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RESEARCH

Macronutrient regulation by mesocarnivores in a rodent-poor area

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Abstract
Understanding how predators cope with variation in the availability of key prey species is pivotal for understanding the adaptive significance of their feeding strategies. In the framework of nutritional ecology, we explored the yearly diets and macronutrient (protein, lipids and carbohydrates) ratios of mesocarnivores (*Martes* spp. and red fox *Vulpes vulpes*), in a protected area (Mount Fenera Natural Park, NW Italy) where the availability of small mammals was unexpectedly low. Small mammal abundance was assessed by live trapping and hair-tube surveys, while diet analysis was based on faecal samples (117 and 104, respectively) collected along transects. All predators compensated for the low availability of their usual main source of protein by switching to alternative, nutritionally equivalent prey: arboreal rodents for martens and earthworms and wild boars for foxes. The higher-than-average use of these prey species indicated that the recorded diets were the result of the search for complementary nutritional resources. Accordingly, both martens and the red fox regulated their nutrient intakes so as to get close to their respective intake targets, suggesting that the nutritional content of food resources may play a major role in shaping the responses of predators to changes in prey abundance. Such dietary flexibility is likely a key factor enabling them to persist across a wide range of habitats, including those undergoing rapid man-driven modification.

Keywords Nutrient balancing · Prey switching · Dietary flexibility · Nutritional geometry

Introduction

Since the 1930s much effort has been devoted to understanding predator–prey relationships, which are considered to play a major role in determining the structure and dynamics of animal communities (Vermeij 1994; Abrams 2000; de Ruiter et al. 2005; Salo et al. 2010). Following the pioneering work of Solomon (1949) and Holling (1959), predator–prey relationships have been investigated in terms of functional and numerical responses, which describe, respectively, how either the rate of prey capture or predator abundance vary with prey abundance (Oaten and Murdoch 1975). Early studies focused on the impact of predation on small mammals, with the aim of unravelling the mechanisms driving the cyclic fluctuations of rodent abundance in northern Europe (e.g. Hansson 1987; Hanski et al. 1991; Boutin 1995; Korpimäki and Krebs 1996) as well as the effects of these cycles on several predators, including rodent-specialist birds (e.g. Korpimäki and Norrdahl 1989, 1991) and mammals (e.g. Korpimäki et al. 1991; O'Donoghue et al. 1997, 1998; Millon and Bretagnolle 2008).

Small mammals represent the main food resource for many coexisting mammalian, avian, and reptilian predators also in temperate forest ecosystems (Macdonald et al. 2000; Mukherjee et al. 2004; Sidorovich et al. 2008; Karell et al. 2009; Pavey and Nano 2013), where yearly variation in rodent abundance is mainly driven by mast production (Wolff 1996; McShea 2000; Elias et al. 2004, 2006; Falls et al. 2007), with bottom-up effects on several predators (King 2002; Jensen et al. 2012). Accordingly, declines in small mammal availability have been reported to affect both the abundance and diversity of higher trophic levels (Hayward et al. 1997; Salamolard et al. 2000; Butet and Leroux 2001; Sánchez-Zapata et al. 2003; Torre et al. 2024).

However, long-lived, generalist predators can respond to fluctuation in prey availability also by tuning their foraging

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strategies and switching to alternative prey species when the abundance, vulnerability, or net energy input of their main prey decrease (e.g., Korpimäki and Norrdahl 1989, 1991; O'Donoghue et al. 1998; Solonen and Karhunen 2002; Malo et al. 2004; Lourenco et al. 2015; Resano-Mayor et al. 2016; Ratajc et al. 2022). Following optimal foraging models (Křivan 1996), generalist predators should select their prey based on energetic profitability (selective diet choice; Stephens and Krebs 1986), and simulations suggest that they should switch to low-quality prey only when the density of the more profitable prey drops below a critical threshold (Fryxell and Lundberg 1994, 1997). In the last two decades, this dominant role of the energetic value of prey has been challenged by nutritional studies, which have demonstrated that in many species foraging is also guided by the need for including specific macronutrients and other chemicals in the diet (Kohl et al. 2015). Animals typically regulate the amounts and balance of macronutrients (i.e. protein, lipids, and carbohydrates) in their diets by either selecting nutritionally balanced foods or combining complementary foods to achieve a species-specific macronutrient intake target (Raubenheimer and Simpson 1997, 2003a, b). Macronutrients ratios have been recorded to affect both the feeding habits of predators (Mayntz et al. 2005; Schmidt et al. 2012; Razeng and Watson 2014) and their fitness (Montoro et al. 2020; Balestrieri et al. 2024).

Switching to food resources that are not nutritionally equivalent or complementary to the main prey (i.e., do not allow predators to achieve a balanced intake of macronutrients) may affect functional responses and have important dynamical implications (Abrams 1987). Notwithstanding, there is still little information on the nutritional effects of the decline or absence of preferred prey items and predators' appetites for nutritionally inadequate prey types (see, e.g., Pulliam 1980; Fryxell et al. 1994). How does dietary flexibility, that is the ability of exploiting alternative foods for surviving in unsuitable (less-than-optimal) food environments (sensu Raubenheimer and Simpson 2020), settle with the goal of achieving a balanced diet? When the profitability of a major suitable prey decreases, do predators actively select alternative complementary prey or simply switch to the most available option? A deeper insight into the feeding ecology of predators, including trophic interactions, can be obtained by a multidimensional approach, integrating the per cent contribution of food items to diets with their nutritional composition (Remonti et al. 2011; Machovsky-Capuska et al. 2016).

