Environmental factors influencing the use of habitat in the red fox, Vulpes vulpes

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(With 8 figures in the text)

The seasonal variation in habitat selection and its determinants were assessed weekly for a sample of three dog-foxes and two vixens in an ecotonal area of the Tuscan coast, in Italy. The most utilized habitats were the maquis (scrubwood), meadows and pinewood. In the cold season the maquis was preferred to any other habitat, but in the warm months foxes made extensive use of meadows. On the other hand, no clear seasonal pattern of use was detectable for the pinewood. Food habits showed a seasonal variation: juniper berries were the staple food, forming by far the greatest part of the diet during the whole study, except in late spring through midsummer, when beetles and grasshoppers predominated. Availability indices for each main food category were calculated on a weekly basis. Distribution of juniper berries was found to be clumped, whereas insects were dispersed. It was also assessed that the former occurred almost entirely in the pinewood, while the latter inhabited mainly meadows and, to a lesser extent, the pinewood. Measures of fox activity in the three habitats were also taken. The fox diet correlated well to the seasonal abundance of the important food resources, which in turn was significantly correlated to meteorologic factors (temperature, number of rainy days). Surprisingly, the seasonal activity in the pinewood was inversely correlated to local food availability, i.e. juniper berries. This can be explained by the clumpedness of this food resource which, when abundant, allows foxes to become quickly satiated and to retreat to other, more preferred habitat such as the maquis. Such results caution against assuming that extensive time spent in a habitat is an indication of proportional feeding dependence on it.

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Introduction

It has been suggested that food dispersion and abundance determine group size in the red fox *Vulpes vulpes* (L., 1758) (Macdonald, 1981, 1983; Carr & Macdonald, 1986; but see also Lindström, 1986). The same variables have been proposed as the main factors underlying territory size (see Macdonald, 1983, and Kruuk & Macdonald, 1985, for reviews). On the other hand, Lindström (1982) and von Schantz (1984a) criticized this view as providing a somewhat simplified picture: for example, when the quality of food patches is low (which is often the case in areas of low productivity such as the boreal forest), then the total availability and not the distribution of food would probably account for most of the variation in the territory size of foxes. While Macdonald (1981) showed that fox distribution was correlated with household density in a suburban area near Oxford, Harris (1981) could not find the same relationship in an urban area (Bristol). However, the influence of food distribution and abundance on the habitat use of the fox has not yet been satisfactorily explored. Furthermore, the few studies where fox movements and food availability have been investigated in a wild and undisturbed environment were all carried out in relatively homogeneous habitats or were not focused primarily on habitat use (e.g. Sargeant, 1972; von Schantz, 1981a, b, 1984b; Mulder, 1982).

The aim of our study was to assess the variation in habitat selection in an undisturbed, natural and heterogeneous environment (i.e. at least six ecosystem types within a radius of less than 500 m). We assumed that this combination of features is suitable to test the effect of food availability, in terms of abundance and dispersion, on habitat use by the red fox.

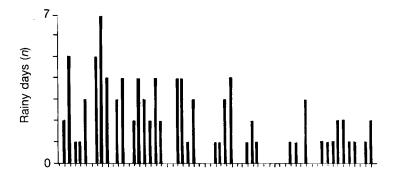
The food habits of the red fox in the Mediterranean region have been the subject of a number of studies (e.g. mountain areas: Leinati et al., 1960; Amores, 1975; Braña & Del Campo, 1980; coastal areas: Ciampalini & Lovari, 1985; Rau, Delibes & Beltran, 1985; Calisti et al. 1990, for a theoretical review).

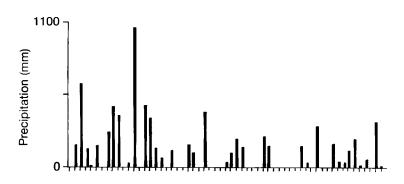
However, no attempt has been made so far to measure food availability in parallel to the feeding habits and ranging behaviour of the red fox, and to evaluate their relationships, as we have done in this study. One might also expect some abiotic factors to have an influence on fox activity and use of habitat (e.g. temperature: Eguchi & Nakazono, 1980; cf. also Eiberle & Matter, 1985, for direct and indirect effects of temperature and rainfall). Therefore we have also analysed the correlations of fox spatial behaviour with variations in temperature and rainfall.

