

Feeding ecology of the red fox in the Soana Valley, Gran Paradiso National Park

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ABSTRACT

Red fox (*Vulpes vulpes*) feeding ecology has been studied frequently in Europe, and in particular in the alpine region. However, in few areas this subject has been thoroughly investigated as in the Gran Paradiso National Park (NW Italy), where the food habits of this generalist species have been repeatedly analyzed since the 1950s, giving today the opportunity of identifying long-term variations in red fox diet. After the last report on this carnivore's diet in the GPNP (1990s), the protected area has been colonized by new potential prey (roe deer, red deer and wild boar) and by a new possible competitor for food resources (wolf). Therefore, we tried to evaluate red fox ecological responses to these colonization processes, focusing in particular on its feeding behaviour. We investigated the food habits of this species in the Soana Valley, the sector of the GPNP where the occurrence of roe deer, red deer, wild boar and wolf proved to be more stable and abundant in the past few years, comparing our results with those reported in the previous studies carried out in the park. Ungulates, and in particular alpine chamois, were the main food resources in the study area, followed by fruits, insects and small-mammals. Diet composition and trophic niche breadth significantly changed during the seasons, mainly due to the effects of snow cover on prey availability. The comparison with previous studies carried out in the GPNP highlighted the capability of the red fox to rapidly adapt to use new available prey (especially roe deer), while the ecological interactions with the wolf are still unclear, needing further research.

Key words: *Vulpes vulpes*, diet, niche breadth, temporal variations, ungulates, NW Alps.

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1 INTRODUCTION

Diet analysis is a major issue for research in the ecology of mammalian predators, especially because food availability is considered to influence their population size (Lindström, 1989), social organization (McDonald, 1983; Kowalczyk et al., 2000) and inter-specific relationships (Schoener, 1974; Dalén et al., 2004). Accordingly, carnivores' feeding ecology has been thoroughly analyzed in the last century, providing a large amount of scientific literature concerning a wide range of ecosystems. In this context, the diet composition of the red fox (*Vulpes vulpes*), one of the most widely distributed predators in the world, has been frequently studied in Europe. This species is largely known as a generalist predator, showing a clear opportunistic behaviour that enables its occurrence in a wide range of habitats (e.g. Richards, 1977; Reynolds, 1979; Calisti et al., 1990; Jędrzejewski and Jędrzejewska, 1992; Borkowski, 1994; Cavallini and Volpi, 1996; Leckie et al., 1998; Contesse et al., 2004; Balestrieri et al., 2005; Dell'Arte et al., 2007; Hartová-Nentvichová et al., 2010; Kidawa and Kowalczyk, 2011; Needham et al., 2014), also including alpine ecosystems (Leinati et al., 1960; Storch and Kleine, 1991; Lucherini and Crema, 1994; Cagnacci et al., 2003; Russell and Storch, 2004; Prigioni et al., 2008; Balestrieri et al., 2011).

Notwithstanding these studies, in few alpine areas has red fox ecology been thoroughly investigated as in the Gran Paradiso National Park (NW Italy; hereafter GPNP). Indeed, in GPNP this species has been studied since the 1950s, providing detailed information on both food habits (Leinati et al., 1960; Cagnacci et al., 2003) and habitat preferences (Boitani et al., 1984; Cagnacci et al., 2004). In particular, red fox feeding ecology has been analyzed repeatedly in the past sixty years within the park (Leinati et al., 1960; Cagnacci et al., 2003), giving the rare opportunity to detect possible variations in this carnivore's diet on a long temporal scale.

In the past two decades, the changes occurring in the composition of the local mammal community in the GPNP may have influenced both the feeding behaviour and the diet of the red fox. First, new ungulate species, namely roe deer (*Capreolus capreolus*), red deer (*Cervus elaphus*) and wild boar (*Sus scrofa*), have recently expanded in the protected area, as a consequence of restocking programmes carried out in the surroundings of the park for hunting purposes. This process could have increased the diversity of available prey, for instance in winter, when ungulate carcasses represent an important food resource (Cagnacci et al., 2003), and in spring, when roe deer fawns are exposed to red fox predation (Panzacchi et al., 2008).

In addition, during the past ten years, the GPNP has been also colonized by a new potential ecological competitor for the red fox: the wolf (*Canis lupus*), occurring with at least one stable pack in the study area. This species, formerly extinct in the western Alps, progressively re-expanded northwards through the Apennines, coming from surviving populations in central Italy (Boitani, 1992; Valière et al., 2003; Fabbri et al., 2007). Thanks to a more effective legal protection and substantial changes in land-use in mountain areas (e.g. decrease of human activities and

forests expansion), today the wolf is able to play again the key role of top predator in alpine ecosystems, likely overlapping in part its trophic niche with the red fox (Patalano and Lovari, 1993; Bassi et al., 2012).

In this paper, we aim to evaluate the ecological responses of the red fox to the colonization processes mentioned above, focusing in particular on its diet in the Soana Valley, the sector of the GPNP where the occurrence of roe deer, red deer, wild boar and wolf has proved to be more stable and abundant in recent years. Therefore, we identified the main food resources exploited by the red fox in this study area, also analyzing seasonal variations in its diet composition. Furthermore, we compared our results with those obtained in the previous studies carried out in the park, in order to detect possible changes in red fox feeding ecology due to the availability of new potential prey and/or to the occurrence of a new possible competitor.

2 MATERIAL AND METHODS

2.1 Study area

The GPNP is undoubtedly one of the better preserved natural areas in the Alps, covering about 710 km² on a mountain range reaching 4,061 m a.s.l. Five main valleys originate from the slopes of the Gran Paradiso massif, among which the Soana Valley represents the easternmost sector of the protected area. This portion of the park is included in the study area, overall extended on 152.6 km² across a large diversity of habitats along the altitudinal gradient, ranging from deciduous (cover ~10%; mainly beech) and coniferous (cover ~15%; mainly larch) forests to alpine shrublands (cover ~10%; mainly green alder and alpine rose) and grasslands (cover ~30%), siliceous scree, cliffs and glaciers (overall ~35% in cover).

