Habitat selection by the red fox Vulpes vulpes (L. 1758) in an Alpine area

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Received 11 June 2002, accepted 5 April 2004

Habitat selection and the influence of habitat variables on red fox ranges were assessed in the Gran Paradiso National Park, Western Alps, Italy, all year round. Nine hundred twenty-two scats were mapped as "signs of presence" by monthly surveys of fixed transects in the main habitat types and altitude belts. Forested habitats and lower altitudes (1000-1500 m a.s.l.) were selected, whereas upper altitudes were avoided, during the cold season. This pattern was attributed to the availability of ungulate carrion, widely used as food by foxes, at low altitude, while upper altitudes provided poor resources in the cold season. During the warm season, no clear pattern of habitat selection could be detected. The selection for forested habitats could therefore be explained by the availability of resources other than food, e.g. resting and denning sites. The strong seasonality of an Alpine altitudinal succession, where resource availability varies over short distances, may lead to home ranges containing a variety of habitat types along the altitudinal gradient, providing resources throughout the year. Foxes possibly hold "vertical" home ranges, where certain habitat types became strategic, especially under limiting climatic conditions.

KEY WORDS: red fox, *Vulpes vulpes*, scats, habitat selection, range attendance, climate, altitude, Alpine habitat.

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INTRODUCTION

Home range shape and size are the result of habitat selection by an animal in its search for an area containing all the resources necessary to reproduce and survive throughout the year (second order selection, JOHNSON 1980). In a patchy environment, the Resource Dispersion Hypothesis (MACDONALD 1981, 1983) predicts that the dispersion of food patches will determine territory size, whereas their richness will limit the group size of carnivores, foxes included. Other studies have showed that population density (DONCASTER & MACDONALD 1992) and location of resting sites (MEIA & WEBER 1993, LUCHERINI et al. 1995) may also affect the territory size of red foxes. Selection resulting from habitat use is another level of selection (JOHNSON 1980) and is likely to be affected by the temporal distribution of resources, as well as their abundance and concentration, within different patches (CAVALLINI & LOVARI 1991, LUCHERINI et al. 1995). In heterogeneous areas, where a number of resources are available at the same time in different habitats, foxes apparently selected a diversity of habitats rather than any one in particular (CA-VALLINI & LOVARI 1994, LOVARI et al. 1996, LUCHERINI & LOVARI 1996). In the mountains, the altitudinal gradient determines a successional variety of habitats (BEGON et al. 1986), where human-induced environmental changes increase fragmentation. Thus, the presence and availability of natural resources can vary abruptly over short distances and Alpine weather conditions, extreme in winter, affect the temporal distribution of resources (VALLETTO et al. 1992, for a description of biodiversity in the Alpine area, where our study was conducted).

Very few studies of range use have been carried out on the red fox in a mountain habitat (MACDONALD et al. 1980, WEBER & MEIA 1996). Amongst these studies, only one has been conducted in the Alps, in part of our study area (BOITANI et al. 1984), but this study was not aimed at habitat selection. It may be expected that in mountains (i) the range use of foxes will include a variety of habitats providing resources throughout the year; (ii) those habitats will be used differently throughout the year, as a consequence of climatic conditions; (iii) the relationship between the seasonal use of resources and habitat will be stronger in severe climatic conditions. Our purpose was to test these predictions through a seasonal assessment of habitat selection by using an indirect sign of presence such as the scat distribution (e.g., FRITTS & MECH 1981, EDGE & MARCUM 1989, MERIGGI et al. 1991).

STUDY AREA

The study area included all the valleys of the Gran Paradiso National Park, from an altitude of 1000 m a.s.l. to the upper limit of vegetation (2500-2800 m a.s.l.). The Gran Paradiso National Park, 720 km², is located in the Western Italian Alps; the climate is typically Alpine continental, characterised by winters with a thick snow cover present on the ground for 5-6 months/year and a mean temperature below 0 °C for 4-5 months/year (Fig. 1, CAGNACCI et al. 1999). Because of the shortness of the spring and the autumn, two main seasons can be considered: a cold one, from September-October to February-March, and a warm season, from March-April to August-September.

