

Small size and monogamy: spatial organization of Blanford's foxes, *Vulpes cana*

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Abstract. Interspecific comparisons between canids suggest allometries in the characteristics of neonates, such that species with lower body weights tend to produce relatively heavy neonates, in relatively small litters whose combined weight is relatively low. Canids weighing less than 6 kg have generally been reported as monogamous with occasional polygyny; on the basis of a parental investment hypothesis, the interspecific allometries suggest that the smallest canids should have the greatest tendency to be polygynous. This prediction was explored by studying Blanford's foxes, which at ca 1 kg are lighter than any previously studied. Data from 11 radio-tracked foxes studied over 2 years indicated that they were organized as strictly monogamous pairs in territories of about 1.6 km² which overlapped minimally. Three out of five territories contained a single non-breeding yearling female during the mating season, but there was no evidence of polygyny. It is suggested that the departure of Blanford's fox from the allometric trends can best be explained in terms of adaptations to its habitat rather than as a direct consequence of small size.

Although foxes were previously thought to be solitary (e.g. Fox 1975), recent studies have shown that several species, such as the red fox, *Vulpes vulpes*, and the Arctic fox, *Alopex lagopus*, may form groups, generally composed of one adult male and several related females (Hersteinsson & Macdonald 1982; Macdonald 1983). For example, among red foxes, male offspring almost always emigrate while some females may stay as non-breeding helpers or, occasionally, as additional breeding females which may rear cubs separately or communally (Macdonald 1979, 1980; Niewold 1980; Zabel & Taggart 1989). Moehlman (1986, 1989) has described a general relationship between body weight and mating systems among canids: 'Small species are usually monogamous, but are on occasion polygamous' and monogamous species may have female helpers, while the heaviest species tend towards polyandry with male helpers. She adopts the theories of Trivers (1972) to argue that this association between small size and polygyny arises because small canids tend to have fewer and relatively heavier pups, which therefore require less parental investment, than the more altricial pups of larger canids. Therefore, males of small species can invest in more than one female. In large species, litters are larger and the pups are more altricial and

require relatively greater post-partum investment, so that helpers are essential. Moehlman's (1986) application of Trivers' (1972) parental investment hypothesis leads to the prediction that polygyny will be more frequent among Blanford's foxes (weight of 1 kg) than among larger representatives of the more-than-6-kg weight class of canids.

The Blanford's or Afghan fox occurs in warm mountainous regions of Pakistan, Afghanistan, Iran and southwestern Russia (Roberts 1977). Recently it was also discovered in Israel, Sinai, Oman and Saudi-Arabia (Mendelssohn et al. 1987; Harrison & Bates 1989). In Israel it is restricted to rugged mountain ridges and canyons in the Negev and Judean deserts. The species is generally considered to be rare (Ginsberg & Macdonald 1990) and aside from the fact that it is nocturnal and largely insectivorous (Ilany 1983; Mendelssohn et al. 1987), nothing is known of its behavioural ecology. Here we present data on the ranging behaviour of 11 Blanford's foxes which suggest that this species has a monogamous rearing system.

METHODS

Study Site

The study was carried out in the Ein Gedi Nature Reserve (31°28'N, 35°23'E, elevation of 100–350 m below sea level) in Israel. This site is characterized

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by steep rocky mountain slopes, deep canyons and sheer cliffs. The topography consists of a 500 m limestone cliff aligned parallel to the Dead Sea. Four large springs and two canyons with permanent water are the main water sources. The vegetation is typically Saharo-Arabic and tropical in origin. Along the water courses, vegetation cover reaches 100% but is only 0.5–10% on the surrounding slopes and cliffs. Maximum average summer temperatures reach 38.9°C, mean relative humidity can be as low as 29% and mean annual precipitation is 81 mm (Karta 1985).

