Original investigation

Food habits of wolves and selection of wild ungulates in a prey-rich Mediterranean coastal area

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ABSTRACT

Large carnivores are increasing throughout the western Holarctic, re-colonising large parts of their former ranges. Ecological (e.g., predator-prey relationships) and socio-economic (e.g., livestock depredation) consequences of this process need to be monitored, to identify suitable management/conservation actions. We studied food habits and selection of main prey by wolves in a Mediterranean protected coastal area (Uccellina Hills in the Maremma Regional Park, *c.* 70 km², central Italy, May 2016- April 2018), including sclerophyllic scrubwood, pinewood, wetlands and mixed rural-wood habitats. Potential prey include wild boar, fallow deer and roe deer (*c.* 25–30 individuals/100 ha, in summer, all species together), livestock (mainly cattle and sheep, *c.* 20 heads/100 ha, overall) and several species of meso-mammals. Overall, wild ungulates dominated the diet (*c.* 90% of absolute occurrence, relative occurrence or volume), with the fallow deer being the main prey (absolute occurrence, AO: 55%; relative occurrence, RO: 42%; volume, V: 44%) followed by the wild boar (AO: 48%; RO: 36% V: 33%). Livestock was rarely used (2%, both AO and V); the coypu (AO: 8%; RO: 6%; V: 6%) was another important food item. Fallow deer and wild boar dominated summer diet, whereas the use alternative prey increased in winter. Fallow deer were selected, wild boar were used according to their availability, whereas roe deer were used less than availability. Prey selection was probably driven by the greater accessibility and detectability of fallow deer, which are gregarious and attended mainly open habitats on lower ground, in respect to wild boar/roe deer. Most likely, availability of a diverse spectrum of meso-large prey and a comparatively lower accessibility of livestock are key-factors to limit livestock consumption.

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Introduction

Top predators are fundamental players of ecosystems and usually depend on meso-large herbivores to meet their energy requirements (Carbone et al., 2007). Prey selection may be expected to occur when predators can choose a prey providing a high ratio of benefits over costs related to its capture (Stephens and Krebs, 1986). Several factors can influence prey selection, such as prey abundance, which affects searching and encounter rates, or vulnerability, which is influenced by prey behaviour, ecology, size, age and accessibility (e.g., Mech, 1970; Huggard, 1993; Karanth and Sunquist, 1995; Jędrzejewski et al., 2000; Cooley et al., 2008; Mattioli et al., 2011). On the last several decades, the wolf *Canis lupus* has been recolonising large sectors of its previous distribution range, especially in Europe (Chapron et al., 2014). Socio-economic issues are generated by the ensuing conflict with humans because of livestock depredation and, often, retaliatory killing (Ripple et al., 2014). In turn, many temperate systems have faced (and will soon face) the return of this carnivore, the action of which may trigger important effects on other components of ecosystems (e.g., Creel et al., 2005; Hebblewhite et al., 2005; Kuijper et al., 2013, 2016; Ripple et al., 2014). Understanding and monitoring wolf-prey relationships is important to predict potential ecosystem consequences of the presence of this top predator, also in the light of assessing human-wolf conflict (Kuijper et al., 2016).

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Wolves prey especially on large and medium-sized wild ungulates, showing a remarkable capacity to adapt to different prey and ecological contexts (Mech, 1970; Okarma, 1995; Meriggi and Lovari, 1996; Mech and Peterson, 2003; Meriggi et al., 2011; Newsome et al., 2016). Livestock is often dominant in wolf diet, especially where/when substantial wild prey is not abundant (e.g., Meriggi and Lovari, 1996; Meriggi et al., 2011; Llaneza and López-Bao, 2015; Torres et al., 2015, for Europe). In particular, it has been suggested that, if a rich and diverse guild of wild ungulates is available, livestock consumption may decrease (Meriggi and Lovari, 1996; Meriggi et al., 2011; Newsome et al., 2016). Although the wolf is often considered a generalist predator, especially in systems including multiple potential prey it can select the most profitable/vulnerable one (e.g., Huggard, 1993; Jędrzejewski et al., 2000; Kunkel et al., 2004; Mattioli et al., 2011). Most research on wolf food habits has been conducted in northern, temperate systems, as well as mountainous habitats (Mech and Peterson, 2003; Meriggi and Lovari, 1996; Newsome et al., 2016, for reviews), whereas comparatively less information is available for lowland Mediterranean habitats (Lagos and Bárcena, 2015; Stahlberg et al., 2017). These systems are very important because they include areas where human settlements/villages are interspersed with natural/semi-natural habitats and where a sharp increase of both ungulate (Apollonio et al., 2010) and wolf numbers (Chapron et al., 2014; Galaverni et al., 2015) have been recorded in recent decades. In particular, analyses of food habits are required especially for areas under-represented in the scientific literature, to show potential adaptations of wolves to local ecological conditions and evaluate the potential for conflict with human activities (Newsome et al., 2016).