The altitudinal gradient influences the vegetation cover. Forest habitats are prevalent at lower altitudes: broad-leaved woods (mainly mixed woods, along the lowest border of the Park, including beech *Fagus sylvatica* and domestic trees, such as cherries *Prunus avium* and plums *Prunus domestica*), as well as conifer woods (larch *Larix decidua* and Norway spruce

Habitat selection in the red fox

Picea abies are the dominant forest species). Open habitats dominate above 1800-2000 m a.s.l.: shrubby areas (mainly berries *Rubus idaeus* and *Rubus fruticosus*, bilberries *Vaccinium myrtillus*, shrubs of *Berberis vulgaris* and wild roses *Rosa* sp.) and pastures (Alpine praires). The remaining part is covered by a combination of rocky praires.

The Gran Paradiso National Park has been protected since 1921, and it is characterised by dense populations of mountain ungulates, mostly Alpine ibex *Capra ibex* (3000-4000 ind.) and chamois *Rupicapra rupicapra* (7000-8000 ind.) (BASSANO 1992, PERACINO 1992). The severe climate of winter and early spring determines the death of many ungulates through the action of avalanches, lack of food and diseases (PERACINO et al. 1992). Numerous ungulate carcasses are found mainly in late winter and spring, between 1000 and 2000 m a.s.l. (PERACINO et al. 1986). Small mammals are common in the Park in deciduous woods, as well as in shrubs and open habitats, also at high altitudes (over 1500-1800 m a.s.l.), whilst they are comparatively scarce in conifer woods (DEBERNARDI et al. 2003). During the research period, no large carnivores were present in the park.

MATERIAL AND METHODS

Data collection

Thirteen transects (30 km in total) dispersed over the whole study area and crossing the habitat types and altitude zones of the area, were chosen for the detection of signs for the presence of foxes. Transects were only placed on footpaths to ensure a consistent detectability of the signs of presence in the different habitat types. We considered scats as signs of the recent presence of foxes (e.g., THOMPSON 1952, JHALA & GILES 1991, MASSOLO & MERIGGI 1998), relatively independent of ground conditions and food intake by foxes (CAVALLINI 1994). Transects were covered monthly from August 1996 to August 1997 and fox scats were mapped and then removed.



Fig. 1. — Monthly changes of temperature and snow cover in the Gran Paradiso National Park (1996-1997; mean of different meteorological stations).

Signs of presence were classified within the eight habitat types and three altitude belts crossed by the transects (Table 1). Moreover, the study area was divided into sample squares (SS) of 25 ha each by means of a 500 m spaced grid, according to the UTM grid. The size of the SS was in accordance with the mean home range of the red fox (195.4 \pm 152.8, BOITANI et al. 1984) in the Gran Paradiso National Park. We selected the SS crossed by transects to calculate an Attendance Index (AI) for each square:

$$AI = \frac{\text{n of scats in the SS}}{\text{km of transect in the SS}}$$

In each SS, we measured the surface area of eleven habitat types and three altitude belts (1000-1500, 1500-2000 and > 2000 m a.s.l.) by a G.I.S. (IDRISI B). The habitat variables (broad-leaved woods, 6.3%; sparse broad-leaved woods, 2.3%; conifer woods, 39.4%; sparse conifer woods, 5.5%; scrublands, 8.1%; meadows, 7.3%; Alpine prairies, 23.2%; bushy prairies, 3.5%; rocky prairies, 1.6%; debris, 0.8%; rocky areas, 1.8%) were mapped on the basis of a vegetation map (1:25000) of the Park (MONTACCHINI et al. 1967) and direct surveys. Finally, we calculated for each SS the Shannon Index of Diversity:

$H' = -\sum p_i \log_2 p_i$

where p_i is the proportion of habitat *i* in the SS.

We worked out the data annually, seasonally and monthly. The seasons were determined according to temperature and snow cover (Fig. 1). In addition, consecutive months were grouped together, in order to avoid overlap across years. The cold season ranged between September 1996 and February 1997, the warm season between March and August 1997.