Besides roe deer, red deer and wild boar, alpine chamois (*Rupicapra rupicapra*) and alpine ibex (*Capra ibex*) represent potential food resources for the red fox in the study area, together with hares (*Lepus europaeus* and *Lepus timidus*), alpine marmots (*Marmota marmota*) and several small mammal species. Alpine grouses (*Tetrao tetrix* and *Lagopus muta*) and rock partridge (*Alectoris graeca*) also occur in the Soana Valley, representing more potential prey for this carnivore. In addition, further food resources may be available near human settlements, e.g. poultry, sheep or garbage.

2.2 Data collection and faecal analysis

Scats were collected along five transects, coinciding with available paths and covering a total length of about 45 km. These transects were traced across a wide range of habitats, between 850 m and 2,350 m a.s.l., investigating all the available biotopes for the red fox in the Soana Valley. Scats were collected fortnightly, from July 2014 to July 2015. In the laboratory, each scat was washed through three sieves, with progressively smaller meshes (1.00 → 0.54 → 0.21 mm), in order to enhance the detection of both large (e.g. hairs, bones, seeds) and small (earthworm

chaetae) food remains (Battisti et al., 2019). Afterwards, we inspected the three resulting sub-samples under a stereo-microscope, sorting the different kinds of remains and estimating their relative volume within each faecal sample (following Kruuk and Parish, 1981). The sediment held in the thinnest sieve mesh was also examined at 35× magnification.

The identification of food remains was performed using different methods. Insect remains, seeds and reptile scales were compared with reference collections, while mammalian hairs and bird feathers were recognized by means of a 400× microscope and identification guides. Concerning feathers, we referred to Day (1966), Robertson et al. (1984) and Dove and Koch (2011), even if a large amount of samples was too damaged during the digestion process to be identified to order level. Hairs were recognized following Debrot (1982), Teerink (1991), De Marinis and Agnelli (1993) and De Marinis and Asprea (2006). The ability in hair identification of each operator was assessed through a *blind test* procedure (error threshold: 5%). In addition, several faecal samples also contained small mammal teeth, which were useful in achieving species identification, following the keys provided by Erome and Aulagnier (1982) and Rolland (2008).

In order to study the relationship between red fox diet composition and climatic variables, namely temperature, rainfall, and snow cover, we downloaded meteorological data from the ARPA Piemonte Climatic Database (www.arpa.piemonte.it), considering the Piamprato weather station (1,560 m a.s.l.) as representative of the whole study area.

2.3 Data analysis

Red fox diet was assessed in terms of both frequency and volume: absolute percent frequency of occurrence (%OC: number of occurrences of each food category/total number of faeces × 100) and percent volume (%V: estimated volume of each food category/total estimated volume × 100) (Kruuk and Parish, 1981; Cagnacci et al., 2003). In addition, in order to produce a graphical representation of red fox diet comparable with previous works (e.g. Kruuk and Parish, 1981; Cagnacci et al., 2003), the mean volume per scat (total estimated volume of each food category/number of occurrences × 100) was calculated as an additional parameter. Data were grouped according to three different time periods: (1) the whole year; (2) the cold season (from November to April) and the warm season (from May to October); and (3) each sampling session. Trophic niche breadth was calculated by the standardized Levins index (B_{sta}) (Colwell and Futuyma, 1971), using both frequency and volume row data. B_{sta} varies between 0 (minimum niche breadth) and 1 (maximum niche breadth), providing a useful summarizing measure about the variety of food items exploited by the red fox in each sampling session.

In order to identify which climatic parameters drive seasonal variations in red fox diet, we applied four binomial Generalized Linear Models (GLMs), including the %OC and %V of the four main food categories occurring in red fox diet

(ungulates, small mammals, insects and fruits) as dependent variables. In this case, the binomial distribution was selected due to the occurrence of proportional data (Zuur et al., 2009). Moreover, the effects of climatic conditions on seasonal variations in red fox niche breadth (B_{sta}) were evaluated through a further Linear Model (LM), with temperature, rainfall (continuous variables) and presence/absence of snow cover as fixed factors. Before running the models, all dependent and independent factors were tested for collinearity by means of a Pearson's correlation test (comparisons among continuous variables) and a non-parametric Mann-Whitney U-test (comparison between continuous and categorical variables) in order to avoid possible results misinterpretations. Model assumptions were verified by plotting the residuals versus fitted values and each covariate, following the recommendations provided by Zuur et al. (2009).

Finally, a LOESS regression was drawn to enhance the graphical representation of seasonal variations in red fox diet, especially concerning the four main food categories and niche breadth. All statistical analyses were performed using the R software (version 3.4.0) (R Core Team, 2017).

3 RESULTS

3.1 Diet composition

In this research, we carried out 26 sampling sessions, collecting overall 1,014 red fox scats. Considering the whole year (Figure 1A; Appendix 1), ungulates were a primary food resource for red foxes in the study area (%V: 31.21; %OC: 50.00), followed by fruits (%V: 15.46; %OC: 34.71), insects (%V: 13.63; %OC: 55.03) and small mammals (%V: 13.30; %OC: 37.67).

Among ungulates, we observed a clear predominance of the alpine chamois (*Rupicapra rupicapra*; %V: 22.35; %OC: 36.19), while roe deer (*Capreolus capreolus*; %V: 5.19; %OC: 9.57), wild boar (*Sus scrofa*; %V: 1.46; %OC: 3.35), alpine ibex (*Capra ibex*; %V: 0.48; %OC: 0.99) and red deer (*Cervus elaphus*; %V: traces; %OC: 0.10) were less consumed. Concerning other mammals, small rodents (%V: 11.26; %OC: 31.76) constituted another important prey category, while other mammalian species (such as alpine marmots, hares, etc.) were little represented in the whole diet (%V: 2.56; %OC: 4.04).

