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Caregivers recognize and bias response towards individual young in a cooperative breeding mammal, the banded mongoose

J. S. Gilchrist[1,2], E. Otali[3] & F. Mwanguhya[4]

1 Department of Zoology, University of Cambridge, Cambridge, UK
2 School of Life Sciences, Napier University, Edinburgh, UK
3 Kibale Chimpanzee Project, Kibale Forest National Park, Uganda
4 Banded Mongoose Research Project, Queen Elizabeth National Park, Uganda

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Correspondence
Jason S. Gilchrist, Current address: School of Life Sciences, Napier University, 10 Colinton Road, Edinburgh EH10 5DT, UK.
Email: j.gilchrist@napier.ac.uk

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Abstract

In research on parental care and cooperative breeding an issue is whether caregivers recognize individual young and therefore preferentially care for those young that will maximize inclusive fitness gains. This field study experimentally evaluates whether caregivers within groups of the cooperative breeding banded mongoose (a communal breeding species that produces litters of mixed parentage) exhibit individual recognition and increased responsiveness to the pup to which they are normally associated within a stable escort–pup pairing. A focal pup was presented to its group under controlled circumstances following temporary removal. The focal escort of a specific pup was more responsive to controlled presentation of that pup than other adults (a control escort, other escorts and non-escorts), spending a greater amount of time in close proximity. This study therefore demonstrates individual recognition and increased responsiveness by adult caregivers to associated pups in the banded mongoose. Thus, caregivers may selectively provide care for specific young within a litter, potentially increasing their inclusive fitness.

Introduction

The adaptive value of both individual and kin recognition lies in the ability of an individual to interact with other individuals in a manner that maximize its' inclusive fitness. We expect individuals to invest in their own young to maximize their lifetime inclusive fitness (Winkler, 1987; Clutton-Brock, 1991). However, fitness may also be increased by directing 'altruistic' behaviour towards those with which future reciprocal 'altruistic' interactions are more likely to occur (Trivers, 1971), or in the more specific case of kin recognition, more closely related individuals (Hamilton, 1964; Komdeur & Hatchwell, 1999; Griffin & West, 2003; Hepper, 2005). In spite of the great interest, evidence of individual and kin recognition is lacking in an adult to young context (in respect of care) with regards to parental or alloparental care in vertebrates [other than in the ability of parents or helpers to recognize familiar young via associative learning or simple 'rules of thumb' in some species (Komdeur & Hatchwell, 1999)]. While care may be biased towards a specific class of young, for example, the more needy or valuable sex (Clutton-Brock, 1991; Brotherton *et al*., 2001), or by size (Stamps *et al*., 1985; Drummond, Gonzalez & Osorno, 1986), evidence of individual or kin recognition towards specific young within a brood or litter is lacking. Even in species with broods or litters with mixed paternity, caregivers rarely differentiate between young but adjust their overall level of care to the brood or litter relative to their expected maternity or paternity (Davies *et al*., 1992). When biased care towards specific young occurs, or towards needier or larger individuals, this bias may be driven by the young rather than the caregiver (Clutton-Brock, 1991; Kacelnik *et al*., 1995; Ostreiher, 1997; Slagsvold, 1997; Drummond, 2006). We present an experimental field test of caregiver discrimination and individual preference for young within a communal breeding mammal with litters of mixed parentage.

Banded mongooses (*Mungos mungo*) are apparently unique among cooperative breeding vertebrates in that particular pups are cared for by specific individuals (usually adults) in a one-to-one pup–escort association (Cant, 1998; Gilchrist, 2004). However escorts do not appear to exhibit a preference to provision particular pups within a communal litter, and simply follow a 'feed the nearest pup' rule (Gilchrist, 2004). Thus, the pup and not the escort is generally responsible for maintaining pup–escort association – the pup actively follows and defends its escort against the approach of other pups (Gilchrist, 2004). But do escorts display a preference to care for specific pups?

We investigate the maintenance of this unusual system by testing whether banded mongoose escorts display an active preference to respond to the pup with which they regularly associate. We test the null hypothesis that escorts exhibit equal response towards pups within a communal litter (i.e. they do not preferentially care for the pup with which they were associating). Our experiment involves temporary removal of two pups from banded mongoose groups, with subsequent presentation of a single pup (in a controlled environment) to the group to test whether the pup provokes a higher intensity response from the pup's escort than from other group members. If our predictive hypothesis is supported, the escort of a pup will be more responsive than other group members to its associated pup.

