



Mutual recognition of pups and providers in the cooperatively breeding banded mongoose

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Adults providing food to offspring are predicted to allocate care in a way that maximizes their fitness. Providers across taxa have been demonstrated to show preferences for particular young depending on the degree of relatedness, offspring sex or size. However, little is known about the cues providers use to discriminate among individual offspring. In the banded mongoose, *Mungos mungo*, a cooperatively breeding carnivore, dependent pups form long-lasting and exclusive associations with particular adults, their 'escorts', and receive the majority of care from these individuals. We performed acoustic analyses of pup distress calls and escort contact calls and found that pup distress calls are highly and escort contact calls are moderately individualized. In subsequent playback experiments, both pups and escorts were more responsive to calls of their association partners than to calls of other individuals. These results suggest that pups and escorts recognize each other vocally and mutually and that both pups and providers contribute to the maintenance of the pup–escort associations. Pups may benefit from vocal recognition of their escorts since this reduces the time spent alone, vulnerable to predators and without being fed. Escorts may be more responsive to their associated pup's calls than to another pup's calls because they preferentially care for this particular individual and/or because they were primed by constant exposure to its calls.

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Parents providing food to offspring are predicted to use a feeding regime that maximizes their long-term reproductive output (Clutton-Brock 1991; Weary & Krebs 1992). Parents may feed offspring of a brood equally (e.g. Leonard et al. 1994; Malacarne et al. 1994; Ostreier 1997) or they may preferentially feed offspring of a particular sex, age or size (reviewed in Lessells 2002). Preferences may differ between providers when parents differ in the cost of reproduction or in the benefits they gain from different types of offspring (Lessells 2002). In the extreme case of brood division, as observed in some bird species (reviewed in Lessells 2002), the two parents may provision separate sets of the brood almost exclusively. In a recent study on brood-dividing redstarts, *Phoenicurus ochruros*, Draganoiu et al. (2006) showed that parents discriminate acoustically between fledglings associated with them and fledglings associated with the other parent.

In a variety of bird and mammal species, nonreproductive helpers contribute to rearing offspring of other individuals, and these helpers are predicted to allocate care in a way that maximizes the benefit of helping (Brown 1987). For example, helpers may care preferentially for closely related young (Emlen & Wrege 1988; Russell & Hatchwell 2001) or increase investment when helping close kin (Reyer 1984; Komdeur 1994). Helpers may also preferentially care for future helpers, as has been suggested in meerkats, *Suricata suricatta*, where females are philopatric and contribute more to cooperative care than male helpers, and females preferentially feed female offspring (Brotherton et al. 2001).

For both parents and helpers, the scope for favouritism is restricted by the availability of options and the ability to discriminate among offspring. Whereas most broods containing multiple offspring probably include individuals of both sexes, variation in age or size may be small, particularly in small broods, and broods of a single pair of parents may offer little variability in relatedness. Furthermore, the potential for kin recognition may be restricted if no reliable association cues are available

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(Komdeur et al. 2004) and preferential feeding of certain individuals requires that the offspring can be distinguished individually (Draganoiu et al. 2006).

Parent–offspring recognition in mammals is usually mediated by olfactory (e.g. Romeyer et al. 1994; Levy et al. 1996; Jackel & Trillmich 2003), vocal (e.g. Insley 2000, 2001; Searby & Jouventin 2003; Fischer 2004) or a combination of olfactory, vocal and visual cues (e.g. Keller et al. 2003). In most cases, however, recognition is confounded with kinship since parents were shown to discriminate between their own and alien offspring but not between individual offspring to which they were equally related. Only few studies to date have demonstrated true individual recognition between offspring and their providers, independent of kinship or other confounding variables such as sex, age or size (e.g. Draganoiu et al. 2006). We studied individual recognition between pups and providers in a species that offers an opportunity to test for individual recognition independent of these confounding effects.

The banded mongoose, *Mungos mungo*, is a small (<2 kg) cooperatively breeding herpestid, in which up to 10 females of a group breed synchronously (Cant 2000) and nonreproductive individuals contribute substantially to rearing the offspring (Cant 2003; Gilchrist 2004). Banded mongooses are interesting subjects for the study of individual recognition because most pups consistently associate with the same adult or subadult ‘escort’. These associations are formed in the first few days after the pups emerge from the den and commonly remain stable for the whole period of dependence (about 6–8 weeks; Gilchrist 2004; Hodge 2005). During foraging, pups spend most of the time in the immediate vicinity (<1 m) of their escorts (Gilchrist 2004; Hodge 2005). As a consequence, pups get the vast majority of food from their escorts and very little from other group members (Bell 2006). Helpers commonly feed the pup nearest to them, which is usually their associated pup, and only rarely a pup further away (Gilchrist 2004). Overall, escorts give away more food than nonescorting individuals (Gilchrist 2004). Compared to pups that do not form an escorting association (usually the smallest of a litter), escorted pups get more food, grow faster, reach age of sexual maturity earlier and have a higher survival rate (Hodge 2005). Observations suggest that these associations are formed and maintained by the pups because the pups follow their escorts in 99% and escorts follow their pups in only 1% of all cases (Gilchrist 2004). However, experimental evidence showing which of the two parties maintains the association and how it is maintained is lacking. At short distance, pups and escorts may recognize each other by smell. However, long-distance recognition is required for the reunion after temporary separation, for example when the escort wandered off foraging while the pup was consuming a large prey item. In a habitat with a lot of structures obstructing vision (Rood 1975; Cant 2000), vocal recognition is probably the most efficient mechanism for this task.