Field Methods

Foxes were trapped using 100 collapsible box traps (Tomahawk, 80 × 22 × 22 cm), positioned in canyons and on rocky slopes, usually under a large boulder to provide shade for captives. Most traps were left in situ for 2–3 years and set for 3–6 days, baited with dead chicks, at approximately monthly intervals. All new captures were measured, weighed and individually marked using numerical metal ear tags (tag-loss was nil). Foxes were categorized as (1) adult if tooth wear was substantial and weight was more than 0.9 kg, (2) subadult if tooth wear was minimal and weight ranged between 0.7 and 0.9 kg, or (3) juvenile if teeth were small and partly emerged and weight was equal or less than 0.7 kg. Adults that were recaptured frequently were fitted with radio-collars (60 g, life span 6 months, Wildlife Materials, Inc., U.S.A.).

Each tracking session involved radio-tracking one individual, starting 1 h before sunset and ending 1 h after sunrise (or later if the fox was still active), with fixes being taken every 15 min. The locations of all other radio-tagged foxes in the vicinity were also recorded. Each fox was radio-tracked once a month. The rugged terrain required all tracking to be done on foot, using a headlamp. The foxes were relatively tolerant and so it was possible to stay within a few hundred metres of focal individuals. Fixes were generally accurate to ±20 m as proven by frequent sightings, but when foxes travelled in particularly inaccessible areas their locations were allocated to a square of 100 × 100 m. Light intensifier goggles (El-Op, Rehovot, Israel) and a powerful flashlight were used to facilitate direct observations.

Data Analysis

Home range size was evaluated using three different methods: (1) 80% minimum convex polygon

of total range (Geffen 1990), (2) 100% minimum convex polygon of nightly range, and (3) summed area of 100 × 100 m grid cells. The respective merits of these techniques have been widely reviewed (e.g. Macdonald et al. 1980; Kenward 1987) and discussed further in the context of Blanford's foxes in Geffen (1990). Nightly distances were calculated as the sum of the distances between each two sequential fixes collected per night. For comparison of seasonal and sex effects on nightly range and distance we collapsed the seasonal daily values of each fox into a mean, and compared these using two-way analysis of variance.

Stability in home range location and configuration for each fox was evaluated using the prevailing range method (Doncaster 1990; Doncaster & Macdonald 1991). This involves a running tally of the number of grid cells coming into use for the first time or being abandoned definitively from the home range, and is conceptually similar to the minimum number alive estimate in capture-mark-recapture analyses, in that the number of grid cells used per night is equivalent to the number of animals caught in a trapping session. The results are expressed as nightly percentage survival of grid cells; so low survival rate indicates that the home range is drifting. This analysis used grid-cell home ranges based on the influence cell method (Voigt & Tinline 1980, Queen's Rule) where the eight contiguous 'influenced' cells around each cell containing a fix are given a utilization score of one-eighth the value of a fix. Peripheral influence cells were trimmed prior to calculations of cell survival (DRIFT.BBC-Computer package; Doncaster 1990). First and last survival estimates for each set of data were discarded because of the dependence of range size on the cumulative fix total (Doncaster 1990).

Overlap between two home ranges is presented as the mean of their percentage overlaps, and calculated separately for each of the home range methods. A pair of foxes was defined as an adult male and female that were observed, by both trapping and radio-tracking, to occupy a shared range for at least 3 months. To test for monogamy, as reflected by the spatial relationships between neighbouring Blanford's foxes, we generated values for a random juxtaposition of ranges as follows: each range was rotated, by a random number of degrees, about its arithmetic centre of activity. After each rotation the overlap with neighbouring home ranges was calculated. This procedure was repeated

10 times, and the mean randomly rotated percentage overlap was compared with the observed overlap using the Wilcoxon signed rank test (Siegel & Castellan 1989). If the observed and the randomly rotated values were not significantly different we concluded that home ranges were juxtaposed without regard to the configuration of neighbouring ranges. Alternatively, a larger observed than expected overlap indicated attraction between individuals, whereas smaller overlap than expected indicated avoidance (Madison 1980).

RESULTS

During 1987–1988 on 189 trapping days in Ein Gedi we caught 31 foxes, of which 11 were fitted with radio collars, in 317 recaptures. Some were recaptured as many as 18–37 times. Nine young ear-tagged foxes that were frequently trapped showed comparable site-fidelity (70–100% of trapping episodes for each fox were within one range) to the ranges of five adult pairs (Fig. 1). One male and three females that were first caught as juveniles (3–4 months old) or subadults (5–7 months old) spent the next 11–14 months (including the breeding season) within an adult pair's home range. All five adult resident females lactated during the spring breeding season (1987 and 1988) but, out of 10 young females that were residents for 2–14 months, during 1987 and 1988, only one lactated. This lactating yearling apparently vacated the parents' range during the breeding season. Of adults (older than 1 year) only members of each resident pair were frequently caught in each range. Adults that were recaptured fewer than five times were considered as non-residents; all were caught in a relatively short period during mid-winter (November–January).