Methods

Data collection

The banded mongoose lives in mixed sex groups with multiple breeding males and females (Rood, 1975). Up to 10 females within a group can give birth synchronously in the same den producing a communal litter of mixed parentage (Cant, 2000; Gilchrist, Otali & Mwanguhya, 2004; Gilchrist, 2006). A number of individuals in the group contribute to rearing the pups, by babysitting, allonursing, escorting and provisioning (Rood, 1974; Gilchrist, 2001, 2004; Cant, 2003).

This experimental study was conducted in Queen Elizabeth National Park, Uganda (0°12′S, 27°54′E). All mongooses were located, trapped and marked (Cant, 2000; Cant, Otali & Mwanguhya, 2001). The research and procedures were licensed by the Uganda Wildlife Authority and the Uganda National Council for Science and Technology and follow the code of ethics and guidelines outlined by the Association for the Study of Animal Behaviour and the Animal Behaviour Society (ASAB, 2006).

Twenty-four pup-removal experiments were conducted in four banded mongoose groups between 29 April 2002 and 19 April 2003. Each experiment incorporated two focal pups and two focal escorts, and therefore two pup presentation trials ($n = 47$ trials, with one experiment lacking one trial). In addition, response was scored for all other group members (excluding pups) per trial, including other escorts whose pups were present throughout the two trials per experiment. The four groups observed for these experiments (groups 11, 1b, 1h and 4b) were chosen because their habituation level allowed targeted pup capture and close observation. Group size (count of number of individuals over 90 days age) varied from 14 to 36 (26.80 ± 1.26), with between 3 and 13 (7.48 ± 0.60) dependent pups present at the beginning of each experiment. The 24 – pup-removal experiments (47 – pup-presentation trials) were run over 10 communal litters, with one to four experiments (two to eight trials) per litter. All trials were conducted on post-weaned pups, after emergence from the den, within the period of pup dependence upon adults (30–90 days, Gilchrist, 2004), with pups aged 48 ± 1.17 days (mean ± SE), range 34–66.

An escort is defined as a group member (aged over 90 days old) that regularly associates with a specific pup (aged 90 days or less). Escorting is mainly performed by adult individuals over 1-year old (Gilchrist & Russell, 2007). Escorts provide care for pups in the communal litter by provisioning, sheltering, carrying, grooming and playing (Gilchrist, 2004). Groups were usually observed for 1 h in the morning and 1 h in the afternoon each day during the period of pup dependence. At the end of each observation, each group member was scored as 'in association' or 'not in association' based upon whether consistent adult–pup pairing was observed between individuals, where association is defined as close proximity (≤ 30 cm) between group member and pup. These summaries of association enabled identification of escort–pup pairs with strong and stable association. An association index for each individual was calculated as: number of observations in association/total number of observations. The association index potentially varies from 0 to 1. In practice, the index varied from 0 to 0.86. The total number of observations per individual (per communal litter) varied between 16 and 34. For analyses, in addition to using association index as a continuous variable, individuals with an association index of zero were categorized as non-escorts, and individuals with an association index of greater than zero were categorized as escorts.

To differentiate between a vacant escort (an escort whose pup has been temporarily removed) having a more intense response than other group members to a pup and an escort responding specifically to its paired pup, two pups were simultaneously trapped and removed from the group. For each experimental trial, we selected two escorts that each displayed a strong stable association with a pup (i.e. that consistently maintained close proximity to a specific pup over a period of days). The two escorts were classified as focal escorts and the two associated pups as focal pups. After 2 days of observation on the focal escorts and all pups, the two focal pups were removed for 2 days. For each presentation trial, one focal pup was then presented to the group in a Havahart cage trap ($60 \times 20 \times 20$ cm) for 10 min during which time we conducted 1 min instantaneous scan samples of individual identities within a 1 m and 5 m marked grid around the focal pup in the trap. An individual was scored as within the grid if its forelimbs occurred within the boundary. Trials were conducted within each group's home range and with all group members present. Free pups were not scored in these trials as they were not considered independent of other group members. Two observers collected this data positioned together *c.* 30 m from the grid and used binoculars (8×40) for observation. One observer collected data on individuals within the 1 m grid and the other observer collected data on individuals within the 5 m grid. In all but three experiments, the two trials were conducted on different days. In the same day trials, the group was allowed to settle for a minimum of 1 h and the protocol repeated for the second focal pup. Both focal pups were then released to rejoin the group. After the release, 2 days of observation followed on the focal escorts and all pups. Observers were not 'blind' to pup–adult association during these trials, but the strict criteria used in scoring presence within grid minimize the possibility of bias. Within a group, a minimum of 1 week elapsed between experiments.