We investigated whether pups and escorts recognize the calls of their association partners and whether both parties contribute to the maintenance of the escorting

associations. Pups emit distress calls when they become separated from the group but not when they are separated from their escort while they still have other group members nearby (C. A. Müller, personal observation). Adults constantly emit contact calls while they are foraging, both when with pups and when foraging by themselves, at a rate of 5–15 calls per min (C. A. Müller, unpublished data). We first recorded pup distress calls and adult contact calls and analysed both call types for individual differences (for spectrograms see Fig. 1). We then temporarily removed pups and escorts in separate experiments and conducted playbacks to test whether pups recognize their escort’s calls and vice versa. Additionally, these experiments allowed us to test which of the two parties contributes to the maintenance of the escorting association. Because pups clearly benefit from these associations, we predicted that pups would recognize their escort’s contact calls and that they would preferentially respond to playbacks of these calls compared to contact calls of other adults. If escorts recognize their associated pup vocally, we predicted that escorts would also preferentially respond to their associated pup’s distress calls. We used pup distress calls rather than the much more frequently occurring begging calls for these experiments because distress calls are presumably used to attract adults and because begging calls in pilot experiments did not induce obvious responses by escorts.

METHODS

We studied a wild population of individually marked banded mongooses on and around Mweya Peninsular in Queen Elizabeth National Park, Uganda (0°12’S, 29°54’E) between March 2004 and September 2005. For details on the study site and marking procedures see Cant (2000). We collected data and performed experiments on six groups that were habituated to observers following at a few metres distance. Group size ranged 15–53 individuals. Animals were classified as adults (>12 months, sexually mature), subadults (6–12 months), infants (3–6 months) and pups (<3 months). Pups are dependent on food provided by other group members, and adults as well as subadults may escort pups.

Recordings

We recorded pup distress calls when the pups were trapped for individual marking at an age of 25–53 days. Escort contact calls were recorded during foraging, at 0.5–1 m distance from the caller (for spectrograms see Fig. 1). In 2004 we used a Sennheiser ME 66/K6 directional microphone (Sennheiser Corp., Old Lyme, CT, U.S.A.) connected to a Sony TCD-D100 digital audiotape recorder (Sony Corp., Tokyo, Japan) and transferred the recordings onto a personal computer using an ESI Waveterminal U24 (Ego Systems Inc., Seoul, Korea). In 2005 we used a Marantz PMD670 audio recorder (D&M Professional, Kanagawa, Japan). All recordings were sampled at 16 bit and 48 kHz.

