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

attempts, only eight (1.9%) were initiated by subadults. Subsequently, we excluded these eight initiation attempts and analysed the 411 initiation attempts made by adult individuals. To investigate how often individuals tried to initiate group movement we calculated a proportion of initiation attempts for all adult individuals. This was calculated by dividing all initiation attempts of each adult individual by the number of all adult initiation attempts occurring in its group, when the focal individual was present. We then investigated the influence of sex, relative age (i.e. whether an individual belonged to the older or the younger half of all adult group members at the time the initiation attempt occurred) and age ranks on the proportion of initiation attempts.

During periods of synchronized pregnancy and lactation, we tested whether the observed frequency of initiation attempts made by individuals of a particular reproductive state differed from the frequency expected by chance. To do so, we first noted the sex, and for females the reproductive state, of the initiator and counted the individuals present in each category (reproductive female, nonreproductive adult female, adult male). Second, we determined the total number of initiations of individuals of a particular category and counted the individuals present in a certain category during all initiation attempts within that group. We then calculated the observed and the expected percentages of initiation attempts for each of the categories within the six social groups. During the gestation period (approximately 60 days), pregnancy becomes evident from around the fourth week of gestation, as females have visibly swollen bellies (Gilchrist 2001) and gain weight. Hence, we analysed data from the last 4 weeks of pregnancy and assigned, after each initiation attempt, the reproductive state of the initiator and the number of pregnant females, nonpregnant females and males present. For initiation attempts occurring during periods of lactation, we determined the number of lactating females within the group by direct observation of females suckling pups and by investigating signs of lactation on trapped and anaesthetized females. Anaesthetized females were processed immediately and released immediately afterwards, typically within a few minutes (for trapping techniques see Jordan et al. 2010). We analysed data derived from periods of lactation from the first 6 weeks after females had given birth when lactation is strongest and pups almost exclusively depend on milk for nutrition. Data from periods in which particular females were still lactating (within the first 6 weeks of lactation), but already clearly pregnant again, were omitted. We did not analyse data collected during the few periods of nonsynchronized breeding when some females were pregnant and others were lactating.

Weighing Methods and Weight Data of Initiators

As part of a long-term project, individuals have been habituated to be weighed in the field (see Hodge 2005, 2007) with a portable electronic balance (Sartorius TE4101, Sartorius AG, Goettingen, Germany) near to their den. We continually attracted individuals to the spot where weights were taken by distributing small quantities of bait in the form of a few rice corns with sauce on the ground during the weighing process. In response to a reward of a drop of milk (cow milk powder dissolved in water) put in the portable balance, individuals either stepped on it themselves or were lifted onto it by the observer. While licking the milk individuals remained calm and weights could be read without fluctuations. With few exceptions, adult individuals were weighed regularly and their offspring were habituated to be weighed. The whole weighing process usually lasted between 5 min and 15 min depending on the group's size. To analyse whether short-term foraging success may influence the likelihood of initiating group departure, we compared the morning weight of an initiator (W_{ini}) with its morning weight

from the previous day ($W_{iniprev}$) and calculated the initiator's weight change (C_{ini}):

$$W_{ini} - W_{iniprev} = C_{ini}$$

C_{ini} was calculated only if the initiator did not initiate group departure on the previous day ($W_{iniprev}$). For each initiator, we analysed the first initiation attempt for which weights were collected.

Initiators' weight data

We compared an initiator's weight change (C_{ini}) with its control weight change (C_{cont}) calculated on 2 days in succession ($W_{cont}-W_{contprev}$) on which this individual did not initiate group departure:

$$W_{cont} - W_{contprev} = C_{cont}$$

In males, the control weight change (C_{cont}) was calculated from the next period in time in which weights of an initiator were collected. In females, the control weight change (C_{cont}) was calculated from the next period in which we weighed an initiator in the same reproductive state (pregnancy, lactation, nonreproductive but adult). Furthermore, in females, we analysed their first initiation attempt observed during the three reproductive states if data were available. We chose not to compare the weight of the initiator with the individual's average weight as seasonal food availability and differences in female reproductive state may influence an individual's body weight. Instead, comparing weights within a short time frame controls for these constraints mentioned above.