Statistical analyses

We tested the null hypothesis that foxes use the habitat types in proportion to their availability. The observed and expected frequencies of use were compared by the chi-square goodness-of-fit test (SIEGEL & CASTELLAN 1988). When the chi-square reached significant values ($P \le 0.05$), we calculated the Bonferroni simultaneous confidence intervals for the proportions of observed use (OUP) to outline which habitat type showed significant differences between the expected and observed proportions of use (NEU et al. 1974, BYERS et al. 1984, ALLDREDGE & RATTI 1986). The Bonferroni confidence intervals were calculated through the following formula:

where *n* is the total number of signs of presence; *P_i* is the proportion of observed use for the *i*th type of habitat; *Z* is the upper standard normal table value, corresponding to a probability tail area of $\alpha/2k$ with $\alpha = 0.05$ and 0.01; *K* is the number of considered habitat types.

$$P_i - Z_{\alpha_{2k}} \sqrt{P_i(1-P_i)/n} < P_i < P_i + Z_{\alpha_{2k}} \sqrt{P_i(1-P_i)/n} < P$$

We performed correlation analyses (Pearson product moment coefficient) between the attendance index and the habitat variables measured in the sample squares, to assess the influence of each habitat variable on the presence of foxes in the study area. Moreover, we subdivided the AI values in two sets by the 25th percentile two obtain two groups of SS: those of low and those of high attendance; on these two groups we performed both for the cold and warm season and for the whole year, one-way analyses of variance (one-way ANOVA) and Discriminant Function Analyses (DFA, method of Wilks' Lamba minimisation) to highlight the habitat characteristics that the foxes require. For these analyses the habitat variables were checked for their distribution and those with significant deviation from the normality (Kolmogorov-Smirnov test) were transformed depending on their approximate distribution. For the DFA we selected the habitat variables that showed differences between low and high attendance squares at the minimum probability level of 0.1 (GREEN 1974, NOON

Table 1.

					Table 1									
Distribut	tion of signs c	of presen	ice and to	otal leng	th of tra	nsects w	/ithin ea	ch habit	at type a	nd altitu	ıde belt.			
Habitat	Length (m)	Aug 1996	Sept	Oct	Nov	Dec	Jan	Feb	Mar	Apr	May	Jun	Jul	Aug 1997
Broad-leaved woods	3305	2	12	15	ε	11	28	10	9	14	0	6	15	21
Sparse broad-leaved woods	2900	4	4	16	б	б	6	18	14	Ŋ	0	0	0	0
Conifer woods	9350	33	52	35	8	18	47	16	39	52	24	22	39	25
Sparse conifer woods	2900	0	7	4	4	2	4	6	2	6	12	0	2	4
Alpine prairies	5845	19	11	28	2	3	3	б	17	10	15	4	19	12
Bushy prairies	1765	1	7	ŝ	1	1	4	ŝ	2	2	7	2	2	8
Rocky prairies	1220	1	1	б	0	0	0	0	1	0	0	0	0	0
Scrublands	2975	Ŋ	7	20	0	2	0	0	-	0	0	4	б	Ŋ
I alt. belt (1000-1500 m a.s.l.)	11310	27	46	57	6	20	49	39	42	42	17	23	47	48
II alt. belt (1500-2000 m a.s.l.)	10575	26	35	22	12	15	45	16	28	41	17	11	12	12
III alt. belt(> 2000 m a.s.l.)	8375	12	15	45	0	S	-	-	12	9	24	7	21	15
Total	30260	65	96	124	21	40	95	56	82	89	58	41	80	75

1981). This procedure allows the use of a reduced number of variables, maintaining a sufficiently high number of cases for each independent variable (WILLIAMS et al. 1990). We also calculated a correlation matrix among independent variables to outline linear dependence (MASSOLO & MERIGGI 1995).

