased pup survival over and above these effects, perhaps because of changes in group composition. For example, eviction may result in smaller groups of more compatible or less conflictual individuals. Permanent eviction also resulted in a higher ratio of males to females in the group. Consequently, since males contribute more than females to offspring care and territory defence, we might expect the presence of relatively more males, per female, in the group to result in greater litter survival during the vulnerable den period.

Finally, we found that eviction was associated with increased levels of intergroup conflict, manifested as an increase in the number of aggressive intergroup interactions involving the evicting group and the evicted cohort. For banded mongooses, and other social species, the fitness costs of engaging in intergroup interactions can be considerable (Aureli, Schaffner, Verpooten, Slater, & Ramos-Fernandez, 2006; Cassidy, MacNulty, Stahler, Smith, & Mech, 2015; Mosser & Packer, 2009; Nichols et al., 2015; Thompson, Marshall, et al., 2017; Wrangham, Wilson, & Muller, 2006). There are likely to be significant additional costs of eviction suffered by the evicting group through repeated interactions with their own evicted cohort. Quantifying these costs, for example territory loss or increased energetic expenditure through recurrent intergroup fighting, is an avenue for future research. Eviction could, therefore, have important knock-on fitness consequences beyond the eviction process itself.

Conclusions

The evolution of eviction in structured populations will depend on the full suite of fitness impacts for the initiators of aggressive eviction, the evictees and the other population members that are affected by large scale changes in group composition or the presence of new groups in the population. Understanding these fitness impacts is challenging because, as in our case, information on the fate of evictees or the impacts on other groups is available only for those individuals that remain within the bounds of a core study area, which represent a biased sample. A goal for future work will be to add information on individuals that are less successful, or travel further from their natal group after eviction. Despite these challenges, long-term individual-based studies of cooperative breeders offer the best opportunity to assess the usefulness of theoretical models of eviction and improve conceptual understanding of the evolution of eviction and its role in social evolution in structured populations.

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DATA ACCESSIBILITY

The data used in this paper are available on Figshare at https://doi.org/10.6084/m9.figshare.5442178.

Appendix

Table A1
The effect of eviction on female reproductive success

Response	Fixed effect	β	SE	χ^2	*P*
Number of emergent pups born in the 12 months following eviction to which a female was assigned maternity	Intercept	−7.91	1.43		
	Eviction category			14.46	**<0.0001**
	Not evicted	0.00	0.00		
	Temporarily evicted	−0.85	0.36		
	Permanently evicted	−1.69	0.52		
	Age (days)	0.00002	0.0002	0.02	0.88
	Weight (g)	0.003	0.0007	18.86	**<0.0001**
	Rainfall (mm)	−0.02	0.01	1.63	0.20
	Eviction category * age			0.54	0.77
	Not evicted	0.00	0.00		
	Temporarily evicted	0.0005	0.0007		
	Permanently evicted	0.0008	0.002		
Number of emergent pups born over the remaining lifetime following eviction to which a female was assigned maternity	Intercept	−1.08	1.53		
	Eviction category			1.84	0.40
	Not evicted	0.00	0.00		
	Temporarily evicted	−0.23	0.57		
	Permanently evicted	−0.71	0.53		
	Age (days)	0.0003	0.0006	0.23	0.63
	Weight (g)	0.004	0.001	9.33	**0.002**

Models predicted the number of emergent pups born in the 12 months following eviction and over the remaining lifetime. They were fitted using a Poisson error structure with the $\log_e$ of lifetime (days) following eviction (up to 12 months in the model of reproductive success in the 12 months following eviction) as an offset term. In the model of reproductive success in the 12 months following eviction group identity, eviction event and female identity were included as random intercepts ($N = 90$ females ($N = 53$ not evicted, $N = 23$ temporarily evicted and $N = 14$ permanently evicted) in 15 eviction events in five groups). In the model of reproductive success in the remaining lifetime following eviction group identity, eviction event and an observation level random effect were included as random intercepts ($N = 31$ females ($N = 9$ not evicted, $N = 15$ temporarily evicted and $N = 7$ permanently evicted) in 12 eviction events in five groups). Significant terms are given in bold.

