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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.

Keywords: banded mongoose; cooperative breeding; Herpestidae; individual recognition; *Mungos mungo*; playback

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; Ostreiher 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.

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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.