Initiator's versus group members' weight change

To analyse whether relative weight change may influence the likelihood of initiating group departure we compared the weight change of an initiator (C_{ini}) with the weight change of all other adult group members weighed during the same 2 days. To do so, we calculated for each initiator a relative weight change score (RS_{ini}) as suggested by Barelli et al. (2008):

$$RS_{ini} = (R_i - 1)/(N - 1)$$

R_i denotes the weight change rank of the initiator and N denotes the number of weighed adult group members. Therefore, RS_{ini} varied from 0 if the initiator had the most negative weight change to 1 if the initiator had the most positive weight change of all group members. We then compared an initiator's weight change score (RS_{ini}) with the mean weight change score of 0.5.

Short-term Deprivation of Food/Feeding Experiment

To test whether nutritional constraints caused by low foraging success may influence the likelihood of initiating group departure we carried out short-term deprivation of food/feeding experiments. We analysed whether individuals that were deprived of food in the afternoon were more likely to initiate group departure on the following morning than individuals that were fed by the observers. To account for differences in the foraging abilities between individuals we captured all individuals taking part in the experiment and fed half of them, whereas the other half were deprived of food. Individuals were captured in the afternoon around 1430 hours and released in the evening near the den around 1900 hours (as the study site lies just about 20 km south of the equator the daylength does not change much and it always gets dark a few minutes after 1900 hours). As less than 2% of the observed initiation attempts were undertaken by nonadults only adult individuals were captured for the experiment. We captured individuals using box traps

(67 × 23 cm and 23 cm high; Tomahawk Live Trap Co., Tomahawk, WI, U.S.A.). We did not capture the individual that was fitted with a refurbished radiocollar and we left a few other adults to stay with the offspring. Trapped individuals were carried to a nearby vehicle and driven to the laboratory, where individuals were then transferred to a cloth bag until fully anaesthetized to minimize stress (see Jordan et al. 2010 for details on trapping techniques). During this removal of the group, we replaced the individuals' colour-coded plastic collars in adults, and shaved a small area of fur on the rump in subadults during anaesthesia, for individual identification. After these procedures, which took about 5 min, individuals were placed back into the traps. Traps were covered by fabric and water to drink was provided inside. Afterwards half of the captured group members were fed and the other half were deprived of food in alternating order according to their age. To know how much food should be provided, we measured the weight gain of banded mongooses during a previous afternoon's foraging. We weighed individuals of the six experimental groups around 1430 hours and again before they went back into their den around 1900 hours (duration between the measurements: mean ± SD = 260.1 ± 10.7 min, N = 59). The individual's weight gain ranged between −22 g and +68 g (mean - ± SD = 23.8 ± 22.8 g, N = 59). Thus, we simulated a good afternoon's foraging success by providing 50 g of fried egg for the individuals that were to be fed. To account for different energetic requirements among females we did not conduct the experiment when females were highly pregnant or lactating. Afterwards we radiotracked those individuals that had not been captured close to their evening den and released the captured individuals near them around 1900 hours. We observed the individuals going into the den and stayed near the den for another 15 min.

On the following morning we arrived near the den at dawn and waited there until individuals emerged. The identity of the individual initiating group departure was noted by both observers. We intended to conduct the experiment twice in a paired design in the six experimental groups so that each captured individual was deprived of food once and fed once. After carrying out an experiment we waited at least 3 weeks before conducting another experiment of this type. In seven cases the experiment could not be analysed and was repeated for the following reasons. In three cases the initiator of group departure could not be identified by one or both of the observers, in three cases an individual that was not captured on the previous afternoon initiated group departure on the following morning, and, in one case, interference with other wild animals did not allow close-range observation of group departure. Of the intended 12 experiments we were able to conduct 11, as in one group the experiment failed four times in a row for reasons mentioned above.

