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ARTICLES

Paternal den attendance is the best predictor of offspring survival in the socially monogamous bat-eared fox

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Although considerable data are available on the subject for birds, almost nothing is known about the adaptive nature of paternal care in mammals. I studied the adaptive significance of paternal care in a socially monogamous population of bat-eared foxes, *Otocyon megalotis*. Between the birth and weaning of cubs males spent significantly more time in the den vicinity than females, and, with the exception of lactation, were involved in all aspects of cub care. Multivariate analyses revealed that, compared to parental size and age, territory quality and maternal den attendance, paternal den attendance was the best predictor of both the number and proportion of cubs surviving to weaning age. I suggest that the parental roles of bat-eared foxes are related to the species' diet, and propose that the beneficial nature of male care may be sufficient to make social monogamy the optimal mating strategy for males as well as females.

Male parental care is unusual in mammals, occurring in 5–10% of species (Kleiman & Malcolm 1981; Woodroffe & Vincent 1994). This is thought to be because female mammals' commitment to gestation and lactation leaves males with little opportunity to care for their offspring (Orians 1969; Trivers 1972) and considerable opportunity to desert partners and search for additional mates (Maynard Smith 1977; Clutton-Brock 1989).

Paternal care is most prevalent in the rodents (Elwood 1983), canids (Kleiman & Malcolm 1981) and primates (Dunbar 1988), and it is often, but not always, associated with living in pairs (Kleiman & Malcolm 1981). Perhaps because of this (Reichard 2003), the requirement for male care has been repeatedly suggested as a factor that may favour the evolution or maintenance of social monogamy (Kleiman 1977; Wittenberger & Tilson 1980; Clutton-Brock 1989; but see Komers & Brotherton 1997). To understand how the necessity for male care affects the mating options of males and females, however, it is necessary to know whether, and to what extent, paternal assistance influences breeding success (Davies 1991; Reichard 2003).

Although substantial data are available relating paternal care to offspring survival in birds (reviewed in Bart & Tornes 1989), few studies have shed light on the adaptive nature of male care in mammals (Clutton-Brock 1991). Gubernick & Teferi (2000) have shown, using male removal experiments, that the absence of fathers reduces offspring survival by 60% in socially monogamous California mice, *Peromyscus californicus* (see also Woodroffe & Vincent 1994, for a review of studies on paternal care in captive rodents). Huber et al. (2002) found that, in polygynous European ground squirrels, *Spermophilus citellas*, burrow preparation by males increased the foraging time of gestating females and the subsequent weight of their emerging pups. Other evidence regarding the adaptive nature of male care is more anecdotal, such as the observation of widowed females failing to rear offspring without male assistance (black-backed jackal, *Canis mesomelas*: Moehlman 1986; fat-tailed dwarf lemur, *Cheirogaleus medius*: Fietz 2003).

The basic canid social unit is the monogamous pair (Kleiman & Eisenberg 1973), and in most species fathers, and sometimes nonbreeding helpers, assist in the rearing of offspring (reviewed in Moehlman 1986, 1989). An important element of paternal care is often the provisioning of partners and young (Asa & Valdespino 1998). This, combined with the fact that canids have large litter sizes and long periods of dependency (relative to other mammals, Kleiman & Eisenberg 1973) suggests that males have an important parental role. However, although there are data relating canid reproductive success to food availability (Englund 1970; Angerbjorn et al. 1991; Maas 1993), no studies have demonstrated that paternal care enhances breeding success.

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The bat-eared fox, *Otocyon megalotis* is a small (ca. 4 kg) insectivorous fox found in eastern and southern Africa. Like other small canids, they usually breed in monogamous pairs (Lamprecht 1979; Malcolm 1986), but occasionally in small polygynous groups (Maas 1993; Pauw 2000). Field studies of the species have revealed that, relative to other canids, the parental roles of males and females (with the exception of lactation) are reversed. Male bat-eared foxes spend a lot of time at breeding dens, huddling with, carrying and grooming cubs and accompanying them on foraging trips (Lamprecht 1979; Malcolm 1986; Maas 1993; Pauw 2000; Wright 2004). In contrast, lactating females spend most of their time away from dens foraging. The special role of males has been attributed to the fact that their small food items (termites) are not readily transported back to the den in any form other than milk (Maas 1993; see also Kauhala et al. 1998).