During pup-release trials, focal-pup behaviour varied within and between pups. Focal-pup activity within the trap varied from inactivity (standing or crouching) to high activity (running back and forth), and from no vocalization to high vocalization (emitting a repetitive high pitched call).

During removal of the focal pups, the two removed pups were kept together; in a wire indoor cage (a Havahart cage trap, as above) with cloth bedding, and supplied with *ad libitum* food (egg and fish) and water. During this period, disturbance to the pups was minimized while monitoring was maintained. Two-day removal was necessary in order to monitor effects of pup removal on interaction and association between the focal escorts and other pups. The optimal point at which to conduct the pup-presentation trials was at the end of the removal period, before pup release, thus minimizing disturbance to the group and the removed pups. Removal of a pup for 2 days had no obvious ill effects in the short or long term, to either the pup or other group members. Pup weight on capture and release did not differ (paired *t*-test: $t=0.01$, d.f. = 37, $P=0.99$; mean weight change $=-0.0526\pm4.83$ g, with mean capture weight $=278.3\pm9.4$ g). On release, pups usually returned to their previous escort and the association resumed as before removal (83% of trials). Survival probability between removed and non-removed pups did not differ in the 7 days after release of the removed pups (IRREML: $\chi^2=0.43$, d.f. = 1, $P=0.51$, $n=178$, 48 removed pups and 130 non-removed pups treating each trial as independent (an individual pup can be a removed pup in one trial and a non-removed pup in other trials), with experiment fitted as a random effect, $n=26$ experiments). Mean survival probability of removed pups was 0.93, mean survival probability of non-removed pups was 0.95. Experimental and non-experimental litters did not differ in pup survival probability during and beyond the period of pup dependence (between 30 and 120 days age) (GLM: $F_{1,13}=0.03$, $P=0.86$, $n=98$ pups in 15 litters, with nine experimental litters and six non-experimental litters). The mean survival probability of pups in experimental litters was 0.59; mean survival probability of pups in non-experimental litters was 0.63. Removal and release had no effect on habituation of group members.

For each presentation trial, group members were classified as focal escort (escort of the presented focal pup), control escort (escort of the other removed pup), other escort (escort of a pup that had not been removed) and non-escort (adult not recorded as in association with a pup). Individuals were categorized in age classes as pup (0–90 days, dependent upon adult care), infant (91–182 days, between dependence and independence), sub-adult (183–364 days, independent but generally non-reproductive) or adult (>364 days, reproductive age adults, the age class responsible for the majority of pup escorting (Gilchrist, 2004; Gilchrist & Russell, 2007).

Statistical analysis

Data analyses were performed using GenStat 6.0. Analyses of response index tested whether the probability that a group member occurred within the grid differed between individuals. Generalized linear mixed models were fitted to the data using the IRREML procedure with logit link function. The dependent variate was fitted using a binomial function. The numerator was the number of scans that an individual was recorded within the 1 m or 5 m grid. The denominator was the total number of scans for the individual (11 scans over the 10 min). The proportion of scans in which an individual occurred within 1 or 5 m of the focal (presentation) pup was fitted as the response index. Fixed effects fitted to models included escort status (focal escort, control escort, other escort and non-escort), escort status II (escort/non-escort) and escorting index (on a continuous scale potentially varying between 0 and 1). Each term was run in a separate model due to the non-independence of the escorting variables. Ageclass, age (as a continuous variate) and sex were also run as fixed effects, with the age effects run in models separate from the escorting variables due to covariance (escorting is more common in the adult age category).

Analyses of response time tested whether the speed of individual responsiveness (the first time at which an individual occurred within the grid) of group members differed between individuals. Linear mixed models were fitted to the data using the REML procedure. The dependent variate was the first minute within which an individual entered the grid (from 0 to 10 min). Fixed effects fitted to models were as above.

In all models we included group identity ($n=4$), communal litter identity ($n=10$), experimental trial (number of pups presented, $n=47$) and individual identity of potential responders ($n=151$, including 79 adults, 43 subadults and 29 infants) as terms in the random model. This accounts for repeated sampling across error terms (Schall, 1991) and therefore avoids pseudoreplication. A random term was dropped from models when identified as a negative or zero component of variance. All two-way interactions between fixed effects were tested but were non-significant and are therefore not presented.