Statistical Analyses

Statistical tests were performed using R 2.7.1/2.9.1 (The R Foundation for Statistical Computing, Vienna, Austria, http://www.r-project.org). To analyse factors that might affect an individual's frequency in initiating group departure we carried out generalized linear mixed-effect models (GLMMs) with quasibinomial error structure and logit-link function. We controlled for the repeated sampling of the same group with 'group' fitted as a random factor (Crawley 2002) using the packages lme4 (Bates et al. 2008) and MASS (Venables & Ripley 2002). Nonsignificant factors were omitted from the final models (Crawley 2002). All interactions were nonsignificant and were thus omitted from the final models (Engqvist 2005). From the resulting F values we calculated the P values according to Faraway (2005). To investigate whether the age ranks of the adult individuals correlated with their proportion of initiation attempts within the six social groups, we conducted Spearman rank correlations. Individuals born on the same day were

assigned age ranks randomly within their age range. We analysed the influence of the different reproductive states on initiation attempts by comparing the observed percentages of initiation attempts of individuals of a particular reproductive state with their expected percentages of initiation attempts according to their frequency within the social group. Because of the sample size and the distribution of data we used exact Wilcoxon signed-ranks tests (Sokal & Rohlf 1995; Mundry & Fischer 1998). To compare the initiators' weight changes (C_{ini}) with their control weight changes (C_{cont}) we carried out linear mixed-effect models (LMM) using the packages nlme (Pinheiro et al. 2006) and MASS (Venables & Ripley 2002). To analyse whether the initiators' weight change scores (RS_{ini}) were significantly lower than the mean weight change score of 0.5 we conducted a t test. To test whether individuals that were experimentally deprived of food were more likely to initiate group departure compared to the likelihood of doing so expected by chance we conducted a one-tailed exact binomial test.

RESULTS

Initiation of group departure was highly variable with 103 of 142 (73%) adult individuals initiating group movement at least once. Only a few individuals either showed a substantially higher initiation rate than predicted or never attempted to initiate a group movement (Fig. 1). Overall, the proportion of initiation attempts was not influenced by the relative age of an individual (GLMM: $F_{1,139} = 1.6$, $P = 0.2$). Within the six groups, the age ranks of the adult individuals correlated only in one group with their proportion of initiation attempts (group D: $r_S = 0.54$, $N = 28$, $P = 0.003$; group B: $r_S = 0.28$, $N = 33$, $P = 0.12$; group F: $r_S = 0.12$, $N = 27$, $P = 0.54$; group H: $r_S = −0.25$, $N = 29$, $P = 0.19$; group S: $r_S = 0.05$, $N = 9$, $P = 0.9$; group V: $r_S = 0.38$, $N = 16$, $P = 0.18$). The proportion of initiation attempts was not influenced by the sex of an individual (GLMM: $F_{1,139} = 2.6$, $P = 0.11$).

The initiation attempts of females, however, were influenced by their reproductive state. During synchronized breeding attempts, pregnant females tended to initiate group departure more often than expected (exact Wilcoxon signed-ranks test: $T^+ = 19$, $N = 6$, $P = 0.094$), whereas nonpregnant females did not initiate group departure more often than expected ($T^+ = 9$, $N = 6$, $P = 0.79$). Males tended to initiate group departure less often than expected during periods of synchronized pregnancy ($T^+ = 1$, $N = 6$, $P = 0.063$; Fig. 2). During periods of synchronized breeding lactating females initiated group departure more often than expected (exact Wilcoxon signed-ranks test: $T^+ = 21$, $N = 6$, $P = 0.031$), whereas nonlactating females did not initiate more often than expected ($T^+ = 6$, $N = 6$, $P = 0.79$) and males initiated less often than expected during these periods ($T^+ = 0$, $N = 6$, $P = 0.031$; Fig. 3).