RESULTS

Habitat selection

Overall, foxes significantly selected both types of dense forested habitats, while almost all sparse forest and open habitats were avoided (Table 2). The same pattern occurred in the cold and the warm seasons, but the selection of broad-leaved woods was limited to the cold period. The lowest altitudinal belt was selected and the highest one avoided in both cold and warm periods (Table 3). The use of the intermediate altitude belt was proportional to its availability, except during the warm season, when it was avoided.

On a monthly basis, the distribution of scats in the habitat types was significantly different from that expected for a use proportional to the availability, except in November, possibly because of the low sample size in that month (Aug 1996 χ^2 = 25.664, P < 0.01; Sep χ^2 = 31.791, P < 0.01; Oct χ^2 = 16.062, P < 0.05; Nov χ^2 = 6.071, NS; Dec χ^2 = 15.935, P < 0.01; Jan χ^2 = 67.187, P < 0.01; Feb χ^2 = 43.938, P < 0.01; Mar χ^2 = 27.009, P < 0.01; Apr χ^2 = 43.230, P < 0.01; May χ^2 = 34.614, P < 0.01; Jun χ^2 = 22.323, P < 0.01; Jul χ^2 = 33.167, P < 0.01; Aug 1997 χ^2 = 35.992, P < 0.01).

For 9 months out of 13, foxes did not use altitude belts in proportion to their availability (Table 3). Almost always, from September to April, the highest altitudinal belt was avoided. In the remaining months, it was used in proportion to its availability. In the transition between the cold and the warm seasons, as well as in June and July, the lowest altitudinal belt was selected. The intermediate zone was generally used in proportion to its availability, although it was positively selected in January and avoided in October, July and August 1997.

Table 2.

 χ^2 test of the distribution of signs of presence between habitat types and Bonferroni confidence intervals analysis between expected (EPU) and observed (OPU) proportion of use of habitat types (year, seasons).

Habitat types	EPU	OPU year	OPU cold season	OPU warm season
Broad leaved woods	0.109	0.158 (**)	0 183 (**)	0.153 NS
Sparse broad-leaved woods	0.109	0.138 () 0.082 NS	0.123 NS	0.045 **
Conifer woods	0.309	0.445 (**)	0.407 (**)	0.473 (**)
Sparse conifer woods	0.096	0.052 **	0.051 **	0.061 *
Alpine prairies	0.193	0.158 *	0.116 **	0.181 NS
Bushy prairies	0.058	0.047 NS	0.044 NS	0.054 NS
Rocky prairies	0.040	0.007 **	0.009 **	0.002 **
Scrublands	0.098	0.051 **	0.067 NS	0.031 **
	χ^2	150.587 **	76.877 **	96.798 **

Parentheses indicate a positive selection. * P < 0.05; ** P < 0.01.

Table 3.

 χ^2 test of the distribution of signs of presence between altitude belts and Bonferroni confidence intervals analysis between expected (EPU) and observed (OPU) proportion of use of altitude belts.

Altitude belts	5	E	PU	OP	U yea	r	OPU	cold s	eason	0	PU wa	rm se	ason
I (1000-1500 II (1500-2000 III (> 2000 m	m)) m) ı)	0. 0. 0.	374 349 277 x ²	0.5 0.3 0.1 78.	505 (** 317 N 178 ** 175 **	*) S *	0 0 0 44	.509 (* .336 N .155 * I.565 *	**) IS **		0.515 0.285 0.200 36.929	5 (**) 5 ** 9 **	
Altitude belts 1996 1997	EPU	OP Au	U g	OPU Sep	J)	OPU Oct	J	OP No	U v	OPU Dec	J :	OPU Jar	J
1000-1500 m 1500-2000 m > 2000 m	$0.374 \\ 0.349 \\ 0.277 \\ \chi^{2}$	0.415 0.400 0.185 2.771	NS NS NS NS	0.479 0.365 0.156 7.954	NS NS ** *	0.460 0.177 0.363 4.510	NS ** NS NS	0.429 0.571 0.001 8.941	NS NS ** *	0.500 0.375 0.125 5.109	NS NS * NS	0.516 0.474 0.011 34.030	(*) (*) **
Altitude belts 1997	OP Fe	U b	OP Ma	U	OP Ap	U	OP Ma	U y	OPU Jun	[OPU Jul		OPU Aug
1000-1500 m 1500-2000 m > 2000 m χ ²	0.696 0.286 0.018 29.814	(**) NS **	0.512 0.341 0.146 9.259	(*) NS ** *	0.472 0.461 0.067 19.537	NS NS **	0.293 0.293 0.414 5.472	NS NS NS NS	0.561 0.268 0.171 6.284	(*) NS NS *	0.588 0.150 0.263 18.946	(**) ** NS **	0.640 (**) 0.160 ** 0.200 NS 23.525 **