Where the fixed effect in a model was significant and contained three or more levels, *post hoc* pairwise comparisons were made between the levels using the *t*-test with the degrees of freedom set to lowest degrees of freedom of the error strata, which in this case equals 24 (the number of experiments, the random term with the highest component of variance). Using this value for the degrees of freedom is a conservative approximation (Brown & Prescott, 1999). The critical value applied to *post hoc* pairwise *t*-tests was therefore 2.06 (with d.f. = 24 for all pairwise tests, two-tailed). The mean values are provided ± standard error in text and Figure (error bars). All tests are two-tailed with significance defined as $P\leq0.05$.

Results are presented for the response of individuals to the focal (presented) pup, measured as presence and earliest presence within the 1 m grid. Results for the 5 m grid are consistent with the 1 m grid, but for simplicity only the latter are presented. All age categories (barring pups) are included in analyses. Results for escorting variables are consistent when restricting analyses to adults.

Results

Factors affecting proximity to focal pup (presence within grid)

Overall, responsiveness (occurrence within 1 m grid) was low. Focal escorts occupied the 1 m grid on 4.3% of scans [increasing to 6.5% of scans (minutes) if entries within each minute subsequent to the scan point are included]. The occurrence of an individual within 1 m of the focal pup differed significantly with respect to escort status ($\chi^2 = 8.35$, d.f. = 3, $P = 0.039$). The focal escort was more likely to be within 1 m of the focal pup than the control escort, other escorts and non-escorts (Fig. 1; focal escort vs. control escort $t = 2.51$, $P = 0.019$; focal escort vs. other escorts $t = 2.40$, $P = 0.025$; focal escort vs. non-escorts $t = 2.52$, $P = 0.019$; all other t statistics <0.95, with $P > 0.35$). In contrast, on average, escorts were no more likely than non-escorts to occur within 1 m of the focal pup (escort vs. non-escort category $\chi^2 = 0.43$, d.f. = 1, $P = 0.51$; escorting index as a continuous variable $\chi^2 = 1.96$, d.f. = 1, $P = 0.16$). Occurrence within 1 m of the focal pup was also not related to ageclass, age (as a continuous variate) or sex (ageclass $\chi^2 = 0.04$, d.f. = 2, $P = 0.98$; age $\chi^2 = 0.66$, d.f. = 1, $P = 0.42$; sex $\chi^2 = 0.33$, d.f. = 1, $P = 0.57$).

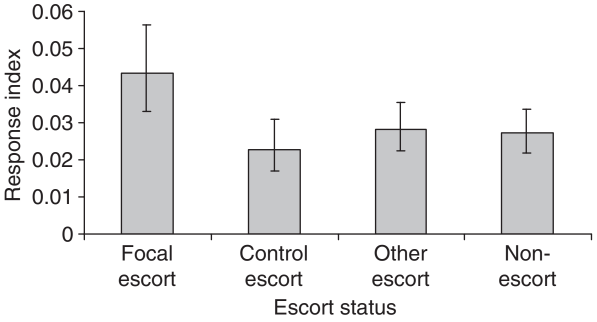

Figure 1 The response index for banded mongoose group members of differing escort status. Response index is the proportion of scans in which an individual occurred within 1 m of the focal (presentation) pup. Focal escort: escort of the focal pup. Control escort: escort of the absent removed pup (non-focal pup). Other escort: escort of a pup that had not been removed. Non-escort: group member not recorded as in association with a pup.

Factors affecting rapidity of response to focal pup (time of entry into grid)

For individuals that came within 1 m of the focal pup, the rapidity of response did not differ among escorting categories (focal escort vs. control escort vs. other escorts vs. non-escorting adults $\chi^2 = 1.03$, d.f. = 3, $P = 0.79$; escort vs. non-escort category $\chi^2 = 1.02$, d.f. = 1, $P = 0.31$; escorting index as a continuous variable $\chi^2 = 0.86$, d.f. = 1, $P = 0.35$). However, rapidity of response was affected by age, with older individuals on average entering the 1 m grid sooner than younger individuals (age $\chi^2 = 11.72$, d.f. = 1, $P = 0.001$, effect size $= -0.00034 \pm 0.00010$). In contrast, neither ageclass or sex had an effect (ageclass $\chi^2 = 1.82$, d.f. = 2, $P = 0.40$; sex $\chi^2 = 0.01$, d.f. = 1, $P = 0.91$).

