

Recolonizing wolves and opportunistic foxes: interference or facilitation?

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The mechanisms of interactions among carnivore species range from facilitation (mainly through increased availability of prey carcasses) to competition. We assessed the potential for facilitative/competitive interactions between the two most widespread carnivores in the world, the wolf and the red fox, in a prey-rich area recently recolonized by the apex predator. One could expect that the superior competitor would ecologically suppress the inferior one, leading to avoidance of the former by the latter. In a Mediterranean coastal area (2017–2018), we assessed spatiotemporal and dietary interspecific overlap and investigated whether the recovery of wolves affected food habits of foxes. Spatiotemporal overlap was extensive (0.84–0.89). Wild ungulates were the staple of the wolf diet (~88–90%); foxes used mainly invertebrates and fruits (~78%), with ungulates being a substantial food category (13% of diet; 66% of occurrences among vertebrate prey). Interspecific dietary overlap was low (0.23), but extensive (0.89) for vertebrate prey. In comparison to a preceding wolf-free period, the volume and occurrence of large mammals in the diet of foxes showed a 2.8- to 3.5-fold increase. Apparently, foxes did not avoid wolves, which provided additional food to the foxes as prey leftovers. In a rich community, the presence of wolves may increase the food spectrum of foxes. Temporal variation of facilitation vs. competition should be assessed in relationship to spatiotemporal changes of predator–prey numbers.

ADDITIONAL KEYWORDS: carnivores – facilitation – food habits – food web – interspecific competition – intraguild interactions.

INTRODUCTION

In natural communities, interspecific coexistence is facilitated by resource partitioning, e.g. the use of different food resources, habitats and/or space, in addition to different temporal activity patterns (Gause, 1934; Pianka, 1973; Schoener, 1974). Nevertheless, interspecific overlap in resource use is common, leading to a range of complex facilitative and competitive effects (Arsenault & Owen-Smith, 2002; Wilmers & Getz, 2005; Ripple *et al.*, 2014). Interspecific killing is frequent between carnivorous mammals, with larger species usually dominant over smaller ones through

intraguild predation or interference competition (for reviews, see Palomares & Caro, 1999; Donadio & Buskirk, 2006). Although facilitative effects of larger species over smaller ones can occur (Wilmers *et al.*, 2003; Ripple *et al.*, 2014), smaller species often adopt behavioural tactics to avoid encounters with larger ones (e.g. Durant, 1998; Vanak *et al.*, 2013; Karanth *et al.*, 2017).

Apex predators are key components of ecosystems, with their actions potentially influencing organisms belonging to lower trophic levels (Hebblewhite *et al.*, 2005; Kuijper *et al.*, 2013; Ripple *et al.*, 2014; Ferretti *et al.*, 2020). The effects of large carnivores on the behaviour and/or ecology of their prey are triggered by predation (e.g. Sinclair *et al.*, 2003; Fortin *et al.*, 2005).

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In contrast, the outcome of interactions with other carnivores can be more complex (Ritchie & Johnson, 2009; Sivy *et al.*, 2017; Prugh & Sivy, 2020) and can trigger further consequences at the ecosystem level (Levi & Wilmers, 2012; Sivy *et al.*, 2018). Evolutionary theory and empirical studies suggest two alternative scenarios for interactions between apex predators and smaller carnivores. Avoidance of interference by larger competitors would be expected to promote ecological partitioning (Durant, 1998; Vanak *et al.*, 2013; Karanth *et al.*, 2017). However, carcass remains left by apex predators can provide feeding opportunities for subordinate carnivores through scavenging, thereby promoting facilitative interactions (Wilmers *et al.*, 2003; Selva *et al.*, 2005; Pereira *et al.*, 2014). According to the first scenario (hereafter, 'avoidance hypothesis'), smaller sized carnivores should be expected to adopt behavioural ploys to limit the risk of encounters with larger ones. According to the second scenario (hereafter, 'facilitation hypothesis'), smaller species would be expected to show ecological overlap with larger ones. Supporting evidence for these alternative expectations would improve our understanding of interspecific interactions that shape relationships between carnivores.

