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 km² 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 $1\frac{1}{4} \times \frac{1}{4}$ 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

parturition or during the period of cub rearing, strongly suggesting that foxes on the study site were exclusively socially monogamous (Wright 2004).

For 17 breeding events I attempted to record initial litter size, the number of cubs reaching 14 weeks (when they are fully weaned, Maas 1993), and the number of cubs reaching 7 months (when foxes are fully grown and starting to disperse, Wright 2004). Birth dates were inferred from changes in the behaviour and size of breeding females, which after parturition became visibly smaller and started resting inside dens rather than above ground (Wright 2004). Because bat-eared fox females give birth underground, I recorded initial litter sizes as the number of cubs first seen emerging from the den (at approximately 3 weeks of age), or the maximum number of cubs seen thereafter (if cubs were observed before 6 weeks of age). Subsequent litter sizes were tracked through the observation of family groups, which were visually located at least once a week.

Measuring Parental Investment

I quantified the parental contribution of foxes by measuring the proportion of the night they spent in the vicinity of their breeding dens. This technique was deemed appropriate because bat-eared foxes on the study site were strictly nocturnal (Wright 2004), and most forms of care provided by adults involved them being close to or with cubs at den sites (Lamprecht 1979; Malcolm 1986; Maas 1993; Pauw 2000; this study). This measure does not provide an estimate of female suckling time, as suckling constitutes a small (Maas 1993) and (in this study) unknowable proportion of the time females spent at the den. Den attendance data were collected from birth until cubs were fully weaned (at 14 weeks), when they start to forage further from their dens (Maas 1993; Wright 2004).

Den proximity was calculated in two ways. In most cases (for nine males and seven females) I located radio-tagged adults by triangulation, and then calculated straight-line distances to known den sites. A minimum of 20 'den proximity fixes' was collected from each parent (males: $\overline{X} \pm SD = 34.8 \pm 8$; females: 33.6 ± 8.1), with at least 3 h between successive fixes, and up to two fixes taken on one night. To control for temporal variation in parental behaviour during the night, I divided the night into three time blocks (1830–2230, 2230–0230, 0230–0630 hours), and collected similar amounts of data during each period (at least one quarter of each individual's total).

For a further six individuals (three males and three females), den attendance data were collected during observation sessions at breeding dens. Observation sessions lasted 3 h 10 min, during which I recorded the location of parents at 10-min intervals (giving 20 records per observation session). I carried out six to eight observation sessions on each individual, with at least two during each time block. When foxes could not be seen, I estimated their proximity (± 50 m) according to the strength of signal from their radiotransmitter. Although the accuracy of this technique was not quantified, the flat terrain of the study site, the limited range of the transmitter (which had a maximum signal distance of approximately 1000 m) and the subsequent location of some foxes suggest that the technique was acceptably accurate.

I classified den attendance (for both data collection methods) as the proportion of total fixes that parents were within a 100-m radius of the den. This measure was highly correlated with the proportion of time spent within 200 m of dens (for radiotracking data from 16 adults: $r_{14} = 0.96$, $P < 0.001$), and results of all analyses presented are qualitatively similar regardless of which measurement was used. Because individuals would be expected to spend some time in the den vicinity by chance, and this proportion would increase with decreasing territory size, I carried out all statistical tests with male and female den attendance figures adjusted for territory size. Adjustments were made by subtracting the proportion of time an individual would be expected in the den vicinity by chance (assuming random territory usage equal to the fraction of an individual's territory that fell within a 100-m radius of the den; range of territory sizes 1.44–5.8 km^2; range of den attendance deductions 0.5–2.2%) from its total den attendance figure. In no case did this adjustment qualitatively affect the results.

