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Author(s): Eli Geffen and David W. MacDonald

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ACTIVITY AND MOVEMENT PATTERNS OF BLANFORD'S FOXES

ELI GEFFEN AND DAVID W. MACDONALD

*Wildlife Conservation Research Unit, Department of Zoology,
South Parks Road, Oxford, UK OX1 3PS*

Blanford's fox (*Vulpes cana*) is strictly nocturnal. Onset of activity is strongly correlated with light (sunset), but variation in the time when activity ceases, in nightly distances traveled, and in the total duration of nightly activity are not easily explained and may be related to nightly foraging success. Weather conditions have no significant effect on activity patterns of these foxes. Blanford's foxes tend to leave the vicinity of their daytime lairs shortly after activity begins and return there during the second half of the night. Some individuals travel a predictable route, especially during the first half of the night. We hypothesize that this time-tabling in the movement of pair members is a mechanism that minimizes interference between foxes while foraging.

Key words: *Vulpes cana*, Israel, desert carnivore, activity pattern, movements

Predators synchronize their foraging with the activity of their main prey (Curio, 1976). Large Canidae, especially species that hunt cooperatively, are active both by day and night (*Canis latrans*—Andelt, 1985; *Canis lupus*—Mech, 1970; *Cuon alpinus*—Johnsingh, 1982) or are diurnal (*Lycaon pictus*—Estes and Goddard, 1967). Most small canids are generally nocturnal or crepuscular (*Urocyon cinereoargenteus*—Trapp and Hallberg, 1975; *Vulpes rüppelli*—Lindsay and Macdonald, 1986; *Vulpes macrotis*—Morrell, 1972), although some also may forage by day (*Alopex lagopus*—Eberhardt et al., 1982; *Otocyon megalotis*—Koop and Velimirov, 1982; Lourens and Nel, 1990). Ruppell's fox (*V. rüppelli*) is partly insectivorous and occupies hot deserts (Lindsay and Macdonald, 1986), whereas the bat-eared fox (*O. megalotis*) is largely insectivorous and sometimes forages by day in regions such as the Kalahari Desert (Nel, 1984). Blanford's fox (*Vulpes cana*) also is largely insectivorous and occupies hot deserts (Geffen et al., 1992a).

The Blanford's fox was only recently discovered in Israel, Sinai, Oman, and Saudi Arabia (Harrison and Bates, 1989; Ilany, 1983). Although there were scattered re-

ports of this 1,000-g canid from Afghanistan, Pakistan, Iran, and the southwestern Soviet Union (Heptner and Naumov, 1974; Roberts, 1977), little was known of its habits (Ginsberg and Macdonald, 1990), and its activity rhythms and movement patterns were largely unknown (Ilany, 1983; Mendelssohn et al., 1987). Blanford's foxes in Israel were spatially organized into pairs with a supernumerary young fox, usually a female (Geffen and Macdonald, 1992).

We have studied the activity of Blanford's foxes to examine whether it is nocturnal or partly diurnal like the only other predominantly insectivorous Old World canid, the bat-eared fox. We examined three factors that may favor nocturnality in the Blanford's fox, and each of them also may shed light on the exceptional diurnal behavior of the bat-eared fox: avoidance of diurnal heat load (small-bodied mammals face relatively high dehydration rates and difficulties in cooling their bodies sufficiently—Noll-Banholzer, 1979); avoidance of predation by diurnal raptors; synchronization with periods of prey availability. We can distinguish the heat stress versus prey availability hypotheses by comparing the behavior of Blanford's foxes during different seasons, but

we cannot test the diurnal-predator hypothesis because there is no control area lacking raptors.

In addition, insectivory has been invoked to explain group foraging by bat-eared foxes (because their prey tend to be clumped—Lamprecht, 1979; Waser, 1980) and solitary foraging and avoidance (to avoid scramble competition and time wasted by visiting areas previously exploited by conspecifics—Lamprecht, 1979; Cody, 1974). Indeed, this argument traditionally was used to explain why canids taking small prey were solitary (Fox, 1975). Therefore, we studied the movement patterns of Blanford's foxes to ascertain whether they forage together and, if not, whether their movements are time-tabled to minimize interference between the foraging activities of group members. Finally, because the availability of invertebrate prey to mammalian predators is affected by weather conditions (Kruuk, 1978; Macdonald, 1980), we tested whether the variations in duration of nightly activity or distance traveled nightly by the Blanford's fox can be explained by weather.