We considered the main apex predator in temperate ecosystems, i.e. the wolf *Canis lupus* Linnaeus, 1758, and the local most widespread mesocarnivore, i.e. the red fox *Vulpes vulpes* (Linnaeus, 1758) (Hoffmann & Sillero-Zubiri, 2016; Boitani *et al.*, 2018). The former is mainly dependent on large mammals (Newsome *et al.*, 2016), whereas the latter uses a broader range of food resources, from fruits to invertebrate and vertebrate prey, according to their availability (Macdonald, 1977; Cavallini & Lovari, 1991; Díaz-Ruiz *et al.*, 2013). Predation on newborn ungulates by foxes has been reported, corresponding to ungulate birth periods (Aanes & Andersen, 1996; Jarnemo *et al.*, 2004). A low interspecific dietary overlap has been detected in two mountainous Mediterranean areas, with low (Patalano & Lovari, 1993) and high availability (Bassi *et al.*, 2012) of wild ungulates, respectively. Wolves can kill red foxes (Palomares & Caro, 1999 and references therein; Wikenros *et al.*, 2017), which would be expected to elicit avoidance reactions to the former by the latter. However, foxes can benefit from carcasses of wolf prey (Jędrzejewski & Jędrzejewska, 1992; Selva *et al.*, 2005; Wikenros *et al.*, 2013). Looking for scavenging opportunities might stimulate overlap between these two carnivores on one or more axes of the ecological niche (diet, space and/or time). Multifactorial studies would help in elucidating the behavioural and ecological mechanisms of interactions between these canids. Moreover, the recent recovery of the wolf in Europe (Chapron *et al.*, 2014) provides the opportunity for comparing ecological parameters of the red fox in the presence vs. absence of the apex

predator, thus increasing our potential to understand the effects of the latter on the behaviour and ecology of the former.

We investigated temporal, spatial and dietary relationships between the wolf and the red fox in an area holding a rich community of wild ungulates and other medium-sized mammals (Ferretti *et al.*, 2019). The food habits and habitat use of foxes had been analysed in this area (Cavallini & Lovari, 1991; Lovari *et al.*, 1994) before the local return of apex predators (2005–2006; Caniglia *et al.*, 2013), which has provided the opportunity to compare the food habits of red foxes in the absence and presence of the apex predator. According to the 'avoidance hypothesis', we would expect low levels of spatial, temporal and dietary overlap between the wolf and the fox, and no difference in the consumption of large mammals with respect to wolf-free times. Conversely, according to the 'facilitation hypothesis', we would expect high levels of spatial, temporal and dietary overlap between wolf and red fox, with an increase in the use of large mammals with respect to wolf-free times.

MATERIAL AND METHODS

STUDY AREA

Our study was conducted in the central-southern sector (~70 km²) of the Maremma Regional Park (MRP, central Italy; 42°39'N, 11°05'E; Fig. 1). The area is bordered by the Tyrrhenian Sea at its western side, and a large part of its territory is occupied by the Uccellina Hills (maximal altitude 417 m a.s.l., Poggio Lecci). The local climate is mediterranean, with mean daily temperature ranging from 9 °C in January to 24 °C in August, and monthly rainfall ranging from 9.3 mm in July to 81.8 mm in November (average for 2014–2018: data from <https://sir.toscana.it>). The vegetation is composed mainly of Mediterranean sclerophyllic scrubwood (58% of the area) dominated by holm oak *Quercus ilex*, also with strawberry tree *Arbutus unedo*, rosemary *Rosmarinus officinalis*, juniper *Juniperus* spp., erica *Erica multiflora*, and rockrose *Cistus* spp. The area also includes pinewood [~11% (mainly domestic pine *Pinus pinea*, over an understorey of *Phyllirea angustifolia*, *Erica multiflora*, *Myrtus communis* and *Juniperus oxycedrus*, and interspersed with marshland and sandy dunes], olive groves and pastures (15%; partly recolonized by wood and bushes), set-aside grassland (4%) and crops (12%; mainly cereals and sunflowers) (Sforzi *et al.*, 2013; Melini *et al.*, 2019). Besides the wolf and the red fox, the mammalian community includes three wild ungulates, i.e. the wild boar *Sus scrofa*, the roe deer *Capreolus capreolus*, and the fallow deer *Dama dama*, and many medium-sized species, i.e. the crested porcupine *Hystrix cristata*, the coypu *Myocastor*