The weight change during the 2-day period in which the focal individual initiated group departure on the second day did not differ from the control weight change on the 2 days on which the same individual did not initiate group departure. Overall, the initiators' weight changes during the initiation period were not more negative than the control period weight changes (LMM: $N = 50$, estimate ± SE = 3.6 ± 5.2, $t_{49} = 0.69$, $P = 0.5$). The males' and females' weight changes during the initiation period were not more negative than the weight changes during the control period (males: LMM: $N = 26$, estimate ± SE = 5.8 ± 7.7, $t_{25} = 0.75$, $P = 0.46$; females: LMM: $N = 24$, estimate ± SE = 1.2 ± 7, $t_{23} = 0.17$, $P = 0.87$). In pregnant females, lactating females and nonreproductive females the weight changes during the initiation period were not significantly more negative than the control period weight changes (pregnant females: LMM: $N = 10$, estimate ± SE = 2 ± 6, $t_9 = 0.34$, $P = 0.75$; lactating females: LMM: $N = 15$, estimate ± SE = 5.6 ± 10.8, $t_{14} = 0.52$, $P = 0.61$; nonreproductive females: LMM:
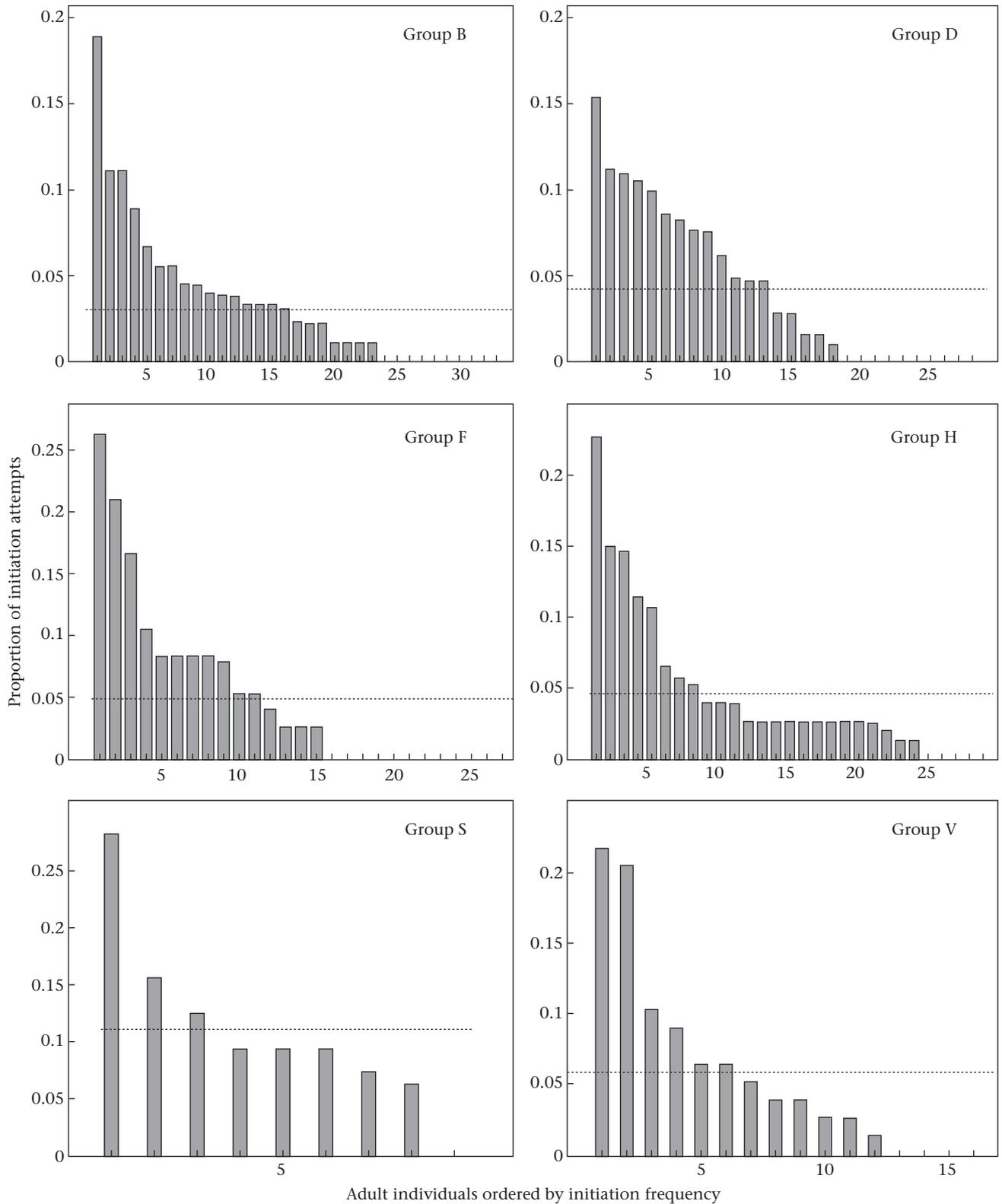
Figure 1. The individual variation in the proportion of initiation attempts ordered by the initiation frequency of the adult individuals for the six social groups (groups B, D, F, H, S, V). The dashed line (− − − −) indicates the predicted proportion of initiation attempts if all group members initiated equally often.