An opportunity to investigate how the nutritional content of available food resources drives the feeding of predators was offered us by the recording, through live-trapping and hair-tube surveys, of the unexpectedly low abundance and diversity of the small mammal community of a protected area of NW Italy (IT1120003). Mice and voles usually are a major source of protein for many coexisting predators (Sidorovich et al. 2008), including mesocarnivores (*Martes* spp., Gazzola and Balestrieri 2020; *Vulpes vulpes*, Balestrieri et al. 2024), which, in turn, usually show intake targets high in protein (Remonti et al. 2016) and have adapted to use protein as a primary source of both nitrogen and energy (Eisert 2011).

Defining the macronutrient intake of wild-living animals is not an easy task, particularly for mammalian carnivores; their mainly nocturnal and secretive lifestyles usually hinder the recording of their meals at large temporal and spatial scales. However, it has been demonstrated that scat-based, dietary studies assessing the volume or biomass of food items can be used to assess their macronutrient intakes at population level (Remonti et al. 2011). This indirect method has the potential to contribute substantially to our understanding of the nutritional niches of elusive animals and has been applied to several mammals (see Balestrieri et al. 2019), including martens and foxes. The intake targets of the pine- and stone marten have been estimated at 49% protein (P), 40% lipid (L), and 11% carbohydrate (C) and 44%P:37%L:19%C energy, respectively (Gazzola and Balestrieri 2020), while the protein energy intake of the red fox is as high as that of hypercarnivores (52%P:38.7%L:8.9%C; Balestrieri et al. 2024).

Referring to these benchmarks, we expected the low availability of mice and voles to elicit two alternative feeding strategies:

1) *nutrient balancing*, that is a variety of complementary food resources would allow mesocarnivores to defend their macronutrient balance by switching on alternative, nitrogen-rich sources ("reactive homeostasis" sensu Moore-Ede 1986);
2) *nutrient generalism*, that is the ability of tolerating a relatively wide range of nutrient intakes would enable mesocarnivores to dismiss the shortage of a major protein resource and rely on imbalanced foods.

Methods

Study area

Mount Fenera Natural Park (3378 ha) takes its name from the highest peak (899 m a.s.l.), which rises from the banks of the River Sesia (45°43'13" N, 8°16'35" E, NW Italy). The clover-shaped protected area can be split in three sectors (N, SW, SE; Fig. 1), differing in habitat characteristics: the SE sector includes the main steep, carbonatic relief, lying over a metamorphic basement (the "Serie dei Laghi"), the northern sector is mainly covered by chestnut (*Castanea sativa*) woods, which, in the SE sector, are interspersed with vineyards and small settlements.

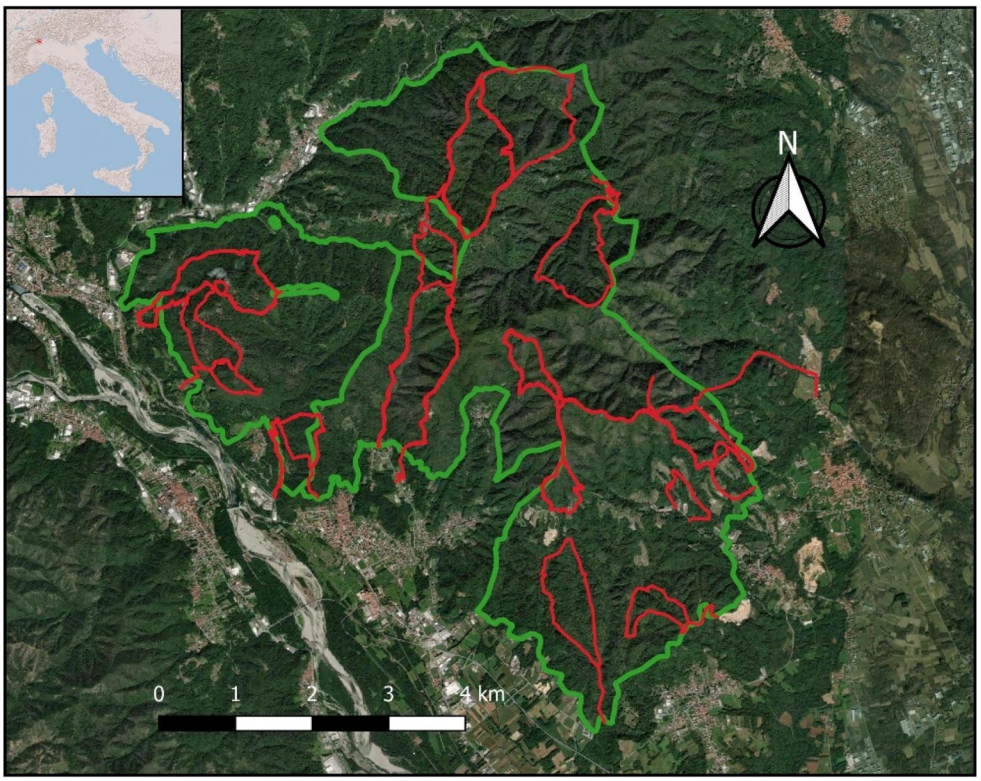

Fig. 1 Surveyed transects (red) within Mount Fenera Natural Park (green borders)