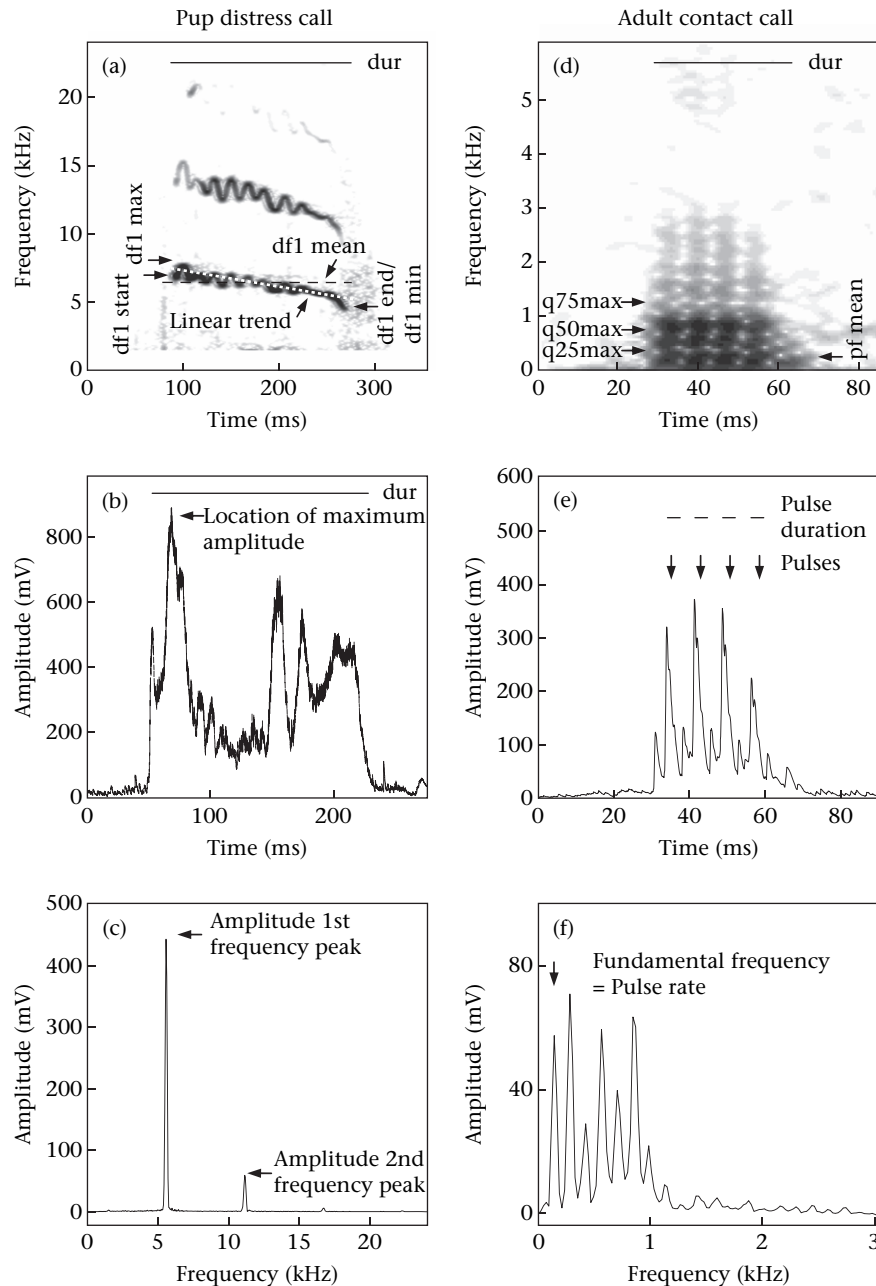


Figure 1. Spectrogram, amplitude envelope and amplitude spectrum of a pup distress call (a–c) and an adult contact call (d–f). Some parameters measured in the acoustic analyses are indicated. Spectrograms were created in Avisoft with time resolution 0.67 ms, frequency resolution 47 Hz and FFT length 1024 (distress call) or 256 (contact call). dur: duration of call; df1: frequency of first dominant frequency band; pfmean: mean peak frequency; q25/q50/q75 max: maximum frequency of first, second and third quartile. Note that, for the acoustic analyses, the parameters shown in b and c were measured from the digitized spectrograms and pulse rate (f) was measured from the amplitude envelope.

Acoustic Analyses

Calls with a good signal-to-noise ratio were selected in Avisoft SASLab Pro 4.38 (R. Specht, Berlin, Germany) and call parameters were measured using Avisoft and LMA 2005 (K. Hammerschmidt, Göttingen, Germany; for a detailed description of algorithms and calculation of parameters see Schrader & Hammerschmidt 1997). In total we

measured 20 parameters for the pup distress calls and 19 parameters for the adult contact calls (see Appendix and Fig. 1). Both programs offer a batch processing option, which enforces a degree of standardization missing when calls are analysed individually (Specht 2006). Some relevant parameters could be measured in only one of the two programs, whereas call duration and frequency of the first dominant frequency band (distress

calls) or quartile frequencies (contact calls) were measured with both programs. Calls were excluded if the values of one or more of these parameters differed by more than 5% between the measurements of the two programs. All measurements were done from spectrograms with fast Fourier transform (FFT) length 1024, frequency resolution 47 Hz and time resolution 1.33 ms (distress calls) or 0.67 ms (contact calls). In total, we measured 20 distress calls from each of 12 pups of one litter and from each of eight pups of a litter from a different group. Within both litters, the distress calls of all pups were recorded on the same day and all pups were born within 2 days. We further measured 20 contact calls from each of eight adults from one group, all potential escorts. Good-quality contact calls could be obtained from only few individuals of the other five groups, which prevented us from doing analyses of individual differences within these groups. For all parameters, we determined the potential for individual coding (PIC) as the ratio of between-individuals and within-individuals coefficients of variation (Robisson *et al.* 1993).