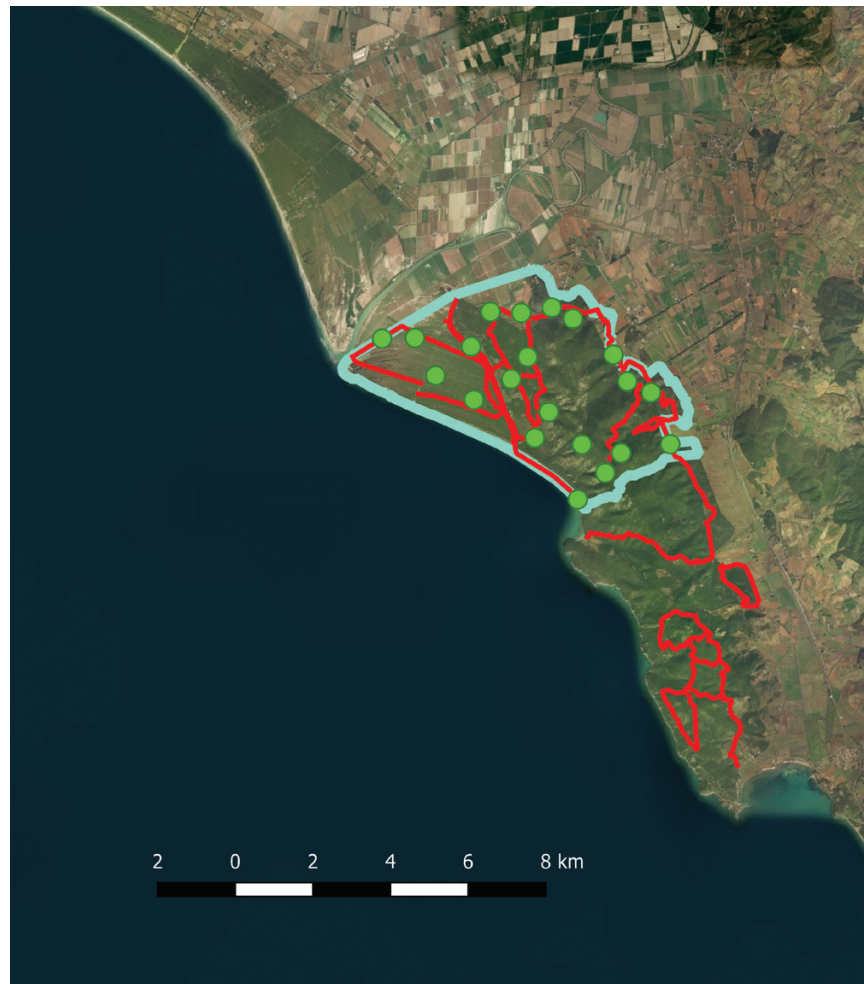


Figure 1. Location of itineraries for scat collection (red lines); borders of the camera trapping study area (pale blue line, coinciding with the area considered for the comparison with Cavallini & Lovari, 1991), with locations of camera traps (green circles).

coypus, the European brown hare *Lepus europaeus*, the Eurasian badger *Meles meles*, the wildcat *Felis silvestris*, the stone marten *Martes foina*, the pine marten *Martes martes*, and various species of smaller mammals. During our study period (2017–2018), ungulate summer densities (i.e. post-birth) were approximately ten to 13 wild boar/100 ha, approximately ten fallow deer/100 ha and six to eight roe deer/100 ha, estimated through faeces counts (Ferretti *et al.*, 2019; Fattorini & Ferretti, 2020). Fallow deer and wild boar have been culled, and wild boar trapped, for population control purposes to reduce damage to habitats, species of conservation interest, and agricultural crops. In the last decade, intensive culling has been followed by a sharp reduction in densities of both wild boar (2010: ~30 individuals/100 ha; 2018–2019: ~10 individuals/100 ha; Ferretti *et al.*, 2016; Fattorini & Ferretti, 2020) and fallow deer (2010: ~15 individuals/100 ha; 2018–2019: ~9–10 individuals/100 ha; Ferretti & Fattorini, 2020).

