Innovative parental care in a myrmecophageous mammal

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Abstract

Male bat-eared foxes, *Otocyon megalotis*, are known to contribute extensively to parental care. Yet, the exact roles that males and females play in raising offspring remain relatively unexplored. Here, we describe interactions between adult foxes and their presumed offspring based on a pilot study on 3 family groups of a wild population in South Africa. We report the first recorded instance of dung provisioning

observed in canids. A male bat-eared fox provided dung to his offspring during a foraging trip, presumably to give them access to the ensconced insects. Further, this male provisioned the young foxes with large, live insects. Similar to other researchers, we never observed provisioning by females, but the females in this population did interact socially with their young in addition to suckling. We emphasize the importance of anecdotal reports of novel behavioural responses in wild canids, as an accumulation of such evidence may reveal patterns of innovative behaviour presently unrecognized in this family.

Keywords: Canidae, dung provisioning, myrmecophagy, *Otocyon megalotis*, parental care

Introduction

The bat-eared fox, *Otocyon megalotis*, faces an unusual ecological conundrum during the cub-rearing season. Similar to aardwolves, *Proteles cristatus* (Richardson 1987a), this medium-sized carnivore has a specialized myrmecophageous diet (Clark 2005), which is a low-energy food source that puts extreme physiological pressure on lactating females (McNab 1984). Unable to devote much time and energy to maternal care, female foxes are highly reliant on males' care of their offspring (Maas 1993), and paternal den attendance has been linked to increased offspring survival (Wright 2006). While investing in paternal care, male foxes face certain challenges linked to their myrmecophageous diet, as their primary food source is too small to profitably bring back to the den. Unlike most canids such as wolves, *Canis lupus*, and blackbacked jackals, *Canis mesomelas* (Malcolm 1985), bat-eared fox males are reported to seldom provision pups at the den (similar to the insectivorous hoary fox, *Pseudalopex*

vetulus, Courtenay et al. 2006). In bat-eared foxes, paternal care appears to primarily focus on non-feeding help, e.g., anti-predator behaviour, grooming, playing, and huddling; only rarely do males contribute small vertebrate prey to the pups (Pauw 2000; Maas 1993; Wright 2006). Their diet does allow family groups to forage socially; both males and females accompany young foxes on early foraging excursions (Maas 1993; Nel 1999), presenting offspring with potential social learning opportunities. Bat-eared foxes therefore present researchers with a rare model system for investigating the entire spectrum of paternal care behaviours in canids.

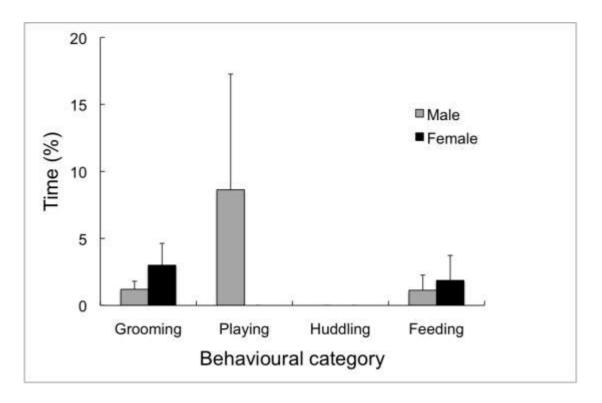
In this descriptive study, we present a brief report on the social interactions between bat-eared fox cubs and their (presumed) parents in three family groups. We use a framework suggested by Kentner *et al.* (2010), assessing paternal care not in isolation, but as part of a bi-parental system in which male and female behaviours may affect and complement each other. In particular, we note certain novel behaviours that have never been described in myrmecophageous mammals.