Following the recent Park Management Plan, the area hosts 16 Natura 2000 habitats, 804 native plant species, 107 birds and 35 mammals, out of which 19 are bats (Mosini et al. 2024). Based on camera-trapping carried out in 2023 (Balestrieri et al. 2023), the red fox, European badger (*Meles meles*) and stone marten (*Martes foina*) can be considered widespread throughout the protected area, while the pine marten (*Martes martes*) was recorded in only three (10%) of the 30 1-km^2 surveyed grid cells, suggesting its recent recolonization of the area.

Small mammal sampling

Between May and November 2023, the diversity of the small mammal community of the study area was assessed using either hair-tubes for glirids and squirrels or Sherman (23 × 7.5 × 9 cm; Sherman Co., USA) and cone-shaped pitfall traps (15 × 40 cm) for terrestrial rodents and insectivores, respectively.

Two types of 300 mm long hair-tubes were used, differing in diameter: 60 mm tubes, targeting European dormouse *Glis glis* and red squirrel *Sciurus vulgaris*, and 30 mm tubes for common dormouse *Muscardinus avellanarius*. The two hair-tubes were set close together on three linear transects, one for each of the three sectors of the Park (Fig. 1), with nine trapping sites spaced 30 m. The large hair-tubes were positioned on trunks or horizontal branches of trees (2–2.5 m above ground level), whereas small tubes were tied to shrubs (ca. 80 cm a.g.l.). Hazelnut cream was used as bait, and an adhesive strip was placed at each end of the tube to collect hairs. We checked the hair-tubes three times, every 10 days, for a total of 1620 trap-nights per season (4860 tn in total; no trapping was carried out in winter). The collected hairs were identified at the species level using a microscope (20× and 40× magnifications) to observe the scale pattern of the cuticle and medulla (De Marinis and Agnelli 1993).

As for hair-tubes, pairs of Sherman and pitfall traps were set close together along three linear transects containing 13 trap points each spaced 30 m apart. They were baited with a mixture of sunflower, maize and oat seeds, and bacon. Both traps were supplemented with a small piece of apple and cotton wool to ensure hydration and thermal insulation, respectively. Traps were activated for 4 consecutive nights and checked every morning, for a total of 312 trap-nights per season (936 tn in total). All trapped individuals were sexed, weighed, fur-clipped to avoid double-counts during the same session and released at the site of capture.

The use of a range of trapping devices aimed to minimise the effect of interspecific variation in the trap-proneness towards different trap types (Anthony et al. 2005; Janova et al. 2010). Trapping effort was consistent with previous studies (e.g.: Heroldová et al. 2007p. 8; Balestrieri et al. 2017).

All activities complied with the current Italian laws and were approved by the Park authorities.

Scat sampling

To assess the feeding habits of the red fox and the two martens (the badger was excluded because in the study area it mainly relies on invertebrates; Ferrarini 2023), faecal samples were collected between October 2023 and December 2024 along six transects (total length = 33.9 km; mean length ± SE = 4.2 ± 0.6 km), coinciding with paths and dirt roads evenly distributed within the protected area (Fig. 1). Surveys were not carried out during periods of high rainfall and postponed for at least one week following heavy rains.

Only the faeces which could be assigned with certainty to either *Martes* sp. or fox, based on morphological and size characteristics were selected. Previous faecal DNA-based studies showed that diameter allows to distinguish fox scats from martens' (< 10 and > 15 mm, respectively) with sufficient certainty (Remonti et al. 2022).

The adequacy of sample size was assessed using Simpson's diversity index (SI):

$$SI = 1 - \sum_{i=1}^{S} p_i^2$$

where p_i is the proportion of individual prey taxa in the *i*th category and *s* is the total number of prey taxa. A diversity curve was then calculated by increments of two samples randomly taken. SI was calculated for each sample, which was then resampled 1000 times by the bootstrap method to obtain the mean and 95% confidence interval. We determined the adequacy of sample size by whether an asymptote was reached in the diversity curve (Glen and Dickman 2006; Hass 2009). The SI increment curve was calculated from the incremental change in each mean SI with the addition of two more samples.

Diet analysis

Each sample was washed through a series of sieves with mesh size decreasing from 0.5 to 0.3 and 0.1 mm. The undigested remains in the 0.5 mm sieve were first examined under a stereomicroscope. Fruits were identified based on seed and epicarp morphology and were compared with a reference collection. Insects were classified at the order level by examining the morphology of their wings, legs, and/or parts of the exoskeleton. Birds were identified at the order level based on the shape of the nodes of the barbules (Dove and Koch 2011). The morphology and internal structure (medulla) of mammal hairs were examined using an optical microscope and the identification keys of Debrot et al. (1982) and Teerink (2003). When possible, the identification was confirmed by observing teeth morphology (Chaline 1974). The thinnest fraction was searched for earthworm chaetae, following Battisti et al. (2019). Briefly, the micro-fraction was diluted in a known volume (V) of water, from which three 1 ml samples were searched for chaetae; the total number of preyed earthworms (Ne) was assessed as:

$$Ne = (V \times mean\ number\ of\ chaetae \times 1.31)/400,$$

where 1.31 is a conversion coefficient accounting for the mean percentage of chaetae lost during the various steps of the analysis; and 400 corresponds to the average number of chaetae per earthworm in northern Italy (Battisti et al. 2019).