Discussion

This study demonstrates that adult banded mongooses are capable of individual recognition. The focal escort was more responsive (spent more time in close proximity) to the presented focal pup than were other escorts, the control escort, and non-escorts within the group. That the focal escort responded to the focal pup, when on average escorts were no more responsive than non-escorts, highlights the role of individual recognition, as escorts are apparently not predisposed to assist pups under these circumstances. Neither can the increased responsiveness of focal escorts be explained by age or sex. In particular, the focal escort was more responsive than the control escort (an escort whose associated pup was similarly absent in the two days prior to the focal pup presentation) to the focal pup. Thus the focal escort was responding specifically to the identity of the caged pup, rather than responding to a pup in the absence of the pup recently in association with the focal escort. Otherwise we would expect a similar response from the control escort whose recently associating pup was also absent. Thus banded mongooses are capable of individual recognition, as adult escorts display an increased sensitivity or concern towards the pup that is normally paired with them in association.

Focal escorts were not quicker to respond to the presentation of the focal pup than other group members. However, rapidity of response (time to enter the 1 m grid) was quicker in older group members as latency to enter the grid decreased with age.

While focal escorts were more responsive (in terms of time spent in the grid) to the focal pup than other adults, on average responsiveness was low. Whilst conditions in the pup-response trials were controlled, their artificial nature, and variation in pup activity and vocalization, may have increased variation in escort response, and decreased intensity of escort response. Nevertheless, while responsiveness was low, escorts do recognize individual pups, and respond to the pup to which they were recently paired more so than other individuals, and more so than when they are not the focal escort.

The identification cues used by the focal escort (and other group members) to identify an individual pup within these trials are not known. Similarly, whether the mechanism is familiarity via association or *a priori* genetic imprinting (e.g. via phenotypic matching) is unknown. However, visual, auditory and olfactory cues are all possible targets for individual recognition within mammals (Komdeur &

Hatchwell, 1999; Tang-Martinez, 2001; Maletinska *et al.*, 2002; Mateo, 2002, 2004, 2006). Acoustic recognition has been shown to play a role in the escort–pup relationship within the banded mongoose (Muller & Manser, in press) and may be a more effective indicator of identity than visual or olfactory cues over medium-to-long distances in the relatively complex, vegetated habitat in which the banded mongoose lives.

Observations of banded mongoose suggest that escorts feed the nearest pup and that pups probably select an escort based upon escorts' intrinsic provisioning rates (Gilchrist, 2004). However, if escorts bias response and possibly care towards a specific pup (e.g. the provisioning rate of the escort may be affected by the identity of the nearest pup), the pup choice of an escort may not be so simple. The care and provisioning rate of individual escorts with respect to pups of different identity need to be evaluated to determine whether escort preference towards pups affects pup choice in selection of and competition for an escort. In addition, escorts may bias care towards pups that maximize the escort's inclusive fitness, for example, pups to which the escort is more closely related (Hamilton, 1963, 1964).

Previous research suggested that kin-directed altruism was unlikely to play a role in the distribution of pup care within the banded mongoose because banded mongoose pups (rather than escorts) actively maintain association, and adults follow a 'feed the nearest pup' rule (Gilchrist, 2004). However, if adults can recognize specific pups within the communal litter, kin-recognition remains possible (although individual recognition does not necessarily beget kin recognition) (Grafen, 1990). If kin recognition occurs in the banded mongoose, the coevolutionary linkage between indicators of relatedness (enabling kin recognition) and kin-directed altruism suggests kin selection may operate (Axelrod, Hammond & Grafen, 2004). The possible role of kin recognition, including parent–offspring recognition, obviously requires further investigation, particularly in light of the likely high level of relatedness between individuals within banded mongoose groups (Gilchrist *et al.*, 2004; Gilchrist, 2006), and the relatively low levels of genetic variation (Waldick, Johnson & Pemberton, 2003). The alternative benefits to an escort of individual recognition (excluding kin-directed altruism) towards pups, for example derived from familiarity, also require evaluation.

While this study presents evidence for individual recognition of young by caregivers, and preferential response to specific young by caregivers, pups still play a dominant role in maintaining escort–pup association by actively following and defending their escort (Gilchrist, 2004). Thus banded mongoose pups are capable of individual recognition of, and preferential association with specific adults. Acoustic playback experiments in the field confirm that pups and escorts recognize each other acoustically (Muller & Manser, in press). As in other species (e.g. sheep, *Ovis aries*, (Nowak *et al.*, 2007), adult–young recognition and response is likely mutual.

While the pup is the major determinant of the distribution of pup care within banded mongoose groups (Gilchrist, 2004), escorts are not totally passive and unbiased in their behaviour towards pups within the communal litter. Adults may indeed direct care to those pups within the communal litter from whom they will gain the maximum fitness benefits. This has implications for other vertebrate cooperative breeding species (mammals, birds and fish), where the possible role of individual recognition and biased care may have been overlooked. Caregivers may selectively provide care for specific young within the litter, potentially increasing their inclusive fitness.

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