Foxes were tracked on 141 tracking nights. Home range locations and configurations of 11 foxes at Ein Gedi were stable during 1987–1988 (Fig. 2), except for male 2 following the death of his mate in 1987 (the instability in the range of male 2 was the result of his moving to another range). Even lactating females did not decrease their home range size (spring; Table I). The foxes travelled 7–11 km per night, covering about 1 km² (Table I). Home range sizes (data were transformed to their natural logarithm for two-way analysis of variance) did not differ between the sexes ($F_{1,32}=2.54$, $P>0.05$) or seasons ($F_{3,32}=0.67$, $P>0.05$). No differences

between the sexes ($F_{1,32}=3.43$, $P>0.05$) or between seasons ($F_{3,32}=0.12$, $P>0.05$) in nightly distance travelled were detected.

The overlap in home range between members of a pair at Ein Gedi was clearly greater than the overlap with any other category of neighbour (Fig. 1, Table II). Comparison between the observed percentage overlap and that generated by the random rotations revealed that the home ranges of mates were significantly more congruent than expected by chance, while the overlap with neighbouring home ranges did not differ significantly from random (Table III).

The dens used by Blanford's foxes at Ein Gedi were usually on a mountain slope and consisted of large rock and boulder piles or scree. Dens were used both for rearing young during spring and for day-time harbourage throughout the year. During winter and spring both members of a pair tended to occupy the same den, or adjacent dens, at the same site (64.5%, $N=48$ days and 69.0%, $N=58$, respectively), while during summer and autumn they often denned at separate locations (49.1%, $N=53$ and 61.0%, $N=41$, respectively), a seasonal difference which is statistically significant ($\chi^2=16.73$, $df=6$, $P<0.05$). Frequent changes from day to day in den location were more common in summer and autumn. Frequencies of occupation of the dens at the same site ($\chi^2=0.79$, $df=3$, $P>0.05$) or at different sites ($\chi^2=6.81$, $df=3$, $P>0.05$) on consecutive days did not differ significantly between the sexes, but did differ between seasons ($\chi^2=14.12$, $df=3$, $P<0.05$ for males and $\chi^2=26.78$, $df=3$, $P<0.05$ for females).

DISCUSSION

On the basis of the following evidence we conclude that the Blanford's foxes in our study area had a monogamous rearing system: (1) home range overlap between members of pairs was significantly greater than expected by chance; (2) both pair-members used the same den area and shared a den during the breeding season (winter–spring); (3) there were no intersexual differences in home range size or nightly travel distances (except in spring); (4) a shift in home range location was observed only once following the death of a pair member; and (5) slight physical dimorphism (Geffen et al., in press).

As an extremely lightweight canid, at the lower extreme of Moehlman's class weighing less than 6 kg, the parental investment hypothesis predicts