From the described set of parameters, we excluded those that had little potential for individual coding ($PIC = 1.0$; see Appendix). Furthermore, where two variables were highly correlated ($r > 0.8$), the less distinctive of the two (smaller PIC) was excluded. The remaining variables were entered simultaneously into a discriminant function analysis (DFA) in SPSS 13.0 to determine the individual distinctiveness of the calls. We used this 'direct' method based on all information available because it is less sensitive to random effects and correlating variables than the alternative 'stepwise' procedure and does not suffer from the latter's multiple testing issues (Mundry & Sommer 2007). We determined the probability of assignment to the correct individual based on the discriminant functions using the 'hold-out sample' method. That is, 80% of the calls were randomly chosen and used to calculate the discriminant functions, which were then used to assign the remaining 20% of the calls to an individual. This procedure was iterated five times and the average percentage of correct assignment found was compared to correct assignment by chance (bootstrapping with 10 000 runs).

Playback Experiments

We performed playback experiments after escorting associations had been stable for at least 3 days (i.e. a pup's nearest adult for at least 70% of the time during foraging was the same on 3 consecutive days). At that date, pups were aged 39–60 days. Of all pup–escort pairs in a group, only those for which good-quality recordings of calls had been obtained were tested. Within this subset, we randomly chose focal pairs from which one partner was temporarily removed and its calls played back to the remaining partner and control pairs from which one partner was removed at the same time but no calls were played back. Removals took place when the groups were foraging, between 0700 and 1100 hours or between 1600 and 1800 hours. Playback experiments were conducted on average 80 min (range 30–140 min) after the removal

using the Sony/Marantz recorder and portable speakers (Creative Travelsound; Creative Technology Ltd., Singapore). In total, we performed 13 pup removal and 12 escort removal experiments in six groups (one to four pup removals and escort removals per group). Pup–escort pairs were treated as statistical units. No individual pup or escort was tested twice as focal animal. However, three escorts and one pup served once as focal and, in another experiment, as control individual.

For the pup removal experiments, two pups that were in stable associations were removed concurrently. Removed individuals were put in a live-trap and carried away out of hearing range (>500 m). The speakers were hidden in a cardboard box and placed on the ground, partly camouflaged next to a bush. Playbacks of the focal pup's distress calls were started when both the focal escort (escort of the pup whose calls were played back) and the control escort (escort of the pup that had also been removed but whose calls were not played back) were foraging or resting at equal distance from and within 15 m of the speakers. Control and focal escorts did not differ in age (Wilcoxon signed-ranks test: $T = 18$, $N = 13$, $P > 0.1$), weight (paired t test: $t = 0.13$, $N = 11$, $P = 0.90$; two individuals could not be weighed) and sex (six of 13 control escorts and seven of 13 focal escorts were males). We recorded latency to approach and time spent next to the speakers for the focal and the control individuals. Animals that came to within 1 m of the speakers were considered to have approached them. Playbacks of pup distress calls lasted 60 s and consisted of loops of 10 calls per 20 s played three times. Playback sequences were compiled in CoolEdit 2000 (Syntrillium Software Corp., Scottsdale, AZ, U.S.A.). Within sequences, call intervals were varied randomly between 0.5 and 3.5 s, covering most of the natural range of call intervals. The volume of the playbacks was set to 50–60 dB at 50 cm using a Voltcraft 329 sound level meter (Conrad Electronic, Hirschau, Germany). This was about 5 dB above the naturally observed average volume of these calls, which ensured that the played cues were salient against a background of begging pups. Qualitatively, responses to these calls did not differ from responses to natural distress calls (C. A. Müller, personal observation). Distress calls used for the playbacks had been recorded no more than 20 days prior to the experiments.

The same procedure was used for the escort removal experiments, during which two escorts were removed concurrently. We played back contact calls of the focal escort to the focal and control pups when they were at equal distance from the speakers. Control and focal pups did not differ in age (maximum difference: 3 days; median: 0 days; $N = 12$) or weight (paired t test: $t = 0.10$, $N = 9$, $P = 0.93$; three pups could not be weighed). Each playback of the focal escort's contact calls was preceded by a control playback of contact calls of a nonescorting adult to determine the two pups' baseline response to contact calls. Experimental playbacks were performed 10 min after the end of the control playbacks. We performed the control playbacks consistently before the experimental playbacks, rather than in random order, because the latter typically elicited a strong response which might have

influenced subsequent reactions. Playbacks of adult contact calls lasted 180 s and consisted of loops of five calls per 20 s played nine times. Playback sequences were compiled in CoolEdit. Within sequences, call intervals were varied randomly between 1 and 7 s, covering most of the natural range of call intervals. The volume of the playbacks was set to 40–45 dB at 50 cm (about 5 dB above the naturally observed average volume of these calls). Contact calls used for the playbacks had been recorded no more than 4 months prior to the experiments.