We studied food habits and prey selection of wolves in a protected area in central Italy, along the coast of the Thyrrenian sea. The area includes 3 species of wild ungulates at high densities, i.e. the wild boar *Sus scrofa*, the fallow deer *Dama dama* and the roe deer *Capreolus capreolus* (c. 30 individuals/100 ha, together), as well as livestock (sheep, cattle, horses, c. 20 heads/100 ha, together). We predicted that (i) the diet of wolves would be dominated by wild ungulates, considering their very high density (Meriggi et al., 1996, 2011); (ii) food habits of wolves would be mainly determined by prey availability, i.e. prey use should reflect availability with, possibly, the selection of the most abundant/accessible one.

Methods

Study area

Our study was carried out in the central-southern part (c. 70 km^2) of the Maremma Regional Park (MRP, Central Italy; 42°39'N, 11°05'E), i.e. the Uccellina Hills (maximum altitude: 417 m a.s.l., Poggio Lecci). The local climate is Mediterranean and the area is bordered by the Thyrrenian Sea at its western side. Vegetation is composed mainly by Mediterranean sclerophyllic scrubwood, dominated by holm oak *Quercus ilex* and including, among the others, strawberry tree *Arbutus unedo*, rosemary *Rosmarinus officinalis*, juniper *Juniperus spp.*, rockrose *Cistus spp.* and other trees/shrubs typical of Mediterranean habitats (50.2%). This scrubwood includes three main wood types: oakwood, with the prevalence of holm oak trees with a height >7 m; shrubwood, with the prevalence of holm oak and strawberry tree, with a height of <7 m; garigue, with bushes (Ferretti et al., 2011a). Other habitats are pinewood (8.4%: mainly domestic pine *Pinus pinea*), abandoned olive groves and pastures (partially re-colonized by wood species and bushes: 9.2%), set-aside grassland (3.9%), marshland/wetlands (3.8%) and crops (24.4%, mainly cereals and sunflower).

A pack of wolves settled in the area in 2015; a second pack settled north of the Ombrone river in 2017 and may visit the northern sector of Uccellina hills (Ferretti, 2016; Regione Toscana, 2017; Fazzi et al., 2018). Wild ungulates include wild boar *Sus scrofa*, fallow deer *Dama dama* and roe deer *Capreolus capreolus* (c. 30 ind.s/100 ha in summer, together, during our study: see Results). Livestock is also present (c. 20 heads/100 ha): free-ranging cattle and horses (c. 1000 heads, overall) are locally and irregularly moved through some pastures and part of pinewood/scrubwood. Calf births occur in winter-early spring and calves are kept together with the mothers up to 6–8 months of age. Usually, adult cows actively defend calves towards predators (Meriggi et al., 1991, 1996). Although no exclusion measure has been adopted locally against calf depredation, farming procedures tend to favour herd cohesion, by limiting separation between mothers and offspring especially until weaning (October). Two sheep herds are also present (c. 800 heads, overall) and alternative preventive measures are adopted (direct surveillance by the shepherd during the day, livestock guarding dogs and/or fences). Other meso-mammals include the coypu *Myocastor coypus*, the European brown hare *Lepus europaeus*, the crested porcupine *Hystrix cristata* and, among carnivores, the red fox *Vulpes vulpes*, the Eurasian badger *Meles meles*, the wildcat *Felis silvestris*, the stone marten *Martes foina* and the pine marten *Martes martes*. Fallow deer and wild boar are culled (both) and captured (wild boar) for population control purposes (Ferretti et al., 2016; Pecorella et al., 2016) throughout the year. Since autumn 2017, coypu culling has been also implemented by Park wardens for eradication purposes.

Scat collection

From May 2016 to April 2018, wolf scats (N = 334) were collected monthly along itineraries located across the main habitats and distributed homogeneously along the chain of Uccellina hills, for a total of c. 60 km length and, opportunistically, during usual activities of territory patrolling by Park Wardens. Scat identification in the field was made based on a set of characteristics such as size, texture, shape, content, position and their characteristic odour (cf. Lovari et al., 2009, 2013, 2015). For a subsample (n = 25) of wolf scats, suitable for genetic analyses, identification was confirmed (100%) through DNA genotyping (ISPRA, unpublished; Fazzi et al., 2018). Each sample was collected using a plastic bag and identified with the date of collection, a numerical code and the location, recorded by a portable GPS device. Samples were stored in a freezer (−20 °C) for further analyses.

Scat analyses

In the laboratory, the content of each scat was assessed according to Lovari et al. (2009, 2013, 2015). Fine sieves, with 1 mm and 3 mm meshes, were used to wash scats and separate hair from bones, hooves and other undigested material. Hairs and other undigested remains, useful for the identification of prey, were then dried and stored for the following identification, which was based on the evaluation of their macroscopic morphological aspect and microscopic features, their comparison with a reference collection of hair of potential prey present in the area, as well as with reference manuals and specific identification keys for wild and domestic ungulates (Teerink, 2004; De Marinis and Asprea, 2006a, 2006b). Reference slides were made from hair samples of potential prey species from dead individuals met in the study area and surroundings. Slides were prepared according to Teerink (2004) and De Marinis and Asprea (2006a). Microscopic evaluation was based upon the analysis of medulla, cuticola and cortex features (Teerink, 2004; Lovari et al., 2009, 2013, 2015), through a 100–400 × microscope.