Study area

The study area lay in the centre of the Maremma Natural Park, Grosseto county, along the Tyrrhenian coastline, Central Italy (42° 39′ N, 11° 05′ E). Precipitation (mm), number of rainy days and maximum and minimum temperatures during the research period are set out in Fig. 1. This is an area of great ecological diversity, in which all major Mediterranean coastal ecosystems are present: meadow, maquis, pinewood (inclusive of the retro-dunal strip), olive grove, wetland and beach. In the area, shooting has been forbidden since 1975, no pesticides have been used and the movements of tourists are limited. Therefore, the direct impact of man on the activities of animals is relatively small. The home ranges of the foxes were about 200 ha (P. Cavallini, S. Lovari & M. Lucherini, unpubl. data). It was estimated that about 10 adult foxes lived in the study area of 500 ha.

For a more detailed description of the area, see Arrigoni et al. (1976), and for a phytosociological outline, see Arrigoni, Nardi & Raffaelli (1985).





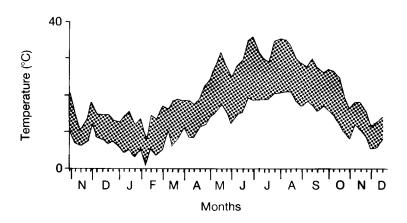


Fig. 1. Number of rainy days, precipitations (mm) and temperatures (max. and min.) in the study area during the research period.

Material and methods

From November 1985 through December 1986 (59 weeks) we recorded the movements of 5 adult red foxes (3 males and 2 females, i.e. about half the local fox population) (Table I). We also analysed the fox diet as well as the availability and distribution of the main food resources (cf. Ciampalini & Lovari, 1985). The temperature and the rainfall in the study area were also recorded.

Habitat use

Radio-tracking was carried out for 48 h per week, in periods of 8 h, with a fix on each animal every 2 h, to have 1 fix per hour over the 24 h/animal/week. For each fix, we recorded the activity of the animal (following the criteria described in Garshelis & Pelton, 1980) and the habitat frequented. For the present paper, only fixes in which the fox was active were used for our analysis. We also calculated the percentage of active fixes in each habitat, on a weekly basis. All foxes were neck-snared in the same area (10 ha) and their pattern of activity proved highly correlated (see Lucherini et al., 1988). Ideally data on each fox should have been analysed separately, but practical problems in the statistical treatment and graphical presentation of the data prevented such an approach. Therefore we followed previous authors (e.g. Garshelis & Pelton, 1981; Clutton-Brock, Guinness & Albon, 1982) in pooling the data relevant to different individuals.

Diet

Each week 20 faeces were collected, stored in polythene bags and deep-frozen, to be thawed later on and analysed as described in Kruuk & Parish (1981) and in Ciampalini & Lovari (1985). Because of the present regulations in Italy, radioactive isotopes cannot be used in the field, e.g. to label foxes and to trace back their faeces. However, we collected scats only in the areas frequented by the study foxes in the 7 days preceding the collection. This procedure should have maximized the probability of collecting the scats of the animals under study. The low frequency of their excursions from their respective home ranges (P. Cavallini, S. Lovari & M. Lucherini, unpubl. data) increased this probability.

Food availability

The availability of the most important food resources reported in the study area (Ciampalini & Lovari, 1985; Calisti et al., 1990; Ferrario & Mondonico, In prep.) (i.e. Orthoptera, Coleoptera and juniper berries), was estimated through weekly indices of relative abundance. The Orthoptera and the Coleoptera were

Table I

Tracking periods of the study foxes

	Trackin	g period	
Individual	From	То	No. of active fixes
Female 1	4/11/85	20/12/85	84
Female 2	11/2/86	20/12/86	538
Male 1	4/11/85	24/1/86	147
Male 2	4/11/85	20/12/86	722
Male 3	26/1/86	20/12/86	575
Total			2066

censused by direct counts of the number of individuals seen along a 2-km transect passing through the study area. The availability of juniper berries was assessed by counting weekly the number of berries collected in nets suspended under 6 randomly selected female juniper trees.

Food distribution

For the same resources (Orthoptera, Coleoptera and juniper berries), we counted the number of items in a series of random plots (1 m²) (40 plots for the juniper, 150 plots for Orthoptera and Coleoptera). From the ratio 'variance/mean' (S^2/\bar{X}) of the number of items per plot we obtained an estimate of the clumpedness of the resource. To find the distribution of juniper in the habitats, we also measured the number of juniper trees in 211 squares of 25 m² evenly distributed in the whole study area.