For both experiments, if neither the control nor the focal individual had responded to the playback, it was started a second time 5–10 min later (four of the 13 distress and three of the 12 contact playbacks). In these cases, only the response to the second playback was used for later analyses. During one distress playback, neither the control nor the focal escort approached the speakers even at the second attempt and, thus, both individuals were recorded as having not responded to the playback. In this case the focal adult visually responded to the first playback and started searching behaviour but failed to approach the speakers. Neither the focal nor the control escort responded to the second playback. Also during two contact playbacks, neither pup approached the speakers at the second attempt. Response latency for individuals that did not approach the speakers during the playback was set to the duration of the playbacks (60 s for escorts during pup removals, 180 s for pups during escort removals). All three response variables, probability and latency to approach and response duration, were nonnormally distributed and therefore analysed with nonparametric tests (Fisher's exact test and Wilcoxon signed-ranks test).

Ethical Note

Trapping and marking procedures followed the guidelines of the Association for the Study of Animal Behaviour and are described in detail elsewhere (Cant 2000). Distress calls were recorded for 2 min when pups were trapped for individual marking. Therefore, no additional trapping was required for this purpose. The durations of removals were kept to a minimum. Dependent pups are sometimes also naturally separated from the rest of the group for 1–2 h, for example when the group leaves the pups behind at a shelter while foraging and returns later to pick them up (C. A. Müller, personal observation). All removed pups and escorts returned to their previous association partners after the experiments and removals had no discernible effect on pup, escort or group habituation.

RESULTS

Acoustic Analyses

Pup distress calls

For the litter of 12 pups, DFA was performed with 15 parameters entered simultaneously (see Appendix Table A1). The corresponding discriminant functions assigned

75.0% (range 70.8–81.9%) of the cross-validated calls to the correct individual compared to 8.5% expected by chance (bootstrapping; $P < 0.0001$). For the litter of eight pups, 80.0% (range 71.9–87.5%) of the cross-validated calls were correctly assigned, compared to 12.5% expected by chance ($P < 0.0001$). The most discriminating parameters (most highly correlated with the first two discriminant functions) were mean and maximum frequency of the first dominant frequency band for both litters, followed by measures of frequency modulation for one litter and amplitude ratio between the first and the second dominant frequency band for the other litter.

Escort contact calls

DFA was performed with 12 parameters entered simultaneously (see Appendix Table A2). The corresponding discriminant functions assigned 42.5% (range 34.4–46.9%) of the cross-validated calls to the correct individual compared to 12.5% expected by chance (bootstrapping; $P < 0.0001$). The most discriminating parameters were two temporal parameters (number of pulses and call duration) and a measure of relative amplitude (mean amplitude of the first frequency peak) while frequency-related parameters were less important.

Playback Experiments

Response of escorts to pup distress calls

The focal escort approached the speakers during 12 of the 13 experiments, whereas the control escort approached during five of the experiments (Fisher's exact test: $P = 0.011$). The focal escorts were quicker to approach the speakers than the control escorts (Wilcoxon signed-ranks test: $T = 3$, $N = 13$, $P < 0.01$; Fig. 2a) and stayed longer near the speakers ($T = 10$, $N = 13$, $P < 0.05$; Fig. 2b).

Response of pups to escort contact calls

During the control playbacks of nonescort contact calls, two of 12 focal pups and one of 12 control pups approached the speakers (Fisher's exact test: $P > 0.5$). During the playbacks of escort contact calls, nine of the 12 focal pups and three of the 12 control pups approached the speakers (Fisher's exact test: $P = 0.039$). The focal pups were quicker to approach the speakers than the control pups (Wilcoxon signed-ranks test: $T = 1.5$, $N = 12$, $P < 0.01$; Fig. 2c) and stayed longer near the speakers ($T = 5$, $N = 12$, $P < 0.05$; Fig. 2d).

DISCUSSION

We showed that the distress calls of banded mongoose pups and, to a lesser extent, the contact calls of adults are individually distinct and that pups and escorts recognize each other by these vocalizations. We suggest that this is a case of true individual recognition of offspring by providers because age differences among pups were minimal (<3 days), responses were not directed to individuals of a particular sex and differences in relatedness among

