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LOCAL FEEDING SPECIALIZATION OF THE RED FOX (*VULPES VULPES*) IN RESPONSE TO EASTERN COTTONTAIL (*SYLVILAGUS FLORIDANUS*) INTRODUCTION (NW ITALY)

ALESSANDRO BALESTRIERI, LUIGI REMONTI, CLAUDIO PRIGIONI

Dipartimento di Biologia Animale, Università di Pavia, Piazza Botta 9, 27100 Pavia
E-mail: prigioni@unipv.it

ABSTRACT - To appreciate the influence of the introduction of the Eastern cottontail (*Sylvilagus floridanus*) on the food habits of the red fox (*Vulpes vulpes*), between June 1998 and February 2000 fox diet was investigated by means of scat analysis (N=115) in a 250 ha wide Natural Reserve of NW Italy, and compared with data collected in the same area prior to cottontail colonization (1988-1989). Comparison included also the diet of badgers (*Meles meles*), considered as potential competitors for food resources.

Alien lagomorphs (mean percent volume, Vm% = 68%) represented by far the most exploited resource, only three other food items reaching values of mean percent volume barely higher than 5%. Cottontails frequency of occurrence did not vary according either to season or to their reproductive cycle (II-IX *vs*. X-I), whilst diet niche breadth varied inversely proportional to the use of this key-resource. Overall fox trophic niche breadth varied from 0.64 in 1988-89 to 0.31 in 1998-00 (B, Levin's index). These findings led us to consider the feeding habits of the fox in the study area as a result of local specialization of a typical generalist carnivore, according to the predictions of optimal foraging theory. No variation occurred in the badger niche breadth since cottontail introduction, whilst niche overlap between foxes and badgers decreased from 0.59 to 0.13 (O, Pianka's index), possibly reducing competition for food in summer.

Key words: *Vulpes vulpes*, diet, local specialization, alien lagomorph, *Sylvilagus floridanus*.

RIASSUNTO - ***Specializzazione alimentare a livello locale della Volpe* Vulpes vulpes *in risposta all'introduzione del Silvilago* Sylvilagus floridanus *(Italia nord occidentale)***. Per valutare gli effetti dell'introduzione del Silvilago (*Sylvilagus floridanus*) sul comportamento alimentare della volpe (*Vulpes vulpes*), nel periodo giugno 1998 – febbraio 2000, la dieta del carnivoro è stata definita tramite l'analisi di 115 feci raccolte nella Riserva Naturale "Garzaia di Valenza" (Provincia di Alessandria, Italia nord occidentale) di circa 250 ha. I risultati ottenuti sono stati confrontati con quelli conseguiti nella medesima area prima dell'introduzione del Silvilago, oltre che con quelli disponibili sulla dieta del Tasso (*Meles meles*), che può essere ritenuto un potenziale competitore per le risorse alimentari.

I lagomorfi sono risultati la categoria alimentare maggiormente consumata (volume medio percentuale, Vm% = 68%), mentre solo tre altre categorie hanno raggiunto valori di Vm di poco superiori al 5%.

Non sono emerse variazioni stagionali o relative al periodo riproduttivo (febbraio-settembre *vs*. ottobre-gennaio) del Silvilago, anche se l'ampiezza di nicchia complessiva è risultata inversamente proporzionale al consumo di lagomorfi. L’ampiezza di nicchia della Volpe è scesa da 0,64 nel 1988-89 a 0,31 nel 1998-00. Nel complesso, la dieta della Volpe nell’area di studio può essere considerata l’espressione di una specializzazione a livello locale, così come previsto dalla teoria del foraggiamento ottimale.

Non è emersa alcuna variazione per l’ampiezza di nicchia del Tasso, mentre il grado di sovrapposizione (indice di Pianka) tra il mustelide e la Volpe è nettamente diminuito (da 0,59 a 0,13). In questi termini la specializzazione della Volpe potrebbe rendere minima la competizione alimentare con il Tasso, in particolar modo in estate, quando la siccità limita la disponibilità di lombrichi.

Parole chiave: *Vulpes vulpes*, nicchia trofica, dieta, specialista, introduzione, *Sylvilagus floridanus*.

INTRODUCTION

The red fox (*Vulpes vulpes*) is considered a prototypical generalist, feeding on a wide variety of food resources according to their local and seasonal availability (Ables, 1975; Lloyd, 1975 and 1980; Macdonald, 1977).