Parentheses indicate a positive selection. * P < 0.05; ** P < 0.01.

Table 4.

Correlation matrix among independent variables (Pearson product moment coefficient). Only variables with significant correlations are showed.

Habitat variables (%)	Pastures	Scrublands	Alt. belt 1500-2000	Alt. belt 2000-2500	Alt. belt > 2500	Н
Broad-leaved woods	*	NS	(***)	**	*	NS
Sparse broad-leaved woo	ds NS	NS	(***)	**	NS	(*)
Conifer woods	***	*	NS	(*)	***	*
Sparse conifer woods	NS	NS	NS	NS	NS	(**)
Meadows	NS	NS	(**)	NS	*	*
Alpine prairies	NS	NS	**	NS	(***)	NS
Scrublands	NS	NS	NS	NS	(***)	NS
Rocky areas	NS	NS	NS	NS	NS	(*)

Parentheses indicate a positive correlation. H: Shannon Index of Diversity. * P < 0.05; ** P < 0.01; *** P < 0.001.

Correlations among habitat variables

Broad-leaved woods were positively correlated to the first altitudinal belt and negatively correlated with the other two belts, whilst conifer woods were positively associated with the intermediate belt and negatively correlated only with the third one (Table 4). Open habitats were negatively correlated with the lowest altitudinal zone and strongly correlated to the highest one, with the exception of meadows. The Shannon Index of Diversity was negatively correlated with homogeneous habitats, e.g. dense woods and prairies, and positively correlated with scattered and fragmented habitats.

Influence of habitat variables on the range attendance

All year round, only dense conifer woods were positively correlated with the fox Attendance Index (AI) (r = 0.28, P < 0.05). In the cold season, the AI was positively associated to dense broad-leaved woods (r = 0.30, P < 0.05) and to the lowest altitudinal belt (r = 0.31, P < 0.05). AI was negatively correlated with the highest altitudinal belt (r = -0.37, P < 0.01). No significant correlations between AI and the habitat variables were detected during the warm season.

Subdividing the sample squares in accordance with low and high values of the AI by the 25th percentile, we obtained respectively 16 and 46 cases in the two groups, both for the year and for the cold and warm seasons. For the whole year the AI in the sample squares of low attendance averaged 8.3 (SE = 1.34) and 46.0 (SE = 4.25) in those of high attendance. Four habitat variables showed significant (P < 0.05) differences between the two groups of sample squares; in particular conifer woods and the lowest altitude belt had greater percentages in the squares of high attendance whereas sparse conifer woods and rocky areas were more present in the squares of low attendance. Moreover, other three habitat variables showed differences at the probability level of 0.1 between the two type of squares: broadleaved woods, with higher percentages in the high attendance squares, and scrublands and the highest altitude belt, with higher percentages in the low attendance ones (Table 5). The Discriminant Function Analysis (DFA) carried out with these as independent variables, significantly separated the two groups of squares with 75.8% of cases correctly classified (68.8% for the low and 78.3% for the high attendance squares). The variables with the greatest discriminant power were rocky areas, conifer woods, and sparse conifer woods (Table 6).