Food items of wolves were categorised at the specific level for meso-large mammals (i.e. ungulates, carnivores, meso-mammals); additionally, we considered the following categories: Mustelids, Small mammals (i.e. the other rodents); Birds; Invertebrates; Fruits; Plant material. The diet of wolves was described considering the whole study period (May 2016-April 2018, N = 334 scats) and 6-month periods (hereafter called šeasons; i.e. šummer: May-October, n = 145 scats; ẅinter: November-April, n = 189). No method for the assessment of food habits from scats is free from potential biases and ideally several methods should be used at the same time to show an approximate picture of the diet (e.g., Meriggi et al., 1996; Ciucci et al., 1996, 2018; Lovari et al., 2013, 2015). For each category (apart from Plant material and Not identified), we calculated initially the absolute and relative occurrence in diet (Lucherini and Crema, 1995). For each i-th prey category, the absolute occurrence (AO_i) was obtained through the ratio between the number of occurrences of each category (n_i) and the total number of scats analysed (N): $AO_i = (n_i / N) \times 100$. The relative occurrence (RO_i) resulted from the ratio between the number of occurrences of each category (n_i) and the total number of occurrences of all categories (N_{tot}): $RO_i = (n_i / N_{tot}) \times 100$.

We estimated also the relative volume of each category, in each scat, visually, considering volumetric classes proposed by Kruuk and Parish (1981), i.e. 1–5%; 6–25%; 26–50%; 51–75%; 76–95%; >95%, using the median point of each of these classes, i.e. 2.5%, 13%, 38%, 63%, 85.5% and 98% (Kruuk and Parish, 1981). The mean volume in diet of each category was estimated (see also Lovari et al., 2013, 2015). The estimated volume of each food item, when present, was plotted versus its absolute occurrence to show its relative importance (Kruuk and Parish, 1981). Estimates of the biomass of ingested food categories are often used to describe the diet of carnivores (e.g., Karanth and Sunquist, 1995; Ciucci et al., 1996). However, besides uncertainties affecting the calculation of biomass consumed, from scats (cf. Chakrabarti et al., 2016; Lumetsberger et al., 2017), it is often impossible to know (*i*) the age-sex class that was preyed upon; (*ii*) whether other animals (e.g., foxes or wild boar) also fed on a carcass; or (*iii*) whether the wolf fed alone or with conspecifcs, e.g., a pair or a pack (Lovari and Mori, 2017; Khan et al., 2018). Nevertheless, to compare results with those obtained with other methods, we also estimated the relative biomass of each prey category, considering mammals (Ciucci et al., 1996) and three models developed by Floyd et al. (1978); Weaver (1993) and Ruehe et al. (2003) (Supplementary Material 1). We built a correlation matrix among values obtained through the different methods, which provided highly correlated results (Supplementary Material 1). To limit redundancy of analyses, we show results of Absolute Occurrence, Relative Occurrence and Relative Volume in the main text, and those of Relative Biomass in the Supplementary Material 1.

The adequacy of sample size was determined through a Brillouin diversity index (Hb, index range: 0–4.5; Brillouin, 1956; cf. Glen and Dickman, 2006; Hass, 2009):

$$Hb = (\ln N_{tot}! - \sum \ln n_i!)/N_{tot}.$$

Each year and season, a diversity curve was calculated by sampling with replacement over a range of 3–81 (May 2016-April 2017 and summer) and 3–107 (May 2017-April 2018 and winter) samples, in increments of two. Cumulative diversity (Hb) was plotted against the number of scats. For this analysis, livestock types were pooled in a single 'Livestock' category, meso-mammals were pooled in a single 'Meso-mammals' category, whereas other minor items were pooled together into 'Other'. Diversity curves showed a stabilisation of results, with an increase <1%, for samples greater than 61 scats, in both years (Fig. 1).

We also calculated the dietary breadth of the wolf, through the standardised Levins index (Hurlbert, 1978) as:

$$B_S = (B-1)/(R-1)$$

where B is the Levins index (Levins, 1968), i.e. $B = 1/\sum (n_i / N_{tot})^2$; R is the number of possible food categories (i.e. resource states, Hurlbert, 1978; Krebs, 1999). For these analyses, we considered the following categories: Wild boar; Fallow deer; Roe deer; Livestock; Meso-mammals; Small mammals (i.e. small rodents and insectivores); Other vertebrates; Invertebrates; Fruits.