In Italy, its diet has been investigated in a variety of environments, including riverine habitats (Prigioni and Tacchi, 1991), Mediterranean coastal areas (Ciampalini and Lovari, 1985; Calisti *et al*., 1990; Cavallini and Volpi, 1996), the Alps (Leinati *et al*., 1960; Cantini, 1991, Cagnacci *et al*., 2003) and the Apennines (Patalano and Lovari, 1993; Rosa *et al*, 1991). All these studies confirm the opportunistic feeding behaviour of the fox, which, on average, relies on fruits and invertebrates in the Mediterranean area and on mammals, mainly rodents, and fruits in mountain and hilly habitats (Calisti *et al*., 1990).

Alien species can deeply alter native ecosystems by means of a variety of mechanisms. Among the possible interactions between alien and native species (Ebenhard, 1988), acting as prey for native predators is probably the most overlooked, ecologists’ attention having been engrossed by the often dramatic effects of allochtonous predators on ecological communities (see Park, 2004). Greater attention has been paid to the alteration of freshwater habitats, where the effects of the introduction of crustaceans (Delibes and Adrian, 1987; Correia, 2001) or fish species (Breathnach and Fairley, 1993) on the feeding behaviour of some predators have been documented.

In north-western Italy, six species of mammals have been introduced in the last two centuries (Bertolino, 1999), of which four (*Sylvilagus floridanus, Myocastor coypus, Sciurus carolinensis* and *Callosciurus finlaysoni*) are susceptible of predation by foxes.

Prey switching is a foraging behaviour commonly associated with generalist predators (Murdoch, 1969) and, according to their feeding adaptability, foxes should be able to readily prey on new abundant and profitable resources. To test this hypothesis i) we analysed fox diet in an area of NW Italy where the eastern cottontail *S. floridanus* is actually abundant in spite of recent colonization (Silvano *et al*., 2000; Meriggi, 2001) and ii) we compared fox trophic niche and feeding habits with available data (Canova and Rosa, 1994) prior to the introduction of eastern cottontails in our study area, also considering niche overlap with the badger *Meles meles* (Canova and Rosa, 1994; Balestrieri *et al*., 2004) as a potential competitor for food resources.

STUDY AREA

The study area coincides with a Natural Reserve ("Garzaia di Valenza", SE Piedmont region, NW Italy) and covers about 250 ha on the left side of the River Po (Fig. 1). The whole territory is flat, extensively covered by cereal crops (13.4%), rice fields (17.0%), and poplar *(Populus* sp.) plantations (25.3%). Woods (17.1%) are dominated by willows (*Salix cinerea*, *S. alba*), poplars (*Populus alba* and various hybrids) and alder (*Alnus glutinosa*), bordering an abandoned river meander and three naturalized artificial lakes (9.4%). Black locusts (*Robinia pseudoacacia*) are widespread along roads and man-made embankments. Gravely soils are covered with high herbaceous vegetation mainly formed by *Euphorbia cyparissias*, *Carex liparocarpos* and drought-resistant Graminaceae associated with black locust shrubs (9.5%). Flood-drifts are scattered near the river-bed (8.1%).