Researchers have disagreed about whether or not paternal assistance is necessary for successful breeding in the bat-eared fox. Moehlman (1989) showed that, relative to other canids, female bat-eared foxes produce large litters of well-developed young. Combining this with one observation of a widowed female successfully rearing a litter of five cubs (made and later documented by Maas 1993), Moehlman (1989) concluded that females are capable of providing most of the required parental investment. Maas (1993), however, suggested that the success of this widowed female resulted from unusually high food availability, and that under normal circumstances lactating females are unlikely to be able both to care for cubs at dens and to satisfy their own nutritional demands.

I investigated the adaptive significance of paternal care in a population of bat-eared foxes in Laikipia, Central Kenya. Initially I examined inter- and intrasexual variation in parental behaviour, how parental behaviour varies with cub age, how the parental behaviour of mated partners is coordinated, and the forms of care provided by parents. Using linear regression models, I then investigated the extent to which paternal and maternal den attendance, size and age, as well as two potential measures of territory quality, influence the number and proportion of cubs surviving to weaning age.

METHODS

Study Site

I carried out the study on Loisaba, a private ranch in Laikipia district, central Kenya (36° 50′ E, 0° 63′ N, altitude 1700 m), between January 2001 and November 2002. The main study site consisted of approximately 25 km^2 of largely open grassland, with scattered shrubs and light acacia bush. Mean annual rainfall on the study site between 1985 and 2001 was 493 ± 181 mm, making the area semi-arid. November is the month of peak rainfall, but most rain usually falls between March and July (Wright 2004).

Capture and Marking of Study Animals

Adult foxes were captured with padded foothold traps (size 2, Soft Catch, Woodstream Corporation, Lititz, Pennsylvania, U.S.A.), to which they were attracted by a variety of olfactory lures (Wright 2004). Foothold traps were set shortly before sunset, and checked at 2-h intervals throughout the night. Trapped foxes were immobilized with a combination of ketamine (0.5 mg/kg) and medetomidine ('domitor' Orion pharmaceuticals, Espoo, Finland; 0.3 mg/kg) hand injected into the femoral muscle. All individuals were weighed, sexed, measured, aged (according to incisor wear, Harris 1978) and given a unique combination of coloured ear tags (Rototags, size 1¼ × ¼ inch; Dalton Supplies Ltd, Henley-on-Thames, U.K.). At least one adult from each pair was fitted with a collar-mounted 150 MHz radiotransmitter (Biotrack, Wareham, U.K.). Before release, foxes were injected with atipamezole ('antisedan', Orion pharmaceuticals), to reverse the effect of the medetomidine. They were then held in a wooden box for 1 h, until the effects of the ketamine had worn off, before being released at the capture site.

Ethical Note

Capture and handling techniques were approved by the Kenya Wildlife Service and the Kenya Ministry of Education, Science and Technology. Although box traps would have been the preferred method of trapping, because of the bat-eared foxes' timid nature and insectivorous diet they are extremely difficult to lure into this trap type (Malcolm 1986), and trials with box traps (two traps set nightly for approximately 1 month) were unsuccessful (Wright 2004). Foothold traps were attached to springs, to prevent struggling animals from damaging their legs. The most serious injuries sustained during trapping were breaks in the skin on the trapped foot ($N = 2$), which we cleaned with cotton wool soaked with alcohol; both animals injured this way survived and went on to breed successfully. No mouth injuries caused by gnawing traps were observed. Although trapped bat-eared foxes tended not to struggle excessively, or vocalize, researchers using this capture technique should be aware that animals are vulnerable to predation. To reduce this risk, between trap checks, I positioned my stationary vehicle in the vicinity of the trapping site, so that distressed animals could be heard and assisted, although assistance was never necessary.

Radiocollars weighed 140 g (3.9% of the average and 4.4% of minimum adult body weight). Although effects of radiocollars on survival and reproductive success were not quantified, litter sizes at birth and dispersal were similar to those reported elsewhere (e.g. Maas 1993), and collars had no readily observable effect on their wearers. I did not attempt to remove radiocollars at the end of the study because I judged that the stress and danger associated with trapping were likely to be greater than that of wearing a radiocollar.

Breeding and Measures of Reproductive Success

Between January 2000 and November 2002, 27 breeding attempts (by 13 pairs of foxes) were known to occur on the main study site. No more than two adults were observed in a social group, either during the 10 weeks before