Data were expressed in terms of both frequency of occurrence and relative volume. For each faecal sample, percent volumes were estimated based on the number and mean weight of food items "as ingested", following the method proposed by Kruuk and Parish (1981). The minimum number of items of each food type was estimated from diagnostic hard parts (e.g. jawbones for mammals, seeds for fruit). Generally, this estimation is straightforward for small items, which are ingested as a whole, while for larger items, such as the carcasses of large mammals, the volume was estimated as 100% minus the estimated total percent volume of all other items. Results were expressed as:

- Percent frequency (F%): (number of faeces containing a particular food item/total number of faecal samples) × 100;
- Estimated percent volume (V%): total volume of each food item as ingested/number of faeces containing that item;

The product F% × V%/100 (mean percent volume, Vm%) outlines the proportional volume of each food item to the overall diet (Kruuk and Parish 1981).

Macronutrient calculation

For each food category, protein, carbohydrate, and lipid contents of major food items were obtained from the available scientific literature (Fidanza and Versiglioni 1989; Colli et al. 2006; Remonti et al. 2011; ESM 1). Following Remonti et al. (2011), for each faecal sample macronutrient percentages were calculated based on the relative volume of the recorded items and converted into metabolized energy using Atwater's coefficients. Macronutrient ratios were then plotted using right-angled mixture triangle plots (RMT; Raubenheimer 2011), which allow to show three components (protein, lipids, and carbohydrates) in a two-dimensional Cartesian space. Percent lipid and carbohydrate energy were plotted on the

two main axes (X and Y), while the protein component was displayed on the third "implicit" axis (Z). The recorded macronutrient ratios were then compared to the respective intake targets (Gazzola and Balestrieri 2020; Balestrieri et al. 2024), for which standard deviation error bars were calculated from available, original data.

Results

Small mammal community

Trapping highlighted the poor diversity of the small mammal community. Thirty-five wood mice (*Apodemus sylvaticus*) were identified, out of a total of 39 captures (0.04 ind/tn). Males were heavier (mean ± SE: ♀ 20.7 ± 1.9 g; ♂ 28.8 ± 1.9; U = 25.5, $P = 0.007$) and more abundant than females (sex-ratio: 1.3:1). Most mice were trapped in spring (71.4%), in the SE sector of the Park (21 vs. 7 each in the other two sectors; $\chi^2 = 16.8$, $P < 0.001$). Additionally, one lesser white-toothed shrew (*Crocidura suaveolens*) was trapped in the SE sector of the Park. Hair-tubes yielded 22 hair samples, belonging to three species: *Glis glis* ($N = 16$, 0.006 ind/tn), *Muscardinus avellanarius* ($N = 3$, 0.001 ind/tn) and *Apodemus* sp. ($N = 3$). Trapping success did not differ significantly among the three sectors. Red squirrels were not trapped but were widespread in the protected area (as assessed by direct observations and camera-trapping; Mosini et al. 2024).

Predators' feeding habits

Overall, 117 (winter: 28, spring: 37, summer: 25, autumn: 27) and 104 (winter: 30, spring: 19, summer: 19, autumn: 36) faecal samples were collected and analysed for martens and red fox, respectively. For each season, Simpson diversity index reached an asymptote, and the incremental change declined below 1% at ≈ 10 samples (ESM 2, 3), indicating that the sampling effort was adequate.

Wild fruits (Vm% = 17.2) - particularly *Prunus* sp. (Vm% = 8.8) -, and rodents (Vm% = 29.0) - mostly squirrels (Vm% = 11.9) and dormice (Vm% = 16.1) -, formed the bulk of martens' yearly diet (Fig. 2A). Significant seasonal variation in the frequency of occurrence of food resource was recorded for cultivated fruits ($\chi^2 = 12.60$, $P = 0.006$), earthworms ($\chi^2 = 17.49$, $P < 0.001$), lagomorphs ($\chi^2 = 13.67$, $P = 0.003$), as well as for squirrels ($\chi^2 = 12.68$, $P = 0.005$) and dormice ($\chi^2 = 16.17$, $P = 0.001$; Table 1). The resulting yearly macronutrient ratio was 43.9% for protein, 41.7% for lipids, and 14.4% for carbohydrates (Fig. 3A). In three out of the four seasons the protein intake was lower than the intake target, to be compensated for in spring. Overall, the recorded macronutrient intake did not differ from the target (Fig. 3A).