On the whole, trees and shrubs offering

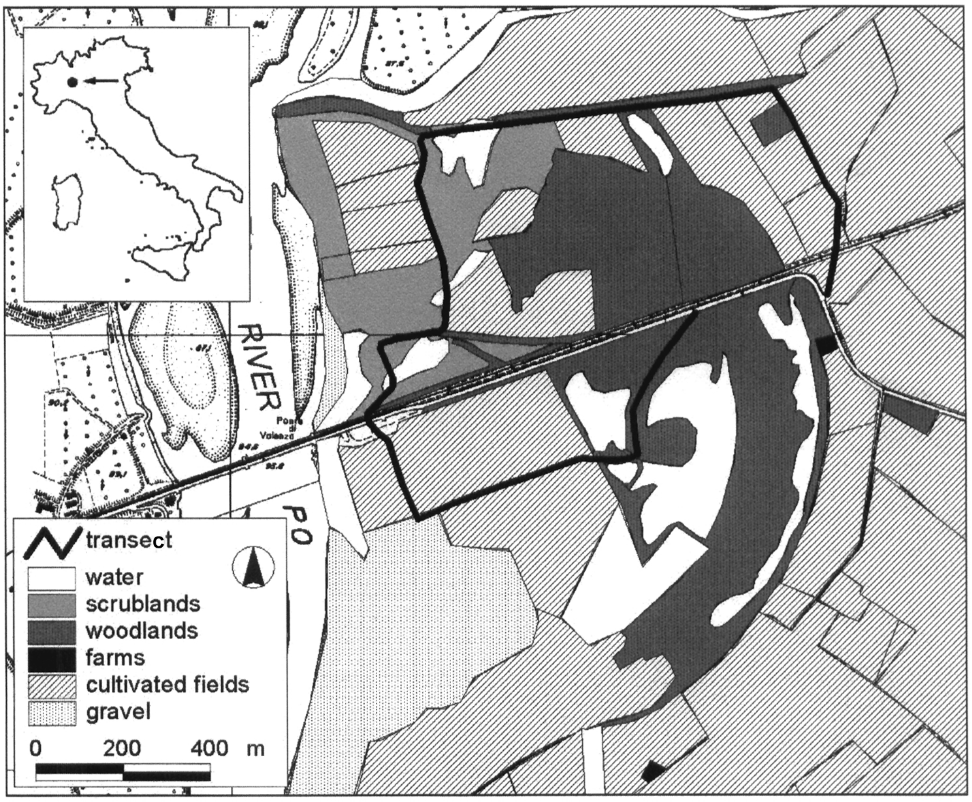

Figure 1 - Environmental characteristics of the study area. The bold line represents the transect selected for searching for fox faeces.

edible fruits are rare and include the following species: *Phytolacca americana*, *Crataegus monogyna*, *Rubus idaeus*, *Rubus* sp., *Cornus sanguinea*, *Ligustrum vulgare*, *Sambucus nigra* and *Viburnum lantana*.

The eastern cottontail, a lagomorph native to the American continent, was introduced to Piedmont region (SW of Turin) in the mid '60s (Meriggi, 2001; Spagnesi, 2002). During the '80s it expanded westward and at the end of the decade, its range included the low hills which rise north of the study area (Prigioni *et al*., 1992). In the mid '90s, mean cottontail densities (4.3 ind./km^2) were still quite lower than those of the hare *Lepus europaeus* (15.6 ind./km^2; Silvano *et al*., 2000). In 2004, along the River Po, about 9.5 km north-west of the study area, mean densities of 22.2 cottontails/km^2 (N = 3; SE = ± 5.6) and of 2.2 hares/km^2 (N = 3; SE = ± 2.1) were recorded (Bertolino S., pers. comm.), pointing out the opposite trend characterizing the two lagomorph populations in NW Italy. Nowadays, the species is present also in western and central Lombardy, rivers and channels representing the main way of dispersal.

In the study area the cottontail appeared in the mid '90s. At the end of 2000 there were more than 15 ind./km^2 (Zappia, 2001), patchily distributed according to the presence of vegetation cover. Prior to this colonization, the study area hosted a good population of wild rabbit *Oryctolagus cuniculus*, which became extinct at the beginning of the '90s because of successive epidemic diseases. Hares have always been sporadic, as a probable consequence of the scarcity of suitable habitats (1-2 ind./km^2; Gola L., pers. comm.).

METHODS

Faeces were collected monthly from June 1998 to February 2000 along a 4.1 km long transect crossing the main habitats of the study area (Fig. 1). A total of 115 faecal samples was stored in polythene bags and refrigerated until processing.

Scat analysis was performed according to Kruuk and Parish (1981) and Prigioni (1991b).

Samples were washed with three sieves of 1.5, 0.3 and 0.1 mm mesh and food remains were inspected to count or estimate the total numbers of each kind of food.

Mammal hairs were compared at 20x and 40x magnifications with the keys of Debrot *et al*. (1982), while reptiles and amphibians were detected by the keys of Di Palma and Massa (1981). Birds' feathers were identified with reference to Day (1966). The undigested remains of insects (wings, legs and cuticle parts) and wild or cultivated fruits (seeds) were identified using personal collections. Sediment remaining in the sieve with the smallest meshes was examined under a binocular microscope to detect earthworm chaetae.

