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Habitat selection and home range in the Blanford's fox, *Vulpes cana*: compatibility with the resource dispersion hypothesis

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Summary. This paper presents analyses of habitat-use and home range size in the Blanford's fox. We predicted, from the resource dispersion hypothesis (RDH), that home ranges would encompass similar areas of combined fruitful habitats, but widely different areas of useless habitats, and thus that home ranges would be larger where such fruitful patches are fragmented and widely dispersed. Home range estimates of 0.5–2.0 km^2 were calculated for 16 adult Blanford's foxes, using three different methods. There were no significant differences in home range size between sexes or study sites. One habitat, dry creekbed, was the most frequently visited in all home ranges. Dry creekbed provided abundant prey for the foxes and only sparse cover for their predators. Both the available area of creekbed in each range, and the area of creekbed patches that was used by the foxes, were independent of home range size. However, the variance in home range size was explained by the mean distance between the main denning area and the most frequently used patches of creekbed. These results are in accord with some predictions of the resource dispersion hypothesis.

Key words: Blanford's fox – Habitat selection – Home range – Food patch – Resource dispersion hypothesis

The Blanford's or Afghan Fox, *Vulpes cana*, 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 and Bates 1989). In Israel it is restricted to rugged mountain ridges and canyons in the Negev and Judaean deserts. The species is generally considered to be rare (Ginsberg and Macdonald 1990) and aside from the fact that it is nocturnal (Ilany 1983; Mendelssohn et al. 1987) and largely insectivorous (Ilany 1983) nothing is known of its behavioral ecology.

Home range sizes vary between species, habitats and methods of analysis. Ranges of red fox, *Vulpes vulpes*, vary from 0.1 to 34 km^2 (Voigt 1987). Species that inhabit less favorable habitats usually hold larger home ranges. Arctic fox, *Alopex lagopus*, ranges are between 18 and 23 km^2 (Garrott and Eberhardt 1987), while Ruppell's fox, *Vulpes ruppelli*, ranges in Oman are even larger (53.8–84.4 km^2; Lindsay and Macdonald 1986). Intraspecific differences in home range size between locations may also be related to differences in productivity. Among canids, Macdonald (1981) reported red foxes' ranges averaging 0.45 km^2 in food-rich rural suburbia of the English midlands, but ranges of >10 km^2 in the upland moors of north England. Insofar as habitat type is an indicator of productivity it has been used to predict differences in fox population density and, by inference, home range size (Macdonald et al. 1981; Harris and Rayner 1986). However, differences in productivity alone may not explain why home range sizes vary so much in a given site. In carnivores that hunt communally for large ungulates, home range size may be correlated with group size (Macdonald 1983). This relationship was interpreted as indicating that the advantages of larger group size outweighed the cost of defending the larger territory necessary to sustain them. The home range size of some other carnivores appears to correlate with the distribution of key habitats (red fox: Macdonald 1981; arctic fox: Hersteinsson and Macdonald 1982; European badger: Kruuk and Parish 1982). For example, arctic foxes in Iceland beachcombed on the seashore for invertebrates and carrion at low tide. Regardless of the total size of home ranges each included about the same length of productive coastline; thus the configuration of the coast and the distribution of productive sections determined the size of the total range. These findings (Macdonald 1981; Hersteinsson and Macdonald 1982; Kruuk and Parish 1982) led to the general proposal that the dispersion of food patches determined territory size, whereas their richness limited group size [the resource dispersion hypothesis (RDH), as presented by Macdonald 1983 and Macdonald and Carr 1989]. Where resource availability