The red fox mostly relied on cultivated fruit (Vm% = 20.6) - particularly grapes (Vm% = 10.9) -, wild boars (Vm% = 16.5), and earthworms (Vm% = 16.5; Fig. 2B). Statistical analysis showed significant differences in the seasonal frequency of use of wild fruit ($\chi^2 = 30.5$, $P < 0.001$), particularly *Prunus* sp. ($\chi^2 = 35.0$, $P < 0.001$), and earthworms ($\chi^2 = 13.3$, $P = 0.004$; Table 2). Red fox macronutrient ratio was assessed as 49.3% protein, 33.0% lipid, and 17.7% carbohydrate energy (Fig. 3B). In summer, the protein intake was lower than the target, to be compensated for, as for martens, in spring. Overall, in the study area, fox diet was poorer in lipids and richer in carbohydrates with respect to the intake target (Fig. 3B).

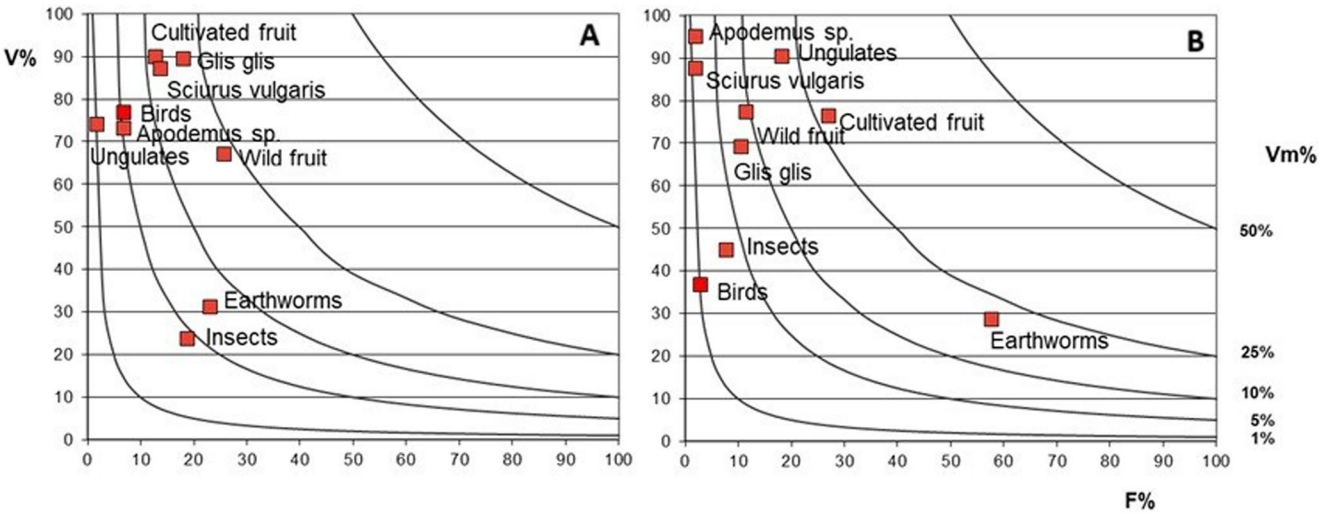

Fig. 2 Yearly diet of *Martes* spp. (**A**) and red fox (**B**) in the study area. Percent frequency of occurrence (F%) versus the estimated percent volume (V%) of 9 major food categories; isopleths connect points of equal percent mean volume (Vm%) in the diet

Table 1 Seasonal diet of *Martes* spp. in Mount Fenera Natural Park, expressed as both percent frequency of occurrence (F%) and percent volume (V%)

Food items	Spring		Summer		Autumn		Winter	
	F%	V%	F%	V%	F%	V%	F%	V%
Mushrooms	0.0	0.0	0.0	0.0	0.0	0.0	3.6	100.0
Fruit	35.1	66.2	64.0	70.9	48.1	76.5	42.9	82.1
undetermined	16.2	83.3	0.0	0.0	7.4	100.0	0.0	0.0
Rosaceae	18.9	51.4	48.0	61.6	14.8	31.3	14.3	97.5
Rosa sp.	2.7	30.0	0.0	0.0	11.1	10.0	7.1	95.0
Prunus sp.	16.2	55.0	36.0	77.7	0.0	0.0	0.0	0.0