Measuring Territory Quality

I recorded two potential measures of territory quality: (1) termite density and (2) territory size. I measured termite density by calculating the average number of *Macrotermes* termite foraging holes in 25 randomly placed 1-m^2 plots on each fox's territory. My own identification of termite heads in fox faeces and extensive behavioural observations revealed that *Macrotermes* termites were bat-eared foxes' main prey on the study site. Maas (1993) showed that, in the Serengeti, the density of *Hodotermes* termite foraging holes correlated with litter size at emergence and the time females spent suckling cubs. This measure may thus indirectly reflect female investment. To calculate territory sizes I used the 95% Kernel method (Worton 1989) which, compared to the Minimum Convex Polygon method, is thought to provide a better estimate of an individual's regular foraging range (Kernohan et al. 2001). Using the ArcView GIS extension *Animal Movement* (Hooge & Eichenlaub 1997), I calculated territory sizes from 60 nocturnal radiotracking fixes collected during the 20 weeks prior to parturition. At least 3 h separated successive fixes, and up to three fixes were collected on any one night (once during each nocturnal time block). Termite densities were measured once on each territory (during the first breeding season that the pair was monitored, in the 20 weeks prior to parturition), whereas territory sizes were recalculated for each breeding event.

Data Analyses

Unless otherwise stated, statistical tests are two-tailed. Prior to parametric testing, proportional data were arcsine transformed to meet assumptions of normality (Sokal &

Rohlf 1995). To examine the factors associated with breeding success, I used linear regressions, with robust standard errors to account for the repeated sampling of groups (using Stata 8.0, Stata Corporation 2003). This method yields the same regression coefficients as standard linear regressions, but controls for differences in the variance/standard errors caused by arbitrary intragroup correlation (Rogers 1993; Williams 2000). Means are given $\pm$ SD.

RESULTS

Sex Differences in Den Attendance

The proportion of time spent within 100 m of their dens varied considerably between males (range 14.8–57.1%; chi-square test: $\chi_8^2 = 30.8$, $P < 0.0001$; Fig. 1a). In contrast, variation in female den attendance was not significant (7.5–23%; $\chi_6^2 = 4.54$, $P = 0.60$; Fig. 1b). Although there was some overlap in the amount of time individual males and females spent at or near dens, on average, males spent significantly more time close to breeding dens than did females (males: $\overline{X} \pm SD = 30.1 \pm 15.6\%$; females: $17 \pm 4.9\%$; t test: $t_{14} = -2.15$, $P = 0.05$).
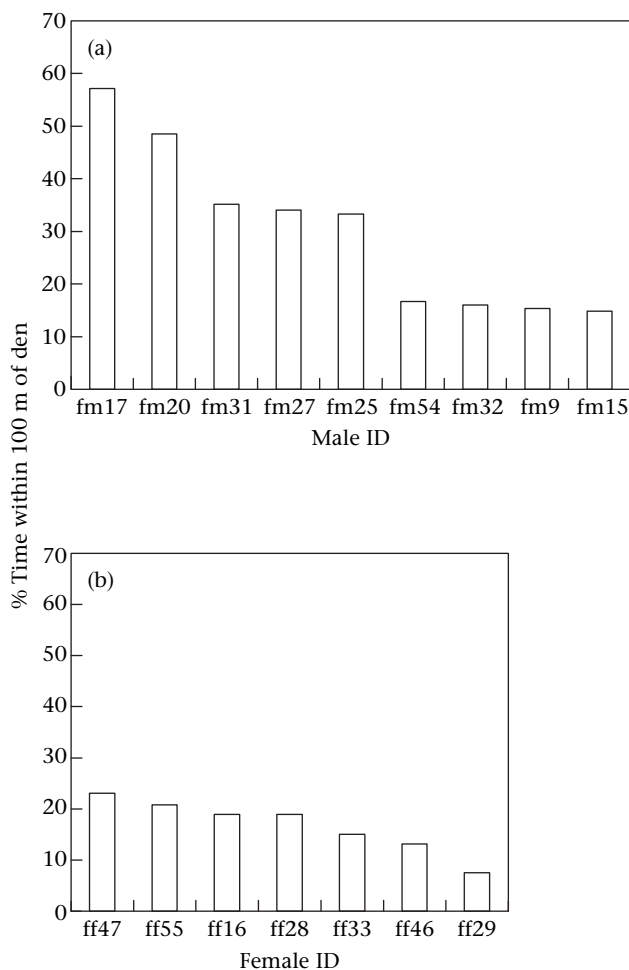

Figure 1. Percentage of time that (a) nine males and (b) seven females were found within a radius of 100 m of their breeding dens.