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varies continuously between habitats rather than occurring as rich islands in an empty ocean, it is harder to model spatio-temporal heterogeneity in resource dispersion (Carr and Macdonald 1986). Furthermore, prey availability tends to be very difficult to measure, whereas habitat patches may be easily defined. Therefore, testing the prediction that resource dispersion determines home range size and configuration is easiest where habitat types are distinct, where each is a reliable indicator of food availability and where one habitat is rich and others are effectively useless. We elected to test this hypothesis on Blanford's foxes because they satisfy these conditions. The habitats in their home ranges are readily categorized into four types, Blanford's foxes are mainly insectivorous, and Geffen et al. (in press a) using sticky plates showed that one habitat, dry creekbed, is characterized by a relatively high abundance of their prey. Geffen et al. (in press a) placed twice a month, coinciding with the full and new phases of the moon, five sticky plates at selected sites in each of the gravel and boulder scree and dry creekbed habitats. These plates were collected at dawn the next morning and all invertebrates identified to ordinal level and counted. The indices of abundance were calculated as monthly percentages of the number of beetles and ants. The number of beetles (annual mean of 5.08) and ants (7.78) collected at night in dry creekbed was consistently and significantly larger than in any other dry habitat that was examined (annual mean of 1.00 and 0.56 beetles and 1.82 and 3.82 ants for gravel scree and boulder scree, respectively).

This paper presents analyses of habitat-use and home range size in the Blanford's fox. We predicted, from RDH, that home ranges of Blanford's foxes would be configured to encompass patches of spring and dry creekbed, and without reference to areas of boulders and scree. Furthermore, we predicted that home ranges would encompass similar areas of combined fruitful habitats, but widely different areas of useless habitats, and thus that home ranges would be larger where such fruitful patches are fragmented and widely dispersed. These predictions can be tested by comparison between home ranges and between the two study sites.

Material and methods

Study site

The study was carried out at two desert sites in Israel: one in the vicinity of the Ein Gedi Nature Reserve (31°28′ N, 35°23′ E, 100–350 m below sea level), the other in the Eilat Mountains Nature Reserve along the Netafim Creek (29°35′ N, 34°53′ E, 500–800 m above sea level).

Both sites were characterized by steep rocky mountain slopes, deep canyons and sheer cliffs. At Ein Gedi a 500-m cliff runs parallel to the Dead Sea; the Eilat site was in a system of deep canyons in the heart of a mountain range. The dominant rock formation at Ein Gedi was limestone; at Eilat it was a mixture of limestone, sandstone, metamorphic rock and granite (Karta 1985).

The sites differed markedly with respect to water supply: at Ein Gedi there were four large springs and two canyons with permanent water. The vegetation was typically Saharo-Arabic and Tropical in origin. Along the water courses, vegetation cover reached 100% but was only 0.5–10% on the surrounding slopes and cliffs. At Eilat there was only one dripping spring. The water from that spring is collected into a concrete basin built by bedouin. Although both sites endures the same extremes in temperature and relative humidity, Ein Gedi receives, on average, three times more rainfall (mean annual precipitation is 81 mm versus 25 mm at Eilat; Karta 1985).

Field methods

Foxes were trapped using collapsible box traps (Tomahawk, 80 × 22 × 22 cm). Ten traps were used at each study area. Traps were scattered in canyons and on rocky slopes, usually under a large boulder in order to provide shade for captives. Most traps were left in situ for 2–3 years; traps were set for 3–6 days and baited with dead chicks at approximately monthly intervals. All new captures were measured, weighed and individually marked using numbered metal ear tags (subsequent tag-loss was nil). Adult individuals that were recaptured frequently were fitted with radio-collars under anaesthesia (0.2 ml/kg of Ketamin hydrochloride, 50 mg/ml). Transmitters (60 g, life span 6 months, Wildlife Material Inc.) were equipped with motion-sensitive switches that facilitated instant detection whether foxes are active or at rest.

Radio-collared individuals were tracked monthly for at least one session. Each session involved tracking one individual, starting 1 h before sunset and ending 1 h after sunrise (or later if the fox was still active). Fixes were taken on the focal fox every 15 min. The locations of all other radio-tagged foxes in the vicinity were also recorded whenever possible. The rugged terrain required all tracking to be done on foot, using a headlamp. The foxes were relatively tolerant to our presence and so tracking was generally done from within a few hundred meters and fixes were generally accurate to ± 20 m (when foxes travelled particularly inaccessible areas their locations were allocated to a 100 × 100 m square).