The temperatures and rainfall were recorded daily with a max.-min. thermometer and raingauge.

To evaluate the weekly variations in trophic and habitat niche breadth of the radio-collared foxes we used the Levins (1968) index, as suggested by Ricklefs (1980) and Putman & Wratten (1983). The index has the following formula:

$$B = \frac{1}{\sum_{i=1}^{n} p^2(i)}$$

where p(i) is the proportion of records in each category.

We also calculated the percentage of total activity (number of active fixes, divided by the total number of fixes, $\times 100$), and the percentage of diurnal activity (number of active fixes during the day, divided by the number of activity fixes, $\times 100$).

We used the Spearman Rank Correlation Coefficient (r_s) (Siegel, 1956) to test correlations; all correlations referred to in the text proved significant.

All statistics were performed by the Stats-Plus programme for Apple II-e computer, except for the cluster analysis, performed by a BMDP programme (procedure amalgamation rule: minimum distance, Dixon & Brown, 1979).

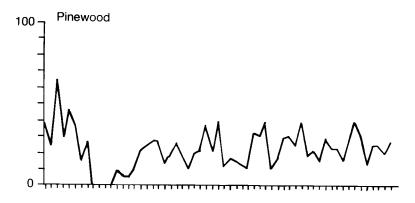
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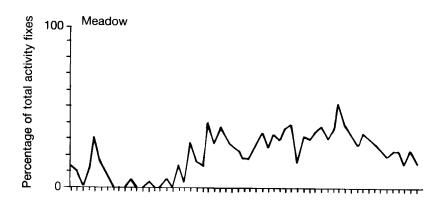
Habitat use

The most utilized habitats were the maquis $(45\cdot1\%)$ of all 'active' fixes), meadow $(21\cdot7\%)$ and pinewood $(20\cdot9\%)$ (Fig. 2), so we have restricted our further analysis to these three habitats only. In the cold season foxes made extensive use of the maquis, which was, however, also considerably utilized at other times of the year. The meadow was used mainly in the warm months, and a decrease in use of the pinewood was apparent between December and February. However, no clear seasonal pattern of use could be assessed for the latter habitat.

Diet

A total of 1180 scats were collected. Juniper berries, Orthoptera and Coleoptera were the staple foods (Fig. 3). All of these showed a very clear seasonality. Juniper berries were by far the greatest part of the diet during the entire research period, except in late spring through mid-summer, when beetles (May-July) and grasshoppers (June-July) predominated (Fig. 2). Orthoptera remained an important food resource up to November. Figure 4 shows the frequency of occurrence and relative volume of food categories in samples pooled over the whole research period. As expected from





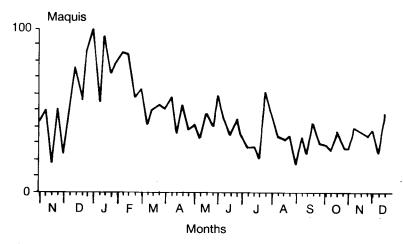
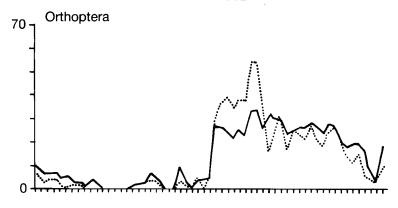
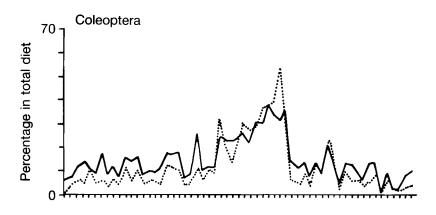


Fig. 2. Percentage of active fixes in the three habitats most used by radio-collared foxes.





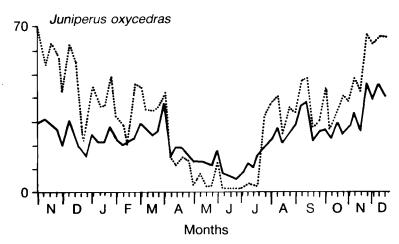


Fig. 3. Percentage of occurrences (——) and volumes (· · · ·) of the three main food categories in the fox diet.

previous information (cf. Material and methods) fruits, especially juniper berries, Orthoptera and Coleoptera were the most important food categories, making up over 72% of the total diet.