METHODS

The study was conducted at the Ein Gedi Nature Reserve (31°28'N, 35°23'E, elev. 100–350 m below sea level) in Israel. This site is characterized 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 sources of free water. The vegetation is typically Saharo-Arabic and tropical in origin (Zohary, 1980). Along water courses, vegetative cover approaches 100%, but was only 0.5–10% on the surrounding slopes and cliffs. Mean maximum summer temperature is 38.9°C, with a mean relative humidity of 29%. Mean annual precipitation is 81 mm (Karta, 1985).

Foxes were trapped using 10 collapsible box traps (Tomahawk, 80 by 22 by 22 cm), positioned in canyons and on rocky slopes, usually under large boulders to provide shade for captives. Most traps were left in situ for 2–3 years and were set for 3–6 days, baited with dead chicks,

at about monthly intervals. Adults that were recaptured more than five times were fitted with radiocollars (60 g, life span 6 months, Wildlife Materials Inc., Carbondale, IL). Transmitters were equipped with motion-sensitive switches that facilitated detection of whether a fox was moving or at rest.

Each tracking session involved radiotracking 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. Each fox was radiotracked monthly. The rugged terrain required all tracking to be done on foot, using a headlamp. The foxes were relatively tolerant, so it was possible to stay within a few hundred meters of focal individuals. At night these foxes showed no fear of humans and occasionally they passed within a few meters of us without exhibiting alarm behavior. Fixes generally were accurate to ± 20 m, as verified by frequent sightings, but when foxes traveled particularly inaccessible areas, their locations were allocated to a 100 by 100-m square corresponding to a similar scale grid on an aerial photograph. Light intensifier goggles (El-Op, Rehovot, Israel) and a powerful flashlight were used to facilitate direct observations.

For each tracking night we calculated: the total distance traveled by the fox; total duration of activity; average speed of travel; nightly home range (the minimum polygon constructed from the fixes collected that night); onset and termination of activity; sunset, sunrise, and total period of darkness (data from an almanac published by The Survey Department of Israel); a moonlight index calculated from the total period of visibility of the moon each night multiplied by an index of lunar phase estimated between 0 (new moon) and $\frac{1}{2}$ (full moon). We defined four seasons at 3-month intervals (Table 1) and compared seasonal-activity periods by two-way analysis of variance after averaging seasonal values of each fox (data were transformed to their $\sin(x)$ for this analysis). The total time that each fox was active of the total time of darkness was expressed as a percentage, and the Kruskal-Wallis test (Siegel and Castellan, 1989) was used to detect seasonal differences. We examined the correlation between nightly variables using the Spearman rank correlation (Siegel and Castellan, 1989) and evaluated the effect of weather variables on the activity duration (data were transformed to their $\sin(x)$ for this analysis) and nightly distance traveled

TABLE 1.—Mean period of nightly activity (min) and percentage of activity per night of males and females in Ein Gedi, Israel, per season (1987–1988); n = number of nights, winter = December–February, spring = March–May, summer = June–August, and autumn = September–November.

	Winter		Spring		Summer		Autumn	
	$\bar{X} \pm SD$ (n)	%	$\bar{X} \pm SD$ (n)	%	$\bar{X} \pm SD$ (n)	%	$\bar{X} \pm SD$ (n)	%
Male	569.1 \pm 98.0 (16)	69.88	562.8 \pm 63.3 (23)	84.55	524.2 \pm 63.9 (19)	85.49	644.1 \pm 44.0 (16)	87.52
Female	567.2 \pm 146.4 (16)	70.33	501.3 \pm 72.7 (19)	75.16	541.5 \pm 45.1 (20)	88.00	572.5 \pm 153.5 (12)	78.09
Total	568.1 \pm 122.6 (32)	70.11	535.0 \pm 73.7 (42)	80.31	533.1 \pm 55.0 (39)	86.78	613.4 \pm 109.4 (28)	82.81

by the foxes using stepwise multiple regression (Sokal and Rohlf, 1981).