$N = 10$, estimate $\pm$ SE $= -3 \pm 10$, $t_9 = -0.03$, $P = 0.98$). Furthermore, the weight change score of initiators (RS_{ini}) was not significantly lower than the mean weight change score of 0.5 (observed mean $RS_{ini} \pm$ SE $= 0.479 \pm 0.04$, $t_{49} = -0.494$, $P = 0.62$).

In our deprivation of food/feeding experiment, deprived individuals initiated group departure more often than fed individuals (one-tailed binomial test: test proportion $= 0.5$, $N = 11$, $P = 0.033$). Group departure was initiated in nine cases (82%) by individuals
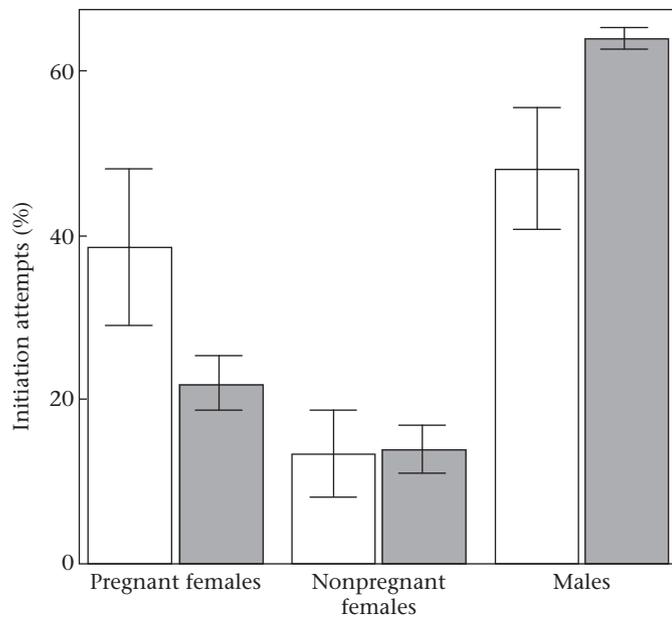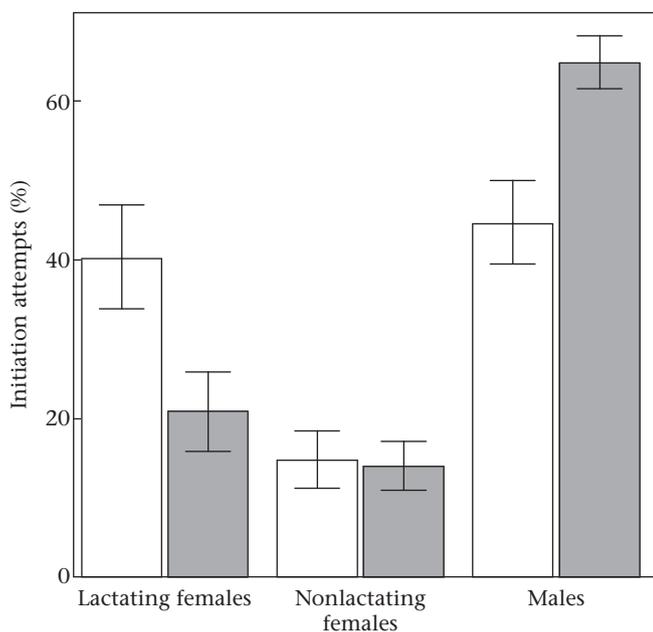
Figure 2. Percentages (mean ± SE) of initiation attempts, during periods of synchronized pregnancy, of pregnant females, nonpregnant females and males (means of six social groups, derived from 95 initiation attempts, including data of 50/92 females/males). White bars: observed percentages of initiation attempts; grey bars: expected percentages of initiation attempts according to the frequencies of occurrence within the six social groups.