Food availability

The relative abundance of the three main food resources (Fig. 5) also showed a clear seasonality. The availability of juniper berries was greatest in the cold months, whereas beetle numbers started increasing in early spring, reached a peak in July and September (when many scarabaeid beetles emerge) and declined during October. Orthoptera showed a sharp increase in June and a decrease in October, while being uniformly abundant in between.

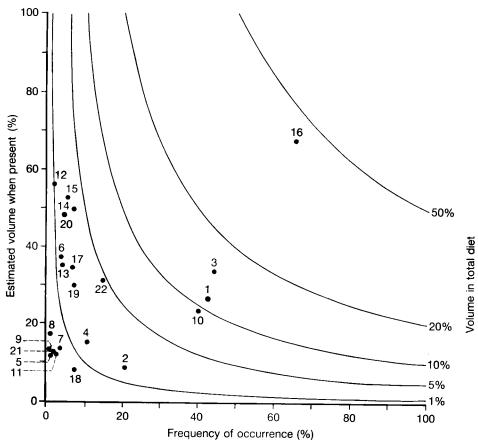
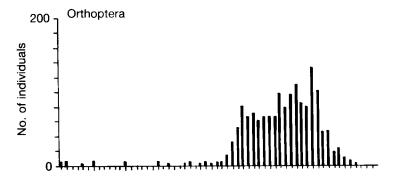
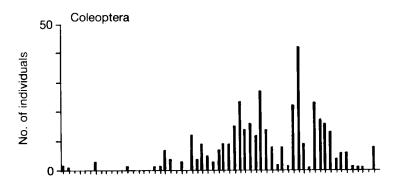


FIG. 4. Estimated volume of fox food categories, whenever eaten, versus their frequency of occurrence. Isopleths connect points of equal relative volume in the overall diet. 1: Coleoptera (adults); 2: Coleoptera (larvae); 3: Orthoptera; 4: Dermaptera; 5: Lepidoptera (larvae); 6: Cicadidae (larvae); 7: other insects; 8: earthworms; 9: Mollusca; 10: Chilopoda; 11: other invertebrates; 12: amphibians and reptiles; 13: birds; 14: large mammals; 15: small mammals; 16: Juniperus oxicedrus (berries); 17: Juniperus phoenicea (berries); 18: pine seeds; 19: Arbutus unedo (fruits); 20: blackberries; 21: olives; 22: other items.





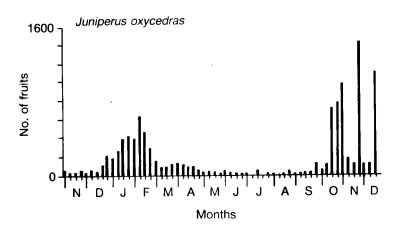


Fig. 5. Availability (number of items) of the three main fox food resources.

TABLE II

Number and percentage of insects (Orthoptera, Coleoptera) sighted during transect censuses in the habitats most used by the radio-collared foxes

	Ortho	ptera	Cole	optera
Habitat	n	%	n	%
Meadow	1298	76.0	157	50.0
Maquis	49	2.8	36	11.5
Pinewood	353	20.8	120	38.3
Total	1700		313	

Food distribution

The ratio S^2/\bar{X} for the juniper berries was 8.9 (>>1, thus indicating a clumped resource). Not surprisingly the number of berries was correlated with the percentage of juniper cover $(r_s=0.996, P<0.001, n=40)$, Spearman rank correlation coefficient). The juniper trees were present in significant numbers only in the pinewood (D=1.36, P<0.01, Kolmogorov-Smirnov test). They were almost absent in the other habitats $(0.17 \ge D \ge 0, P>0.20)$. The ratio S^2/\bar{X} was 1.4 for both the Orthoptera and the Coleoptera which thus were classified as dispersed resources. The distribution of these insects in the habitats most used by the foxes studied showed that both Coleoptera and Orthoptera occurred mainly in the meadow, followed by the pinewood, but were very scarce in the maquis (Table II).

Trophic and habitat use niches

Figure 6 shows that the trophic niche, measured on both the occurrence (%) and the estimated volume (%), oscillated around the same value throughout the study period, with an increase in the cold months; the habitat use niche did not show any major variation.