Data analysis

Home range size was evaluated using three different methods:

1. 80% minimum convex polygon of total range. The 80% value was selected because plots of cumulative percentage of fixes versus home range size revealed, in 70% of cases, a plateau at 60–80% and a sharp increase thereafter (Fig. 1). To calculate the 80% ranges, fixes were first ranked according to distance from an arithmetic mean center of activity, and the most peripheral point was dismissed prior to successive recalculations of the mean arithmetic center of the remaining points until the most peripheral 20% had been discarded (Ford and Krumme 1979; Kenward 1987).
2. 100% minimum convex polygon of nightly range, averaged for all nights.
3. Summed area of 100 × 100 m utilized grid cells. Hectare grid cells were selected as appropriate to the degree of accuracy of the collection of radio-fixes (see above).

The respective merits of these techniques have been widely reviewed (e.g. Macdonald et al. 1980; Kenward 1987). A salient advantage of the grid cells over the polygonal method is the former's lesser distortion due to the effect of excursions. However, the grid method is sensitive to both cell and sample size (Voigt and Tinline 1980; Newdick 1983). In this study, data sets with less than 200 fixes appeared to underestimate home range sizes when the 100 × 100 m grid cells method was employed. We chose to use all three methods because there is no consensus on a standard method. The same data analyzed by two methods may yield very different range size estimates (Macdonald et al. 1980). Therefore, similar size estimates produced by several methods increased our confidence that the home range estimates are correct, and facilitate comparison with other studies. To accommodate the three-dimensionality in the home ranges, we calculated altitudes and distances of ten random locations along the cliffs from 1 : 50 000 topographic maps, averaged the angle of the slope for each site and corrected home range sizes according to contribution of the slope.

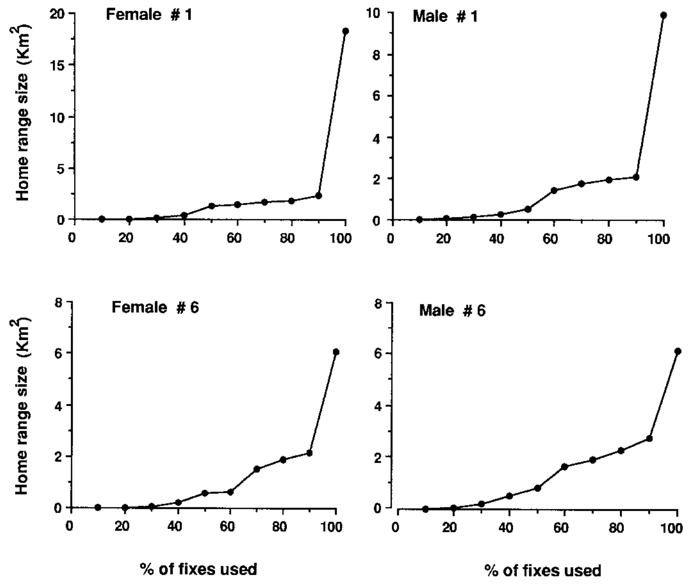

Fig. 1. Example of changes in home range size in relation to the percent of data subsampled for four foxes in Ein Gedi. Home range size estimates are based on the minimum convex polygon method

Habitat composition of each range was based on the 100 × 100 m grid. This grid was superimposed on an aerial photograph, and each cell categorized according to the predominant habitat. Expected values for nightly habitat use were calculated by multiplying the availability of each habitat in the home range by the mean nightly total time spent active by the fox (Catt and Staines 1987). Observed and expected frequencies were compared using chi-square tests. An index of intensity of use of each habitat *(IU)* was calculated as follows:

$$IU = \frac{\text{mean percent of night spent in habitat}}{\text{habitat availability in home range (\%)}}$$

The mean night length in June, as a fraction of monthly night length, was used as an adjustment to equalize sampling effort for seasonal comparisons of the time spent in each habitat per night. We compared intensity of use indices between the pairs at both sites using non-parametric methods (Mann-Whitney and Kruskal-Wallis tests). For sexual and seasonal comparisons of the time spent at each habitat we averaged the seasonal nightly values for each fox and looked for statistical differences using repeated-measure two-way analysis of variance. We were unable to run this comparison for the Eilat data because of small sample size.