Whitebeam fruits (*Sorbus aria*; %V: 4.28; %OC: 7.69) and wild cherries (*Prunus avium*; %V: 2.57; %OC: 4.54) formed the bulk of fruit biomass in red fox diet, while raspberries and blackberries (*Rubus* sp.; %V: 1.63; %OC: 8.19), together with wild strawberries (*Fragaria vesca*; %V: 0.66; %OC: 6.31), frequently occurred within faecal samples, but always with small volumes.

Insects (%V: 13.63; %OC: 55.03) consisted mostly of coleopterans (%V: 7.89; %OC: 41.22), being mainly represented by ground beetles and dung beetles. Among other invertebrates, earthworms were the most consumed prey (%V: 0.82; %OC: 43.89), despite the limited relative volume in the overall diet.

Other minor food categories in red fox diet were birds (%V: 0.87; %OC: 6.31), reptiles (%V: 0.64; %OC: 6.02) and garbage (%V: 0.54; %OC: 2.47).

3.2 Seasonal variations

According with Pearson's correlation test, we noticed a significant collinearity between the absolute percent frequency of occurrence (%OC) and the percent volume (%V) for all the considered food categories (ungulates: $r = 0.96$, $P < 0.001$; fruits: $r = 0.94$, $P < 0.001$; insects: $r = 0.95$, $P < 0.001$; small mammals: $r = 0.80$, $P < 0.001$). Among fixed factors, a significant intercorrelation was found between temperature and presence/absence of snow cover (non-parametric Mann-Whitney U-test: $U = 6$, $P < 0.001$), while the rainfall-snow cover (non-parametric Mann-Whitney U-test: $U = 72$, $P = 0.560$) and the temperature-rainfall (Pearson's correlation test: $r = 0.13$, $P = 0.516$) comparisons showed no collinearity. Therefore,

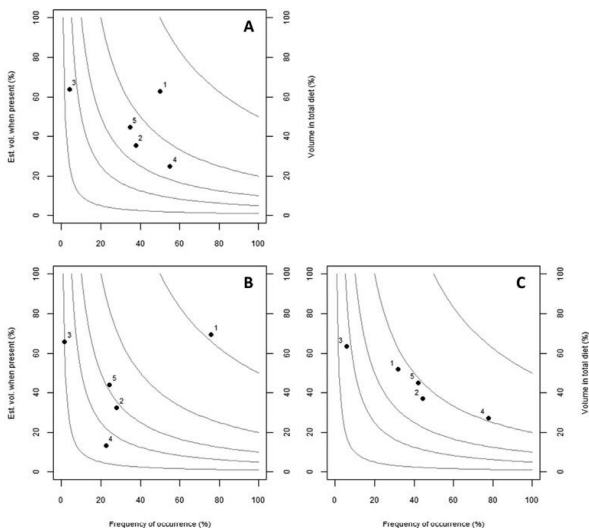


Figure 1 Graphical representation of the relationship between the mean volume per scat of each food category (Est. vol. when present) and its frequency of occurrence (%OC) in red fox diet during (A) the whole year, (B) the cold season and (C) the warm season. Isopleths connect the points with equal estimated volume in its overall diet (%V). In these graphics, only the main food categories in terms of %V are reported, namely '1' ungulates, '2' small-mammals, '3' other mammals, '4' insects, and '5' fruits.

only %OC was included in the GLMs as dependent variable, producing absolutely comparable results with those concerning %V. In addition, temperature was excluded from the final models, in order to avoid possible results misinterpretations due to its collinearity with snow cover.

Red fox food habits in the Soana Valley clearly differed between the cold and warm seasons (Figure 1B–C; Figure 2). During winter, ungulates formed the bulk of the diet (mostly alpine chamois), while small mammals, insects and fruits were the main food resources in summer. Consequently, the trophic niche was narrower during the cold season, as reported by the Levins index values (Figure 2E). Snow proved to be the main climatic factor affecting red fox diet in the study area

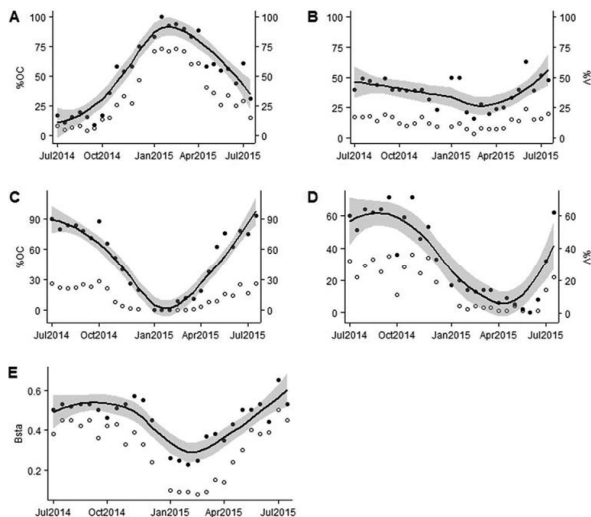


Figure 2 Seasonal variations in the intake of the four main food resources exploited by the red fox in the Soana Valley: (A) ungulates, (B) small mammals, (C) insects and (D) fruits. In (E), the seasonal trend of the trophic niche breadth (Levins index values) is also reported. Black points refer to per cent frequencies of occurrence (%OC), while the white ones represent estimated volumes (%V). A LOESS regression curve has been drawn on the %OC data to better visualize the seasonal trends (95% confidence interval in grey).