In the cold season the AI averaged 3.0 (SE = 0.63) in the squares of low attendance and 20.4 (SE = 1.59) in the high attendance ones. Three habitat variables showed significant differences (P < 0.05) between the two types of squares: broad-leaved woods and the lowest altitude belt had greater percentages in the high attendance squares, whereas scrublands were more present in the low attendance ones (Table 5). The DFA was performed with these variables and with three others that showed differences at the probability level of 0.1: conifer woods, rocky areas, and the highest altitude belt. The discriminant function derived from the analysis significantly discriminated the low and high attendance squares, with percentages of cases correctly classified of 72.6% in total, of 68.8% for the low, and 73.9% for the high attendance squares. The variables with the greatest discriminant power were the altitude belt from 1000 to 1500 m a.s.l., scrublands, and broad-leaved woods (Table 6).

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Habitat variables (%)		Year		Coi	ld season		Warı	n season	
	Low	High	р	Low	High	Р	Low	High	Р
Broad-leaved woods	1.9 (1.23)	7.9 (2.07)	0.104	0.9 (0.76)	8.2 (2.08)	0.044	1.9 (1.23)	7.9 (2.07)	0.104
Sparse broad-leaved w.	1.7 (1.28)	2.6 (1.16)	0.654	1.2 (1.24)	2.8 (1.17)	0.475	3.7 (2.28)	1.9 (0.97)	0.412
Conifer woods	23.8 (5.78)	44.7 (4.66)	0.018	28.1 (6.47)	43.3 (4.68)	0.091	25.0 (4.62)	44.3 (4.84)	0.029
Sparse conifer w.	11.7 (4.97)	3.4 (1.26)	0.025	7.5 (3.29)	4.8 (1.88)	0.476	11.7 (4.97)	3.4 (1.26)	0.025
Meadows	3.7 (2.46)	8.6 (2.46)	0.270	5.8 (3.30)	7.9 (2.36)	0.633	4.5 (2.51)	8.3 (2.46)	0.391
Alpine prairies	30.6 (7.64)	20.6 (4.49)	0.264	27.5 (7.84)	21.7 (4.50)	0.519	29.2 (7.86)	21.1 (4.47)	0.368
Bushy prairies	4.1 (2.26)	3.3 (2.01)	0.818	4.3 (2.26)	3.2 (2.00)	0.756	2.5 (2.11)	3.8 (2.02)	0.724
Rocky prairies	2.4 (2.26)	1.4 (0.72)	0.566	2.4 (2.27)	1.4 (0.72)	0.584	2.4 (2.26)	1.4 (0.72)	0.566
Scrublands	13.9 (5.68)	6.0 (2.05)	0.109	16.7 (5.85)	5.1 (1.88)	0.015	13.1 (5.27)	6.3 (2.20)	0.168
Debris	0.3 (0.24)	1.1 (0.46)	0.367	1.4(0.84)	0.7 (0.37)	0.410	0.2 (0.19)	1.1 (0.46)	0.245
Rocky areas	6.2 (3.18)	0.3 (0.16)	0.003	4.5 (3.17)	0.9 (0.40)	0.075	6.2 (3.18)	$0.3 \ (0.16)$	0.003
Habitat diversity*	1.4 (0.12)	$1.1 \ (0.09)$	0.115	1.3 (0.13)	1.1 (0.09)	0.262	1.4(0.11)	1.1(0.09)	0.076
Altitude belt 1000-1500	15.1 (8.41)	41.3 (6.49)	0.034	9.4 (6.79)	43.3 (6.51)	0.006	21.3 (9.87)	39.2 (6.42)	0.152
Altitude belt 1500-2000	53.9 (11.89)	45.1 (6.15)	0.482	59.8 (10.64)	43.0 (6.32)	0.183	49.3 (11.75)	46.7 (6.21)	0.834
Altitude belt > 2000	31.0 (11.53)	13.6 (4.54)	0.095	30.8 (10.29)	13.7 (4.88)	0.100	29.4 (11.14)	14.2 (4.70)	0.143
* Shannon Index of Divers	sity.								