Intensity of use of each patch was evaluated by calculating the cumulative time each fox spent active at the patch relative to the total activity time in the creekbed habitat. Using this index, we ranked the creekbed patches at each home range according to their intensity of use and calculated the straight-line distances between the main denning area (where most inactive fixes were collected) and the five most intensively used creekbed patches. An average of these distances for each home range was used as an index of distribution of the most important patches to the foxes. We correlated this index with home range size in order to evaluate whether the distribution of patches affected range size.

Results

Most home range estimates ranged between 0.5 and 2 km², regardless of the method used (Table 1). One individual (Male #2, Ar) gradually shifted his home range within 1 month following his mate's death. Although the new location was 3 km away, during the following 3 months he continued to visit (on two out of the three nights during which he was tracked) his previous home range, with each visit lasting approximately 4 h. Subsequently, excursions to the previous range were not observed for 6 months and consequently this male was excluded from the analysis (Table 1). On the last night on which Female #1 was tracked, she made an excursion to an area 4 km from her home range; this night was excluded from the analysis. In all other cases the foxes occupied the same range throughout the period of radio-tracking. Each range was shared by a pair of adult foxes. In addition, we know of one male and four females that were first trapped as juveniles (3–4 months old) or sub-adults (5–8 months old) and that spent 6–12 months within an adult pair's home range. Out of ten young females that were residents for a period of 2–12 months only one bred. We have no case of an adult (> 1 year) that was frequently caught in a particular range and that was not one of the adult residents.

Home range size did not differ significantly between sexes at either site (Table 1). Comparisons between sites were equivocal: polygonal methods indicated similar mean home range sizes for the two study sites, but the grid method indicated significant differences between them (Table 1). It seems likely that the home range areas in Eilat yielded by the grid cells method were underestimates caused by inadequate numbers of fixes per fox. There were no cases in Ein Gedi where ranges drawn as convex polygons contained large areas not used by the fox, and this confirmed that the polygonal estimates were reliable and so only they were used in subsequent analyses. The average angle of slope was 35° in Ein Gedi and 18° in Eilat. To accommodate this three-dimensionality when comparing between sites we increased each home range in Ein Gedi and in Eilat by 22% and 5%, respectively (Table 1). Home ranges in Ein Gedi were distributed along the 500-m cliff line (Fig. 2), whereas in Eilat, home ranges adjoined one large dry creek.

The home ranges at Ein Gedi comprised an average (± SD) of 63.44% ± 3.22 gravel scree, 3.63% ± 2.59 boulder scree, 28.38% ± 4.05 dry creekbed and 4.54% ± 3.46 stream and spring; these proportions (number of grid cells of each habitat) differed significantly between home ranges ($\chi^2 = 67.0$, $df = 33$, $P < 0.0005$). At Eilat, home ranges comprised an average of 48.31% ± 9.44 gravel scree, 5.02% ± 2.35 boulder scree, 44.98% ± 7.28 dry creekbed and 1.48% ± 1.40 spring, but these proportions did not differ significantly between home ranges ($\chi^2 = 3.64$, $df = 12$, $P > 0.05$).

Average time (min, ± SD) per night spent by foxes at Ein Gedi in gravel scree was 148.8 ± 109.8, in boulder scree 46.0 ± 63.8, in dry creekbed 359.9 ± 141.9 and near a water source 13.0 ± 27.9. In Eilat, foxes spent per night 83.8 ± 37.4 in gravel scree, 32.0 ± 20.2 in boulder scree, 286.1 ± 74.4 in dry creek bed and 83.9 ± 89.5 near a water source. Dry creekbed was the most frequently visited habitat in all seasons. At Ein Gedi the foxes distributed their time in proportions which differed significantly between the habitats (repeated measure two-way analysis of variance; $F_{(3,84)} = 47.98$, $P < 0.001$). However, no sea-