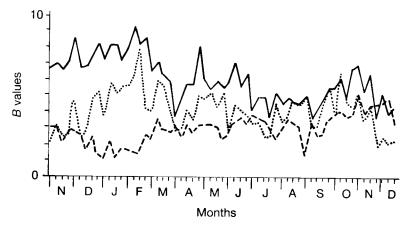
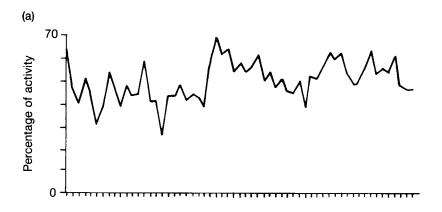


FIG. 6. Niche breadths (Levins, 1968) based on diet (percentages of occurrence (——) and volume (\cdots) and habitat use (---). Low niche breadth: 1; great niche breadth: n (number of categories).

Activity

The total activity of the foxes (Fig. 7) did not show great variations during the study period, except for the warmer months in which the foxes appeared to be slightly more active. The diurnal activity (Fig. 7) followed a similar pattern. The availability of the dispersed food resource (i.e. Orthoptera and Coleoptera) was positively correlated with both total and diurnal activity, while the clumped resource (i.e. juniper berries) was negatively correlated (although significantly only with diurnal activity). The percentage of Orthoptera (a diurnal prey) in the diet correlated well with total activity; the correlations of diurnal activity with use of the main food resources show the same trends as those with availability.



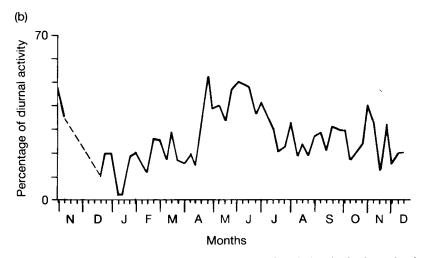


FIG. 7. Percentage of (a) active fixes in total fixes and (b) active fixes during the day in total active fixes.

Correlations between the main environmental and behavioural variables. Both r. (Spe TABLE III

	OA	CA	Ϋ́	Me	Ma	ΡW	8	00	o	ov	C	Σ	NO	N	H	mT	MT	RD	풉
Me	+++	+++	+++				į		ĺ										
Ä	+++	+ + + + -0.403	++																
ΡW	QS 0:241	NS 0·165	QS -0.237																
8	+++			+++		OS 0-229													
CO		+++		NS 0.157		NS 0.023													
or			++	NS -0.196		NS 0-182													
0	+++			+++		+													
C		+++		+		NS 0.053													
λſ			++	++		NS 0.156													
O	+ + + -0.520	+ + + -0.492	++	+++		QS -0:231													
N N	NS -0.003	NS -0.078	++	NS -0-113	NS 0·178	QS -0·229													
Z	+ + + 0.463	++	NS -0.063				+++	NS -0.010	NS 0·148	++++	NS -0.012	NS 0-013	+++	OS -0.221					
Tm	+++	+ + + 0·729	++++	+++ 0.79 4	++++	QS 0·250	++++	++	+	+++	++	+++	+ + +	NS -0-132	+ + +				
ΤM	++++	+ + + 0·738	+++	+ + + 0·738	+ + + +0.442	NS 0·145	++++	+++	+++	+ + +	+ + +	+ + + +	+ + + +	NS -0-0-7	+ 6				
RD	++0:342	+ -0.285	++	+	+	NS 0-012	+ + -0.279	NS -0.034	NS -	QS -0.739	NS	SN	+ 67 + 67 + 67 + 67 + 67 + 67 + 67 + 67	NS C	NS				
P.	QS 0·247	NS -0.199	+ 0·281	QS -0-224	NS 0:119	NS 0.014	NS -0.142	NS -0.118	NS -0.011	NS -0.150	SZ -0-088	SZ 0	0.316	NS 0	NS -0-201				
Ac	++++	+ + + 0.442	NS -0.155	+ + + 0.451	++	NS 0·107	+ + 0-331	NS 0-040	NS -0·166	+ +	NS 0.155	+ -0.259	QS -0.241	NS 0.076	+ + 0	+ +	+++	NS -0-213	NS O
Ψ .	DA ++ +++ ++ * 0.369 0.532 -0.419 0	++++	++0.419	0.311	QS -0·254	+	+ 0·307	+ 0·329	+-0.309	++	++	+ -0.296	NS -0.150	OS -0.236	NS 0.205	++	+ + + 0	NS -0.121	NS -0.035