Results of the Discriminan for the whole year a	nt Function Analys nd in the cold and	es (DFA) between s warm seasons (hał	quares with low (n bitat variables select	= 16) and high (n = ed by one-way ANO	= 46) values of the <i>A</i> DVA, minimum sign	the transformation of transformat
Habitat variables (%)		Year	Cold	season	Warn	1 season
	Standard DFA coefficients	Corr. coeff. with the DFA	Standard DFA coefficients	Corr. coeff. with the DFA	Standard DFA coefficients	Corr. coeff. with the DFA
Broad-lived woods	- 0.203	- 0.283	0.204	0.434	- 0.539	- 0.332
Conifer woods	-0.278	- 0.415	0.301	0.362	- 0.415	- 0.448
Sparse conifer woods	0.467	0.393			0.450	0.462
Scrublands	0.290	0.278	- 0.466	- 0.526	I	
Rocky areas	0.728	0.535	- 0.597	- 0.382	0.609	0.628
Habitat diversity*	I	Ι	I		0.125	0.363
Altitude belt 1000-1500	- 0.373	-0.371	0.618	0.605	I	
Altitude belt >2000	0.119	0.290	0.126	- 0.352		Ι
Eigenvalue	0	.570	0	.376	0	.414
Canonical Correlation	0	.602	0	.523	0	.541
Wilks' Lambda	0	.637	0	.727	0	.707
Chi-square	2	5.47	1	8.18	1	9.91
df		7		6		5
Р	0	.001	0	.006	0	.001

* Shannon Index of Diversity.

Table 6.

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In the warm season the AI reached average values of 2.4 (SE = 0.60) and 23.7 (SE = 3.63) respectively for the low and high attendance squares. Conifer woods had greater (P < 0.05) percentages in the squares of high attendance, whereas sparse conifer woods and rocky areas showed higher average values in the squares of low attendance. Furthermore for broad-leaved woods and habitat diversity (Shannon Index of Diversity) we detected differences at the probability level of 0.1 (Table 5). The discriminant function derived from the DFA performed with these variables, significantly separated the squares of low from those of high attendance, with 80.6% of total cases correctly classified (62.5% of low and 87.0% of high attendance squares). The most important variables in the discrimination were rocky areas, sparse conifer woods, and conifer woods (Table 6).

DISCUSSION

The use of indirect signs of presence to define the patterns of habitat selection has some disadvantages. For example it is not possible to relate habitat use to the activity patterns and range use of animals by this method, as it is with radiotracking (WEBER & MEIA 1996). However, this method was appropriate in the present study for three crucial reasons: (1) we could carry out the study in a wide area, including different isolated valleys, in order to maximise the number of individuals sampled and to obtain independent samples; in this way, habitat selection analyses were carried out at population level; (2) the results are not affected by individual variability, which can be detrimental for radio-tracking studies conducted on few individuals; in these cases the results cannot represent the pattern of habitat selection by the population but they can show the habits of some individuals that could be a non-random sample of the population (LOVARI et al. 1996); (3) signs of presence can be mapped precisely, whereas telemetry locations may incorporate a lot of error, especially in mountains and when looking at habitat use in patchy environments, because of the errors due to the reflection (KENWARD 2001).

Moreover the fact that scats were collected only on footpaths could represent a bias because the foxes use tracks to quickly move or mark (MACDONALD 1980). However, we based our choice on the following: (i) footpaths allowed a consistent detection of signs of presence in different habitat types and seasons; (ii) in mountains, habitat patches follow the altitudinal succession, thus limiting the error; (iii) we considered scats on the footpath as signs of fox attendance of the surrounding area, not only of the habitats along the transect.

Foxes selected the lowest altitudes and the forested habitats (positively correlated to each other) mainly in the second part of the cold season, whilst avoidance of the highest altitudes began earlier in the cold period. Correlations between these variables and the Attendance Index of foxes in the cold season showed the same pattern. Conversely, we expected a significant presence in the upper altitudes (open habitats) in the warm period. Surprisingly, however, this was not seen. The one-way ANOVAs and Discriminant Function Analyses showed that in general the wooded habitats and low altitudes are highly visited, whereas the open habitats and high altitudes were poorly visited. This should be because of the correlation between these habitat and altitude, i.e. wooded habitats are associated with lowest altitudes and open ones with highest altitudes. However, in the warm season the altitude was not important in the discrimination between high and low attendance squares, whereas