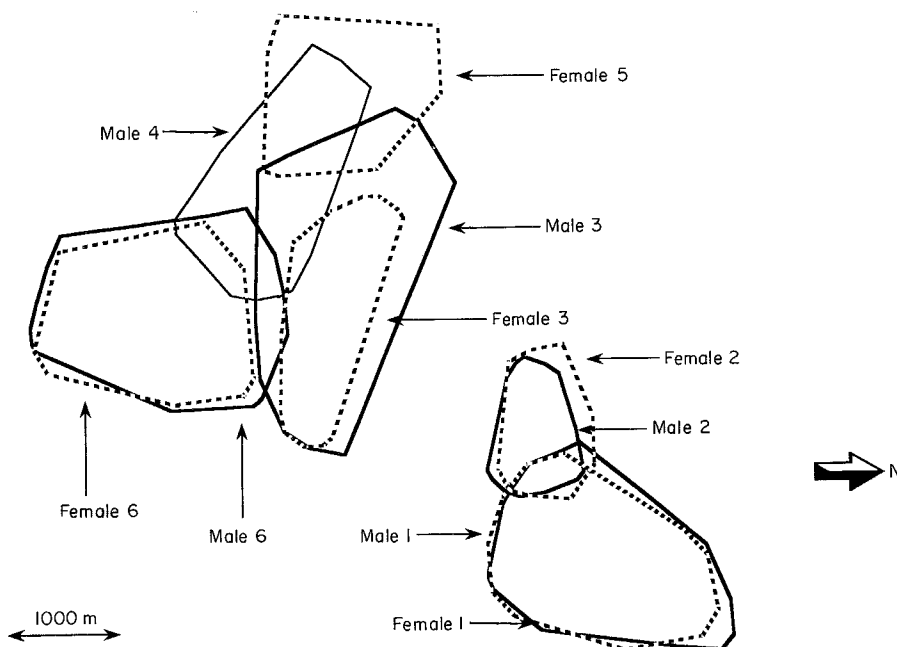


Figure 1. The spatial organization of home ranges (80% minimum polygon) of 10 Blanford's foxes at Ein Gedi during 1987. During the winter of 1988 females 2 and 5 died, male 2 moved to the range of female 5 and a new female (4) joined male 4. The other neighbouring pairs (1, 3 and 6) did not alter their ranges during the 2 years of study.

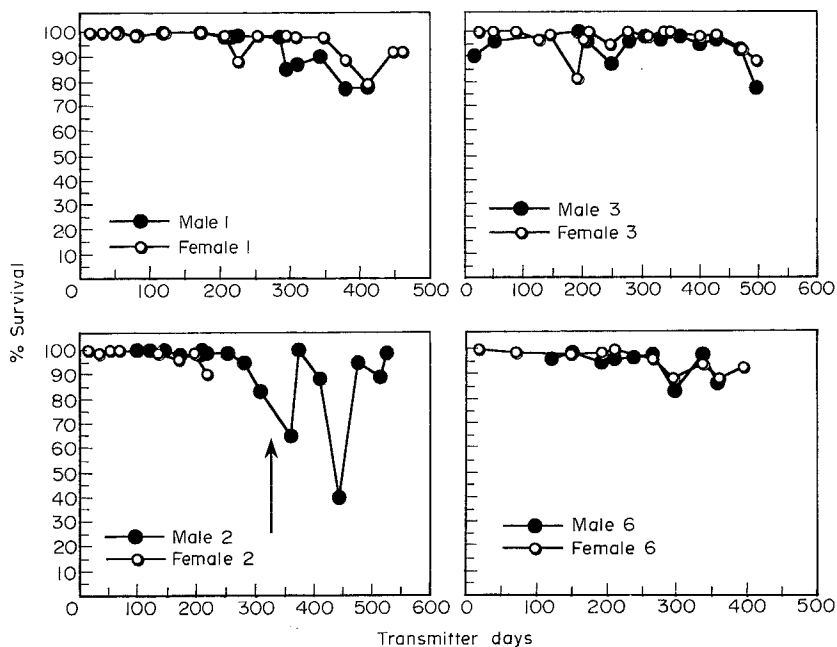


Figure 2. Percentage of grid cells surviving from one tracking night to the next in relation to tracking interval (transmitter days) for four pairs of foxes in Ein Gedi. High versus low values for percentage survival indicate stability in the range used from night to night. The only instability recovered (pointed by the arrow) was in the range of male 2 following the death of his mate (female 2).