Results were expressed as percent frequency of occurrence (F% = number of faecal samples containing a specific food items/total number of faecal samples x 100), percent relative frequency of occurrence (RF% = number of occurrences of an item/total number of items x 100), percent volume (V% = total estimated volume of each food item as ingested/number of faecal samples containing that item) and percent average volume (Vm% = total estimated volume of each food item as ingested/ total number of faecal samples).

Data were grouped annually, seasonally (winter: I-III; spring: IV-VI; summer: VII-IX; autumn: X-XII) and according to the cottontail reproductive period (II-IX *vs*. X-I; Meriggi, 2001) in order to investigate time-related variations in fox diet.

Trophic niche breadth was estimated by Levins' B index (Feinsinger *et al.*, 1981), using the proportions of occurrence (RF) of seven main food categories (fruits, insects, birds, insectivores, lagomorphs, rodents and carnivore carrions).

Trophic niche overlap between the red fox and the badger (Canova and Rosa, 1994; Balestrieri *et al.*, 2004) was assessed by Pianka's O index (1973):

$$O_{jk} = \frac{\sum_{i=1-n} p_{ij} p_{ik}}{\sqrt{\sum_{i=1-n} p_{ij}^2 \sum_{i=1-n} p_{ik}^2}}$$

where p_{ij} and p_{ik} are the proportions of occurrence of ten main food categories (fruits, maize, earthworms, insects, amphibians, birds, insectivores, lagomorphs, rodents and "other items") in the diet of the two species. According to Prigioni (1991b), the same ten items were used to compare B in 1988-89 and 1998-00 both for the fox and the badger (to this purpose, the raw frequency data of Canova and Rosa, 1994, were suitably re-arranged).

The raw frequency data for different seasons were compared using χ^2 tests. Because of the great number of repeated tests on related data, the sequential Bonferroni technique was used to determine the level of significance (Rice, 1989). The influence of the different types of prey on seasonal trophic niche breadth was analysed using a multiple regression, where B was the dependent variable and the proportions of occurrence (p_i) of each food item (after angular transformation: arcsin p^{-1}) were the predictors. The model was fitted with the predictors in decreasing order, according to the strength of correlation (Spearman's rank correlation test) between the dependent variable and each predictor, and following backward elimination of the non significant ones.

RESULTS

In the study area, the diet of foxes assumed a markedly carnivore feature. Mammals (F% = 93.9) formed the bulk of fox diet accounting for 87.7% in Vm% of the overall diet (Tab. 1 and Fig. 2). Among them, lagomorphs (Vm% = 68.0) represented by far the most exploited resource. Rodents (Vm% = 17.2) included mainly the bush-living common dormouse *Muscardinus avellanarius* and the water vole *Arvicola terrestris*. Birds represented a secondary food source (Vm% = 6.61) and included mainly small Passeriformes. The other food categories showed values below 5% in Vm%: amongst invertebrates, coleopteran larvae and imagoes were the most eaten prey, whilst fruits were eaten only occasionally (Vm% = 1.0).

Fox diet did not show marked seasonal or interannual variations; only the frequency of occurrence of the invertebrates varied, with a peak in summer (χ^2= 13.23; P=0.004). The frequency of lagomorph predation did not vary even when partitioning our data according to the cottontail reproductive period (1988/89: $F\%_{II-IX}$ = 75.0; $F\%_{X-I}$ = 92.8; 1999/00: $F\%_{II-IX}$ = 72.7; $F\%_{X-I}$ = 77.8). Lagomorphs represented the main food item in all seasons (Fig. 3).

Bird consumption was inversely related to that of rodents (Tab. 2).

In the analysis of the influence of prey type on seasonal diversity (B_{winter} = 0.30; B_{spring} = 0.55; B_{summer} = 0.44; B_{autumn} = 0.45), five variables - lagomorphs, fruits, insects, birds and rodents (in this order) – were included in the multiple-regression model (Spearman's rank correlation with B was negative for lagomorphs and rodents and positive for the other three variables, ranging between 0.40 and

Table 1- Overall fox diet in the study area; for the abbreviations see Methods; number of faecal samples: 115; number of items: 171.