Estimates of ungulate densities

In summers 2016 and 2017 (June-August), ungulate densities were estimated through pellet group counts, using the faecal accumulation rate technique (Mayle et al., 1999). Pellet groups (i.e. with > 5 pellets) accumulated in sample areas during a defined time interval were counted (Mayle et al., 1999). This technique is considered more reliable than faecal standing crop counts (Mayle et al., 1999; Campbell et al., 2004), because it does not involve the use of pellet group decay rates, which is variable across habitats (in our same study area: Massei et al., 1998), to calculate densities. The sampling strategy was described in Fattorini et al. (2011) and Ferretti et al. (2016), and was based on a two-stage, stratified sampling strategy involving the use of circular plots (5-m radius, N = 258), allocated to strata proportionally to strata size. Strata were determined according to the main habitat categories: Mediterranean scrubwood; pinewood and marshland; abandoned olive groves and pastures; set-aside grassland; cultivated fields (Fattorini et al., 2011; Ferretti et al., 2011a, 2011b, 2016). Furthermore, local features and differences in deer densities detected through preliminary pellet group counts were also considered: Mediterranean scrubwood and abandoned olive groves and pastures were divided in two strata (in the North and in the South of the study area, respectively), while crops were divided in 5 strata (Fattorini et al., 2011; Ferretti et al., 2016). In larger strata (north/south Med. scrubwood, pinewood and cultivated fields 2–3), we adopted a two-stage strategy. In the first stage, the strata were partitioned into spatial units of different sizes (determined on the basis of natural or man-made edges). A sample of units was selected through a probabilistic sequential (draw-by-draw) sampling scheme, with selection probabilities proportional to unit size, and avoiding the selection of contiguous units. The use of selection probabilities proportional to size was adopted to handle the presence of units with different sizes (Skalski, 1994). The selection of contiguous units was avoided, because adjacent units were more alike than units that were far apart, thus giving poor contribution to sample information (Fattorini, 2006; Grafström and Tillé, 2013).

In the second stage, plots were placed within the sampled units through a tessellation stratified sampling: a grid of polygons (e.g., quadrats) of equal size was overlain to each sampled units, and a plot was randomly placed within each polygon (Fattorini et al., 2011). This scheme is able to provide an even distribution of plots within units respect to that provided by a completely random allocation. We allocated a number of plots to strata proportionally to their size. In smaller strata, the first phase was avoided and plots were placed directly on the stratum through the same scheme adopted within the spatial units. Methodological details and theoretical justifications are given in Fattorini et al. (2011), from which an unbiased estimator of faeces abundance and a conservative estimator of its standard error are provided.

On a land use map of the MRP, geographic coordinates were assigned to the centre of each selected plot through the ArcView GIS 3.2 ESRI © software. A portable GPS was used to find plots in the field. During a first survey, plots were carefully searched for any
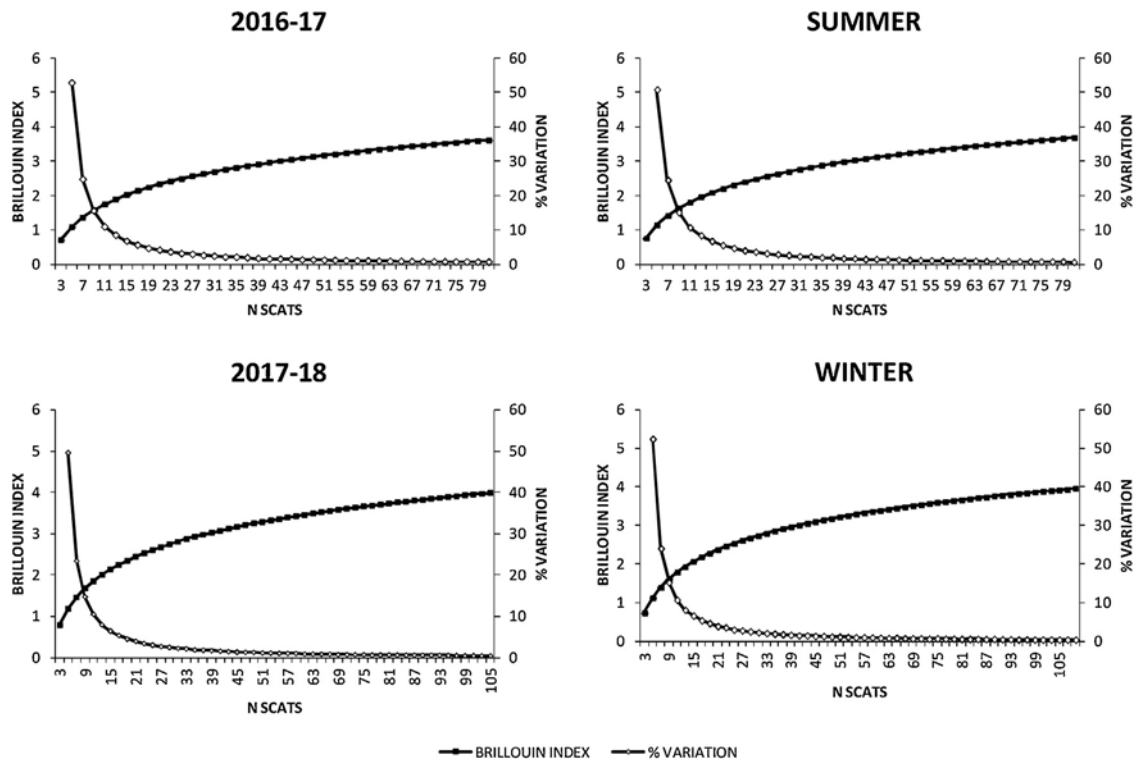
Fig. 1. Diversity curves and percentage incremental changes for wolf scat samples, in May 2016-April 2017 (up, left), May 2017-April 2018 (down, left), summer (up, right) and winter (down, right).