Table 1. Home range size of male and female Blanford's foxes at Ein Gedi and Eilat

	Sex	Grid (100 × 100 m) Area (km²)	# of fixes	80% polygon Area (km²)	# of fixes	Nightly polygon Area (km²)	# of nights	Duration of tracking (months)
Ein Gedi	Male # 1	1.66	677	1.92	541	1.07 ± 0.38	14	28
	Female # 1	1.61	858	1.81	686	1.64 ± 1.10	18	31
	Male # 2 (Dv)	0.92	452	0.55	361	0.68 ± 0.25	10	24
	Male # 2 (Ar)	1.10	422	5.38	337	1.04 ± 0.99	9	9
	Female # 2	0.81	459	0.66	367	0.62 ± 0.84	10	20
	Male # 3	1.90	701	2.75	560	1.10 ± 0.80	15	19
	Female # 3	1.24	865	1.12	691	0.66 ± 0.48	19	19
	Male # 4	1.49	689	1.62	551	1.21 ± 0.42	15	20
	Female # 4	0.68	171	0.93	136	0.69 ± 0.16	4	6
	Female # 5	0.72	212	1.36	169	0.87 ± 1.12	4	4
	Male # 6	1.48	530	2.31	423	1.68 ± 0.58	11	14
	Female # 6	1.39	552	1.86	441	1.22 ± 0.45	12	17
$\bar{X} \pm SD$	Males	1.42 ± 0.36	$n=6$	1.83 ± 0.83	$n=5^a$	1.12 ± 0.66	74	
$\bar{X} \pm SD$	Females	1.07 ± 0.39	$n=6$	1.29 ± 0.48	$n=6$	1.03 ± 0.83	67	
Mann-Whitney	*U* test	$T^+ = 28.0$; $P > 0.05$		$T^+ = 22.0$; $P > 0.05$		$Z = 1.48$; $P > 0.05$		
Eilat	Male # 7	0.36	152	1.23	121	0.80 ± 0.71	2	7
	Female # 7	0.53	257	0.99	205	0.78 ± 0.64	6	20
	Male # 8	0.40	114	0.59	91	0.60 ± 0.23	3	8
	Male # 9	0.54	160	2.07	128	1.80 ± 0.91	4	13
	Female # 9	0.40	90	2.62	72	0.37	1	13
$\bar{X} \pm SD$	Males	0.43 ± 0.09	$n=3$	1.29 ± 0.74	$n=3$	1.12 ± 0.66	9	
$\bar{X} \pm SD$	Females	0.46 ± 0.09	$n=2$	1.80 ± 1.15	$n=2$	0.72 ± 0.61	7	
Mann-Whitney	*U* test	$T^+ = 3.5$; $P > 0.05$		$T^+ = 4.0$; $P > 0.05$		$T^+ = 44.0$; $P > 0.05$		
$\bar{X} \pm SD$	Ein Gedi[b]	1.52 ± 0.49	$n=12$	1.87 ± 0.84	$n=11$	1.32 ± 0.91	141	
$\bar{X} \pm SD$	Eilat[c]	0.47 ± 0.09	$n=5$	1.57 ± 0.87	$n=5$	1.03 ± 0.81	16	
Mann-Whitney	*U* test	$T^+ = 60.0$; $P < 0.001$		$T^+ = 35.0$; $P > 0.05$		$Z = 1.6$; $P > 0.05$		

[a] Area of male # 2 (Ar) was excluded
[b] Corrected for slope by increase of 22.0% in home range size
[c] Corrected for slope by increase of 5.0% in home range size

Ar = home range in Nahal Arugot and Dv = home range in Nahal David. n = number of foxes