Cub Age and Den Attendance

To investigate whether patterns of male and female parental behaviour changed with cub age, I divided the den attendance data into seven biweekly cub age classes (0–2, 2–4, 4–6, 6–8, 8–10, 10–12, 12–14 weeks), and combined data from five females and six males for which statistically similar proportions of fixes were collected during each age class (chi-square tests: females: $\chi_{24}^2 = 30.6$, $P = 0.17$; males: $\chi_{30}^2 = 37.4$, $P = 0.17$).

Apart from a peak when cubs were 2–4 weeks old, the proportion of time that males spent within 100 m of their dens varied little with cub age (range 28.6–40.5%; chi-square test: $\chi_6^2 = 7.18$, $P = 0.3$; Fig. 2). Female den attendance followed a different pattern and varied significantly between cub age classes ($\chi_6^2 = 12.7$, $P = 0.05$; Fig. 2). During the first 8 weeks of cub life, females spent relatively little time in the den vicinity (range 6.45–12%). When cubs reached 10 weeks of age, however, average levels of female den attendance increased, to 28.6% at 10–12 weeks and 30.3% at 12–14 weeks.

Coordination of Den Attendance

To investigate whether the parental behaviour of mated partners (from six pairs) was coordinated I compared the frequencies of simultaneous presence of partners at dens with those expected by chance. I calculated expected frequencies of simultaneous presence by multiplying the frequencies at which male and female partners were found (alone or together) within 100 m of their dens. Observed frequencies of simultaneous presence did not differ from those expected by chance, whether data from the six pairs were combined ($\chi_5^2 = 2.23$, $P = 0.82$) or considered alone (chi-square tests: pair 1: $\chi_1^2 = 0.25$, $P = 0.62$; pair 2: $\chi_1^2 = 0.03$, $P = 0.86$; pair 3: $\chi_1^2 = 0.21$, $P = 0.65$; pair 4: $\chi_1^2 = 0.02$, $P = 0.89$; pair 5: $\chi_1^2 = 1.46$, $P = 0.23$; pair 6: $\chi_1^2 = 0.26$, $P = 0.61$). This suggests that mated partners did not perform parental duties together, but neither did they strictly rotate duties in the den area.
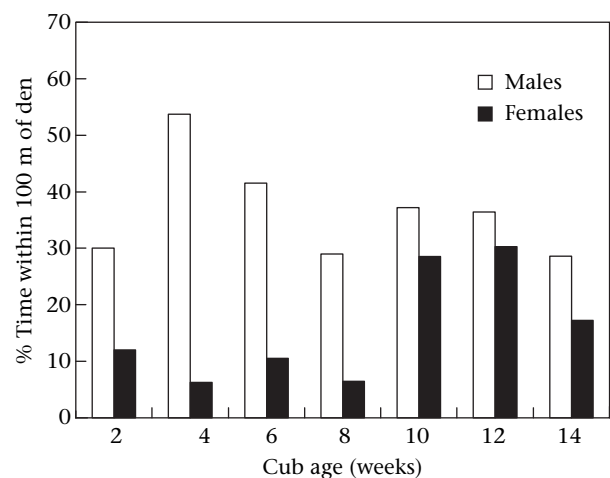

Figure 2. Variation in male and female den attendance with cub age, combining data from six males and five females for which similar proportions of data were collected during each age class.

Forms of Parental Care

Table 1 shows the forms of care that bat-eared fox parents were observed performing or that they were inferred to provide for their cubs. Before cubs first emerged from the den, at 3–4 weeks of age, the principal parental behaviours (aside from lactation) were huddling, grooming, defending and carrying cubs between den sites. When cubs reached 3–4 weeks of age they began taking solid food, as evidenced by indigestible termite heads appearing in their faeces. Initially cubs made short foraging trips in the immediate den vicinity, with one or both parent chaperoning. As cubs got older these foraging trips became more frequent, and occurred at greater distances from the den. There was evidence of direct provisioning by parents, with the chewed remains of small mammals, birds and insects occasionally being found in den entrances, but behavioural observation and inspection of den sites suggested that this was infrequent.