Rubus sp.	0.0	0.0	12.0	13.3	0.0	0.0	0.0	0.0
Apples	0.0	0.0	0.0	0.0	3.7	95.0	0.0	0.0
Pears	0.0	0.0	0.0	0.0	0.0	0.0	7.1	100.0
Figs	0.0	0.0	4.0	100.0	3.7	100.0	0.0	0.0
Grapes	0.0	0.0	12.0	65.0	3.7	90.0	0.0	0.0
Kaki	0.0	0.0	0.0	0.0	18.5	96.0	3.6	90.0
Hedera elix	0.0	0.0	0.0	0.0	0.0	0.0	28.6	75.6
Sambucus sp.	0.0	0.0	4.0	100.0	0.0	0.0	0.0	0.0
Wild fruit	18.9	52.4	40.0	80.9	11.1	10.0	35.7	80.5
Cultivated fruit	0.0	0.0	16.0	73.8	29.6	95.6	10.7	96.7
Earthworms	45.9	24.3	4.0	1.0	14.8	52.5	17.9	44.0
Insects	29.7	14.4	8.0	30.0	18.5	13.0	14.3	60.0
undetermined	0.0	0.0	0.0	0.0	3.7	10.0	3.6	30.0
Orthoptera	0.0	0.0	4.0	40.0	7.4	12.5	0.0	0.0
Coleoptera	5.4	4.0	8.0	10.0	0.0	0.0	3.6	10.0
Hymenoptera	0.0	0.0	0.0	0.0	3.7	10.0	0.0	0.0
Larvae (Coleoptera)	21.6	18.4	0.0	0.0	3.7	20.0	7.1	100.0
Reptiles *(Lacerta* sp.)	8.1	71.7	0.0	0.0	0.0	0.0	0.0	0.0
Passeriformes	10.8	81.3	12.0	63.3	0.0	0.0	3.6	100.0
Mammals	51.4	86.2	52.0	85.8	51.9	95.0	39.3	95.9
Small rodents	16.2	79.2	44.0	92.3	44.4	96.3	32.1	83.3
undetermined	0.0	0.0	0.0	0.0	3.7	100.0	3.6	90.0
Apodemus sp.	10.8	78.8	4.0	50.0	11.1	73.3	0.0	0.0
Myodes glareolus	2.7	70.0	0.0	0.0	0.0	0.0	0.0	0.0
Sciurus vulgaris	2.7	90.0	4.0	95.0	22.2	91.7	28.6	82.5
Glis glis	8.1	83.3	44.0	88.2	18.5	92.0	7.1	100.0
Insectivores	5.4	77.5	0.0	0.0	0.0	0.0	7.1	27.5
Lagomorphs	16.2	95.7	0.0	0.0	0.0	0.0	0.0	0.0
Lepus sp.	10.8	95.5	0.0	0.0	0.0	0.0	0.0	0.0
Sylvilagus floridanus	8.1	92.3	0.0	0.0	0.0	0.0	0.0	0.0
Carrion	2.7	98.0	0.0	0.0	0.0	0.0	3.6	50.0
Sus scrofa	0.0	0.0	0.0	0.0	0.0	0.0	3.6	50.0
Capreolus capreolus	2.7	98.0	0.0	0.0	0.0	0.0	0.0	0.0