FOOD ITEMS	N	F%	RF%	V%	Vm%
Fruits	8	7.0	4.7	15.0	1.0
Undetermined fruits	4	3.5	2.3	15.0	0.5
Phytolacca americana	1	0.9	0.6	20.0	0.2
Viburnum lantana	3	2.6	1.7	13.3	0.3
INSECTS	14	12.2	8.2	38.2	4.6
Orthoptera	2	1.7	1.2	20.0	0.3
Coleoptera	11	9.6	6.4	43.2	4.1
Hymenoptera	1	0.9	0.6	20.0	0.2
BIRDS	14	12.2	8.2	54.3	6.6
Anseriformes	2	1.7	1.2	65.0	1.1
Passeriformes	12	10.4	7.0	52.5	5.5
MAMMALS	108	93.9	63.2	93.4	87.7
Insectivores	6	5.2	3.5	34.2	1.8
Lagomorphs	87	75.6	50.9	89.9	68.0
Rodents	38	33.0	22.2	52.0	17.2
Myoxus glis	2	1.7	1.2	60.0	1.0
Muscardinus avellanarius	13	11.3	7.6	50.4	5.7
Clethrionomys glareolus	1	0.9	0.6	20.0	0.2
Microtus sp.	4	3.5	2.3	60.0	2.1
Arvicola terrestris	15	13.0	8.8	42.0	5.5
Rattus sp.	3	2.6	1.7	75.0	2.0
Apodemus sp.	2	1.7	1.2	82.5	1.4
Mus domesticus	1	0.9	0.6	20.0	0.2
Carnivore carrions (*Martes foina*)	1	0.9	0.6	80.0	0.7

1.00 (Tab. 2). From this initial model, only lagomorphs remained in the final model, which took the form B = -1.2431 arcsin $(p_{lagomorphs})^{-1}$ + 1.4155 (adjusted R^2 of the final model = 0.9907, F = 321.47, P = 0.0031).

Overall fox trophic niche breadth varied from B = 0.64 in 1988-89 to B = 0.31; comparing the relative frequencies of occurrence, prior to cottontail introduction, foxes ate significantly less lagomorphs ($F_{88/89}$% = 27.3; $F_{98/00}$ = 75.6; χ^2 = 26.33; P<0.001) and more maize ($F_{88/89}$% = 24.2; $F_{98/00}$ = 0.0; χ^2 = 29.47; P<0.001).

On the contrary, no significant variation occurred for the badger niche breadth (B = 0.54 in 1988-89; B = 0.49 in 1998-00), even if in 1988-89 badgers ate fewer earthworms ($F_{88/89}$% = 37.7; $F_{98/00}$ = 79.0; χ^2 = 25.82; P<0.001) and frogs ($F_{88/89}$% = 9.4; $F_{98/00}$ = 38.0; χ^2 = 13.98; P<0.001) and more *Prunus* sp. ($F_{88/89}$% = 32.1; $F_{98/00}$ = 4.0; χ^2 = 23.05; P<0.001).

As a consequence niche overlap between foxes and badgers decreased (from O = 0.59 to O = 0.13).

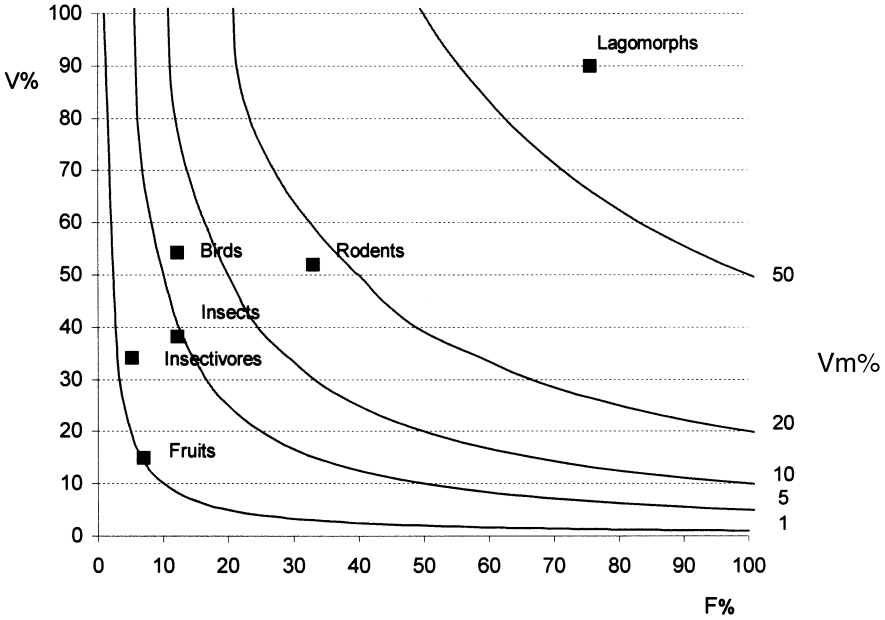

Figure 2 - Estimated volume (V%) of fox food categories, whenever eaten, vs. their frequency of occurrence (F%). Isopleths connect points of equal relative volume (Vm%) in the overall diet.

