



Individual and demographic consequences of mass eviction in cooperative banded mongooses



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ARTICLE INFO

Article history:

Received 13 April 2017

Initial acceptance 6 June 2017

Final acceptance 11 September 2017

MS. number: 17-00333R

Keywords:

conflict

cooperation

demography

eviction

Mungos mungo

social evolution

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.

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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 km² 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 non-parents 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

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