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Variable initiators of group departure in a cooperative breeder: the influence of sex, age, state and foraging success

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For animal species that forage as cohesive units, communal decisions about when to forage and where to go are necessary to maintain group cohesion. While in some species particular individuals or subgroups emerge as consistent initiators of movement decisions, in others, many different individuals initiate coordinated group movements. Theoretical models and some empirical studies suggest that an animal's nutritional need may explain variable leadership. We investigated what individual characteristics influence the likelihood of initiating group departure in the cooperatively breeding banded mongoose, *Mungos mungo*. We found that initiation of group departure was highly variable, and not influenced by sex or age of individuals. However, during periods of synchronized breeding, lactating females initiated group departure more often than expected by chance. Experiments to test whether nutritional constraints explained leadership roles revealed that the initiators of group departure were deprived individuals. This suggests that low energetic reserves caused by low foraging success can have an influence on the individuals' likelihood of acting as initiators. However, analysis of weight data showed that initiators had neither a lower body weight than when not initiating nor a more negative weight change than other group members. These findings indicate that besides short-term foraging success, other factors such as high energetic demands during periods of lactation, asymmetries in foraging abilities or investment in cooperative activities between individuals also determine leadership. We conclude that while nutritional constraints can influence initiation of group departure, various effects of individual differences may equally affect leadership roles.

Many animal species forage and travel in groups (Krause & Ruxton 2002). Forming groups might help to gain protection from predators, improve breeding, exchange information and compete against rivals (Alexander 1974; van Schaik 1983; Richner & Heeb 1995). To preserve these group advantages, social animals need to maintain group cohesion (Alexander 1974; Krause & Ruxton 2002), which can be achieved through the process of consensus decision making. Here, group members choose between two or more mutually exclusive actions with the aim of reaching a consensus (Seeley & Buhrman 1999; Conradt & Roper 2003, 2005), although, in some species with fission–fusion dynamics, individuals may make consensus decisions by splitting up into subgroups (Aureli et al. 2008; Jacobs 2010). In small groups, in which individuals can communicate globally (i.e. directly address all other group members, Conradt & Roper 2005), often an individual acts as 'initiator' or 'leader' of coordinated group movement. Initiators are defined as group members that initiate group activity (for example group movement) whereas leaders are group members that elicit follower behaviour (King & Cowlishaw 2009; Pyritz et al. 2011). In the case of group movement, the term 'leader' should not be restricted to the individual's spatial position but comprise the whole process of collective action (Pyritz et al. 2011).

Groups and societies of animals vary in the extent to which certain individuals are leaders in group decisions (Leca et al. 2003). In some species, certain individuals consistently lead group movements (hamadryas baboons, *Papio hamadryas*: Kummer 1968; Stolba 1979; gelada baboons, *Theropithecus gelada*: Dunbar 1983; grazing heifers, *Bos primigenius*: Dumont et al. 2005), whereas in other species various individuals are at the forefront in such activities (bar-headed geese, *Anser indicus*: Lamprecht 1992; white-faced capuchin monkeys, *Cebus capucinus*: Leca et al. 2003; green woodhoopoes, *Phoeniculus purpureus*: Radford 2004; see Conradt & Roper 2005 for definitions of consistent versus variable leadership). While consistent initiation and leadership in group movement might be influenced by the knowledge of experienced individuals

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about the location of food sources (Reebs 2000; Swaney et al. 2001; McComb et al. 2011), the species' social organization (e.g. influence of social dominance: Schaller 1963; Erhart & Overdorff 1999; Sueur & Petit 2008) and personality characteristics (Ward et al. 2004; Leblond & Reebs 2006; Harcourt et al. 2009; Kurvers et al. 2009), little is known about what may cause variable initiation of group movement.

Recent models and a few empirical studies have emphasized the importance of energetic need in the likelihood of acting as leader (reviewed in King & Sueur 2011). Rands et al. (2003), in a state-dependent game model, found that the behaviour of a pair of foraging animals, if there was an advantage to foraging together, became highly synchronized. As a result of this synchronization, differences in energetic reserves of the two animals developed, resulting in different behavioural roles for each of them. The individual with lower reserves emerged as the temporary leader, deciding when the pair should forage (Rands et al. 2003). Other analyses including more than two individuals also emphasized need as an important factor determining leadership (Conradt et al. 2009; Sueur et al. 2010). Studies of foraging fish showed that individuals with lower reserves often occupy front positions in schools (Gotceitas & Godin 1991; Krause et al. 1992, 1998; Krause 1993). Fischhoff et al. (2007) showed that in plains zebra, *Equus burchelli*, the reproductive state was a key determinant of variable leadership. Lactating females, with high energy requirements, were more likely to initiate group movement than nonlactating females. In dwarf mongooses, *Helogale parvula*, the dominant female appears to make all movement decisions (Rasa 1987). However, as the dominant female is also the sole breeder in the group (Creel & Creel 1991) the energy-consuming reproductive activity may make her the hungriest individual. This hypothesis is supported by a study on meerkats, *Suricata suricatta*, in which dominant females lead the groups more often when lactating than during other periods (Turbé 2006). However, evidence is still ambiguous for whether energetic reserves are important for decision making in social foragers (Rands et al. 2008).