OA: Orthoptera (availability); CA: Coleoptera (availability); JA: juniper (availability); Me: activity in meadow (in total activity); Ma: activity in maquis (in total activity in pine wood (in total activity): OO: Orthoptera (occurrence, in total diet); CO: Coleoptera (occurrence, in total diet); JO: juniper (occurrence, in total diet); OV: Orthoptera (estimated volume, in total diet); CV: Coleoptera (estimated volume, in total diet); JV: juniper (estimated volume, in total diet); ON: trophic niche breadth (based on occurrences); VN: trophic niche breadth (based on estimated volume); HN: habitat niche breadth; mT: minimum temperature (C); MT: maximum temperature (C); RD: rainy days (n); Pr: precipitation (ml); Ac: activity (in total * Except from 18 November to 21 December 1985: $+++=P\leqslant 0.001$; $++=P\leqslant 0.01$; $+=P\leqslant 0.05$; QS = 0.10 > P>0.05; NS = P>0.10

Ξ

fixes); DA: diurnal activity (in activity fixes)

Correlations and cluster analysis

Table III sets out the significance of correlations we drew between the main environmental and behavioural variables. The abundance of Orthoptera and Coleoptera proved directly correlated to maximum and minimum temperatures and negatively correlated to the rainfall (number of rainy days). On the other hand, the abundance of juniper berries showed opposite trends. Moreover, both the occurrence and volume of such items in the fox diet were positively associated with the abundance values.

Furthermore, a close relationship was found between habitat use and the abundance of each main food category. Use of meadows by the foxes was directly correlated with insect abundance and inversely associated with abundance of juniper berries. Use of the maquis showed an inverse correlation with Orthoptera and Coleoptera abundance, and a positive one with the number of

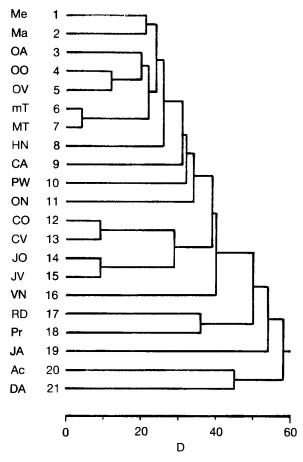


Fig. 8. Dendrogram resulting from the cluster analysis of the main environmental variables. Clustering by minimum distance method. Abbreviations as in Table III. D: amalgamation distance.

juniper berries. Conversely, there was a negative correlation between the number of juniper berries and the use of pinewood.

The picture one may draw from these and the other correlations (cf. Table III) is obscured by the probable interdependence of some variables: e.g. diurnal activity, temperature and rainfall are all related to daylength; number of rainy days, millimetres of precipitation and temperature are all dependent on the season. For this reason we performed a cluster analysis.

Variables from 1 to 15 formed a cluster, although not well delineated (D=40; Fig. 8). Within the main cluster two other clusters could be identified. One (D=25) included the occurrence and volume of Orthoptera in total diet, Orthoptera abundance, maximum and minimum temperature, use of meadow and maquis. The other (D=30) embraced Coleoptera and juniper occurrences and volumes.

It is surprising that the trophic niche indices (in occurrences and in volume) have not formed a cluster. Moreover, the abundance of Coleoptera and juniper berries is quite distant from their presence (occurrence, volume) in the diet.

Discussion

All three habitat types were extensively used by the foxes, but to different extents during the study period. Wooded areas, particularly if provided with an understorey, are known to be heavily used by the red fox (e.g. Schofield, 1960; Pulliainen, 1981; Jones & Theberge, 1982; Artois, 1985), especially for denning activities (e.g. Weber, 1983, 1985; Paquet & Libois, 1986) and for resting (e.g. Blanco, 1986).

Juniper berries were the main winter food for foxes in our study area. They are rich in fats and carbohydrates, but very poor in proteins (Cavani, 1989) which are indispensable for the survival of a carnivore species (e.g. Schaller et al., 1985). In the same study area, Ciampalini & Lovari (1985) and Calisti et al. (1990) found that small mammals were numerous in the fox diet from mid-winter to early spring, but were an unimportant food item in the rest of the year. The small mammals tend to be chiefly located in the maquis in our study area (L. Santini, University of Viterbo, pers. comm.). Therefore, it is most likely that the peak in maquis use, predation on mammals, diet improvement and better thermic conditions in woodland (Robbins, 1983: 124) are all related factors. The increased use of meadows in the warm months can also be related to trophic factors (see below).