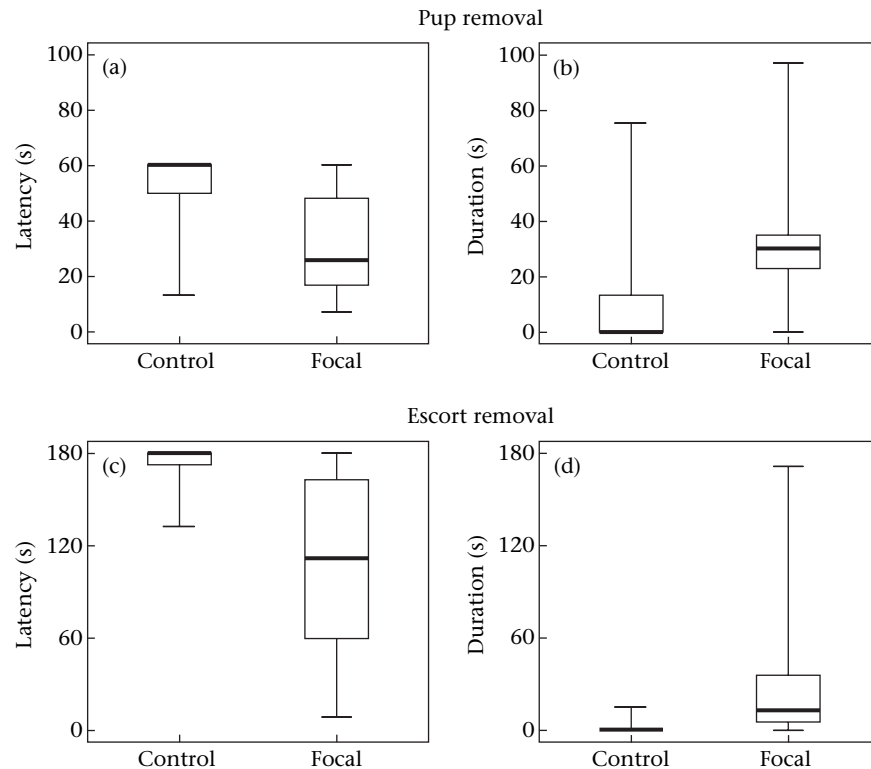


Figure 2. Responses of control and focal individuals to playback experiments. (a) Response latency of escorts to pup-distress playbacks; 60 s corresponds to no approach. (b) Time escorts spent within 1 m of the speakers during pup-distress playbacks. (c) Response latency of pups to escort-contact playbacks; 180 s corresponds to no approach. (d) Time pups spent within 1 m of the speakers during escort-contact playbacks. Shown are median, interquartile range and range.

pups within litters are probably small in this inbreeding species (Waldick et al. 2003).

Mutual recognition of parents and offspring by acoustic means has been demonstrated in a variety of species (e.g. Espmark 1971; Insley 2001; Searby & Jouventin 2003). However, in some cases recognition is unidirectional with parents not recognizing their offsprings' calls (Falls 1982; Torriani et al. 2006). The distinction of unidirectional and mutual recognition has been related to the mobility of offspring and antipredator strategies (Torriani et al. 2006). Unidirectional recognition is predicted where offspring remain stationary and hide, such as in fallow deer, *Dama dama*, and mutual recognition where offspring follow their parents, such as in sheep, *Ovis aries* (Shillito-Walser et al. 1981; Searby & Jouventin 2003), and reindeer, *Rangifer tarandus* (Espmark 1971). Alternatively, unidirectional recognition may be explained by a low probability of confusion where offspring remain stationary and separated from conspecifics and, thus, spatial cues are reliable indicators of an individual's identity (Falls 1982). Instead, mutual recognition may be required where offspring mingle with each other, as for example in species breeding in colonies, forming crèches or living in groups with mobile offspring. Dependent banded mongoose pups follow adults during foraging (from an age of 3–4 weeks; Rood 1974; Cant 2003), mingle with other pups in the group and rely on adults for defence

against predators. Mutual recognition in this species, thus, fits the predictions of the hide–follower hypothesis (Torriani et al. 2006) and the confusion hypothesis (Falls 1982).

Individual recognition of pups' distress calls was matched by high distinctiveness of these calls, particularly in parameters of frequency and frequency modulation. Compared to the distress calls, adult contact calls were much simpler in structure and less individually distinct. Only about 40% of these calls were assigned to the correct individual using discriminant function analysis, suggesting that, unlike in some other carnivores with individual recognition systems (e.g. Insley 1992; Charrier et al. 2003), selection pressure did not lead to contact calls featuring high individual stereotypy in the banded mongoose. Pups nevertheless successfully recognized the contact calls of their escorts, indicating either that we did not measure some parameters relevant for individual recognition of these calls or that selection pressure acted more on the receiver's sensory system and less on the sender's call structure in this species. Alternatively, a moderate assignment accuracy of single calls may be sufficient for individual recognition because calls are repeated and thus signal detection is enhanced (Charrier et al. 2002) or because only one individual needs to be discriminated against all others rather than all individuals against each other (Hammerschmidt & Todt 1995). In any case, whereas

highly individualized calls do not necessarily imply presence of individual recognition (e.g. McCulloch et al. 1999), our results also indicate that low assignment rates of single calls to the correct individual in discriminant function analyses need to be interpreted cautiously and may not necessarily imply absence of individual recognition.