Table 1 Estimated regression parameters, standard errors, z-values, t-values and P-values for the GLMs and the LM concerning the effects of climatic variables on the %OC of the four main food categories in red fox diet and on the trophic niche breadth (b-GLM = Binomial GLM; LM = Linear Model). Significant P-values are reported in bold

| Dependent variables | Explanatory variables | Models | | | |
|--------------------------|-----------------------|----------|------------|--------------|----------------|
| | | Estimate | Std. error | z or t value | Pr (> z) |
| Ungulates (b-GLM) | Intercept | -0.747 | 0.119 | -6.301 | <0.001 |
| | Snow cover | 1.881 | 0.143 | 13.153 | < 0.001 |
| | Mean precipitations | -0.012 | 0.018 | -0.676 | 0.499 |
| Small mammals (b-GLM) | Intercept | -0.302 | 0.112 | -2.703 | 0.007 |
| | Snow cover | -0.504 | 0.134 | -3.754 | < 0.001 |
| | Mean precipitations | 0.002 | 0.017 | 0.104 | 0.918 |
| Fruits (b-GLM) | Intercept | 0.469 | 0.134 | 3.493 | <0.001 |
| | Snow cover | -2.104 | 0.192 | -10.949 | < 0.001 |
| | Mean precipitations | -0.158 | 0.026 | -6.038 | < 0.001 |
| Insects (b-GLM) | Intercept | 1.210 | 0.128 | 9.427 | <0.001 |
| | Snow cover | -2.243 | 0.148 | -15.166 | < 0.001 |
| | Mean precipitations | 0.002 | 0.019 | 0.106 | 0.916 |
| Niche breadth (LM) | Intercept | 0.506 | 0.033 | 15.510 | <0.001 |
| | Snow cover | -0.133 | 0.036 | -3.721 | 0.001 |
| | Mean precipitations | 0.003 | 0.005 | 0.536 | 0.597 |

(Table 1). In particular, snow cover caused a significant reduction in the intake of insects, fruits and small mammals; while, on the other hand, the occurrence of snow on the ground favoured the exploitation of ungulates as a food resource. Snow cover was also the main factor in determining a significant contraction of the trophic niche during the cold season. Conversely, rainfall was related only to fruits consumption.

4 DISCUSSION

In this research, the red fox was confirmed to be an opportunistic predator, able to exploit a wide range of food resources all over the year. Ungulates, fruits, insects and small mammals were the main food categories used by this species in the Soana Valley, corroborating the data reported in the previous studies carried out in the GPNP (Leinati et al., 1960; Cagnacci et al., 2003) and in other alpine areas (Lucherini and Crema, 1994; Russell and Storch, 2004; Prigioni et al., 2008; Balestrieri et al., 2011). The highly adaptable behaviour of the red fox may be an essential feature to ensure the occurrence of this carnivore in alpine habitats, where environmental conditions are often extremely variable among seasons, with consequent remarkable fluctuations in prey availability. As demonstrated by our results and by previous

research (Cavallini and Lovari, 1991; Lucherini and Crema, 1994; Cagnacci et al., 2003; Hartová-Nentvichová et al., 2010), the red fox is able to seasonally modulate its diet composition, exploiting in each period the most accessible food resources in the ecosystem. In summer, since a large variety of trophic resources is usually available in alpine habitats, this species is able to occupy a relatively wide trophic niche, feeding in particular on small mammals, insects and fruits. Conversely, during winter, food availability can be severely limited, forcing foxes to depend almost exclusively on ungulate carrions, with a consequent niche breadth reduction.

Although seasonal variations in food availability can be often related to prey phenology (e.g. for insects and fruits), our data suggest an important role of snow cover in conditioning red fox diet in alpine habitats, even if temperature may represent a confounding factor (high collinearity with snow cover). As reported in literature (Jędrzejewski and Jędrzejewska, 1992; Lucherini and Crema, 1994; Cagnacci et al., 2003), the presence of snow causes a considerable increase in ungulates consumption, while the intake of small mammals, insects and fruits is often severely affected by this environmental factor. Indeed, snow cover is known to enhance ungulate mortality in mountain habitats, especially in late winter/spring (Jacobson et al., 2004; Rughetti et al., 2011), while snow depth can reduce the effectiveness of red fox predation on small mammals (Lindström and Hörnfeldt, 1994). On the other hand, fruit and insect consumption may also be conditioned by low temperatures, since this parameter was found to drive red fox diet composition in areas where snow cover is negligible (Calisti et al., 1990; Serafini and Lovari, 1993).

Besides seasonal variations in the use of food resources, our research also aimed to describe possible changes in red fox feeding ecology on a long temporal scale, thanks to the availability of previous studies carried out within the GPNP in the past sixty years (Leinati et al., 1960; Cagnacci et al., 2003). Despite few differences having been observed during the past forty years (Cagnacci et al., 2003), some important changes recently occurred in red fox diet composition in the Soana Valley, probably ascribable to general variations in prey availability. However, these results must be carefully interpreted, since our sampling area slightly differs from those considered in the previous research (Soana Valley *vs.* whole park).

First of all, Leinati et al. (1960) and Cagnacci et al. (2003) identified alpine chamois and alpine ibex as the main ungulate species consumed in the park by the red fox. Although alpine chamois was found as the main food resource in our study as well, we also recorded the occurrence of roe deer and wild boar, while alpine ibex remains were rarely found. This reduction in ibex intake is likely a consequence of its distribution, as this ungulate is relatively abundant in the GPNP, except for the Soana Valley. On the other hand, our study area has been interested in the past two decades by a rapid expansion of roe deer and wild boar populations, previously absent in the GPNP. In this case, our results confirm the high adaptability of the red fox in exploiting new trophic resources as soon as they become available (Cavallini and Lovari, 1991).

Unfortunately, due to the lack of detailed data on ungulate abundance collected in this study, we are unable to ascertain if alpine chamois is the most exploited

species by the red fox owing to prey selection dynamics or density-dependent factors. However, since this carnivore usually mainly feeds on the most available prey (Cavallini and Lovari, 1991; Leckie et al., 1998; Kidawa and Kowalczyk, 2011), we can hypothesize that in the cold season alpine chamois are more exposed to death by avalanches than roe deer and wild boar, due to their habitat preferences, resulting in a different carrion availability.