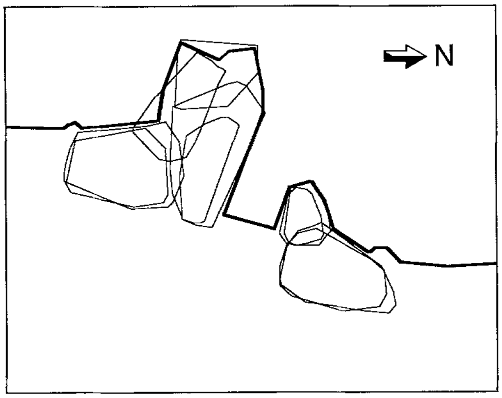

Fig. 2. Home range configurations (80% minimum polygon) of the adult foxes in Ein Gedi during 1987 in relation to the cliff line *(bold line)*. Above these cliffs (west) rolling hills and flat plains dominated the topography

sonal ($F_{(3,84)} = 0.27$, $P > 0.05$) or intersexual ($F_{(1,84)} = 0.01$, $P > 0.05$) effects were detected in the pattern of habitat use.

Foxes spent significantly more time than expected in the creekbed habitat (Ein Gedi: $\chi^2 = 18.0$, $df = 3$, $P < 0.001$; Eilat: $\chi^2 = 9.4$, $df = 3$, $P < 0.05$; Fig. 3). At both sites dry creekbed ($IU = 2.33 \pm 0.54$ and 1.22 ± 0.06 for Ein Gedi and Eilat, respectively) and boulder scree ($IU = 2.44 \pm 2.53$ and 1.12 ± 0.65 for Ein Gedi and Eilat, respectively) were used on average more than gravel scree ($IU = 0.38 \pm 0.22$ and 0.46 ± 0.31 for Ein Gedi and Eilat, respectively). At Eilat, a strong attraction to the only small spring available was apparent for the individuals living around it (foxes # 7 and 8). Springs were heavily used in Eilat ($IU = 9.86 \pm 2.97$) but not in Ein Gedi ($IU = 0.60 \pm 0.42$). Dry creekbed and water source were used at different intensities at each study site (Mann-Whitney test with $n_1 = 10$ and $n_2 = 5$: $U = 28$, $P > 0.05$ for gravel scree; $U = 33$, $P > 0.05$ for boulder scree; $U = 50$, $P < 0.001$ for dry creekbed; $U = 49$, $P < 0.005$ for spring). The five pairs at Ein Gedi (Kruskal-Wallis test; $\chi^2 = 8.8$ for gravel scree, 7.4 for boulder scree, 8.6 for dry creekbed and 5.4 for spring with $df = 4$ and $P > 0.05$), and the two pairs at Eilat did not use similar habitats at different intensities (Mann-Whitney test with $n_1 = 3$ and $n_2 = 2$: $U = 6$, $P > 0.05$ for gravel scree; $U = 6$, $P > 0.05$ for boulder scree; $U = 4$, $P > 0.05$ for dry creekbed).

Home range sizes (80% minimum polygon) at Ein Gedi did not correlate significantly with available area of

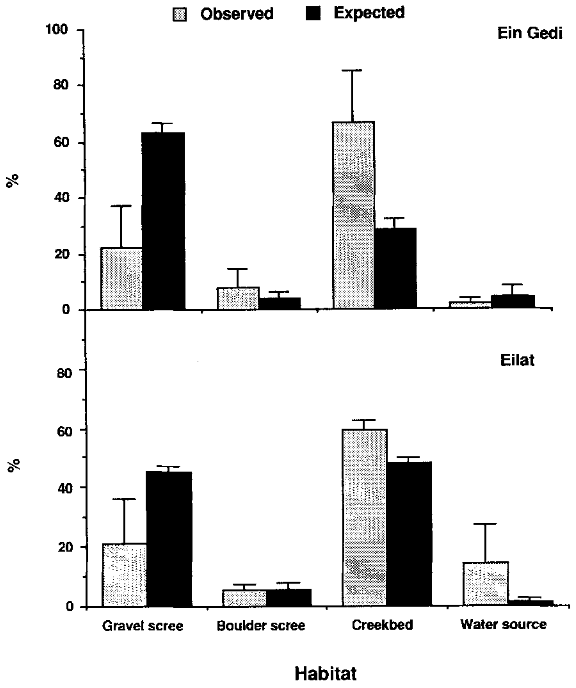

Fig. 3. Average (± SD) observed *(light columns)* and expected *(dark columns)* percent of time per night spent in each habitat at Ein Gedi and Eilat