We examined distances of each fox from the vicinity of the den every 2 h during each sampled night. We defined a distance of ≥ 100 m as away from the den and a distance of < 100 m as near the den. For each fox, the frequencies of near and away from the den at each 2-h interval were compared by a goodness-of-fit test (Siegel and Castellan, 1989). Because each fox was analyzed separately, we used only data from foxes that were tracked for ≥ 10 nights to avoid biases from small samples.

Foxes used their ranges unevenly (Geffen, 1990). Therefore, we divided each pair's home range (80% minimum polygon; a method we used to remove outliers; Geffen, 1990) into five sectors, each representing an important site for the foxes such as a den or a dry creek (dry creek was the most utilized habitat by the foxes—Geffen, 1990). A pair of foxes was defined as an adult male and female that were observed, by both trapping and radiotracking, to occupy a shared range for ≥ 3 months. For each night, the time between the onset of the fox's activity and its arrival at each of the five sectors was calculated. These results were calculated as percentages of the total number of arrivals at each sector in consecutive 30-min periods (from all available nights for each fox). Patterns in arrival time at each sector during the first 6 h after the onset of activity were compared between pair members using a maximum likelihood log-linear model fitted to a Poisson distribution (GLIM-computer package—Healy, 1988). Simplified models of individual movement patterns are presented as home-range plots with arrows indicating the most

frequent direction of movement during the first 6 h after onset of activity.

RESULTS

Foxes were tracked on 141 nights (6,588 fixes for 11 foxes). Differences in duration of nightly activity between the sexes ($F = 0.98$, $d.f. = 1, 32$, $P > 0.25$) or among seasons ($F = 1.39$, $d.f. = 3, 32$, $P > 0.25$) were not significant, but percentages of activity per night were significantly different among seasons (Kruskal-Wallis test, $H = 16.7$, $d.f. = 3$, $P < 0.001$; Table 1). Foxes were observed in 92% of 463 observations walking solitarily.

Variance in monthly onset of activity was small (Fig. 1), and monthly averages closely followed the time of sunset (Fig. 1). Onset of activity (Kruskal-Wallis test, $H = 118.0$, $d.f. = 11$, $P < 0.001$) and termination of activity (Kruskal-Wallis test, $H = 23.4$, $d.f. = 11$, $P < 0.05$) differed significantly among months. Mean differences between onset of activity and sunset, and between termination of activity and sunrise did not vary significantly among individuals ($H = 17.0$, $d.f. = 10$, $P > 0.05$ and $H = 4.8$, $d.f. = 10$, $P > 0.05$, respectively). Foxes never were recorded to emerge from their dens before sunset or after sunrise.

Onset of activity was best correlated with sunset (Spearman rank correlation; $r_s = 0.89$, $n = 141$, $P < 0.001$), but termination of activity was weakly correlated with sunrise

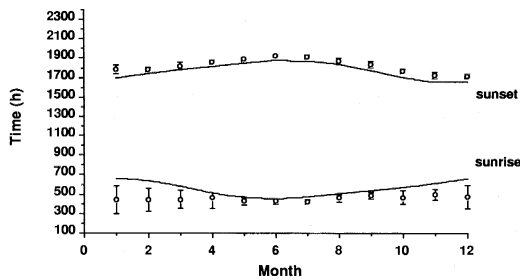


FIG. 1.—Mean (\pm SD) times for onset and termination of activity for all foxes at Ein Gedi, Israel (1987–1988). The solid lines represent the time of sunset (upper line) and sunrise (lower line).

($r_s = 0.28$, $n = 141$, $P < 0.005$). Termination of activity also was correlated with the total nightly activity period ($r_s = 0.66$, $n = 141$, $P < 0.001$). Nightly distances ($\bar{X} \pm SD = 9.3 \pm 2.7$ km) were significantly correlated with the total period of nightly activity ($r_s = 0.44$, $n = 141$, $P < 0.001$). We did not detect any effect of moonlight on duration ($r_s = 0.16$, $n = 141$, $P > 0.5$) or end ($r_s = 0.03$, $n = 141$, $P > 0.8$) of activity. Variations in period of nightly activity and nightly distance could not be significantly explained by any of the weather variables that we examined using stepwise multiple regression (partial correlation $r \leq 0.08$, $d.f. = 1,140$, n.s. in all cases). Heavy rain and strong wind caused foxes to retreat to their dens, but such conditions were brief and rare.