Our experiments demonstrated that both pups and escorts play active roles in the maintenance of escorting associations. The benefits of escorting associations to the pups are well established (Gilchrist 2004; Hodge 2005) and vocal recognition of the escorts by the pups likely accelerates the reunion process after temporal separation and therefore reduces the time during which little food is received and vulnerability to predators is high. In contrast, it is unclear why escorts also contribute to the maintenance of the associations, particularly because escorting is costly as it reduces weight gain (Hodge 2007).

Adults responding preferentially to distress calls of their associated pups may be a consequence of the constant exposure to the structurally similar begging calls of these pups (20–60 calls per min during foraging; Bell 2006). This probably leads to hormonal changes in the exposed individuals, as found in meerkats (Carlson et al. 2006), and therefore escorts may be more responsive to distress calls of pups than nonescorts. Furthermore, even though escorts interact regularly with other pups, they are exposed to begging calls of one particular pup much more than to calls of other pups. Therefore, if pup begging and distress calls have idiosyncratic characteristics, as has been shown in some mammals (Cheney & Seyfarth 1988; Reby et al. 2006) and birds (Weary & Krebs 1992; but see Beecher et al. 1994), an escort may be primed to calls of its associated pup (analogous to vocal identity priming in humans; Ellis et al. 1997). The escorts' preferential response to distress calls of their associated pups may therefore be a by-product of this priming effect and, thus, not necessarily an adaptive response. Nevertheless, this means that escorts contribute to the maintenance of the escorting associations, which stands in contrast to observational data suggesting that associations are maintained by the pups (Gilchrist 2004).

An alternative and more intriguing possibility is that, in this species, escorts respond preferentially to distress calls of their associated pups because they benefit from stable associations with particular young. First, escorts may care preferentially for more closely related pups. There is evidence that breeders are more likely to escort pups than nonbreeders (Gilchrist & Russell 2007). At this date, pedigrees are not available and it is therefore unknown whether providers are more likely to associate with more closely related pups. However, even though multiple males and females are breeding concurrently, high levels of inbreeding and the consequent low genetic variability within groups (Waldick et al. 2003) may offer little opportunity for helpers to dispense care in a kin-biased way. Furthermore, females within groups commonly give birth in synchrony in the same den (Cant 2000) and cues associated with kinship may therefore be unavailable in this system, unless genetic differences are reflected in phenotypic

cues that allow self-referent phenotype matching (Mateo & Johnston 2000).

Second, escorts may care for future coalition partners. Banded mongooses commonly disperse as single-sex factions which may include individuals differing in age by several years (Cant et al. 2001). Therefore, same-sexed pup–escort pairs may end up in the same dispersing faction. However, there is little evidence that associations are preferentially formed with same-sexed partners (Hodge 2003; Gilchrist 2004) and, thus, this is unlikely to explain the adults' interest in forming escorting associations.

An alternative explanation for escorting associations are group-augmentation benefits (Woolfenden 1975; Brown 1987; Kokko et al. 2001). Escorts may benefit from caring for future helpers which will later help raise their pups and defend the territory against neighbouring groups (Rood 1975; Cant et al. 2002). Close associations between pups and escorts may be the most efficient way of raising offspring in this species because escorted pups grow faster and are more likely to survive to independence than non-escorted pups (Hodge 2005). Also, escorting may increase the efficiency of care, for example by permitting the escorts to monitor the food intake of their associated pups, which may be more reliable than using begging rate as a correlate of the pups' hunger level (Kilner & Johnstone 1997; Bell 2006).

We showed that banded mongoose pups and escorts recognize each other acoustically and our experiments demonstrated that both parties contribute to the maintenance of the escorting associations. We offered two interpretations for the adults' increased responsiveness to distress calls of their associated pup. First, it may be a by-product of the escorts being constantly exposed, and thus primed, to begging calls of this pup. Second, it may reflect preferential care for particular pups. It remains to be investigated what benefits escorts accrue from provisioning pups. Our findings have important implications for cooperative breeding theory because helpers may acquire increased benefits by allocating care discriminately among individual offspring.