Despite ungulates proving to represent the main shared food category among coexisting red fox and wolf populations (Patalano and Lovari, 1993; Bassi et al., 2012), our data are inadequate to provide a convincing assessment about a possible ecological interaction between these species in the study area. Further analyses on these topics are therefore needed in the future, arranging a specific sampling design, in order to describe for the first time in the alpine region the effects of sympatry on the feeding ecology of these two carnivores.

At last, it is important to remark that insects showed consumption rates considerably higher than those observed in the past on the whole park area, likely as a consequence of the higher suitability of the Soana Valley for arthropods compared with other park portions (GPNP, *unpublished data*). In addition, the observed progressive reduction in garbage occurrence in red fox scats among studies (Leinati et al., 1960; Cagnacci et al., 2003) may reflect the effective environmental policies carried out by the GPNP in recent decades, sensitizing tourists and local populations towards a proper waste management system. Even if this result can be referred to the Soana Valley only, such an outcome gives evidence that strict rules have been probably useful in limiting the abandonment of refuse in the ecosystem, thus reducing the availability of this kind of food resource for the red fox.

In conclusion, the study of red fox feeding behaviour in the Soana Valley clearly confirmed the high dietary adaptability of this species, even in alpine ecosystems. Prey availability proved to be a key factor in determining diet composition, explaining both the seasonal and long-term variations reported in this paper.

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REFERENCES

- Balestrieri, A., Remonti, L. and Prigioni, C. (2005) Local feeding specialization of the red fox (*Vulpes vulpes*) in response to eastern Cottontail (*Sylvilagus floridanus*) introduction (NW Italy). *Hystrix*, 16(2): 113–126. <https://doi.org/10.4404/hystrix-16.2-4349>

- Balestrieri, A., Remonti, L. and Prigioni, C. (2011) Assessing carnivore diet by faecal samples and stomach contents: a case study with Alpine red foxes. *Central European Journal of Biology*, 6: 283–292. <https://doi.org/10.2478/s11535-010-0106-1>
- Bassi, E., Donaggio, E., Marcon, A., Scandura, M. and Apollonio, M. (2012) Trophic niche overlap and wild ungulate consumption by red fox and wolf in a mountain area in Italy. *Mammalian Biology*, 77: 369–376. <https://doi.org/10.1016/j.mambio.2011.12.002>
- Battisti, A., Giuliano, D. and Balestrieri, A. (2019). Detection of earthworm chaetae in mammal faeces: methodological implications. *Folia Zoologica*, 68(1): 54–58. DOI: 10.25225/fozo.075.2019
- Boitani, L. (1992) Wolf research and conservation in Italy. *Biological Conservation*, 61: 125–132. [https://doi.org/10.1016/0006-3207\(92\)91102-X](https://doi.org/10.1016/0006-3207(92)91102-X)
- Boitani, L., Barrasso, P. and Grimaldi, I. (1984) Ranging behaviour of the red fox in the Gran Paradiso National Park (Italy). *Bollettino di Zoologia*, 51: 275–284. <https://doi.org/10.1080/11250008409439466>
- Borkowski, J. (1994) Food composition of red fox in the Tatra National Park. *Acta Theriologica*, 39(2): 209–214.
- Cagnacci, F., Lovari, S. and Meriggi, A. (2003) Carrion dependence and food habits of the red fox in an Alpine area. *Italian Journal of Zoology*, 70: 31–38. <https://doi.org/10.1080/11250000309356493>
- Cagnacci, F., Meriggi, A. and Lovari, S. (2004) Habitat selection by the red fox *Vulpes vulpes* (L. 1758) in an Alpine area. *Ethology, Ecology and Evolution*, 16: 103–116. <https://doi.org/10.1080/08927014.2004.9522640>
- Calisti, M., Ciampalini, B., Lovari, S. and Lucherini, M. (1990) Food habits and trophic niche variation of the red fox *Vulpes vulpes* (L. 1758) in a Mediterranean coastal area. *Revue d'Ecologie (la Terre et la Vie)*, 45: 309–320.
- Cavallini, P. and Lovari, S. (1991) Environmental factors influencing the use of habitat in the red fox. *Vulpes vulpes*. *Journal of Zoology*, 223: 323–339. <https://doi.org/10.1111/j.1469-7998.1991.tb04768.x>
- Cavallini, P. and Volpi, T. (1996) Variation in the diet of the red fox in a Mediterranean area. *Revue d'Ecologie (la Terre et la Vie)*, 51: 173–189. <http://hdl.handle.net/2042/54833>
- Colwell, R.K. and Futuyma, D. (1971) On the measurement of niche breadth and overlap. *Ecology*, 52: 567–575. <https://doi.org/10.2307/1934144>
- Contesse, P., Hegglin, D., Gloor, S., Bontadina, F. and Deplazes, P. (2004) The diet of urban foxes (*Vulpes vulpes*) and the availability of anthropogenic food in the city of Zurich, Switzerland. *Mammalian Biology*, 69(2): 81–95.
- Dalén, L., Elmhagen, B. and Angerbjörn, A. (2004) DNA analysis on fox faeces and competition induced niche shift. *Molecular Ecology*, 13: 2389–2392. <https://doi.org/10.1111/j.1365-294X.2004.02249.x>
- Day, M.G. (1966) Identification of hair and feather remains in the gut and faeces of stoat and weasels. *Journal of Zoology*, 148: 201–217. <https://doi.org/10.1111/j.1469-7998.1966.tb02948.x>
- De Marinis, A.M. and Agnelli, P. (1993) Guide to the microscope analysis of Italian mammals hairs: Insectivora, Rodentia and Lagomorpha. *Bollettino di Zoologia*, 60: 225–232. <https://doi.org/10.1080/11250009309355815>
- De Marinis, A.M. and Asprea, A. (2006) Hair identification key of wild and domestic ungulates from southern Europe. *Wildlife Biology*, 12: 305–320. [https://doi.org/10.2981/0909-6396\(2006\)12\[305:HIKOWA\]2.0.CO;2](https://doi.org/10.2981/0909-6396(2006)12[305:HIKOWA]2.0.CO;2)
- Debrot, S. (1982) *Atlas des poils de mammifères d'Europe*. Institut de Zoologie de l'Université de Neuchâtel.