In this study, we analysed initiation of group movement by focusing on the initiation of morning group departure from their overnight dens in banded mongooses, *Mungos mungo*. Banded mongooses are small, cooperatively breeding carnivores that live in stable groups (Cant 2003) with little or no reproductive skew among females and no linear dominance hierarchy (Cant 2000). Multiple females, but typically not all adult females, breed in synchrony and all of them usually give birth on the same day (Cant 2000). Banded mongooses are diurnal and emerge from their communal overnight den after dawn and leave the den area to forage as a cohesive group. When foraging, group members are more spread out, but group cohesion is always maintained by contact calls (Rood 1975). As the whole group departs 'en masse' banded mongooses provide a unique opportunity to study factors influencing the initiation of group departure among many individuals in a society with low reproductive skew among females.

We investigated the effects of identity, reproductive state and low energetic reserves caused by low foraging success on the likelihood of initiating group departure. Specifically, we analysed whether age, sex and reproductive state influenced the frequency of initiation attempts of individuals. We also investigated whether an initiator's morning weight was relatively low in comparison to its morning weight taken on noninitiating days, and whether an initiator's weight change from the previous day to the day of initiating was more negative compared to the weight changes of the other group members over the same time period. To test the influence of low energetic reserves, we used short-term deprivation of food/feeding experiments. We predicted that in cooperatively breeding species, such as the banded mongoose, in which females exhibit low reproductive skew (Cant 2000; Cant et al. 2011; Hodge et al. 2011) and lack a clear linear dominance hierarchy, initiation of group departure would be variable and influenced by the female's reproductive state during synchronized breeding periods. Furthermore, if initiation of group departure were to be influenced by low foraging success we would first expect initiators to have a lower morning weight than when they are not initiating. Second, we predicted initiators to have a more negative weight change than other group members over the same time period. Third, we expected that individuals deprived of food would initiate group departure on the following morning more often than experimentally fed individuals.

METHODS

Study Site and Animals

Data were collected from July 2006 to November 2007 on a wild but habituated population of banded mongooses living on and around Mweya Peninsula, Queen Elizabeth National Park, Uganda (0°12′S, 29°54′E). The vegetation of the study site was mainly short grassland interspersed with numerous dense thickets (for details of the study area see Cant 2000; De Luca & Ginsberg 2001). Our study population consisted of 142 adult individuals in six groups, ranging from seven to 44 individuals per group allowing close-range observations. Animals were classified as adults (>12 months), subadults (6–12 months), juveniles (3–6 months) and pups (<3 months). To allow long-term identification of each individual, a tattoo of the group code and individual number were applied to the inner thighs of all individuals during their first capture (see Cant 2000 for further details). To identify individuals in the field, all of them were trapped on a regular basis. Traps containing mongooses were covered with a cloth and driven to the laboratory on the back of a pick-up truck. Individuals were coaxed from the traps into a black cloth bag tied around the entrance, and a mask delivering isoflurane was placed over the muzzle through the cloth (see Jordan et al. 2011 for further details). At the laboratory, adults were fitted with colour-coded plastic collars. Subadults and infants were marked by shaving a small area of fur on the rump and pups were individually marked with hair dye on small areas of fur. Trapping and marking procedures are described in detail elsewhere (Cant 2000; Hodge 2007; Jordan et al. 2010, 2011). To locate groups easily, one individual in each group was fitted with a refurbished Sirtrack radiocollar (Sirtrack, Havelock North, New Zealand) weighing a mean ± SD of 22.85 ± 3.11 g (range 17–28 g), which is 1.46% of the body mass (range 0.95–1.87%; Jordan et al. 2010). Radiocollars were fitted following procedures outlined for meerkats (Golabek et al. 2008) and were rotated among adult group members approximately every 6 months. The study was approved by the Uganda Wildlife Authority.

Behavioural Observations

Data on initiation of group departure from the den were collected by two observers in six social groups on 412 mornings (range 40–102 days per group). To localize the group, we radiotracked them in the late afternoon and followed them until they went into the den around sunset. On the following morning we waited beside the den until individuals emerged, when we weighed them (see below). After being weighed, they stayed closely together until an individual initiated group departure by moving away from the den area (defined as at least 10 m away from the den in any direction).

To obtain data on who initiated group departure we observed 503 initiation attempts. In 84 initiation attempts we could not identify the initiator of group movement. Of the remaining 419