Discussion

Generalist predators can use a wide range of food resources, including fruit, invertebrates, birds and mammals. These foods largely vary in their macronutrient composition: considering only those recorded for the mesocarnivores occurring in the study area, protein content varied from 0.3% to 21.8%, while carbohydrates ranged between ≈0 and 19.2% and average lipid content varied from ≈0 to nearly 13.3%. Such diversity in the nutrient content of available foods implies that predators have separate appetites for different nutrients (Raubenheimer and Simpson 2020) and any change in prey availability may affect the achievement of their macronutrient intake target.

We expected the low availability of small mammals to elicit alternative feeding responses, either *nutrient balancing*, through the exploitation of complementary foods, or *nutrient generalism*, meaning that the species were able to tolerate a range of diet compositions and override the lack of their main nutrient source. Although being considered generalist predators, both martens and the red fox tended to regulate their nutrient intakes so as to get close to their respective intake

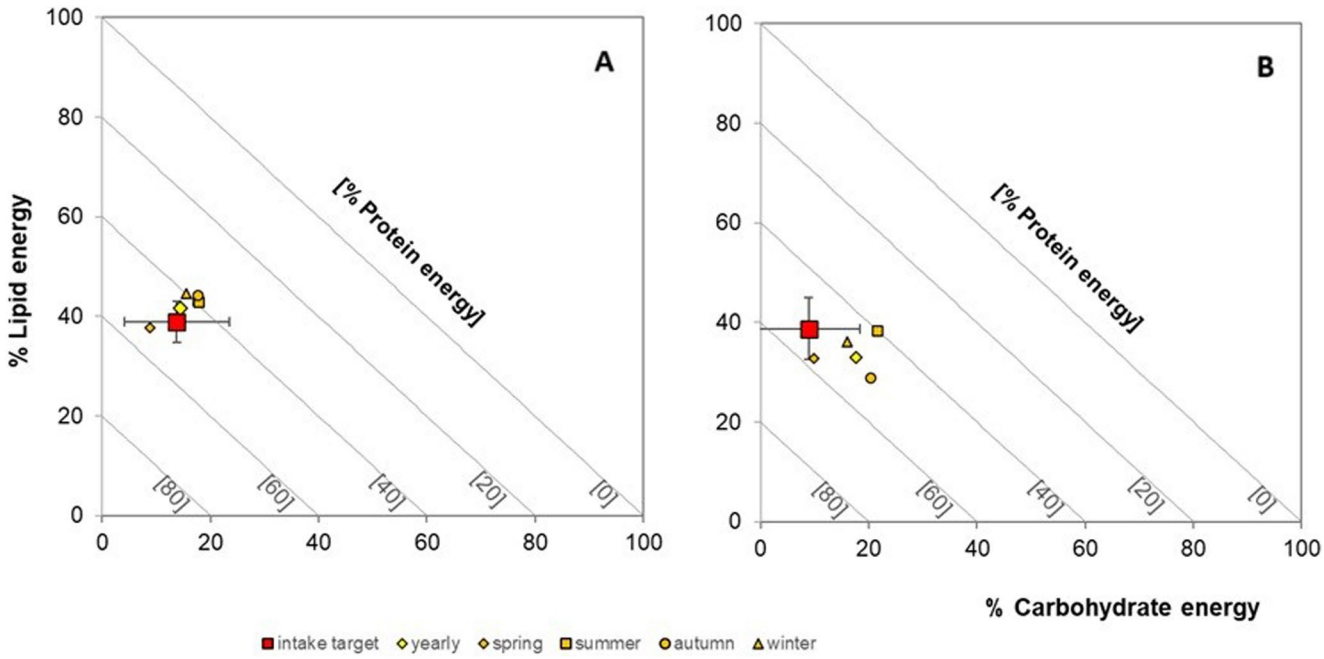

Fig. 3 Right-angled mixture triangle plot showing seasonal and yearly macronutrient ratios for *Martes* spp. (**A**) and red fox (**B**) in the study area with respect to the taxa's intake targets (47.3%P:38.9%L:13.8%C and 52%P:38.7%L:8.9%C, respectively; with standard deviation error bars). Protein percentage, which is represented by diagonal isolines, decreases with distance from the origin

targets. The protein energy intake of martens coincided with the target for the stone marten, consistently with its higher relative abundance in the study area. Red fox diet was richer in carbohydrates than the average, a pattern which, at European range-level, has been recorded for populations living in rural and urban habitats (Balestrieri et al. 2024), and attributed to the disproportionate availability of cultivated fruit. Accordingly, in the study area widespread vineyards and orchards provided for the major food resource in fox diet.

Balanced macronutrient intakes were gained by pursuing alternative prey, namely arboreal rodents for the two mustelids and earthworms and wild boars for the red fox, offering similar nutrient compositions: the average values for the quantity of macronutrients and water in dormice (Cvrtila et al. 2004) and squirrels (USDA 2018) meat are comparable with the chemical composition of the meat of wild boars, while earthworms contain more water, but, as shown by European badgers, are a valuable source of protein (Balestrieri et al. 2019). Wild boars were widespread in the study area (on average, 190 boars culled every year; Mosini et al. 2024), while earthworm abundance was rather low in wooded areas (mean ± SD = 27.2 ± 7.5 ind/m^2; Balestrieri et al. 2026) with respect to average values for European forests (90 ind/m^2; De Wandeler et al. 2016), to increase in wood-pasture ecotones (243.2 ± 26.6 ind/m^2).

While martens have been reported to impact introduced grey squirrels (*Sciurus carolinensis*; Sheehy et al. 2018), the contribution of red squirrels to marten diet is usually low or negligible, with frequency of occurrences ranging between 0 and 19% (on average: 3.7%; Twining et al. 2020), voles being by far the preferred prey whenever available (De Marinis and Masseti 1995; Paterson and Skipper 2008; Balestrieri 2024). In terms of percent mean volume, the importance of squirrels and dormice in marten diet is even lower, averaging 1.3 ± 0.5% and 1.5 ± 0.6% (mean Vm% ± SE as assessed using data in Gazzola and Balestrieri 2020). Consistently with our results, the shift from voles to squirrels in pine marten diet has been reported to depend on their relative abundance (Lindstrom 1989).

Throughout Europe, earthworms are preyed on by several mammals, mostly belonging to the order Insectivora (Macdonald 1983). In the British Isles, foxes actively search for earthworms when microclimatic conditions increase their availability (Macdonald 1980). However, in general the contribution of this resource to fox diet is low, averaging 3 ± 1.5% (mean Vm% ± SE, as calculated from papers reviewed in Balestrieri et al. 2024). On the other hand, ungulate carrion are eaten by foxes whenever available, but they usually represent a major meat source in mountainous habitats (Borkowski 1994; Cagnacci et al. 2003; Balestrieri et al. 2024). Carrion can be considered a clumped food resource with unpredictable dispersion (Lovari et al. 1994); in the study area, where wild boars are routinely culled since the early 1990 s (Monaco et al. 2010; Mosini et al. 2024), ungulates probably consisted of shot and unrecovered adults and starved juveniles.

Table 2 Seasonal diet of the red fox in Mount Fenera Natural Park, expressed as both percent frequency of occurrence (F%) and percent volume (V%)