Table A2
Post hoc test of the effect of eviction on female reproductive success in the 12 months following an eviction

Response	Eviction category	β	SE	*z*	*P*
Number of emergent pups born in the 12 months following eviction to which a female was assigned maternity	Permanently evicted versus not evicted	−1.69	0.52	−3.25	**0.003**
	Permanently evicted versus temporarily evicted	0.84	0.58	1.46	0.30
	Temporarily versus not evicted	−0.85	0.36	−2.37	**0.045**

Post hoc multiple comparison of means with Tukey's all-pairwise comparisons to determine differences in the number of emergent pups to which a female was assigned maternity in the 12 months following eviction. The original model was fitted using a Poisson error structure with the $\log_e$ of lifetime (days) following eviction (up to 12 months) as an offset term, and with group identity, eviction event and female identity as random intercepts (GLMM, $N = 90$ females ($N = 53$ not evicted, $N = 23$ temporarily evicted and $N = 14$ permanently evicted) in 15 eviction events in five groups). Significant post hoc comparisons are given in bold.

Table A3
The effect of eviction on litter survival in the evicting group

Response	Fixed effect	β	SE	χ^2	*P*
Number of pups that survived to emergence	Intercept	−1.65	0.64		
	Timing of birth of litter			19.50	**<0.001**
	Not following eviction	0.00	0.00		
	Following temporary eviction	0.08	0.20		
	Following permanent eviction	1.11	0.26		
	Group size	0.05	0.02	5.98	**0.015**
	Rainfall (mm)	0.04	0.06	0.48	0.49

Model predicted the number of pups that survived to emergence from litters born following a temporary eviction, a permanent eviction or not born following an eviction. It was fitted using a Poisson error structure with the $\log_e$ of the number of females that gave birth to the communal litter as an offset term, and with group identity and eviction event as random intercepts ($N = 48$ litters ($N = 16$ born following a temporary eviction, $N = 12$ born following a permanent eviction and $N = 20$ not born following an eviction) in seven groups). Significant terms are given in bold.

Table A4
Post hoc test of the effect of eviction on litter survival in the evicting group

Response	Timing of birth of litter	β	SE	*z*	*P*
Number of pups that survived to emergence	Not following eviction versus following temporary eviction	0.08	0.20	0.38	0.92
	Not following eviction versus following permanent eviction	1.11	0.26	4.32	**<0.001**
	Following temporary eviction versus following permanent eviction	1.03	0.31	3.31	**<0.01**

Post hoc multiple comparison of means with Tukey's all-pairwise comparisons to determine differences in the number of pups that survived to emergence in litters born following a temporary eviction, a permanent eviction or not born following an eviction. The original model was fitted using a Poisson error structure with the $\log_e$ of the number of females that gave birth to the communal litter as an offset term, and with group identity and eviction event as random intercepts ($N = 48$ litters ($N = 16$ born following a temporary eviction, $N = 12$ born following a permanent eviction and $N = 20$ not born following an eviction) in seven groups). Significant post hoc comparisons are given in bold.

Table A5
The effect of eviction on intergroup conflict

Response	Fixed effect	β	SE	χ^2	*P*
Number of intergroup interactions involving the evicting group and including interactions involving the evicted cohort	Intercept	−0.98	0.44		
	Period			5.71	**0.017**
	Before eviction	0.00	0.00		
	After eviction	0.57	0.25		
	Eviction type			0.58	0.45
	Permanent eviction	0.00	0.00		
	Temporary eviction	0.29	0.39		
Number of intergroup interactions involving the evicting group but excluding interactions involving the evicted cohort	Intercept	−1.04	0.41		
	Period			2.37	0.12
	Before eviction	0.00	0.00		
	After eviction	0.39	0.25		
	Eviction type			1.60	0.21
	Permanent eviction	0.00	0.00		
	Temporary eviction	0.49	0.38		
Number of intergroup interactions involving groups in the population other than the evicting group and including interactions involving the evicted cohort	Intercept	0.22	0.30		
	Period			2.27	0.13
	Before eviction	0.00	0.00		
	After eviction	0.23	0.15		
	Eviction type			2.13	0.14
	Permanent eviction	0.00	0.00		
	Temporary eviction	0.48	0.33		
Number of intergroup interactions involving groups in the population other than the evicting group but excluding interactions involving the evicted cohort	Intercept	0.12	0.32		
	Period			0.98	0.32
	Before eviction	0.00	0.00		
	After eviction	0.16	0.15		
	Eviction type			4.18	**0.041**
	Permanent eviction	0.00	0.00		
	Temporary eviction	0.70	0.34		

Models predicted the number of intergroup interactions involving the evicting group, and involving groups in the population other than the evicting group, in the 30 days before and after an eviction event. They were fitted using a Poisson error structure with group identity and eviction event as random intercepts ($N = 78$ 30-day periods in eight groups; $N = 39$ periods immediately before an eviction and $N = 39$ periods immediately after an eviction). Significant terms are given in bold.