that were deprived of food whereas individuals that were fed by the observers did so in only two cases (18%).

DISCUSSION

In banded mongooses initiation of group departure from the den was highly variable. More than 70% of adult individuals

Figure 3. Percentages (mean ± SE) of initiation attempts, during periods of synchronized lactation, of lactating females, nonlactating females and males (means of six social groups, derived from 129 initiation attempts, including data of 50/92 females/males). White bars: observed percentages of initiation attempts; grey bars: expected percentages of initiation attempts according to the frequencies of occurrence within the six social groups.

initiated group departure at least once. Only a small proportion of group members initiated movement substantially more often than predicted, or never attempted to initiate. The likelihood of initiating group departure did not differ between the sexes nor was it influenced by the relative age of the adult individuals. However, during periods of synchronized breeding, pregnant females tended to initiate group departure more often than expected and lactating females initiated more often than expected compared to their occurrence within the social groups. Our analyses of weight gain of individuals initiating group departure showed first that the initiators' weights in relation to their weight of the previous day were not significantly more negative than their weights in control periods. Second, the relative weight changes of initiators were not significantly more negative than those of the other adult group members. Yet, in contrast to these findings, the results obtained from the deprivation of food/feeding experiments revealed that deprived individuals were more likely to initiate group departure.

Age ranks of the adult individuals correlated with the likelihood of initiating group departure in only one of the six social groups. Similarly high percentages of group members involved in initiation of group movement have been shown in studies on primates (Leca et al. 2003; Jacobs et al. 2008; Stueckle & Zinner 2008). The degree of variability in leadership of group departure might be influenced by the species' social organization as described in lemurs (Jacobs et al. 2008) and macaques (Sueur & Petit 2008; for a review on the influence of social systems on decision making in collective movements see Petit & Bon 2010). For example, in lemur species in which females are dominant over males, females are primarily responsible for the time and direction of departures (Erhart & Overdorff 1999). In a lemur species with no female dominance, leadership is distributed among all group members (Jacobs et al. 2008). In line with these results from primate studies, the social system might also influence leadership in different mongoose species. In the cooperatively breeding dwarf mongooses, with a single breeding female, travel decisions are made by the dominant female (Rasa 1987), whereas based on our results, from a low reproductive skew society, there is evidence that neither social dominance nor personality traits appear to influence initiation of group departure. Banded mongoose social groups lack a clear linear dominance hierarchy and if personality characteristics, such as activity (Beauchamp 2000) or boldness (Ward et al. 2004; Leblond & Reebs 2006) were of importance, leadership should be consistent or at least less variable than observed. Knowledge about important food resources, as for example shown in ravens, *Corvus corax* (Wright et al. 2003), is unlikely to influence their leadership roles, as banded mongooses roam all over their relatively small territories in search of their widely distributed invertebrate and small vertebrate prey (Rood 1975). However, during periods of synchronized breeding, pregnant female banded mongooses tended to initiate group departure more often than expected, although not significantly so, and lactating females initiated more often than expected compared to their occurrence within the social groups.