Table 1. Forms of parental care observed in study foxes, and evidence that they occurred

Behaviour	Definition	Evidence of occurence
Huddling	Resting in contact with cubs to help them maintain body temperature	Observed at den entrances and inferred from fact that parents spent extended periods of time inside dens with cubs
Grooming	Grooming cubs to help remove ectoparasites	Observed at den entrances
Defending	Actively defending cubs from predators	Males observed mobbing black-backed jackals and an African wildcat, *Felis libyca*, that strayed close to dens
Chaperoning	Accompanying cubs on foraging trips in the den vicinity	Observed on many occasions
Provisioning	Bringing solid food back to the den	Established from observation of animal remains (small bird, rodent, large insect) at den entrances, and inferred from behaviour of males, which foraged in the den vicinity while making short trips back to the den
Carrying	Carrying cubs between dens	Inferred from fact that small and immobile cubs were transferred up to 1 km between den sites

Litter Sizes

Mean litter size at first emergence ± SD was 3.8 ± 0.77 ($N = 15$ breeding attempts), with a range of three to five. The average number of cubs surviving to weaning at 14 weeks was 2.6 ± 1.55, giving a preweaning mortality rate of 31.6%. Of the 15 litters monitored, in three (20%) no cubs survived to weaning age, while all cubs survived to weaning in six litters (40%). For the 12 litters that were monitored until dispersal, an average of 1.92 ± 1.51 cubs reached 7 months of age, giving a birth to dispersal mortality rate of 50% and a weaning to dispersal mortality rate of 23.3%.

Correlates of Breeding Success

Litter size at first emergence (for 15 breeding attempts by 11 pairs) was not influenced by paternal or maternal age or weight, termite density or territory size, although the relationship with territory size approached significance (linear regressions with robust standard errors to account for repeat sampling of groups: male age: $F_{1,9} = 0.01$, $P = 0.93$; male weight: $F_{1,9} = 1.52$, $P = 0.25$; female age: $F_{1,10} = 0.03$, $P = 0.86$; female weight: $F_{1,10} = 0.01$, $P = 0.91$; termite density: $F_{1,10} = 0.74$, $P = 0.41$; territory size: $F_{1,9} = 4.32$, $P = 0.06$).

Termite density, male den attendance, and male and female age were all significant predictors of the number of cubs surviving to weaning age, but territory size and paternal and maternal weight showed no significant effect (Table 2). Stepwise elimination of variables (based on partial correlation coefficients, P to remove = 0.1) from a multivariate model rendered the univariate paternal den attendance model the best predictor of the number of cubs reaching weaning age.

Male den attendance, termite density and female age were significant predictors of the proportion of cubs surviving to weaning (Table 2). Stepwise elimination of variables from a multivariate model rendered the univariate paternal den attendance model the best predictor of the proportion of cubs surviving to weaning. In addition, when the three (independently) significant variables were included in a multivariate model ($F_{3,8} = 3.67$, $P = 0.06$, $R^2 = 0.58$), only the partial correlation coefficient for male den attendance remained significant (partial t values: paternal den attendance: $t = 2.30$, $P = 0.05$; termite density: $t = 0.53$, $P = 0.61$; female age: $t = 0.36$, $P = 0.73$).

Male Den Attendance

Because male den attendance was the primary factor influencing the number and proportion of cubs surviving to weaning age, and significant intermale variation existed in this variable, I went on to investigate predictors of male den attendance (using linear regressions with paternal den attendance as a response variable). Territory size and termite density were both significant positive predictors of paternal den attendance, as was male age and the age of their partners (Table 3). Female weight, in contrast, was negatively correlated with paternal den attendance. Initial

Table 2. Linear regressions examining the factors associated with the number and proportion of cubs surviving to weaning age