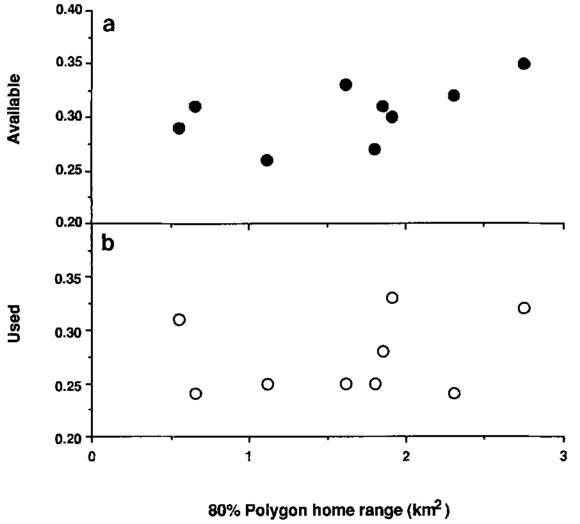

Fig. 4. a Home range size (polygon, km^2) versus available creekbed area ($r = 0.53$, $P > 0.05$), and **b** home range size versus used creekbed area ($r = 0.23$, $P > 0.05$) at Ein Gedi

creekbed in each home range ($r = 0.53$, $P > 0.05$, Fig. 4a) nor with the area of creekbed that was used by each fox ($r = 0.23$, $P > 0.05$, Fig. 4b). For this analysis we have only used large data sets (> 400 fixes) in order to avoid bias in the area estimates of creekbed used (nine foxes; see Table 1 and Fig. 4b). Creekbed patches were used proportionally to their size ($r = 0.71$, $F_{(1,40)} = 39.6$, $P < 0.001$), so that large patches were heavily used while small ones were rarely visited. Mean minimum polygon (80%) home range size of all pairs was significantly correlated with the mean distance between the main denning area at each home range and the five most intensively used creekbed patches ($r = 0.94$, $F_{(1,6)} = 35.8$, $P < 0.005$; Fig. 5).

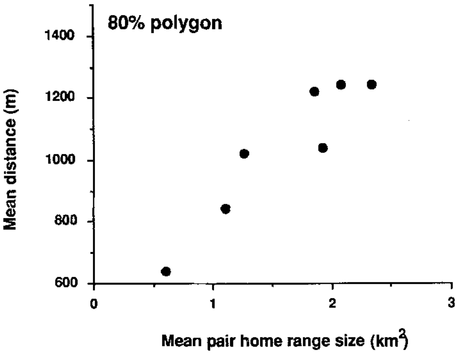

Fig. 5. Mean distance (m) of the five most intensively used creekbed patches from the main denning area versus mean pair home range size (80% polygon; km^2). $r = 0.94$, $P < 0.05$

Discussion

Home range size (corrected for body weight) in the Carnivora is correlated positively with degree of carnivory and negatively with proportion of insects and fruits in the diet (Gittleman and Harvey 1982). An approximate expected size for a Blanford's fox's home range was extrapolated from plots of home range size versus standardized metabolic needs of carnivore species (group size × body weight$^{0.75}$; Gittleman and Harvey 1982). For 1000 g foxes (Geffen et al., in press b), living in pairs, predicted home ranges of 1 km^2 and 0.6 km^2 are obtained from plots of data sorted according to family in the Carnivora and type of diet, respectively; both values are within the range of the observed Blanford's fox's home range size (0.55–2.75 km^2). Harestad and Bunnell's (1979) equation for carnivores (home range size $= 0.011 \times \text{weight}^{1.36}$) yields a home range estimate of 1.65 km^2 for the average Blanford's fox's weight and similar mean values were observed in the field (Table 1; 80% polygon).