pellet group, later removed from the plot. We marked the centre of each plot through a peg or a tape. Local landmarks were noted down to help plot detection in subsequent surveys. A second survey was conducted after *c.* 40 days (according to the local decay rate of deer/wild boar pellet groups: Massei et al., 1998; Minder, 2006) to count pellet groups (>5 pellets, Mayle et al., 1999) in the plots. Pellets of fallow and roe deer were recognized out of shape and size: the former defecates cylindrical pellets, usually with a pointed end and slightly concave at the other, whereas the latter makes small, elongated pellets, rounded at both ends (Mayle et al., 1999). For fallow deer, we used a defecation rate of 25 pellet groups/day recommended by Massei and Genov (1998, data from our same study area). For roe deer, we used an estimated value of 20 pellet groups/day (i.e. an average between two sites with different environmental conditions: Mitchell et al., 1985), recommended for this ungulate (Ratcliffe and Mayle, 1992; Mayle et al., 1999; see also Fattorini et al., 2011; Ferretti et al., 2011a). As to wild boar, we used a value of 6.7 faeces/day estimated in an enclosed area (size: *c.* 23 ha, at a distance of *c.* 40 km from our study area) with dominance of Mediterranean scrubwood, in the summer 2018 (Fattorini and Ferretti, unpublished).

Selection of ungulates

To evaluate the selection of wild ungulates, yearly scales were considered: Year A (May 2016-April 2017, $n = 83$ scats) 2017 and Year B (May 2017-April 2018, $n = 251$), to compare them with densities estimated in summers 2017 and 2018, respectively. Each year, the availability of each ungulate (a_i) was given by the ratio of its density over the total density of wild ungulates. We compared the observed number of occurrence of each prey (n_i) with the expected one according to its availability, through a *G*-test (Sokal and Rohlf, 1995).

Then, we calculated the selection considering Relative Occurrence and Relative Volume. The use of each wild ungulate species

(r_i) was given by the relative occurrence of each of them in the diet, in respect to the total number of ungulate items. For prey use, 0.95 confidence intervals were calculated for each species according to Neu et al. (1974). For each wild ungulate, we calculated the Jacobs' index (Jacobs, 1974):

$$D_i = (r_i - a_i)/(r_i + a_i - 2r_i a_i)$$

D_i values range from +1 (maximum preference) to -1 (maximum avoidance, Jacobs, 1974). For this index, 0.95 confidence intervals were calculated by resampling our records 1000 times through bootstrap.

Results

Wolf food habits

Overall, wild ungulates and coypu dominated the diet of wolves, building up *c.* 90% Relative Occurrence (RO) and 88% Relative Volume (RV), together (Table 1; Supplementary Material 1). The fallow deer and the wild boar were the most used prey, with the former being the top one (Absolute Occurrence, AO: 55.4%; RO: 41.7%; RV: 43.5%), followed by the latter (AO: 48.2%; RO: 36.3%; RV: 32.7%; Table 1; Figs. 2 and 3). The roe deer was used with a much lower frequency than wild boar and fallow deer, being *c.* 6–8% of diet (Table 1; Fig. 2 and 3). The coypu was another important food item (*c.* 6–8% of diet, depending on the index: Table 1; Figs. 2 and 3), whereas livestock was rarely used (*c.* 2% RO and RV, but *c.* 3–9% RB, Table 1; Figs. 2 and 3; Supplementary Material 1).

In summer, wolf diet was composed almost completely by fallow deer and wild boar, in terms of occurrences and volume (fallow deer: *c.* 48–63% of diet, depending on the index; wild boar: *c.* 35–51%; Fig. 2). These ungulates were the staple of wolf diet also in winter (fallow deer: *c.* 37–50%; wild boar: *c.* 31–46%; Fig. 2). Occurrence of roe deer and coypu increased from summer (*c.* 3–4%, for each of them) to winter (*c.* 8–11%; Table 1; Fig. 2). Livestock,

Table 1
Food habits of wolves in a Mediterranean protected area: absolute and relative occurrences, volumes and relative biomasses food items in the diet (TOTAL: May 2016-April 2018, N = 334 scats; Summer: May-October, n = 145 scats; Winter: November-April, n = 189).