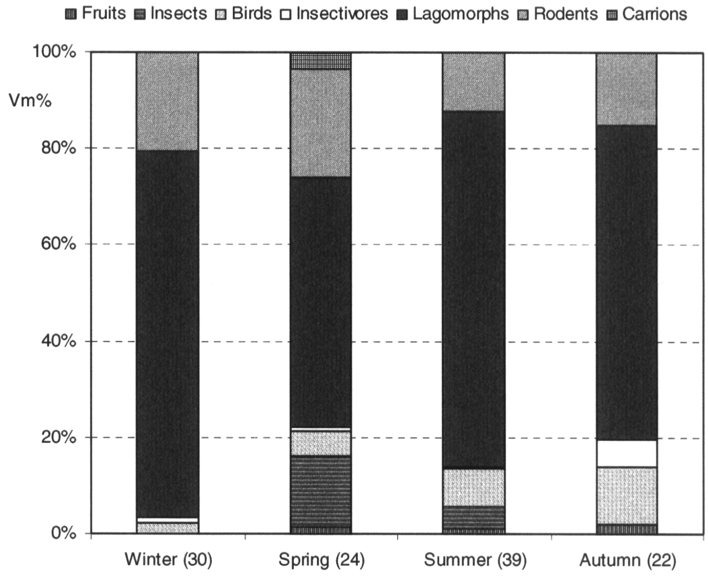

Figure 3 - Percent mean volume (Vm%) of main food items of foxes according to season; in brackets the number of faeces analysed for each season.

Table 2 - Correlation matrix between the seasonal trophic niche breadth (B) and the five food items included in the multiple-regression model (** = P<0.01; N=4, Spearman's rank correlation test).

	B	Lagomorphs	Fruits	Insects	Birds
Lagomorphs	-1**				
Fruits	0.80	-0.80			
Insects	0.63	-0.63	0.11		
Birds	0.40	-0.40	0.80	-0.11	
Rodents	-0.40	0.40	-0.80	0.11	-1**

DISCUSSION

In Italy, lagomorphs generally represent a secondary food resource for foxes, their frequency of occurrence ranging between 0.8% and 25.5% (Pozio and Gradoni, 1981; Pandolfi, 1983; Cantini, 1991; Prigioni and Tacchi, 1991; Prigioni, 1991a; Rosa *et al.*, 1991; Pandolfi and Bonacoscia, 1991; Prigioni *et al.*, 1995a and 1996; Cagnacci *et al.*, 2003).

The intensive predation on lagomorphs, which, according to local availability, can be almost entirely ascribed to the eastern cottontail, was the main feature of fox diet in the study area, suggesting the hypothesis of a certain degree of local specialization.

The prediction of this hypothesis is that i) diet is dominated by one or a small number of foods and that ii) the use of the main resource is relatively stable, i.e. seasonally invariant (Roper, 1994).

The first assumption was supported by the unusually high frequency of occurrence of the cottontail and by the sharply carnivore-bent trophic niche of the fox, which included only three other items (common dormice, water voles and Passeriformes) with mean percent volumes barely higher than 5%. With the exception of insect consumption, no significant time-related fluctuation in the use of main food resources emerged.

Nonetheless, multiple regression showed that diet diversity was inversely related to the use of lagomorphs, suggesting that the consumption of this key-source effectively decreases in spring, when lagomorph availability is lower and foxes rely to some extent on alternative resources, but without showing preferences for a specific prey (Revilla and Palomares, 2002).

From another point of view, diet breadth is considered a relative index of species or population specialization, those showing narrower diet breadths being considered more specialized (Begon and Mortimer, 1986; Futuyma and Moreno, 1988).

To compare different studies is always difficult if there is not access to raw frequency data (Prigioni, 1991b) and, knowledge of prey availability being generally limited, it is often impossible to say what mechanisms determine diet variation between two populations (Virgós *et al.*, 1999).