Roe deer densities decreased from ~ten individuals/100 ha in 2007 to approximately five individuals/100 ha in 2018. No estimates of density are available for ungulates in the 1980s. For the early 1990s, Massei *et al.* (1997a) reported pre-birth minimal densities of 18 wild boar/100 ha, estimated through vantage point counts in March 1993. Figures plummeted to three individuals/100 ha in March 1994, determined by a heavy mortality after a severe drought (Massei *et al.*, 1997a). The number of trapped wild boar/trap/day was 0.6–1.6 in 1991–1993 (June–September: Massei *et al.*, 1997b) and 0.4–0.6 in 2017–2019 (June–September; MRP archives). Summing up wild boar and fallow deer, 584 individuals were shot in 1991–1993 and 495 in 2017–2019 (MRP archives). Overall, these figures suggest no major variations of ungulate numbers between wolf-free and present times.

The wolf was reported as accidental in coastal southern Tuscany at the beginning of the 20th century

(Ghigi, 1911). Wolves were absent from our study area when the Maremma Regional Park was established in 1975 (Arrigoni *et al.*, 1976). Initially, a pack of wolves with signs of admixture with dogs reproduced in the area between 2006 and 2008 (Caniglia *et al.*, 2013). No sign of the presence of this top predator was reported after 2013 (Gallo *et al.*, 2015), suggesting local extinction. On 2015, a pack of wolves settled in the central part of the Park, and 2 years later a second pack formed farther north (Regione Toscana, 2017; Fazzi *et al.*, 2018; Ferretti *et al.*, 2019). During our study, the minimal size of the main pack (i.e. the maximal number of individuals filmed together through standardized camera trapping; see *Spatiotemporal overlap* Section) was six to eight individuals during the cold period (November 2017–April 2018) and four or five individuals in the warm period (May–October 2018, excluding newborn pups). The minimal size of the second pack was seven individuals throughout the study year. The density of wild ungulates was high (~30 individuals/100 ha in summer 2017, pooling the data for the three species; Ferretti *et al.*, 2019). Livestock was also present locally (~20 heads/100 ha), including free-ranging cattle and horses, in addition to two sheep herds (Ferretti *et al.*, 2019). Tourists visit the Park seasonally and mainly concentrate on the beach.

DATA COLLECTION

Food habits of wolf and red fox in sympatry

Food habits were assessed by identification of undigested remains in scats (Kruuk & Parish, 1981; e.g. Cavallini & Lovari, 1991; Ferretti *et al.*, 2019, for our study area). Between November 2017 and October 2018, wolf scats ($N = 292$) and red fox scats ($N = 665$) were collected monthly along itineraries (total length: c. 60 km). The samples were stored in plastic bags marked with a code (date of collection, location and collector's initials) and deep-frozen (-20°C), after which they were analysed in the laboratory. In the field, scats were assigned to fox or wolf according to size, shape, content, location and the characteristic smell (Cavallini & Lovari, 1991; Ferretti *et al.*, 2019). Dubious scats were not collected. No free-ranging/feral dogs were recorded by camera traps in the area (see *Spatiotemporal overlap* Section). DNA genotyping of a subsample of fresh putative wolf scats ($N = 38$; Istituto Superiore per la Protezione e la Ricerca Ambientale, unpublished; Fazzi *et al.*, 2018) confirmed species identification, providing support to our field criteria.

Spatiotemporal overlap

The spatiotemporal overlap between the wolf and the red fox was assessed through camera trapping. Between November 2017 and October 2018, 21 camera