The distribution of home ranges along a cliff in Ein Gedi (Fig. 2) arose because this constituted the only suitable habitat for Blanford's foxes. Above these cliffs rolling hills and flat plains dominated the topography. In contrast, the foxes at Eilat were in the heart of a mountainous area and surrounded by suitable habitat.

The prediction that foxes would use most heavily the habitat in which insects were abundant, and that their home ranges would be configured around these habitats, was not upheld when both spring and dry creekbed were considered. Not only did some home ranges at Eilat have no springs, but most foxes in Ein Gedi used this habitat much less than expected on the basis of its availability. In contrast, all home ranges did appear to be configured around dry creekbed and all foxes utilized this habitat heavily. We propose that this dichotomy arises because the lush vegetation around springs offers ideal cover for predators and thus makes it very dangerous for Blanford's foxes. At Ein Gedi, the favoured ambush location of leopards, *Panthera pardus*, is in dense vegetation. Although we have no direct evidence that leopards prey on foxes, we observed in the field that foxes barked repeatedly towards leopards and never approached them closely. Ein Netafim, the only available spring in the Eilat study area, was visited more than predicted by the foxes living around it. Ein Netafim differed markedly from the springs at Ein Gedi in that it was not surrounded by lush vegetation, but several large caperbushes grew there and provided fruit eaten regularly by foxes (Geffen et al., in press a). If springs were excluded, on the grounds that their resource value is devalued by the high risk of predation, then the prediction of RDH is fully supported by the size of home ranges with respect to dry creekbed.

Our findings that home range size does not correlate significantly with either available area of creekbed or with the creekbed area used by foxes imply that each fox needed a roughly similar area of creekbed in order to survive (Fig. 4a, b). The difference in the correlation coefficients of these two measures may be explained if we look closely on the intensity of use of creekbed patches in any home range. The foxes tended to use the large patches frequently (90–95% of the time in creekbed spent in large patches) and rarely visited the relatively small ones. Hypothetically, if a fox needs to increase its range to include an additional useful (large) creekbed patch then, in such a rugged area, it would inevitably include additional small creekbed patches too. Therefore, using the area of creekbed used by each fox ($\geq 1\%$ of the time in creekbed) emphasized the independence of area of creekbed from home range size. In contrast, the variation in size of all home ranges appeared to be best explained by the mean distance of the important creekbed patches from the common denning area in each range (Fig. 5). This mean distance reflects pattern of patch distribution, which supports our prediction that dispersion of creekbed patches within the home range determines its size.

A second prediction of the patchy case of the RDH is that group size will be limited by the richness of food available in bottle-neck patches. In some cases, variance in the availability of patches may be so great (the binomial case in Carr and Macdonald 1986) and/or patches may be so rich (the rich patch case of Carr and Macdonald 1986, and exemplified by Kruuk and Parish 1982 and Bradbury and Vehrencamp 1976) that the minimum home range that will support a pair will support other adults too. However, insect availability within dry creekbed is relatively high (Geffen et al., in press a), and is probably rather homogeneously dispersed within this habitat. Therefore RDH would predict that the minimum economically defendable area of dry creekbed required to support a pair and their progeny would not readily accommodate additional adult group members, and thus that Blanford's foxes would live in pairs or small groups. Two supplementary predictions might affect this expectation. First, if some advantage of sociality overwhelmed the disadvantage of home range expansion, then larger groups might develop (Macdonald and Carr 1989). In that case the foxes would meet the definition of expansionists (Kruuk and Macdonald 1985). However, Geffen and Macdonald (in press) showed that home ranges of Blanford's foxes did not change in size throughout the year, although the number of supernumerary residents changed. Second, if the minimum social unit of Blanford's foxes, a pair, configures its home range with respect to dry creekbed as appears to be the case, there might nonetheless be sufficient resources in other habitats to satisfy the food security of additional adults, at least in the short term, and especially if they were non-breeders, and thus had lower nutritional requirements. These predictions are in general accord with our observation that Blanford's foxes live in pairs, with which a non-breeding subadult, generally female, is sometimes associated.

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