Food item	Absolute Occurrence			Relative Occurrence			Relative Volume		
	TOTAL	Summer	Winter	TOTAL	Summer	Winter	TOTAL	Summer	Winter
Wild boar	48.2	51.0	46.0	36.3	39.4	34.0	32.7	34.9	31.2
Fallow deer	55.4	62.8	49.7	41.7	48.4	36.7	43.5	49.7	38.4
Roe deer	7.8	4.1	10.6	5.9	3.2	7.8	5.8	3.3	7.7
Sheep	1.2	0.0	2.1	0.9	0.0	1.6	0.8	0.0	1.5
Cattle	1.5	0.0	2.6	1.1	0.0	2.0	1.5	0.0	2.6
Coypu	7.8	4.1	10.6	5.9	3.2	7.8	6.0	2.4	8.8
Badger	3.3	3.4	3.2	2.5	2.7	2.3	2.2	2.2	2.3
Porcupine	0.6	0.0	0.5	0.5	0.0	0.4	0.1	0.0	0.5
Hare	0.3	0.7	0.5	0.2	0.5	0.4	0.3	0.0	0.1
Red fox	0.3	0.0	0.5	0.2	0.0	0.4	0.3	0.0	0.5
Mustelid	0.3	0.0	0.5	0.2	0.0	0.4	0.1	0.0	0.1
Felis sp.	0.3	0.0	0.5	0.2	0.0	0.4	0.3	0.0	0.5
Small mammals	0.6	0.0	1.1	0.5	0.0	0.8	0.3	0.0	0.5
Birds	1.2	1.4	1.1	0.9	1.1	0.8	0.1	0.1	0.0
Invertebrates	1.2	0.7	1.6	0.9	0.5	1.2	0.1	0.0	0.1
Fruits	3.0	1.4	4.2	2.3	1.1	3.1	0.3	0.5	0.1
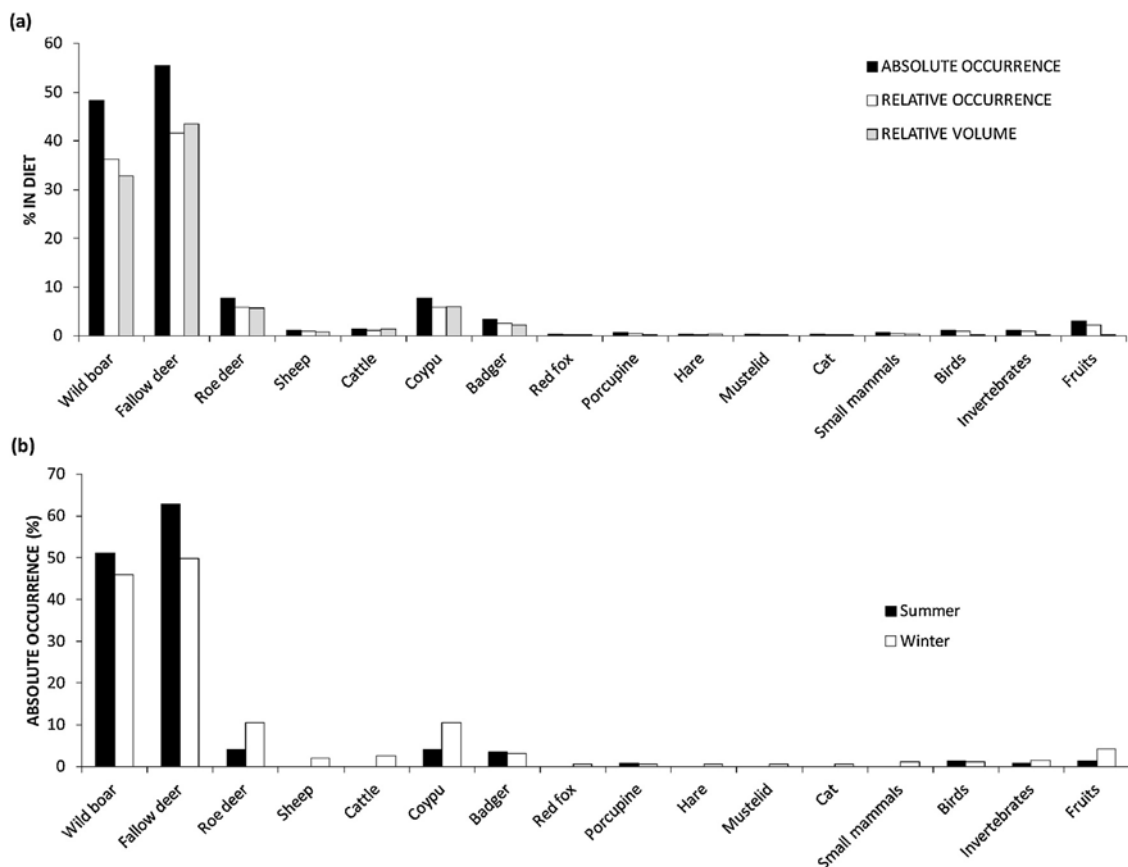
Fig. 2. Food habits of wolves in a Mediterranean protected area: (a) absolute occurrence, relative occurrence and relative volume of food items in the diet (May 2016-April 2018, N = 334 scats); (b) absolute occurrence of food items in summer (May-October, n = 145) and winter (November-April, n = 189) diet.

mainly cattle, was used only in winter (RO: 3.5%; RV: 4.1%; Table 1; Fig. 2). The Standardised Levins index was 0.27 throughout the study, being 0.19 in summer and 0.33 in winter.

Wolf prey selection

In both summer 2016 and 2017, in our study area, the wild boar was the most abundant ungulate (density: 12.5–15.1 individuals/100 ha, depending on year), followed by the fallow deer (9.6–9.8 individuals/100 ha) and the roe deer (7.6–7.7 individu-

als/100 ha, Table 2). In both years, the number of occurrences of ungulate species in the wolf diet differed significantly from the number expected on the basis of their availability (G-test, 2016: $G = 29.4$, $df = 2$, $p < 0.001$; 2017: $G = 112.7$, $df = 2$, $p < 0.002$). Thus, the usage of ungulates by wolves did not reflect their availability, being the fallow deer the most used one, followed by the wild boar and by the roe deer (Table 2). The selection of deer species was consistent between years: fallow deer were selected, roe deer were used less than their availability, whereas wild boar were used according to their availability (Fig. 4).