Nightly home range averaged 1.08 ± 0.74 km² and was significantly correlated with distance traveled nightly ($r_s = 0.62$, $n = 141$, $P < 0.001$), total period of nightly activity ($r_s = 0.27$, $n = 141$, $P < 0.001$), and mean speed of nightly travel ($r_s = 0.53$, $n = 141$, $P < 0.001$). Foxes tended to be away (≥ 100 m) from their daytime den during the first half of the period of nightly activity and near it (< 100 m) towards sunrise (Fig. 2). Once a fox begins activity it soon leaves its daytime denning area (Fig. 2). For all nine foxes, the pattern of their location within their home ranges significantly shifted during successive 2-h blocks throughout the night

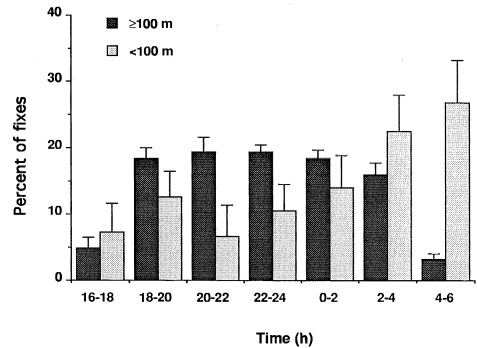


FIG. 2.—Mean (\pm SD) percent of fixes located < 100 m and ≥ 100 m from the daytime resting den throughout the night (in 2 h intervals) at Ein Gedi, Israel.

($\chi^2 \geq 37.4$, $d.f. = 6$ and $P < 0.001$ in all nine cases).

The arrival times at each of five sectors in each home range were measured from the onset of activity for eight foxes at Ein Gedi. Using a maximum likelihood log-linear model (fitted to a Poisson distribution; $\chi^2 \leq 24.6$, $d.f. = 20$, n.s. in all cases) for comparison between the two members of each pair showed that patterns of arrival time to each sector were significantly different between the members of two pairs (pair 1: sector B ($\chi^2 = 13.74$, $d.f. = 1$, $P < 0.05$) and sector E ($\chi^2 = 4.05$, $d.f. = 1$, $P < 0.05$) and pair 4: sector D ($\chi^2 = 11.06$, $d.f. = 1$, $P < 0.05$)). Variation in the movements of each fox confounded detection of additional statistical differences between pair members in their arrival times at sectors, but patterns suggestive of such differences were apparent (Fig. 3; Geffen, 1990).

DISCUSSION

The Blanford's fox in Israel is strictly nocturnal. This trait is shared with most small canids in arid environments (e.g., Lindsay and Macdonald, 1986; Morrell, 1972; Nel, 1984), but not all (Koop and Velimirov, 1982; Lourens and Nel, 1990). The exception, the bat-eared fox, also is primarily insectivorous. Although summer temperatures at Ein Gedi rising to 39°C might preclude activity of Blanford's foxes by day,