locations were selected: a grid (cell size $1.3\text{ km} \times 1.3\text{ km}$) was superimposed on a sector ($\sim 30\text{ km}^2$) of the study area, using a Geographic Information System (GIS). This sector encompassed the study area of previous studies on red fox behavioural ecology (e.g. Ciampalini & Lovari, 1985; Cavallini & Lovari, 1991; Lovari *et al.*, 1994). Camera traps were placed on suitable trees (one camera per grid cell) located along paths potentially used by carnivores, at a height of 30–60 cm from the ground (Torretta *et al.*, 2017). Cameras were rotated monthly across locations in order to monitor each of them for ~30 days consecutively, every 3 months. We used IR-Plus HD-2 cameras (Ziboni Technology srl, Costa Volpino, BG, Italy), triggered by an infrared motion sensor, set to operate continuously (i.e. 24 h/day) and to record 30 s videos with a minimum time lag of 5 s between consecutive shots (Foster *et al.*, 2013). Each month, we considered a minimal distance of $\geq 1\text{ km}$ between each pair of neighbouring cameras. The cameras were inspected every 1–2 weeks to replace batteries and memory cards, and they were relocated every ~4 weeks. The sampling effort at each location was given by the number of days between positioning and relocation of the camera. When/where the batteries ran flat before replacement, the time of the last exposure was determined from the downloaded videos and considered as the last operational date (Li *et al.*, 2010). The total sampling effort was 2053 trapping days (mean $\pm$ SEM, 97.8 ± 4.1 days).

DATA ANALYSES

Food habits of wolf and red fox in sympatry

In the laboratory, samples were dried in an oven at 60°C for >3 h to inactivate parasites. The scats were examined using tweezers, in water, then washed through a 1–3 mm mesh sieve (Kruuk & Parish, 1981) to separate the undigested components, e.g. hair, fragments of bones, teeth, hooves, feathers, plant material or other unidentified items (Kruuk & Parish, 1981). Hairs and other undigested remains were then dried and stored for later identification. Hairs were compared with a reference collection of hair of potential prey present in the area, with reference manuals and specific identification keys for ungulates (Teerink, 2004; De Marinis & Asprea, 2006a, 2006b). Slides were prepared according to Teerink (2004) and De Marinis & Asprea (2006a). Microscopic evaluation was based upon the analysis of features of the medulla, cuticula and cortex (Teerink, 2004), using a $\times 100$ – $\times 400$ microscope. A blind test was performed to test the skills of the observer (G.P., I.B. and M.R.) in scat analyses: a sample of 75 slides and 25 bags including reference hair were shown to each observer for identification. Observers were allowed to conduct analyses when they identified $\geq 95\%$ of reference samples correctly.

The focus of our study was the interspecific comparison of diets and assessment of temporal variations in the use of large mammals by the red fox, rather than a detailed description of the composition of its diet. Thus, we considered the following categories: wild ungulates, livestock, mesomammals (coyote, porcupine, hare and other carnivores), small mammals (other rodents and smaller mammals), other vertebrates, invertebrates, fruits and unidentified. No method to assess the carnivore diet is free from potential limitations or biases; therefore, the use of several estimators is usually recommended (Ciucci *et al.*, 1996; Reynolds & Aebischer, 2008; Klare *et al.*, 2011). For each i -th food category, the absolute frequency of occurrence (AOcc_i) was calculated: $\text{AOcc}_i = (n_i/N) \times 100$, where n_i was the number of faeces including that category and N was the total number of analysed scats. We also estimated the relative volume of each food category visually, considering volumetric classes 1–5, 6–25, 26–50, 51–75, 76–95 and >95% (Kruuk & Parish, 1981; Kruuk, 1989). For each category, we initially estimated the volume when present, i.e. the mean volume whenever that category was found (VP_i). Then, the estimated volume of each food category in the total diet (EV_i) was calculated as $\text{EV}_i = (\text{total estimated volume of each prey species} / \text{total estimated volume of all prey species}) \times 100$ (Kruuk & Parish, 1981; Lucherini & Crema, 1995; Lovari *et al.*, 2015). The same method was used in previous studies in the same study area (e.g. Cavallini & Lovari, 1991; Lovari *et al.*, 1994; Lucherini *et al.*, 1995). Analyses were conducted at yearly and for 6 month periods ('cold period', November 2017–April 2018; and 'warm period', May–October 2018). The adequacy of the sample size was determined through a Brillouin diversity index (Hb ; index range, 0–4.5; Brillouin, 1956; cf. Glen & Dickman, 2006; Hass, 2009): $\text{Hb} = (\ln N_{\text{tot}}! - \sum \ln n_i!)/N_{\text{tot}}$, N_{tot} being the total number of occurrences of all prey categories in all samples. A diversity curve was calculated by sampling with replacement over a range of three to 101 samples for both carnivores, in increments of two. Diversity curves showed a stabilization of results, with an increase of < 1% for samples > 31 scats, for both species. The volume of food categories in the diet (excluding the unidentified category) was compared between carnivores and between 6 month periods through non-parametric multivariate analysis of variance (NPMANOVA; Anderson, 2001; Torretta *et al.*, 2016a) with permutation (10 000 replicates).