The female reproductive state, and lactation in particular, had an influence on leadership of group departure in banded mongoose. Thus, in the closely related dwarf mongooses, where the dominant female produces several litters a year (Creel & Creel 1991), consistent leadership in travel decisions by dominant females might be influenced more by their energy-consuming reproductive activity than their dominance status. This hypothesis is supported in meerkat groups, which have high reproductive skew and in which the dominant female is typically the sole breeder in the group. The dominant female here most frequently takes a leading role during pregnancy and lactation periods, but not during nonreproductive periods (Turbé 2006). These findings suggest that, independent of the degree of reproductive skew among females, the reproductive

state, particularly lactation, appears to have a greater influence on the initiation of group departure than the species' social organization.

Contrary to our prediction, the variable leadership in group departure was not influenced by the weight gain of initiators suggesting that the foraging success of the previous day is not the sole key determinant of roles underlying initiation of group departure in banded mongooses. Although pregnant females tended to initiate and lactating females initiated group departure more often than expected, females in these reproductive states did not weigh significantly less when initiating group departure. Studies have shown that the variability in energetic needs between individuals in a group is highest during pregnancy and lactation (Scantlebury et al. 2002) and that lactation is energetically demanding (Dall & Boyd 2004). As reproducing females may have high metabolic requirements throughout pregnancy and lactation, their overall energetic demands appear to be more influential for leadership roles than their short-term foraging success on the previous day. Consequently, individuals with high energetic demands may become leaders even while having short-term high foraging success. Apart from pregnant and lactating females, nonreproductive females and males did not weigh significantly less when initiating group departure. For some of these individuals, the time available for foraging might often be limited, since, in cooperative breeders in which individuals provide care to offspring that are not their own, the investment in cooperative activities commonly varies among helpers (Cockburn 1998). In banded mongooses, contributions to pup care activities are strongly male biased (Hodge 2007). Until pups are able to forage independently, males contribute more to babysitting and provisioning pups with food items (Rood 1974; Gilchrist 2001, 2004; Cant 2003; Hodge 2005, 2007). Hence, in anticipation of their high contribution to pup care during the day, males may become leaders in determining when and where to forage even when their foraging success on the previous day was high. The same argument might apply for nonreproductive females. They may initiate group departure from the den independent of their previous day's foraging success as mothers that are not pregnant provide more food items to foraging dependent pups than pregnant mothers (Hodge 2007).

In contrast, the results obtained from the deprivation of food/feeding experiments revealed that individuals deprived of food were more likely to initiate group departure. In line with the predictions of the theoretical models (Rands et al. 2003; Conradt et al. 2009; Sueur et al. 2010) energetically needy individuals became leaders in social groups of banded mongooses. By feeding half of the captured adult individuals, we simulated a situation in which the remaining half of the subjects should have had substantially lower energetic reserves. In our experimental design the discrepancy in the foraging success between the two treatment groups was likely to be higher than the differences between individuals occurring naturally. Normally, even individuals that are heavily involved in pup care should find some time to forage for themselves. Hence, leadership roles influenced by such wide differences in foraging success are not likely to occur often under natural conditions.

Although our deprivation of food/feeding experiments provided evidence that 'leading according to need' may also occur in small groups with global communication, our analysis of weight data did not reveal an influence of short-term weight gain on the likelihood of initiating group departure. Hence, it appears that generally the foraging success of the previous day is not the sole key determinant underlying leadership roles in banded mongooses (see King et al. 2009). Instead, factors such as consistently high energetic demands during reproductive periods, asymmetries between individuals in their foraging efficiency and their time available for foraging, as well as the initiator's foraging success in relation to that of other group members, may often be as influential as an individual's low energetic reserves. As such, our results are in line with the predictions of recent game-theoretical modelling on the emergence of leaders in foraging pairs. Given that the qualities of individuals can differ, the resulting changes in behaviour may be complex (Rands et al. 2008). Our findings suggest that, as in the banded mongoose, also in other social species and particularly in other cooperative breeders, the determinants underlying variable initiation of movement decisions might be diverse.

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