Food items	Spring		Summer		Autumn		Winter	
	F%	V%	F%	V%	F%	V%	F%	V%
Mushrooms	15.8	45.0	0.0	0.0	2.8	40.0	3.3	20.0
Fruit	15.8	88.3	68.4	70.8	44.4	70.6	50.0	71.0
undetermined	5.3	90.0	0.0	0.0	8.3	8.3	6.7	92.5
Rosaceae	10.5	87.5	47.4	76.7	13.9	65.0	26.7	72.5
Sorbus sp.	0.0	0.0	0.0	0.0	2.8	50.0	0.0	0.0
Prunus sp.	10.5	87.5	47.4	76.7	0.0	0.0	0.0	0.0
Rubus sp.	0.0	0.0	0.0	0.0	2.8	65.0	6.7	7.5
Apples	0.0	0.0	0.0	0.0	5.6	100.0	13.3	95.0
Pears	0.0	0.0	0.0	0.0	0.0	0.0	6.7	92.5
Figs	5.3	50.0	0.0	0.0	0.0	0.0	0.0	0.0
Grapes	0.0	0.0	21.1	57.5	25.0	77.2	13.3	51.3
Kaki	0.0	0.0	0.0	0.0	2.8	100.0	3.3	95.0
Maize	0.0	0.0	0.0	0.0	13.9	38.0	0.0	0.0
Wild fruit	10.5	88.5	47.4	77.7	2.8	50.0	0.0	0.0
Cultivated fruit	5.3	50.0	21.1	57.5	33.3	82.9	36.7	78.6
Earthworms	68.4	36.0	26.3	24.0	52.8	30.4	76.7	23.8
Insects	5.3	50.0	10.5	55.0	8.3	30.0	6.7	55.0
undetermined	0.0	0.0	0.0	0.0	0.0	0.0	3.3	10.0
Orthoptera	0.0	0.0	5.3	10.0	2.8	10.0	0.0	0.0
Coleoptera	5.3	60.0	5.3	100.0	2.8	20.0	0.0	0.0
Larvae (Coleoptera)	0.0	0.0	0.0	0.0	5.6	30.0	3.3	100.0
Passeriformes	10.5	30.0	5.3	50.0	0.0	0.0	0.0	0.0
Mammals	47.4	84.7	42.1	87.5	38.9	90.5	46.7	89.9
Small rodents	15.8	45.0	31.6	93.3	13.9	64.0	20.0	88.3
undetermined	5.3	30.0	0.0	0.0	2.8	30.0	0.0	0.0
Apodemus sp.	0.0	0.0	5.3	100.0	2.8	90.0	0.0	0.0
Myodes glareolus	0.0	0.0	0.0	0.0	5.6	40.0	0.0	0.0
Rattus sp.	0.0	0.0	0.0	0.0	0.0	0.0	6.7	87.5
Sciurus vulgaris	10.5	52.5	10.5	80.0	8.3	46.7	13.3	88.8
Glis glis	5.3	100.0	21.1	87.5	2.8	80.0	6.7	77.5
Insectivores	5.3	95.0	0.0	0.0	0.0	0.0	0.0	0.0
Lagomorphs	5.3	100.0	0.0	0.0	5.6	62.5	0.0	0.0
Lepus sp.	5.3	100.0	0.0	0.0	5.6	62.5	0.0	0.0
Carrion	21.1	83.0	5.3	90.0	22.2	90.3	20.0	95.5
Sus scrofa	15.8	77.3	5.3	90.0	19.4	90.3	16.7	95.6
Capreolus capreolus	5.3	100.0	0.0	0.0	2.8	90.0	3.3	95.0

The higher-than-average use of these prey species indicates that the recorded diets were the result of the search for complementary-to-terrestrial rodent nutritional resources. Accordingly, mice and voles accounted for less than 5% of the overall diet of all mesocarnivores, a figure which both was consistent with and confirmed the lower-than-expected richness of the small mammal community (2 vs. 4–7 species of terrestrial rodents and insectivores; Canova and Fasola 1991; Debernardi et al. 1997). The absence of the bank vole *Myodes* (*Clethrionomys*) *glareolus* was quite surprising, as it is usually abundant in forested habitats (Mazurkiewicz 1994; Kamenišťák et al. 2020) and was the dominant species in local fossil records (MIS5; Berto et al. 2016). Interference competition of widespread wild boars, which have been recorded to eat hoards collected by small mammals when the above-ground availability of acorns is low (Focardi et al. 2000), may explain both the low richness and abundance of the community and dominance of habitat-generalist wood mice, which are less affected than bank voles by rooting (Selva et al. 2012; Fagiani et al. 2014). Arboreal rodents may be less affected by competition for food with wild boars: dormice hibernate and can suppress their activity and reproduction in mast-poor years (Krystufek 2010), while food availability is not a major constraint on reproduction for squirrels (Hayssen 2008).

Predator–prey relationships are dynamic and behavioral diet shifts, which occur over short time scales may have a major influence on community dynamics and ecosystem

functions (Kondoh 2003; de Ruiter et al. 2005). Our results suggest that the nutritional content of available resources may play a major role in shaping the responses of predators to changes in prey abundance.

The outcomes of the interaction of organisms with their food environment (i.e.: all the abiotic and biotic factors that influence nutrition; Raubenheimer and Simpson 2020) have ecological implications, affecting fitness and, ultimately, population dynamics. Notwithstanding, nutritional ecology usually focuses on individual-level traits, by keeping captive animals on controlled diets (i.e.: foods with known macronutrient compositions) and recording their macronutrient intakes and effects of unbalanced diets on metabolic health (e.g.: Solon-Biet et al. 2014) and demographic traits (e.g.: Le Couteur et al. 2016). While measuring macronutrient ratios with great precision, controlled diets do not allow us to know how animals cope with actual environmental conditions and temporal or local variation in food (nutrient) availability and appreciate inter-population variation in intake targets. Despite being more time consuming and less accurate, scat-based, diet analysis enables to investigate the nutritional requirements of wild-living, elusive animals and how they manage to satisfy them under challenging conditions in the real world (see Machovsky-Capuska et al. 2016). Using a population-level approach we demonstrated that feeding flexibility allowed mesocarnivores to balance their macronutrient intake despite the local shortage of a major food resource. This ability probably plays a major role in making them able to spread in a wide variety of habitats and cope with ongoing, man-driven environmental changes.

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Declarations

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