We also estimated the dietary niche breadth for each species and the dietary overlap between the wolf and the red fox. Dietary breadth was assessed using the Levins index (B ; Levins, 1968), which is estimated as $B = 1/\sum \text{EV}_i^2$. This index can take values up to the maximal number of available categories. We then standardized the dietary breadth to express it on a scale ranging from zero (the species feeds on

one category) to one (available categories used in the same proportion), through the standardized Levins index (B_s ; Hurlbert, 1978): $B_s = (B - 1)/(X - 1)$, where X is the number of food categories. For the dietary overlap, we calculated the Pianka index (O_{jk} ; Pianka, 1973): $O_{jk} = (\sum \text{EV}_{ij} \times \text{EV}_{ik}) / \sqrt{\sum \text{EV}_{ij}^2 \times \sum \text{EV}_{ik}^2}$, where EV_{ij-k} is the proportion of resource i of the total resources used by species j and k , in terms of estimated volume. We considered two levels of analysis: (1) the entire spectrum of the diet, with the previously mentioned categories; and (2) vertebrates, i.e. the category characterized by potential common use from both canids, with wild and domestic ungulates being considered at specific level. For these last analyses, we also calculated the relative frequency of occurrence (ROcc_i) as: $\text{ROcc}_i = (n_i/N_{\text{vert}}) \times 100$, where N_{vert} is the total number of food items belonging to vertebrates. Eventually, we correlated the absolute occurrences of vertebrate food categories between the wolf and the fox diets using Pearson's correlation coefficients.

Red fox diet in presence vs. absence of wolf

We compared our results with those reported by Cavallini & Lovari (1991) in November 1985–December 1986, i.e. the most comprehensive study on local food habits of foxes, conducted in the north-central Uccellina area and in the pinewood. To standardize our data spatiotemporally to those of Cavallini & Lovari (1991), we considered the same study area (Fig. 1) and study period (i.e. number of months). Thus, we also included red fox scats collected in November–December 2018 (i.e. our study period was November 2017–December 2018). These analyses were based on a sample of 576 red fox scats. For consistency with Cavallini & Lovari (1991), the comparison was based on: (1) estimated volume of general categories in total diet, i.e. large mammals (wild and domestic ungulates), other mammals, other vertebrates, invertebrates, fruits and unidentified; and (2) the absolute frequency of occurrence of large mammals in the diet, derived from Cavallini & Lovari (1991). Numbers of scats with or without large mammals were compared between periods using the G -test.

Spatiotemporal overlap

For all videos, the date, the solar time of capture and location of the camera traps were recorded (Foster *et al.*, 2013). To limit pseudo-replication, when the same camera trap recorded consecutive videos (temporal distance < 30 min) of the same species we counted them as one event (Monterroso *et al.*, 2014; Torretta *et al.*, 2017), and we considered the data of the first video for subsequent analyses (Lucherini *et al.*, 2009; see also Tobler *et al.*, 2008; Torretta *et al.*, 2016b; Satgé *et al.*, 2017; Mori *et al.*, 2020). Thus,