Our results are consistent with what was previously reported by Ciampalini & Lovari (1985) and Calisti et al. (1990) as main food resources (Orthoptera, Coleoptera and juniper berries) of the fox in the same (approximately 500 ha) area. The same authors reported a maximum niche breadth in spring and a minimum one in the autumn, which we could not detect when working in approximately the same area about three years later. Such different results may be ascribed to a year-to-year variation in the use of the minor food resources (e.g. Chilopoda, vertebrates). It is surprising that the habitat use niche did not show any major variation during the study period, whereas an increase was to be expected in the cold months, when the relatively poor quality of food resources should have given rise to more intense habitat sampling by the red fox. Such an expectation is supported by the greater niche breadth in that season. Another possible explanation may be that social activities, e.g. territory patrolling, take up substantial time for foxes in such a densely populated area (cf. Macdonald, 1979), thus masking variation in the use of secondary habitats.

Negative correlations were found between the trophic niche (in both occurrence and volume) and the habitat niche breadths. The greatest trend difference between trophic and habitat niche breadths was shown in winter 1985–86, whereas the data relating to early winter 1986–87 were much less contrasting (see Fig. 6). Such a difference means that interannual variation can occur. Perhaps particularly poor food resources in some of the habitats in the first winter could explain this inconsistency.

The availability, dispersion and use of the main food resources are correlated, and they influence the activity pattern of the red fox. This conclusion is consistent with the data reported in Lucherini et al. (1988) who worked on the activity of a sample of three adult dog-foxes in the same area.

A number of authors have assumed or suggested that food habits of the red fox are correlated to resource availability (e.g. Errington, 1935; Goszczynsky, 1974; Macdonald, 1981), but so far only von Schantz (1981a) and Lindström (1982) interannually, and Sargeant, Allen & Eberhardt (1984) spatially, have statistically supported such an important issue. On the other hand, no correlation between seasonal food availability and food habits was shown by previous authors.

Our data indicate that the diet of the fox was correlated to the availability of the most important food resources, which in turn was correlated to meteorologic factors.

Orthoptera and Coleoptera were shown to be present mainly in the meadows, which explains why use of this habitat by the foxes was positively correlated to the availability of insects, while use of the maquis was negatively associated. Similarly, it is understandable that use of the meadow showed an inverse correlation to the availability of juniper berries, as this tree grows chiefly in the pinewood, being very rare in the maquis and totally absent in meadows. Therefore, one could have expected the fox activity in the pinewood to be positively correlated with availability of juniper berries, whereas a negative association should have occurred between the maquis and this food resource. However, our data have shown the opposite. Such an apparent paradox can be explained by the various degrees of clumpedness of the main food resources. In fact, while the insects are dispersed, the juniper berries are very clumped. Furthermore, these berries can be found readily under the juniper trees and are thus a highly predictable food resource for the fox. The time needed to search for and to feed on berries is obviously much less than that for catching insects, which leaves the fox with spare time to spend in other activities, e.g. searching for small mammals in the maquis. Our finding is consistent with Macdonald's arguments (1981) that not only the abundance, but also the dispersion pattern are important in shaping the use of space by the red fox. Therefore, caution must be employed before assuming that the time spent in an area is proportional to the use of local food resources.

From the cluster analysis, it can be seen that maximum and minimum temperatures influenced the availability of Orthoptera and thus the importance of Orthoptera in the diet (occurrence, volume). In turn, this cluster of variables is the most related to the use of habitat, i.e. meadows and maquis.

Furthermore, Coleoptera—in contrast to Orthoptera—are present in the winter diet of foxes (although in low numbers). This could explain the relationship between this food category—but not the Orthoptera—and juniper berries. In fact, the cluster analysis seems to indicate that the importance of juniper in the diet is more related to Coleoptera (occurrence, volume, availability) than to the availability of juniper berries, which most probably are a less suitable food category.

Rain and activity do not seem to group tightly together with any other variable (D=40). This fact might be explained by an imprecise evaluation of the rainfall, i.e. pooling data by weeks, and by factors underlying activity that have not been considered (e.g. hormonal state, cf. Aschoff, 1966).

Summary

The food habits of red foxes were positively correlated to the seasonal abundance of the most important local resources (juniper berries, grasshoppers, beetles), which was correlated to meterologic factors.

The availability, in terms of abundance and dispersion, of the main food resources and their use influenced the activity pattern and habitat choice of red foxes.

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