Table I. Mean ($\bar{X} \pm \text{SD}$, N) nightly home range size and nightly distance travelled for five males and five females per season in Ein Gedi

	Winter	Spring	Summer	Autumn	Total
Nightly home range (km²)					
Male	1.0 $\pm$ 0.7 (16)	1.3 $\pm$ 0.6 (23)	1.1 $\pm$ 0.8 (19)	1.0 $\pm$ 0.5 (16)	1.1 $\pm$ 0.7 (74)
Female	0.9 $\pm$ 0.6 (16)	0.9 $\pm$ 0.8 (19)	1.2 $\pm$ 1.0 (20)	1.1 $\pm$ 0.8 (12)	1.0 $\pm$ 0.8 (67)
Total	1.0 $\pm$ 0.7 (32)	1.1 $\pm$ 0.7 (42)	1.2 $\pm$ 0.9 (39)	1.0 $\pm$ 0.6 (28)	1.1 $\pm$ 0.7 (141)
Nightly distance (km)					
Male	9.7 $\pm$ 3.1 (16)	11.3 $\pm$ 1.7 (23)	8.3 $\pm$ 2.3 (19)	9.5 $\pm$ 1.8 (16)	9.8 $\pm$ 2.5 (74)
Female	8.6 $\pm$ 3.1 (16)	7.9 $\pm$ 3.3 (19)	9.4 $\pm$ 2.6 (20)	8.5 $\pm$ 2.2 (12)	8.6 $\pm$ 2.9 (67)
Total	9.2 $\pm$ 3.1 (32)	9.8 $\pm$ 3.0 (42)	8.9 $\pm$ 2.5 (39)	9.1 $\pm$ 2.0 (28)	9.3 $\pm$ 2.7 (141)

N = Number of nights. Winter = December–February, Spring = March–May, Summer = June–August and Autumn = September–November. Winter is the mating season and spring the pup-rearing season.

Table II. Comparison of mean percentage overlap between mates and with neighbouring males and females using data from two different home range estimates

	Mean percentage overlap	
	Male	Female
Grid (100 $\times$ 100 m)		
With mate	62.7	62.7
With other males	18.7 $\rightarrow$ *	13.6 $\rightarrow$ *
With other females	11.2	9.9
80% minimum polygon		
With mate	77.9	77.9
With other males	16.3 $\rightarrow$ *	8.2 $\rightarrow$ *
With other females	10.0	7.4

* $P < 0.05$, two-tailed probabilities, Mann–Whitney U -test.

that Blanford's foxes are more likely to be polygynous than are larger canids. However, the more altricial its young, the greater the need for post-partum paternal care and the more monogamous we might expect the species to be. In the context of these conflicting pressures we will consider the observed rearing system in the Blanford's fox.

Is there any evidence of polygyny to set against these indications of monogamy? Our results showed that in at least three territories there were additional reproductive-age adults during the breeding season. In each of two territories there was a non-breeding female and in the third territory a second female which subsequently lactated. However, having been trapped frequently (once every 2 weeks to a month) prior to the breeding season, this female was trapped (and found to be lactating) only

once during the next 3 months. Thereafter, she was again recaptured frequently (total of 29 recaptures during 1 year). We interpret this as indicating that she left the territory during the breeding season and returned thereafter. Overall, the five Ein Gedi territories yielded no evidence of polygyny. Nor did two territories we have studied in another population of Blanford's foxes at Eilat (300 km south; Geffen 1990). In total, therefore, we can report on seven territories with no evidence of polygyny. This sample is large and detailed by the standards of field studies of canids, and larger than most of those cited by Moehlman (1986) as indicating evidence of occasional polygyny. We conclude that the Blanford's fox in our study areas is, by the standards of small canids, uncommonly strictly monogamous and rarely if ever polygynous.

What is the social role of the non-breeding adult females sharing the territories of Blanford's fox breeding pairs? The phenomenon of helpers is well documented in canid societies (Macdonald & Moehlman 1983). In the case of the genus *Vulpes* and related small fox-like species the helpers are almost invariably female (e.g. Macdonald 1979); they are equally likely to be male or female in the medium sized *Canis* species (e.g. Moehlman 1979), and are predominantly male in the larger canids such as the African wild dog, *Lycaon pictus* (e.g. Frame et al. 1979). Our observations suggest that natal philopatry is indeed largely confined to non-breeding female Blanford's foxes, but we found no evidence that these females contributed to the care of the young at any stage of their development. Despite following the territory residents closely over two breeding seasons, with frequent observations of the parents in the vicinity of the den, we

Table III. Comparison of observed percentage overlap between categories of home ranges (80% minimum polygon) with the mean percentage overlap produced by random rotation of one range of the two being compared