- Dell'Arte, G., Laaksonen, T., Norrdahl, K. and Korpimäki, E. (2007) Variation in the diet composition of a generalist predator, the red fox, in relation to season and density of main prey. *Acta Oecologica*, 31: 276–281. <https://doi.org/10.1016/j.actao.2006.12.007>
- Dove, C.J. and Koch, S.L. (2011) Microscopy of feathers: a practical guide for forensic feather identification. *The Microscope*, 59(2): 51–71.
- Erome, G. and Aulagnier, S. (1982) Contribution à l'identification des proies des Rapaces. *La Bièvre*, 4(2): 129–135.
- Fabbri, E., Miquel, C., Lucchini, V., Santini, A., Caniglia, R., Duchamp, C., Weber, J.M., Lequette, B., Marucco, F., Boitani, L., Fumagalli, L., Taberlet, P. and Randi, E. (2007) From the Apennines to the Alps: colonization genetics of the naturally expanding Italian wolf (*Canis lupus*) population. *Molecular Ecology*, 16: 1661–1671. <https://doi.org/10.1111/j.1365-294X.2007.03262.x>
- Hartová-Nentvichová, M., Šálek, M., Červený, J. and Koubek, P. (2010) Variation in the diet of the red fox (*Vulpes vulpes*) in mountain habitats: effects of altitude and season. *Mammalian Biology*, 75: 334–340. <https://doi.org/10.1016/j.mambio.2009.09.003>
- Jacobson, A.R., Provenzale, A., von Hardenberg, A., Bassano, B. and Festa-Bianchet, M. (2004) Climate forcing and density dependence in a mountain ungulate population. *Ecology*, 85(6): 1598–1610. <https://doi.org/10.1890/02-0753>
- Jędrzejewski, W. and Jędrzejewska, B. (1992) Foraging and diet of the red fox *Vulpes vulpes* in relation to variable food resources in Białowieża National Park, Poland. *Ecography*, 15: 212–220. <https://doi.org/10.1111/j.1600-0587.1992.tb00027.x>
- Kidawa, D. and Kowalczyk, R. (2011) The effects of sex, age, season and habitat on diet of the red fox *Vulpes vulpes* in northeastern Poland. *Acta Theriologica*, 56: 209–218. <https://doi.org/10.1007/s13364-011-0031-3>
- Kowalczyk, R., Bunevich, A.N. and Jędrzejewska, B. (2000) Badger density and distribution of setts in Białowieża Primeval Forest (Poland and Belarus) compared to other Eurasian populations. *Acta Theriologica*, 45: 395–408.
- Kruuk, H. and Parish, T. (1981) Feeding specialization of the European badger (*Meles meles*) in Scotland. *Journal of Animal Ecology*, 50: 773–788.
- Leckie, F.M., Thirgood, S.J., May, R. and Redpath, S.M. (1998) Variation in the diet of red foxes on Scottish moorland in relation to prey abundance. *Ecography*, 21: 599–604. <https://doi.org/10.1111/j.1600-0587.1998.tb00552.x>
- Leinati, L., Grimaldi, E., Mandelli, G. and Videsott, R. (1960) Indagini sulle abitudini alimentari della volpe (*Vulpes vulpes* L.) del Parco Nazionale del Gran Paradiso. *La Clinica Veterinaria*, 83: 1–24.
- Lindström, E.R. (1989) Food limitation and social regulation in a red fox population. *Holarctic Ecology*, 12: 70–79. <https://doi.org/10.1111/j.1600-0587.1989.tb00824.x>
- Lindström, E.R. and Hörnfeldt, B. (1994) Vole cycles, snow depth and fox predation. *Oikos*, 70(1): 156–160. <https://www.jstor.org/stable/3545711>
- Lucherini, M. and Crema, G. (1994) Seasonal variation in diet and trophic niche of the Red fox in an Alpine habitat. *Zeitschrift für Säugetierkunde*, 59: 1–8.
- McDonald, D.W. (1983) The ecology of carnivore social behavior. *Nature*, 301: 379–384. <https://www.nature.com/articles/301379a0>
- Needham, R., Odden, M., Lundstadsveen, S.K. and Wegge, P. (2014) Seasonal diets of red foxes in a boreal forest with a dense population of moose: the importance of winter scavenging. *Acta Theriologica*, 59: 391. <https://doi.org/10.1007/s13364-014-0188-7>
- Panzacchi, M., Linnell, J.D.C., Odden, J., Odden, M. and Andersen, R. (2008) When a generalist become specialist: patterns of red fox predation on roe deer fawns under