the percentage of wooded and open habitats were significantly different in the two type of squares. This could mean that broad-leaved and conifer woods are required habitats by foxes. Habitat selection is likely to be dependent on availability and quality of food resources (CAVALLINI & LOVARI 1991, LUCHERINI et al. 1995). This view is supported by data on food habits (CAGNACCI et al. 2003): carcasses of ungulates, primarily chamois, were by far the staple food during the cold season; moreover, their use was strictly associated with the presence of snow cover. Carrion is a rich, clumped food resource, with an unpredictable dispersion, influencing fox movements (LOVARI et al. 1994). A large number of carcasses of wild ungulates (chamois and Alpine ibex) are usually found in winter and spring at the bottom of the valleys, where these ungulates move to search for food or are carried by avalanches (PERACI-NO et al. 1986). Foxes have been frequently seen feeding on carrion, especially in the lowest and intermediate altitude zones, whereas only few sightings were recorded in the highest altitude belt in winter and spring (PERACINO et al. 1992). Conversely, in the cold period, avoidance of the upper altitudes may be explained by the scarcity of local food resources. In summer, in the Park, the availability of potential resources for an opportunistic carnivore strongly increases, due to the mild climatic conditions. In fact, the diet was more varied than in winter (CAGNACCI et al. 2003) and included items with differential distribution in the habitat patches of the altitudinal succession. Small mammals (summer staple food) were found in Gran Paradiso National Park mainly in shrubby areas (DEBERNARDI et al. 2003). In summer, other important mammal prey were ungulates (likely to be mainly kids, CAGNACCI et al. 2003) and marmots (CAGNACCI et al. 1999), which were present in the upper altitudes, in that season. Among insects, mainly grasshoppers and ground beetles, which are abundant in meadows and open habitats (GRANDI 1951) were consumed (CAGNACCI et al. 1999). Fruits are obviously concentrated in shrubby areas, but they can also be common in woods. It is therefore likely that the distribution of food resources in summer did not influence habitat selection of foxes in their range use as strongly as under the harsh climatic conditions of the cold season. Other aspects of habitat use, e.g. an overall preference for dense forested habitats and the constant avoidance of open ones, could be only partly explained through variations in diet and food availability. Foxes use wooded areas intensively (e.g. SCHOFIELD 1960, PULLIAINEN 1981, ARTOIS 1985), because of the associated food resources (e.g. fruits). On the other hand, forested habitats may also provide resting and denning sites (MEIA & WEBER 1993, LUCHERINI et al. 1995; LOVARI et al. 1996) or favourable temperature conditions both in winter and in summer (CAVALLINI & LOVARI 1994).

It has already been suggested that the Resource Dispersion Hypothesis (MAC-DONALD 1983) cannot explain ranging behaviour and habitat use in a complex environment with several productive habitats, if only food resources are considered (CAVALLINI & LOVARI 1991, LOVARI et al. 1996). The strong seasonality and the highly fragmented altitudinal succession of an Alpine area, where availability of natural resources varies over short distances, may lead to home ranges containing a variety of habitat types along the altitudinal gradient, providing resources throughout the year. Vertical movements of radio tagged foxes were actually recorded in one valley of our study area (BOITANI et al. 1984). Moreover, CAGNACCI et al. (1999) found that scat composition did not significantly vary with altitude or habitat patches, as would be expected if individual home ranges were restricted to an altitudinal belt. This information lends support to our conclusions. Habitat selection may therefore be an adaptive proximate response to severe climatic conditions, which seasonally alter the relative importance of different habitats to foxes.

ACKNOWLEDGMENTS

We are grateful to the staff of the Gran Paradiso National Park, especially the Direction, the park wardens and B. Bassano, who helped us in many ways. We wish to thank also L. Cagnolaro, former Director of The Natural History Museum in Milan, who provided us with laboratory facilities and technical expertise. Two anonymous referees kindly provided constructive criticism on a previous draft. B. Tolhurst kindly revised the final English draft. Financial support was provided by the Gran Paradiso National Park Agency.

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