	Mean observed (% $\pm$ SD)	Mean rotated (% $\pm$ SD)	Sample size	T+
Male with mate	67.3 $\pm$ 19.9	52.8 $\pm$ 19.5	5	15*
Female with mate	88.6 $\pm$ 10.8	64.8 $\pm$ 8.2	5	15*
Male with other males	16.3 $\pm$ 9.3	13.7 $\pm$ 11.2	8	28
Female with other females	7.4 $\pm$ 10.3	7.7 $\pm$ 8.7	4	5
Male with other females	10.0 $\pm$ 11.1	7.3 $\pm$ 6.2	9	30
Female with other males	8.2 $\pm$ 9.3	12.7 $\pm$ 12.9	7	7

The results are presented for 80% minimum polygon. For each comparison 10 random rotations of one of the home ranges were made, and the overlap calculated after each.

* $P < 0.05$; Wilcoxon signed-rank test (T+).

never saw a non-breeding adult contribute to the cubs in any way. Furthermore, we never observed any adult carry food to the young and we found only one den with remains of prey at the entrance. Rather, it appears that the cubs are entirely dependent for food upon their mother's milk until they begin to forage for themselves. This may be because these foxes live largely on insects (Geffen et al. 1992), which are not large enough to merit transport back to the den, and it seems likely that they do not regurgitate, as red foxes do not do so (Macdonald 1987). While it is possible to imagine various ways in which non-breeders and fathers might foster the well-being of the cubs, we could see no evidence that they did so. We have no indication that the male provides food either to the female or to the cubs, although we have observed males that groomed and accompanied juveniles. Therefore, it appears that the contribution to pup survival of any individual other than the mother is probably minimal (see Macdonald & Carr 1989). Under the parental investment hypothesis, these circumstances act in the same direction as neonate precociality to favour polygyny.

Blanford's foxes occupy territories that tessellate with minimal overlap. It seems likely that the disadvantage of interference competition between neighbours for their insect prey favours this spacing out. We have shown elsewhere that the size and configuration of their territories is determined by the dispersion of patches of a particular habitat, dry creekbed, in which they forage much more than elsewhere (Geffen 1990). For cases where territorial animals forage for patchily dispersed food, Carr & Macdonald (1986) described how variability in

food availability could create conditions in which a territory with the minimum resources necessary to support a pair could support additional group members at no competitive cost to the original occupants. However, where the dispersion of available food is rather homogeneous between patches it is less likely that the minimum territory required to support a pair will also support additional adults (Macdonald 1981, 1983). Under these circumstances, following Macdonald (1983), we would have predicted that most territories would be occupied only by pairs or trios, as was observed. In this case, to incorporate additional adults on a permanent basis would require a territory proportionally richer in resources (i.e. expansionism, *sensu* Kruuk & Macdonald 1985). If the contribution to cub survival of non-breeding females is close to nil, then it is unlikely that the benefit of incorporating them would repay the costs of territorial expansion (Macdonald & Carr (1989) elaborated the same argument to explain why smaller canids may generally be territorial contractors and the opposite argument to explain why larger canids may generally be expansionists).

Returning to the question of why Blanford's foxes are not polygynous, we advance two non-exclusive hypotheses. These are: (1) that their altricial young require more paternal care than would have been predicted for a canid of this size, making monogamy advantageous to the male; and (2) that the dispersion of their prey is such that the territorial expansion generally required to accommodate additional females would diminish the male's capacity to defend his mate and food to the extent that outweighed any benefit from

polygyny. To test these hypotheses exhaustively will require more data.

In conclusion, Moehlman (1986) argued that physiological corollaries of body size result in allometries that dictate interspecific differences in requirements for post-partum care, and therefore determine rearing systems. It seems to us more plausible that body size determines feeding habits and ecological circumstances, and thus that factors such as resource dispersion impose constraints upon social organization which therefore determine the capacity for post-partum care and, in turn, the most advantageous neonate characteristics. In our view, the relatively low degree of post-partum care observed in small canids is not a consequence of physiological corollaries of size that constrain them to produce precocial neonates and thus facilitate polygyny; rather, small size places them in ecological conditions that favour those social systems that offer reduced scope for post-partum care and an adaptive response to this is the production of precocial neonates.

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