Table 2

Densities (and 0.95 confidence intervals), relative availability and relative use (and 0.95 confidence intervals, estimated through the Relative Occurrence) of fallow deer, roe deer and wild boar in the study area, in 2016/17 and 2017/18, estimated through ungulate pellet group counts and analyses of wolf scat contents.

Ungulate prey	Density (0.95 CIs)		Availability		Use (0.95 CIs)	
	2016/17	2017/18	2016/17	2017/18	2016/17	2017/18
Fallow deer	9.8 (2.2)	9.6 (2.2)	0.30	0.33	0.50 (0.13)	0.50 (0.07)
Roe deer	7.7 (3.5)	7.6 (3.2)	0.24	0.26	0.10 (0.08)	0.06 (0.03)
Wild boar	15.1 (5.6)	12.5 (3.8)	0.46	0.41	0.40 (0.13)	0.44 (0.07)
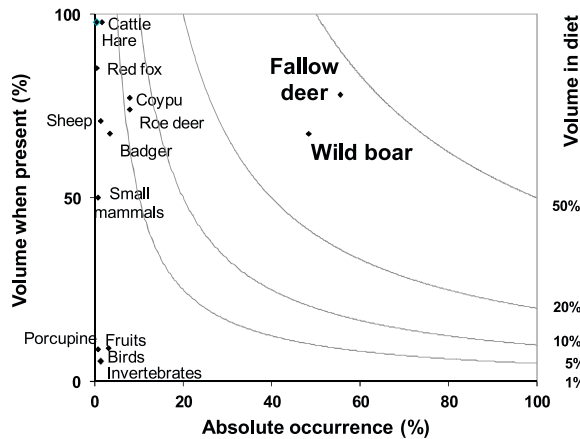
Fig. 3. Food habits of wolves in a Mediterranean protected area: Absolute frequency of occurrence, Volume when present (%) and Volume in diet (%) of food items in the diet (May 2016-April 2018, N = 334 scats).
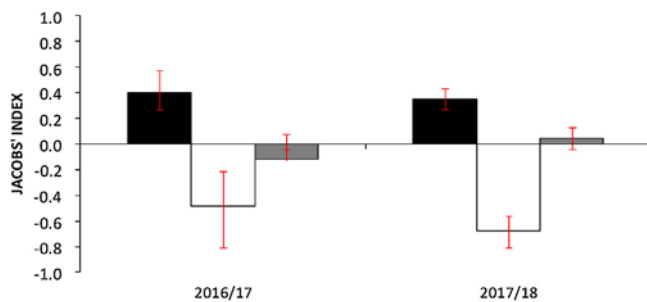
Fig. 4. Selection of wild ungulates (black: fallow deer; white: roe deer; grey: wild boar) by wolves in a Mediterranean protected area, estimated through the Jacobs' index and 0.95 confidence intervals.

Discussion

Throughout our study, in a hilly Mediterranean coastal area including a diverse guild of wild ungulates (3 species), livestock and a rich community of meso-mammals (8 species among rodents, lagomorphs and carnivores), wolves relied largely on wild prey and, among them, wild ungulates were the staple of diet (Meriggi and Lovari, 1996; Meriggi et al., 2011; Torres et al., 2015). Our results agree with those observed in other Mediterranean areas with great abundance of wild prey (e.g., Barja, 2009; Meriggi et al., 2011; Stahlberg et al., 2017). Fallow deer and wild boar built up about 85–90% of wolf diet in summer and were largely used in winter, whereas the use of alternative prey (mainly roe deer and coypu) increased from summer to winter (Manghi and Boitani, 2012). However, wolves did not use ungulates according to their availability.

Encounter rates are expected to be higher for prey living in large groups than for solitary-living ones (Hebblewhite and Pletscher, 2002; Creel and JaJr, 2005). Both wild boar and fallow deer can form large social groups which, especially in summer, usually include a large proportion of newborn/young individuals, that are frequent

prey to wolves (Apollonio et al., 1998; Gazzola et al., 2005; Mattioli et al., 2011). Moreover, wild boar are usually noisy when moving, which makes them easily detectable because of e.g., grunts, smell and squeals. Roe deer tend to be gregarious only during the cold season, when they form groups the size of which increases with habitat openness and homogeneity, but is usually of less than 10 individuals, whereas solitary males/females or females with 1–3 fawns are the usual social groups in the other seasons (Hewison et al., 1998; for our study area: Fattorini and Ferretti, 2019). A greater detectability of roe deer in the cold months than in summer, because of grouping, may explain the increase in the use of roe deer in winter. Interspecific differences in patterns of gregariousness of wild ungulates were probably an important factor influencing the local prey use by wolves.