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Appendix

Table A1. Parameters used in the discriminant function analysis of pup distress calls

Parameter*	Category†	Program‡	PIC§	Values**
<i>Start frequency of 1st dominant frequency band (DF) (Hz)</i>	F	LMA	1.6/1.3	6925 (3594/9046)
<i>End frequency of 1st DF (Hz)</i>	F	LMA	1.9/1.3	3878 (1092/5793)
Maximum frequency of 1st DF (Hz)	F	LMA	2.1/1.6	7331 (4201/9234)
<i>Minimum frequency of 1st DF (Hz)</i>	F	LMA	2.2/1.2	3604 (930/5636)
Mean frequency of 1st DF (Hz)	F	LMA	2.3/1.5	5091 (1981/6424)
Factor of linear trend of 1st DF	GM	LMA	1.3/1.3	−1.04 (−0.24/−2.02)
<i>Alternation frequency between original curve and linear trend of 1st DF</i>	LM	LMA	1.3/1.0	24.7 (9.8/37.9)
<i>Maximum deviation from linear trend (Hz)</i>	LM	LMA	1.4/1.1	1484 (779/2593)
<i>Minimum deviation from linear trend (Hz)</i>	LM	LMA	1.2/1.3	420 (257/585)
<i>Number of changes between original and floating average curve of 1st DF</i>	LM	LMA	1.3/1.1	46.5 (41.4/51.5)
Mean deviation from floating average (Hz)	LM	LMA	1.2/1.1	257 (156/379)
<i>Maximum deviation from floating average (Hz)</i>	LM	LMA	1.3/1.1	1082 (496/2010)
Duration of call (ms)	T	LMA	1.6/1.2	338 (198/493)
<i>Relative location of maximum amplitude</i>	T	Avisoft	1.0/1.1	0.42 (0.20/0.74)
Amplitude ratio between 1st and 2nd DF	RA	LMA	1.4/1.4	2.92 (1.35/5.31)
Entropy at start	E	Avisoft	1.2/1.1	0.27 (0.24/0.31)
Entropy at end	E	Avisoft	1.4/1.1	0.35 (0.29/0.45)
Mean entropy	E	Avisoft	1.6/1.2	0.53 (0.40/0.68)
Minimum entropy	E	Avisoft	1.5/1.2	0.25 (0.23/0.28)
Maximum entropy	E	Avisoft	1.5/1.4	0.50 (0.36/0.59)

*Parameters used for classification of both data sets are shown in bold; parameters used for classification in only one data set are shown in italic.

†F: frequency; GM: global frequency modulation; LM: local frequency modulation; T: temporal; RA: relative amplitude; E: entropy.

‡Software program used to measure the parameter. All parameters were measured from digitized spectrograms.

§Potential for individual coding for the two litters separately.

**Shown are mean and, in parentheses, range of means per individual.

Table A2. Parameters used in the discriminant function analysis of adult contact calls

Parameter*	Category†	Program‡	PIC§	Values**
Maximum peak frequency (Hz)	F	LMA	1.0	608 (531/725)
Minimum peak frequency (Hz)	F	LMA	1.0	151 (103/190)
Mean peak frequency (Hz)	F	LMA	1.1	351 (287/398)
Mean frequency of 1st Quartile (Hz)	FD	Avisoft	1.0	366 (342/398)
Mean frequency of 2nd Quartile (Hz)	FD	Avisoft	1.1	659 (628/717)
Mean frequency of 3rd Quartile (Hz)	FD	Avisoft	1.0	1136 (1091/1204)
Maximum frequency of 1st Quartile (Hz)	FD	Avisoft	1.1	461 (431/499)
Maximum frequency of 2nd Quartile (Hz)	FD	Avisoft	1.2	845 (768/921)
Maximum frequency of 3rd Quartile (Hz)	FD	Avisoft	1.1	2167 (1500/2688)
Minimum frequency of 1st Quartile (Hz)	FD	Avisoft	1.0	241 (203/269)
Minimum frequency of 2nd Quartile (Hz)	FD	Avisoft	1.0	397 (349/452)
Minimum frequency of 3rd Quartile (Hz)	FD	Avisoft	1.1	750 (621/881)
Duration of call (ms)	T	LMA	1.4	44 (36/57)
Number of pulses	T	Avisoft	1.3	5.4 (4.4/7.3)
Pulse rate (Hz)	T	Avisoft	1.1	122 (112/131)
Mean pulse duration (ms)	T	Avisoft	1.3	3.8 (3.2/4.2)
Mean interval between pulses (ms)	T	Avisoft	1.2	7.3 (6.6/8.3)
Mean amplitude of 1st frequency peak	RA	LMA	1.2	554 (377/733)
Maximum amplitude of 1st frequency peak	RA	LMA	1.1	932 (626/1200)

*Parameters used for classification are shown in bold.

†F: frequency; FD: frequency distribution; T: temporal; RA: relative amplitude.

‡Software program used to measure the parameter. Four temporal parameters were measured from amplitude envelopes using pulse train analysis in Avisoft. All other parameters were measured from digitized spectrograms.

§Potential for individual coding.

**Shown are mean and, in parentheses, range of means per individual.