- contrasting conditions. *Canadian Journal of Zoology*, 86: 116–126. <https://doi.org/10.1139/Z07-120>
- Patalano, M. and Lovari, S. (1993) Food habits and trophic niche overlap of the wolf *Canis lupus* L. 1758 and the red fox *Vulpes vulpes* (L. 1758) in a Mediterranean mountain area. *Revue d'Ecologie (la Terre et la Vie)*, 48: 279–294. <http://hdl.handle.net/2042/54730>
- Prigioni, C., Balestrieri, A., Remonti, L. and Cavada, L. (2008) Differential use of food and habitat by sympatric carnivores in the eastern Italian Alps. *Italian Journal of Zoology*, 75(2): 173–184. <https://doi.org/10.1080/11250000701885521>
- R Core Team (2017) *R: a language and environment for statistical computing*. R Foundation for Statistical Computing, Vienna, Austria. Available at: <https://www.R-project.org/>.
- Reynolds, P. (1979) Preliminary observations on the food of the Fox (*Vulpes vulpes* L.) in the Camargue, with special reference to Rabbit (*Oryctolagus cuniculus* L.) predation. *Mammalia*, 43(3): 295–307. <https://doi.org/10.1515/mamm.1979.43.3.295>
- Richards, D.F. (1977) Observations on the diet of the Red fox (*Vulpes vulpes*) in South Devon. *Journal of Zoology*, 183: 495–504. <https://doi.org/10.1111/j.1469-7998.1977.tb04201.x>
- Robertson, J., Harkin, C., Govan, J. (1984) The identification of bird feathers. Scheme for feather examination. *Journal of the Forensic Science Society*, 24: 85–98. [https://doi.org/10.1016/S0015-7368\(84\)72301-2](https://doi.org/10.1016/S0015-7368(84)72301-2)
- Rolland, C. (2008) *Clé d'identification des micro-mammifères de Rhône-Alpes*. CORA Faune Sauvage, 54 pages.
- Rughetti, M., Toigo, C., von Hardenberg, A., Rocchia, E. and Festa-Bianchet, M. (2011) Effects of an exceptionally snowy winter on chamois survival. *Acta Theriologica*, 56: 329–333. <https://doi.org/10.1007/s13364-011-0040-2>
- Russell, A.J.M. and Storch, I. (2004) Summer food of sympatric red fox and pine marten in the German Alps. *European Journal of Wildlife Research*, 50: 53–58. <https://doi.org/10.1007/s10344-004-0037-0>
- Schoener, T.W. (1974) Resource partitioning in ecological communities. *Science*, 185: 27–39. DOI: 10.1126/science.185.4145.27
- Serafini, P. and Lovari, S. (1993) Food habits and trophic niche overlap of the red fox and the stone marten in a Mediterranean rural area. *Acta Theriologica*, 38(3): 233–244.
- Storch, I. and Kleine, C. (1991) Zur Nahrungswahl des Fuchses in den Voralpen. *Zeitschrift für Jagdwissenschaft*, 37: 267–270. <https://doi.org/10.1007/BF02239732>
- Teerink, B.J. (1991) *Hair of West-European Mammals. Atlas and identification key*. Cambridge University Press.
- Valière, N., Fumagalli, L., Gielly, L., Miquel, C., Lequette, B., Poulle, M.L., Weber, J.M., Arlettaz, R. and Taberlet, P. (2003) Long-distance wolf recolonization of France and Switzerland inferred from non-invasive genetic sampling over a period of 10 years. *Animal Conservation*, 6: 83–92. <https://doi.org/10.1017/S1367943003003111>
- Zuur, A.F., Ieno, E.N., Walker, N., Saveliev, A.A. and Smith, G.M. (2009) *Mixed effects models and extensions in ecology with R*. New York: Springer.

APPENDIX 1

Diet composition of the red fox in the Soana Valley between July 2014 and July 2015. For each food category, the estimated volume (%V) and the percent frequency of occurrence (%OC) are reported.

| Food categories | | %V | %OC |
|----------------------------|-------------------------------------|-------|-------|
| INVERTEBRATES | | 14.53 | 67.55 |
| Insects | | 13.63 | 55.03 |
| Orthoptera | | 1.40 | 16.37 |
| | <i>Polysarcus denticauda</i> | 0.03 | 0.30 |
| | <i>Pholidopetra aptera</i> | 0.07 | 0.69 |
| | <i>Decticus verrucivorus</i> | 0.01 | 0.10 |
| | <i>Pseudochorthippus parallelus</i> | 0.01 | 0.20 |
| | Undetermined Orthoptera | 1.28 | 15.58 |
| Dermaptera | | 0.25 | 4.64 |
| Diptera | | 0.01 | 0.30 |
| Hymenoptera | | 0.40 | 3.06 |
| | Formicoidea | 0.02 | 1.18 |
| | Vespoidea | 0.30 | 1.38 |
| | Undetermined Hymenoptera | 0.08 | 0.89 |
| Coleoptera | | 7.89 | 41.22 |
| | Carabidae | 4.00 | 27.51 |
| | <i>Carabus depressus</i> | 1.28 | 11.54 |
| | <i>Carabus intricatus</i> | 0.03 | 0.30 |
| | <i>Carabus problematicus</i> | 0.10 | 1.08 |
| | <i>Carabus</i> sp. | 1.11 | 10.06 |
| | <i>Pterostichus flavofemoratus</i> | 1.07 | 13.41 |
| | Undetermined Carabidae | 0.42 | 4.73 |
| | Silfidae | 0.26 | 3.35 |
| | Scarabeoidea | 2.03 | 7.99 |
| | Curculionidae | 0.01 | 0.30 |
| | Undetermined Coleoptera | 1.59 | 15.58 |
| Larvae | | 3.62 | 20.02 |
| | Lepidoptera | 2.71 | 11.44 |
| | Trichoptera | 0.02 | 0.20 |
| | Diptera | 0.75 | 6.90 |
| | Coleoptera | 0.02 | 0.39 |
| | Undetermined Larvae | 0.13 | 2.37 |
| Undetermined insects | | 0.06 | 1.28 |
| Other invertebrates | | 0.90 | 45.46 |
| Mollusca | | 0.01 | 0.30 |
| | Gasteropoda | 0.01 | 0.30 |
| Oligochaeta | | 0.82 | 43.89 |
| | Lumbricidae | 0.82 | 43.89 |
| Arachnida | | 0.04 | 2.17 |
| | Araneae | 0.02 | 0.49 |
| | Opiliones | 0.01 | 0.59 |
| | Acari | 0.01 | 1.08 |