Our results suggest that fallow deer were preferred to wild boar and, especially, roe deer. This result may appear surprising, because the wild boar and the roe deer have been frequently reported as the main wild prey to wolves in Italy, and in Europe in general (Newsome et al., 2016; Mori et al., 2016, for reviews). In particular, wild boar have been reported as selected in other study areas in Italy, whereas fallow deer have been avoided or little used (e.g., Meriggi et al., 1996; Mattioli et al., 2004, 2011; Stahlberg et al., 2017). In our study area, fallow deer locally can reach densities greater than 40–50 individuals/100 ha, i.e. in ecotones and grasslands (Ferretti et al., 2011a, 2018), where they can form groups up to many tens of individuals (Pecorella et al., 2019). Ecotone areas intensively used by fallow deer herds include mainly abandoned olive groves partially recolonised by scrubwood, meadows and pastures with trees in lowland areas, where bushy patches – likely suitable to wolf attacks – are interspersed with patches of greater habitat openness (cf. Torretta et al., 2017). Additionally, active defence of piglets by mothers, as well as large body size and longer tusks in adult males, may make wild boar a more costly – potentially dangerous – prey than fallow deer, among which females and young individuals cannot rely on potentially defensive weapons such as large antlers. Thus, wolves may address their predatory activity preferentially to fallow deer.

Coypu and roe deer were alternative prey, especially in winter, i.e. when the availability of main prey likely decreased. Large rodents have been reported as significant alternative prey to wolves (e.g., Thurber and Peterson, 1993; Sidorovich et al., 2017). Conversely, the very low use of roe deer may appear surprising (cf. Newsome et al., 2016; Mori et al., 2017). In our study area, behavioural interference has been reported between the fallow deer and the roe deer, with the latter being displaced by the former from shared feeding grounds, also through direct aggression, and being less abundant in areas with high densities of fallow deer (Ferretti, 2011; Ferretti et al., 2011a, 2011b; see also Putman and Sharma, 1987; Focardi et al., 2006; Imperio et al., 2012; Elofsson et al., 2017). In our study area, the greatest densities of roe deer were observed in scrubwood/ecotones (Ferretti et al., 2011a; Ferretti et al., 2018) and this deer showed a selection for dense, scrubby vegetation growing on steep, rocky grounds, avoided by fallow deer (Minder, 2006). Predation by wolves on roe deer has been shown to increase with growing density of this deer species (Meriggi et al., 2015) and to decrease with the increase of forest

cover (Mattioli et al., 2004). Most likely, wolves detected fallow deer groups in open, lowland grounds, easier than roe deer, which mainly attended concealing habitats. If so, moving to competition-free areas would provide roe deer with a refuge from predation as well.

Although wolves can make substantial use of livestock also when wild prey is abundant (e.g., Okarma, 1995; Treves et al., 2004; Bradley and Pletscher, 2005; Nelson et al., 2016), in our study area wolves used livestock only occasionally (e.g., Meriggi et al., 1996; Jędrzejewski et al., 2000; Capitani et al., 2004; Mattioli et al., 2004, 2011; Ansorge et al., 2006; Barja, 2009; Stahlberg et al., 2017). Our results are consistent with great availability of large wild prey reducing consumption of livestock (Meriggi and Lovari, 1996; Sidorovich et al., 2003; Meriggi et al., 2011). Relative accessibility of livestock in relation to that of wild prey, which is influenced by local husbandry techniques, is a key factor influencing livestock depredation (e.g., Okarma, 1995; Newsome et al., 2016). Availability of wild prey alone is insufficient to limit livestock depredation, because it could sustain abundant populations of predators, which would ultimately enhance livestock depredation (e.g., Treves et al., 2004; Bradley and Pletscher, 2005; Suryawanshi et al., 2013; Nelson et al., 2016). In our study area, livestock is mainly composed by herds of cattle, as well as sheep. Calves are the most vulnerable individuals in cattle herds (Meriggi et al., 1991, 1996; Fico et al., 1993). Most likely, herd cohesion and active defence provided by adult cows towards predators makes calves a relatively dangerous prey in respect to wild ungulates (Meriggi et al., 1991, 1996). Calf vulnerability is the highest in birthing periods (winter-early spring), as well as during farming stages when they are separated from mothers (autumn). Although the level of livestock use was low during our study also in these periods, the adoption of protection measures/recoveries in these stages of the farming process would further reduce the risk of calf depredation (Ciucci and Boitani, 1998; Smith et al., 2000; Musiani et al., 2003; Treves et al., 2016). As to sheep, the presence of alternative preventive measures (direct surveillance by the shepherd during the day, livestock guarding dogs and fences) likely deterred attacks. Most likely, livestock was less accessible and vulnerable to wolf predation than wild ungulates, in our study area, which would contribute to explain our results. We suggest that the availability of an adequate and diverse spectrum of wild prey (Meriggi and Lovari, 1996; Meriggi et al., 2011) and the relatively lower accessibility of livestock, also through adequate prevention/protection measures (e.g., Treves et al., 2016), were two concurrent factors contributing to limit wolf-human conflicts.

Author contribution

FF planned this study, collected most data, participated in prey identification, analysed data and wrote the first draft; MR participated in data collection and, together with VM and LB, in prey identification and data analyses; SL participated in study planning, data discussion and writing.

Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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