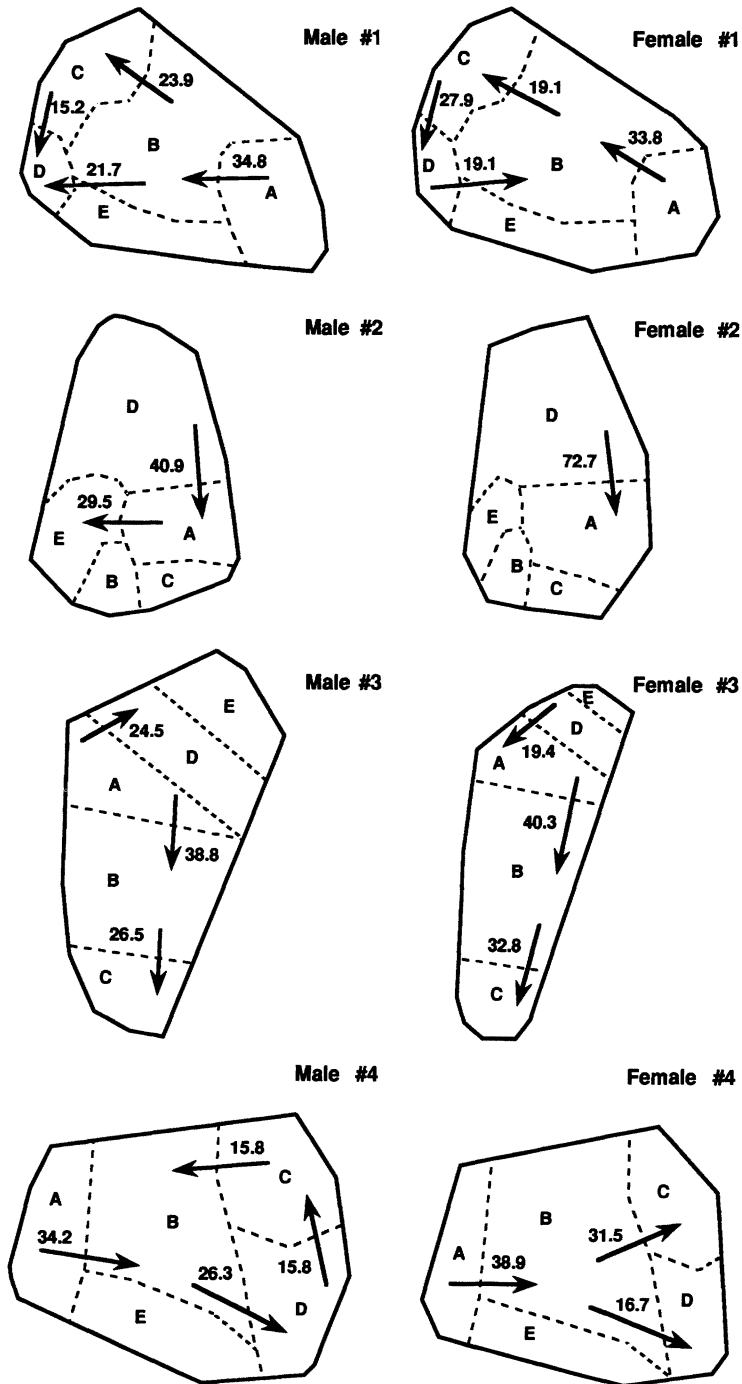


FIG. 3.—Percentage of movements between sectors of each home range of four pairs of Blanford's fox. Bold arrows pointing out the most frequent direction of movement during the first 6 h after onset of activity. Home ranges are 80% minimum polygons, with sector boundaries shown as broken lines.

midwinter temperatures at 15–18°C would seem unlikely to be a constraint. The geographic range of the bat-eared fox encompasses variously hot regions (Smithers, 1983). Although it is possible that bat-eared foxes are more strictly nocturnal in hotter areas and during hotter seasons, this is not known; certainly they occasionally have been observed foraging for swarms of termites (*Hodotermes mossambicus*) in the heat of the day in the Kalahari Desert (Nel, 1978). It seems unlikely that high temperature alone imposes a curfew on diurnal activity by the Blanford's fox. The diurnal sorties of the bat-eared foxes may be favored either because the insects they eat are more often diurnal than those eaten by the Blanford's fox, or because their larger size puts them at lesser thermal disadvantage. In Israel, diurnal invertebrates (e.g., grasshoppers and ants during winter—Geffen et al., 1992a), which apparently were located during the night while inactive, were common in the diet of Blanford's foxes. Furthermore, seasonal changes in dietary composition of Blanford's foxes were not detected (Geffen et al., 1992a). These results imply that if prey availability does not fluctuate much annually and if foxes are able to locate both active (nocturnal) and inactive (diurnal) prey, then food availability cannot be the main force that drives these foxes to strict nocturnality.

The small size of Blanford's fox renders it susceptible to large diurnal raptors such as the golden eagle (*Aquila chrysaetus*) and the Bonelli's eagle (*Hieraetus fasciatus*). In contrast, nocturnal predators (red foxes, *Vulpes vulpes*, and eagle owls, *Bubo bubo*) rarely frequent its habitat, and leopards (*Panthera pardus*), although common, rarely prey upon foxes (Ilany, 1979). Thus, the body size of Blanford's fox makes diurnal activity perilous; even at three times the weight, bat-eared foxes closely watch large birds of prey (Lamprecht, 1979). Cape foxes (*Vulpes chama*) dash for cover when a martial eagle (*Polemaetus bellicosus*) appears

overhead (D. W. Macdonald, pers. obs.), whereas kit (*Vulpes macrotis*) and red foxes are reported to fall prey to golden eagles (Cramp, 1980; O'Farrell, 1987). Although food availability and heat stress might favor nocturnality by the Blanford's fox, only anti-predator behavior would seem a fully adequate explanation of strict nocturnality of the Blanford's fox.