Model term	Number surviving					Proportion surviving				
	N	R^2	F	df	P	N	R^2	F	df	P
Termite density	17	0.19	7.40	1,11	0.02	17	0.21	6.52	1,11	0.03
Territory size	15	0.18	4.32	1,10	0.06	17	0.02	0.35	1,11	0.56
Paternal den attendance	12	0.47	7.81	1,8	0.02	12	0.56	12.9	1,8	0.01
Maternal den attendance	10	<0.01	0.01	1,6	0.94	10	0.01	0.23	1,6	0.65
Paternal weight	15	0.03	0.28	1,9	0.61	15	0.14	2.27	1,9	0.17
Maternal weight	17	<0.01	0.03	1,11	0.86	17	<0.01	0.06	1,11	0.82
Paternal age	15	0.05	5.10	1,9	0.05	15	0.26	4.30	1,9	0.07
Maternal age	17	0.23	6.86	1,11	0.02	17	0.20	5.95	1,11	0.03

All regressions conducted with robust standard errors to account for repeated sampling of groups. $N =$ number of breeding events analysed.

litter size, male weight and female den attendance did not influence the time males spent near their dens. Stepwise elimination of the significant variables from a multivariate model rendered a trivariate model ($F_{3,8} = 11.0$, $P < 0.01$, $R^2 = 0.80$) with male age (partial $t = 3.21$, $P \leq 0.01$), termite density (partial $t = 2.54$, $P = 0.04$) and female weight (partial $t = -2.90$, $P = 0.02$) the best predictor of male den attendance, with male and female age being dropped from the model.

DISCUSSION

My results clearly show that bat-eared fox fathers play an important parental role. Between birth and weaning, males spent significantly more time than females close to breeding dens, and, with the exception of lactation, were involved in all aspects of cub care. Consistent with this, multivariate analyses showed that, compared to territory size, termite density (which influences suckling time, Maas 1993), female den attendance, and parental age and weight, male den attendance was the best predictor of both the number and proportion of cubs surviving to weaning age. Although the intercorrelation of predictor variables (with termite density, male age and female weight significantly influencing male den attendance) makes the interpretation of data more difficult, and causal relationships cannot be inferred from correlational data, the results suggest that paternal care enhances offspring survival.

Table 3. Linear regressions examining the factors associated with male den attendance

Model term	N	R^2	F	df	P
Termite density	12	0.34	8.32	1,8	0.02
Territory size	12	0.49	38.0	1,8	<0.001
Maternal den attendance	9	0.04	0.39	1,6	0.56
Paternal weight	12	<0.01	<0.01	1,10	0.99
Maternal weight	12	0.41	8.11	1,8	0.02
Paternal age	12	0.26	8.00	1,8	0.02
Maternal age	12	0.28	5.68	1,8	0.04
Litter size	12	<0.01	0.01	1,8	0.91

All regressions conducted with robust standard errors to account for repeated sampling of groups. $N =$ number of breeding events analysed.

The parental behaviour of bat-eared foxes on the study site was largely similar to that observed elsewhere, with males primarily responsible for guarding, grooming and huddling with cubs and accompanying them on foraging trips (Serengeti, Lamprecht 1979; Maas 1993; Masai Mara, Malcolm 1986; Kalahari, Pauw 2000). Like previous researchers (Lamprecht 1979; Maas 1993), I suggest that bat-eared fox parental roles are influenced by the species' insectivorous diet. Although limited feeding of cubs was inferred to occur in this study (see also Pauw 2000), males are unable to provision their partners or cubs with termites (the species' major food source). Because termites take a long time to gather, lactating females are obliged to spend most of the night (>85%) foraging (Wright 2004), leaving them with little time to spend with cubs. This makes male involvement in offspring care important, both when cubs are confined to the den, and when they start to forage around the den.