Materials and methods

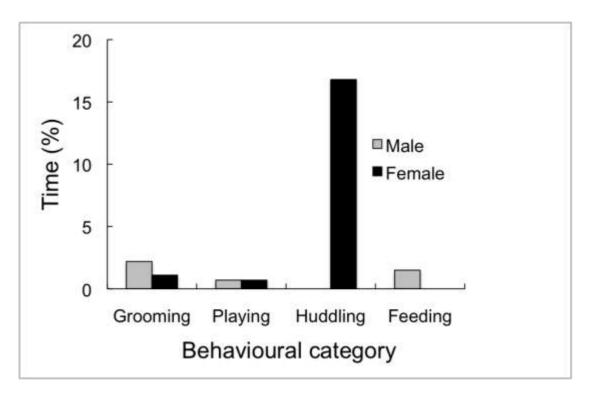
This pilot study was conducted between November 2010 and February 2011 at Benfontein Nature Reserve, Kimberley, in Northern Cape Province of South Africa (28°99'S and 24°81'E). The reserve is an 11 000 ha game farm consisting of dry Karoo, grassland and Kalahari savannah. Four bat-eared foxes (3 males, 1 female) were fitted with collar-mounted VHF transmitters (Sirtrack Ltd, Havelock North, New Zealand). In order to fit these collars, foxes were live-trapped using cage traps baited with offal, and immobilized with 10 mg ketamine hydrochloride and 0.2 mg medetomidine hydrochloride, which was reversed with 1.0 mg atipamezole (Wright

2006). The study was approved by the Animal Use and Care Committee at the University of Pretoria (EC031-07).

Observations centred on three social groups comprising 5, 3, and 2 adult individuals each, with 3, 2, and 4 juveniles, respectively. Each of these social groups had 1 or more radio-collared individuals allowing us to locate their resting site when this location moved. These collared individuals were sexed during capture and could be identified by their collars, while other group members were identified through distinctive fur colour patterns, behaviours (such as urination posture) and scars. In all groups the pups were below weaning age during the study period. Both collared and non-collared group members were habituated to vehicles, and were observed from a distance of 5-50 m for the duration of the study. We collected data following a focal protocol (Altman 1974), noting the duration of all behaviours performed by group members using CyberTracker[©] software loaded on a Personal Data Assistant. Over a period of eight nights, we conducted 14.8 h of observations at den sites, where cubs were interacting with adults for 113 minutes. Additionally, we recorded 4.5 h of observations on foraging trips (across 3 nights) in which cubs were escorted by one or more adult(s). Due to logistical challenges, we only performed foraging observations for one group of foxes. Here we report on socio-positive interactions between adults and offspring, i.e., social grooming, playing (including play-fighting), huddling, and feeding/suckling. We followed the ethogram of Wright (2006) and Lamprecht (1979) in defining these standard canid behaviours. No statistical comparisons were performed, as the data were limited in terms of sample size and cumulative observation hours.



A



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Fig. 1. The percentage of time in which bat-eared fox adults (both males and females) directed socio-positive interactions at the pups while (a) at the den (mean + SE across 3 groups), and (b) on foraging excursions (N = 1 group). Adult males (gray bars) and females (black bars) appeared to spend an equal amount of time grooming pups, but differed in terms of provisioning, playing, and huddling behaviour.

Results

At the den, cubs spent less time interacting with females than with males, even when time spent suckling is included (Fig 1a). We observed one instance in which a male returned to the den with a large insect, which he provided to the cubs. After the cubs allowed the prey item to escape, the male recaptured and returned the insect to the pups, which subsequently ate the prey item. Females were never observed to provide cubs with prey items at the den. While foraging, males and females spent a roughly equal amount of time playing with and grooming the cubs, but the female was the only individual observed to huddle with the young foxes (Fig 1b). Cubs attempted to suckle from the female while foraging, but were rebuffed. During foraging excursions the female again never provided food items to the cubs. However, the adult male provisioned the cubs on three occasions during the observed foraging excursions. Twice, the male caught a large insect and brought it to the pups. Each time the pups allowed the insect to escape, and the male returned it to them to finally ingest successfully. The third provisioning instance was when the male presented the cubs with a large piece of ungulate dung. The pups ate from the faeces after initially playing with it. Presumably, these cubs extracted invertebrates from the dung, but we were unable to verify whether they ate the faecal matter itself, or primarily fed on invertebrates within the dung. Teeth marks were observed in the residual dung that we inspected after the foraging group moved on.