The onset of activity largely is explained by light conditions (sunset), but variation in duration and termination of activity may reflect nightly foraging success. In the field, it was impractical to assess nightly foraging success directly. Three factors might account for the proportionally longer duration of activity during the hot summer season (Table 1): less nighttime is available for foraging; some prey (e.g., beetles—Geffen et al., 1992a) are inactive in subterranean cavities under rocks, thus making their capture more time consuming; pups usually are fully independent by June, so the presence of one or two independent pups in the home range during summer may increase intraspecific competition. Blanford's foxes tend to be lightest in weight during summer (Geffen et al., 1992b), which also may indicate food shortage. All three possibilities are compatible with the data and we cannot distinguish their relative importance.

Red foxes retreated to cover during heavy rain or hail storms (Doncaster, 1985) and their activity decreased in proportion to rainfall, snow depth, and temperature (Ables, 1969; Halpin and Bissonette, 1988). Windy nights, however, may be advantageous when foraging for birds, which then tend to sleep closer to the ground (Doncaster, 1985). In the Judean Desert, climatic conditions at night were mild (mean minimum temperature during winter was 14.4°C) compared to northern zones, and appeared to have little direct effect on the activity of the Blanford's fox, except when conditions were extreme. Temperature and relative humidity are among the most important limiting factors of activity for ground-dwelling

invertebrates (Abushama, 1984; Holm and Edney, 1973; Thomas, 1979; Whitford and Ettershank, 1975); small microclimatic differences could affect the availability of invertebrates (Kramm and Kramm, 1972; Marion, 1986). Blanford's foxes primarily are insectivorous (Geffen et al., 1992a), therefore we would have expected that seasonal changes in the activity patterns and the population of the local invertebrate fauna would affect the activity pattern of foxes. We did not detect significant seasonal changes in the activity of foxes in relation to climatic conditions, which suggest that the comparatively mild climatic conditions during the night at Ein Gedi allow invertebrates to be active year round (Geffen et al., 1992a), and that foxes can meet their daily energetic requirements by foraging for 6–8 h for invertebrates.

Blanford's foxes tended to leave their daytime refuge soon after becoming active. Doncaster (1985) reported that urban red foxes became active immediately after sunset, but stayed in the vicinity of their den until midnight, when human disturbance had subsided. The pattern of movements of Blanford's foxes within each home range was dependent on its configuration. Within narrow home ranges the choice of routes inevitably was restricted by topography. In two cases, members of a pair systematically avoided each other. This avoidance only operated during the first hours of activity when foxes probably were hungry after staying at the den during the day. The different movement pattern of each pair member may aid foxes in minimizing interference with each other while feeding (Lamprecht, 1979). Considering the low resolution of our partitioning of the home range into sectors, along with the multitude of factors that affect the nightly movements of these foxes, we are impressed by the finding of significant avoidance through time-tabling by two of the four pairs. Our impression in the field was that this is a general phenomenon in all pairs. We hypothesize that foraging away

from the denning area, where foxes usually are present, and on different routes are mechanisms for reducing conflicts over food among residents.

Our results indicate that the Blanford's fox is strictly nocturnal and the onset of activity is triggered by dim light (sunset). We propose predation as the most powerful factor influencing nocturnal behavior of Blanford's foxes. A less stark contrast between predation risks by night and day, together with protection afforded by larger size, may explain why bat-eared foxes are less strictly nocturnal. Climatic conditions have little direct effect on activity patterns of Blanford's foxes. Members of a pair generally forage alone, in contrast to another insectivorous canid, the bat-eared fox. We believe that this is because the food of the Blanford's fox is less clumped than that of the bat-eared fox. One food often cited as highly clumped, and facilitating group foraging in the bat-eared fox, is emergent termites. These were a small part of the diet of Blanford's fox (7.8%; Geffen, 1990). Although both members of each pair of Blanford's foxes used all parts of their shared ranges and, overall, did so to similar extents, they used some areas according to different time-tables. In this way they probably reduced competition for a rapidly depleted (invertebrates), but also rapidly renewing, resource.

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