We had the opportunity of comparing

fox diet in the same small area immediately before and after cottontail introduction, pointing out the substantial cut down of fox trophic niche breadth associated to the exploitation of the alien prey. Surprisingly, despite the abundance of available rabbits, prior to cottontail introduction lagomorphs amounted to only 23% of the overall fox diet (Canova and Rosa, 1994).

Cottontails select field margins, hedgerows and stream or canal banks with dense permanent herbaceous and bushy cover (Vidus Rosin *et al*., in press). The few alternative prey that foxes relied on, occur or nest in the same habitat and foxes could have run up against them whilst looking for cottontails. From this point of view, the opportunistic use of secondary food items does not contradict the hypothesis of local specialization (Prugh, 2005).

Dealing with the distinction between specialist and generalist predators may cause confusion and disagreement (e.g. the dispute about the badger; Kruuk and Parish, 1981; Kruuk and de Kock, 1981; Martin *et al*., 1985; Roper, 1994; Fedriani *et al*., 1998; Revilla and Palomares, 2002). The discussion on the feeding behaviour of predators needs clarity upon the meaning of the terms generalist and specialist, both words being used with different definitions by evolutionary and behavioural ecologists (Revilla and Palomares, 2002; Bolnick *et al*., 2003). For the first, specialization is the result of morphological and physiological adaptations which entail the exploitation of a specific resource (i.e. *fundamental specialization*, *sensu* Hutchinson, 1957), whilst behavioural ecologists often call specialization the disproportionate use of a particular resource within a range of potentially available ones; this *realized specialization* may result from a variety of mechanisms provided for by optimal foraging theory (Krebs and Davies, 1993).

According to its models, dietary choices of predators depend on prey profitability, i.e. the net benefit assured by the consumption of each kind of prey. Predators should strongly select the most profitable prey and, eventually, they should add secondary prey items when the net profitability of the key source falls below a threshold (Charnov, 1976; Raymond *et al*., 1990).

Net benefit results from a trade off between many factors (energy content, abundance, distribution, defences and escape rates of different prey and morphology, physiology, handling behaviour, individual experience and preferences of predators; reviewed by Bolnick *et al*., 2003) which make the measure of profitability a hard task. Nevertheless, cottontails offer to predators a biomass which is about 35 times that of most voles and mice and their high reproductive performance should assure prey availability in spite of relatively intense predation (Vidus Rosin *et al*., in press).

With respect to wild rabbits, cottontails do not dig burrows and could be more exposed, particularly their juveniles, to fox predation. In these terms cottontails may be considered a highly profitable food source.

Foxes have no morphological or physiological adaptation to pursue a specific prey such as, for example, small mustelids (*Mustela erminea*, *M. nivalis*), which were sized and shaped for rodents predation in the Pliocene (King, 1983a). Nevertheless, keeping in mind Hutchinson's distinction, there is no contradiction in considering the feeding habits of the fox in the study area as the result of local (*realized*) specialization of a typical generalist carnivore, which, by virtue of its great adaptability, can also set itself at one extreme of the specialist-generalist continuum (on the other hand, in particular environmental conditions small mustelids are known to intensively use alternative "unusual" foods; King, 1983b; Martinoli *et al.*, 2001).

The isoleg theory (Rosenzweig, 1981) predicts that coexistence between competitors is favoured when one of the competing species is a specialist while the other acts as a generalist (Rosenzweig, 1987). Although in the River Po plain foxes and badgers usually coexist, the trophic niche of the latter includes mainly earthworms and maize, while foxes specialize on cottontails, so sharply reducing the overlap between their trophic niches, and minimizing competition for food, particularly in summer, when drought reduces earthworms availability forcing badgers to look for alternative sources of proteins (Balestrieri *et al.*, 2004).

The effects of fox specialization should be more pronounced with respect to niche overlap with stone martens (*Martes foina*), whose diet composition generally includes a higher variety of food sources (rodents, fruits, birds and invertebrates; Bertolino and Dore, 1995; Prigioni *et al.*, 1995b; Prigioni and Sommariva, 1997).

Further research is needed to identify the role played by fox feeding specialization in the general picture of interspecific competition for food among local predators.

Cottontails have been introduced for hunting, but they are rarely shot, hares being a more traditional and appreciated target. Our results suggest that foxes may represent a limiting factor for an alien species whose impact on native lagomorph populations is still unknown.

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