Discussion

Despite the limits of a short observational period and small number of groups (N=3), we observed multiple instances in which male bat-eared foxes – but not females – provisioned pups with food items. While other researchers have occasionally

observed such provisioning of large insects and small vertebrates (Pauw 2000; Maas and MacDonald 2004), our study provides the first recorded evidence of male foxes provisioning pups with antelope dung. To our knowledge, this report also presents the first described instance of dung provisioning in any vertebrate species. While it is possible that the adult foxes and pups ate the faecal matter to obtain necessary intestinal microbes (found in the stomachs of small insectivores, Langer 2002), medium-sized canids are reported to eat dung only under conditions of extreme social, not nutritional, stress (Beerda et al. 1999). Further, other myrmecophageous mammals (Cornelius et al. 1975; Smith et al. 1998) naturally produce the chitinase necessary to digest insects, suggesting that bat-eared foxes, similarly, do not need to obtain intestinal flora from dung. Indeed, it is more likely that experienced foxes extract the insects that occur inside antelope dung (Maas and MacDonald 2004). Dung provisioning, in this case the offering of antelope dung to a group member in order to provide it with the ensconced insects, is a novel response to a particular ecological challenge and represents one of very few observed cases of innovative parenting behaviour in wild mammals. Such "innovation" (Reader and Laland 2001, 2002) may be practiced by only a single individual within this population, but it is possible that other foxes at this study site and in other locations display similar behaviours. However, since dung provisioning has not been noted in previous studies on bat-eared fox behaviour (Maas and MacDonald 2004; Pauw 2000), it could be an innovation that is typical of the Benfontein population but absent elsewhere in the bat-eared fox's distribution range. It would be particularly interesting to ascertain whether other myrmecophageous mammals such as the aardwolf also utilize dung in a similar way, since the potential for adult provisioning in this species is similarly constrained by prey size (van Jaarsveld et al. 1995).

Similar to other reports (Nel 1999; Maas and MacDonald 2004), we observed behaviour displayed by male foxes that is suggestive of teaching (Caro and Hauser 1992) or social learning (Zentall and Galef 1988). We noted multiple occasions in which the male did not simply kill the prey item and provide this to the pups, but brought the live animal back to the young. He allowed the offspring to interact with the prey item and even retrieved it when they failed to kill their prey. Such exposure to the handling of difficult prey can enhance the cognitive development and future foraging and hunting success of naïve individuals (Thornton and McAuliffe 2006). However, rigorous experimental research is needed to confirm the possible existence of teaching in this canid. At the moment, our description of dung provisioning and possible teaching behaviour contributes to a database of anecdotal reports on unusual behaviours in carnivores and, specifically, canids. Large bodies of anecdotal data in primates and birds have been instrumental in driving new research directions in the field of cognitive ecology (Bates and Byrne 2007; Byrne and Whiten 1988; Lefebvre 2011), and we would therefore urge other carnivore researchers to document possibly unique behaviours observed in their study populations.

This study confirmed that both male and female bat-eared foxes spend time grooming and interacting socially with pups, whether it was at the den or on foraging excursions. It is notable that females – not males – huddled with their pups while foraging. In agreement with observations that adult foxes are often playful (Lamprecht 1979), we observed all adults, and males in particular, playing with the pups. These observations contradict some studies that indicate lactating females do not associate with pups aside from allowing them to suckle (Maas 1993). We expected that female bat-eared foxes would spend less time interacting with offspring,

due to the high foraging demands imposed by the cost of lactation. In other myrmecophageous mammals such as the aardwolf, lactating females spend up to 8 hours a night foraging on their small, dispersed prey (e.g., Richardson 1987b). Our observation that female bat-eared foxes, rather than males, spent more time with offspring while foraging, is therefore unusual, but may be an artefact of limited observational hours. In contrast to Wright (2006), we never observed antipredator behaviours or overt guarding in the adults. The absence of this behaviour may be due to our limited observational hours. In both aardwolves (Richardson 1987a; van Jaarsveld et al. 1995) and bat-eared foxes (Maas 1993), it has been postulated that females are dependent on male aid for the survival of her offspring, yet the exact nature of this help has not been fully quantified. This brief pilot study provides evidence for a range of parental behaviour in the bat-eared fox, some of which have not been noted previously. The range of caring behaviours presented here are suggestive of potentially complex parental behaviour in both sexes as well as individual variation in such behaviour, warranting future research dedicated to understanding how parental behaviour in the bat-eared fox contributes to maintain a foraging niche that appears to be energetically suboptimal.

Acknowledgements

We are grateful to De Beers Ecology Division and the Diamond Route for permission to work on Benfontein Game Reserve, and the staff and managers at Benfontein for logistic support. This study was financially supported by an NRF focal area grant awarded to Professor Elissa Cameron, an NRF SARCHi chair in mammal behavioural ecology and physiology awarded to Professor Nigel Bennett and NRF incentive funds as well as a research fellowship from University of Pretoria awarded to F. Dalerum.

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