Although the forms of paternal care I observed were similar to those recorded elsewhere, there is evidence that typical levels of bat-eared fox paternal investment may differ between populations. Maas (1993) found that, when cubs are aged between 0 and 9 weeks, males spend an average of almost 90% of their time within 50 m of dens (based on observational data). This contrasts markedly with the results of this study, where males spent an average of only 30.1% of their time within 100 m of dens (although inaccuracies associated with radiotracking may make the true figure slightly higher). It is possible that this parental variation stems from differences in diet quality. In the Serengeti, bat-eared foxes feed on *Hodotermes* termites, apparently the preferred food of the species across most of its range (Nel 1978; Maas 1993), whereas on my study site foxes feed predominantly on *Macrotermes* species (and appear to live at lower population densities than Serengeti foxes; compare Wright 2004 with Maas 1993 and Lamprecht 1979).

If male care significantly enhanced cub survival, why was so much individual variation in paternal den attendance observed? The fact that paternal den attendance correlated independently with both termite density and male age could reflect the fact that paternal investment is condition and/or experience dependent (Carlisle 1982; Wunderle 1991; Forslund & Pärt 1995). Since bat-eared foxes spend most of their time foraging (Wright 2004),

abstinence from feeding may carry a particularly high cost, which males on lower-quality territories may be less able to afford. Alternatively, male reproductive investment may increase with age because of decreasing future reproductive potential (Pianka 1976; Curio 1988). The negative association between female weight and male den attendance could be interpreted as an attempt by males to compensate for a reduced ability of their partners to invest in young, but without knowing whether female weight influenced milk production this explanation is speculative.

Given that widowed female bat-eared foxes are at least occasionally capable of rearing offspring (Maas 1993), it is clear that social monogamy is not maintained because paternal care is always necessary for successful breeding (Kleiman 1977). The requirement for male care could still make social monogamy advantageous for males, however, if males dividing care between the litters of multiple females suffered reduced reproductive success, so that males with two mates are less successful than those with one, (Wittenberger & Tilson 1980). Is this likely to be the case for bat-eared foxes?

Throughout their range bat-eared foxes are usually seasonal breeders (Wright 2004), so polygynous males would have to divide care between multiple litters simultaneously rather than sequentially. As males spent an average of 30.1% and up to 57.1% of their time in the den vicinity, and assuming a 10% travel time between den sites (Wright 2004), a male dividing care evenly between two dens would spend an average of 10.1% or up to 23.6% of his time at each den. The regression analyses show that a 10% increase in den attendance corresponded to a 16.2% increase in cub survival, with a den attendance of 49.2% resulting in the complete survival of litters. On this basis, males with two mates would increase their reproductive success by between 6% (for average levels of den attendance; proportional increase in offspring surviving in two litters with 10.5% paternal den attendance versus one litter with 30.1% paternal den attendance) and 18% (proportional increase in survival of offspring in two litters with 23.6% paternal den attendance versus one litter with 57.1% paternal den attendance). This calculation, however, does not account for the fact that males are heavily involved in postweaning cub care (Wright 2004), and perhaps advantageous prebirth den preparation (Pauw 2000; Huber et al. 2002). Because sharing these forms of care between litters would further reduce the already small benefits of polygyny, I speculatively conclude that, unless breeding females denned communally (Maas 1993), or males divided care unequally between dens, the requirement for paternal care may make social monogamy the optimal mating strategy for both sexes.

Although the care provided by canid males could be unselected or maladaptive (e.g. Jamieson 1989), their heavy involvement in offspring and mate provisioning (Asa & Valdespino 1998) suggests that they make a significant parental contribution. This conclusion is supported by the observation of widowed females failing to rear young (Moehlman 1986), and by the fact that the presence of nonbreeding helpers, which perform similar 'parental' duties as fathers, enhances offspring survival (red foxes, *Vulpes vulpes*: Macdonald 1979; black-backed jackals: Moehlman 1979; although these studies do not account for the potentially confounding effects of territory quality). The question of whether or not the requirement for male care generally promotes social monogamy in canids is difficult to answer. However, the observation that social monogamy apparently persists in some species without well-developed forms of male care (e.g. Geffen & Macdonald 1992) suggests that other factors, such as dispersion (Brotherton & Manser 1997; Komers & Brotherton 1997; Wright 2004) or noncompliance of females (Davies 1989; Gowaty 1996), also operate to prevent polygyny from occurring.

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