| Food categories | | %V | %OC |
|----------------------------|---------------------------------|--------|-------|
| Crustacea | | Traces | 0.20 |
| | Isopoda | Traces | 0.20 |
| Miriapoda | | 0.03 | 0.49 |
| | Chilopoda | 0.03 | 0.49 |
| Undetermined invertebrates | | Traces | 0.10 |
| VERTEBRATES | | 49.32 | 82.54 |
| Mammals | | 47.66 | 78.80 |
| Small-mammals | | 13.30 | 37.67 |
| Insectivora | | 1.91 | 5.92 |
| | <i>Talpa caeca</i> | 0.07 | 0.10 |
| | <i>Talpa europaea</i> | 0.07 | 0.10 |
| | <i>Talpa sp.</i> | 0.61 | 1.48 |
| | <i>Sorex gr. araneus</i> | 0.10 | 0.39 |
| | Undetermined Insectivora | 1.06 | 3.94 |
| Rodentia | | 11.26 | 31.76 |
| | Arvicolinae | 3.81 | 8.58 |
| | <i>Chionomys nivalis</i> | 0.47 | 0.79 |
| | <i>Microtus arvalis</i> | 0.17 | 0.30 |
| | <i>Microtus savii/multiplex</i> | 0.92 | 2.17 |
| | <i>Myodes glareolus</i> | 0.67 | 1.68 |
| | Undetermined Arvicolinae | 1.57 | 3.94 |
| | Muridae | 1.00 | 2.47 |
| | <i>Apodemus sp.</i> | 0.85 | 2.07 |
| | <i>Mus musculus</i> | 0.15 | 0.39 |
| | Gliridae | 1.34 | 2.47 |
| | <i>Glis glis</i> | 1.10 | 1.97 |
| | <i>Muscardinus avellanarius</i> | 0.05 | 0.10 |
| | Undetermined Gliridae | 0.19 | 0.39 |
| | Undetermined Rodentia | 5.12 | 19.33 |
| Undetermined small-mammals | | 0.13 | 0.69 |
| Ungulates | | 31.21 | 50.00 |
| Suidae | | 1.46 | 3.35 |
| | <i>Sus scrofa</i> | 1.46 | 3.35 |
| Cervidae | | 5.26 | 9.86 |
| | <i>Capreolus capreolus</i> | 5.19 | 9.57 |
| | <i>Cervus elaphus</i> | Traces | 0.10 |
| | Undetermined Cervidae | 0.07 | 0.20 |
| Bovidae | | 24.23 | 39.45 |
| | <i>Capra ibex</i> | 0.48 | 0.99 |
| | <i>Rupicapra rupicapra</i> | 22.35 | 36.19 |
| | <i>Ovis aries</i> | 1.23 | 1.78 |
| | Undetermined Bovidae | 0.17 | 0.49 |

| Food categories | %V | %OC |
|---------------------------------|--------|-------|
| Undetermined ungulates | 0.26 | 1.18 |
| <i>Other mammals</i> | 2.56 | 4.04 |
| <i>Marmota marmota</i> | 2.12 | 3.35 |
| <i>Lepus</i> sp. | 0.07 | 0.10 |
| <i>Felis catus</i> | 0.10 | 0.10 |
| <i>Vulpes vulpes</i> | 0.25 | 0.39 |
| <i>Meles meles</i> | 0.02 | 0.10 |
| Undetermined mammals | 0.59 | 2.96 |
| Birds | 0.87 | 6.31 |
| Anseriformes | 0.07 | 0.30 |
| Galliformes | Traces | 0.10 |
| Strigiformes | 0.07 | 0.10 |
| Passeriformes | 0.31 | 1.87 |
| Undetermined birds | 0.42 | 3.94 |
| Reptiles | 0.64 | 6.02 |
| Lacertidae | 0.27 | 1.87 |
| <i>Anguis veronensis</i> | 0.17 | 1.18 |
| Undetermined Lacertidae | 0.10 | 0.69 |
| Ophidia | 0.07 | 0.59 |
| Undetermined reptiles | 0.30 | 3.65 |
| Undetermined Vertebrates | 0.15 | 1.78 |
| VEGETAL MATERIAL | 35.14 | 92.01 |
| Fruits | 15.46 | 34.71 |
| <i>Actinidia chinensis</i> | 0.26 | 0.89 |
| <i>Corylus avellana</i> | 0.14 | 0.69 |
| <i>Fragaria vesca</i> | 0.66 | 6.31 |
| <i>Juglans regia</i> | 0.03 | 0.10 |
| <i>Malus sylvatica</i> | 0.78 | 1.68 |
| <i>Prunus avium</i> | 2.57 | 4.54 |
| <i>Prunus domestica</i> | 1.78 | 4.44 |
| <i>Pyrus communis</i> | 0.54 | 0.89 |
| <i>Rosa</i> sp. | 0.11 | 0.49 |
| <i>Rubus</i> sp. | 1.63 | 8.19 |
| <i>Sorbus aria</i> | 4.28 | 7.69 |
| <i>Sorbus aucuparia</i> | 0.18 | 0.30 |
| <i>Vaccinium</i> sp. | 0.53 | 1.38 |
| <i>Vitis vinifera</i> | 0.11 | 0.30 |
| Undetermined Fruits | 1.85 | 6.02 |

| Food categories | %V | %OC |
|-------------------------------|--------|-------|
| Other Vegetal Material | 19.68 | 86.00 |
| Grass leaves | 16.30 | 70.71 |
| Other leaves | 3.12 | 14.60 |
| Undetermined Vegetal Material | 0.27 | 1.78 |
| GARBAGE | 0.54 | 2.47 |
| Aluminium | Traces | 0.10 |
| Paper | 0.23 | 0.99 |
| Organic material | 0.09 | 0.20 |
| Plastic | 0.18 | 0.89 |
| Undetermined Garbage | 0.03 | 0.49 |
| UNDETERMINED MATERIAL | 0.48 | 1.28 |