our analyses have been based on 1354 videos (wolf: $N = 339$; red fox: $N = 1015$). To estimate the temporal overlap between the wolf and the red fox, two stages were involved (Ridout & Linkie, 2009; Linkie & Ridout, 2011). First, we used a non-parametric kernel density function to assess daily activity patterns of the wolf and the red fox (Carter *et al.*, 2015), and we assessed whether the temporal activity patterns were distributed homogeneously throughout a 24 h period using the Watson test (Lund *et al.*, 2017). Second, coefficients of overlap (Δ), ranging from zero (no overlap) to one (complete overlap), were used to estimate the extent of overlap between two kernel density estimates (Ridout & Linkie, 2009; Linkie & Ridout, 2011). In particular, we used the Δ_4 coefficient because sample size was always > 75 (Ridout & Linkie, 2009). The 95% confidence intervals (CIs) for Δ were estimated by 1000 bootstrap samples (Meredith & Ridout, 2017; Linkie & Ridout, 2011). Temporal activity patterns of the two species were compared using Watson's two-sample test. For each location, the passage rate of each species (RAI) was estimated as $RAI = NV_c / \text{number of operating days}$, where NV_c is the number of shots collected per species. The correlation between passage rates of the two species in each location was calculated using the Pearson's correlation coefficient. Eventually, we calculated the relative use of each i -th location (U_i) by the two

carnivores, as $U_i = RAI_i / \sum RAI_i$, which we used to calculate indices of interspecific spatial overlap with the Pianka index, as $O_{jk} = (\sum U_{ij} \times U_{ik}) / \sqrt{(\sum U_{ij}^2 \times \sum U_{ik}^2)}$, where U_{ij-k} is the relative use of each i -th location of species j and k . All analyses were performed for periods of 6 months ('cold' and 'warm' periods; see temporal scales of dietary analyses).

RESULTS

FOOD HABITS OF WOLF AND RED FOX IN SYMPATRY

The diets of the two carnivores were significantly different at all temporal scales (NPMANOVA: $F = 198.12$ – 639.54 , $P < 0.001$). At the yearly scale, wild ungulates dominated the diet of the wolf (AOcc: 90%; EV: 88%), followed by mesomammals (AOcc: 10%; EV: 8%), whereas other categories were of minor importance (Table 1; Fig. 2). The wolf diet differed significantly between 6-month periods (NPMANOVA: $F = 13.582$, $P < 0.001$). The importance of wild ungulates was greater in the warm period (EV: 93%) than in the cold one (EV: 82%), when ~15% of the diet was made up of alternative prey (Table 1; Fig. 2).

The diet of the red fox was based mainly on invertebrates (AOcc: 70%; EV: 35%) and fruits (AOcc: 62%; EV: 43%), with wild ungulates being a

Table 1. Food habits of wolves and red foxes in a Mediterranean protected area: absolute occurrences and estimated volume of food items in the diet (TOTAL: November 2017–October 2018; $N_{\text{wolf}} = 292$ scats, $N_{\text{red fox}} = 665$ scats; Cold period: November–April; $N_{\text{wolf}} = 144$ scats, $N_{\text{red fox}} = 331$ scats; Warm period: May–October, $N_{\text{wolf}} = 148$ scats, $N_{\text{red fox}} = 334$ scats)

Species	Food category	Absolute occurrence			Estimated volume		
		Year	Cold period	Warm period	Year	Cold period	Warm period
Wolf	Wild ungulates	90.4	85.4	95.3	87.6	82.0	93.1
	Livestock	3.4	6.3	0.7	3.1	5.6	0.7
	Meso-mammals	9.6	12.5	6.8	8.1	10.8	5.5
	Small mammals	1.0	1.4	0.7	0.1	0.1	0
	Other vertebrates	0.7	1.4	0	<0.1	<0.1	0
	Invertebrates	0.7	1.4	0	<0.1	<0.1	0
	Fruits	4.5	5.6	3.4	0.5	0.1	0.7
	Unidentified	1.0	2.1	0	0.7	1.3	0
Red fox	Wild ungulates	30.1	39.9	20.4	13.0	16.4	9.6
	Livestock	3.0	6.0	0	1.3	2.6	0
	Meso-mammals	3.8	6.6	0.9	2.0	3.4	0.6
	Small mammals	4.2	7.3	1.2	1.1	1.5	0.6
	Other vertebrates	10.7	17.5	3.9	3.2	4.9	1.5
	Invertebrates	69.9	61.6	78.1	35.2	22.2	48.2
	Fruits	62.3	71.3	53.3	42.7	46.8	38.7
	Unidentified	8.4	10.6	6.3	1.5	2.2	0.8

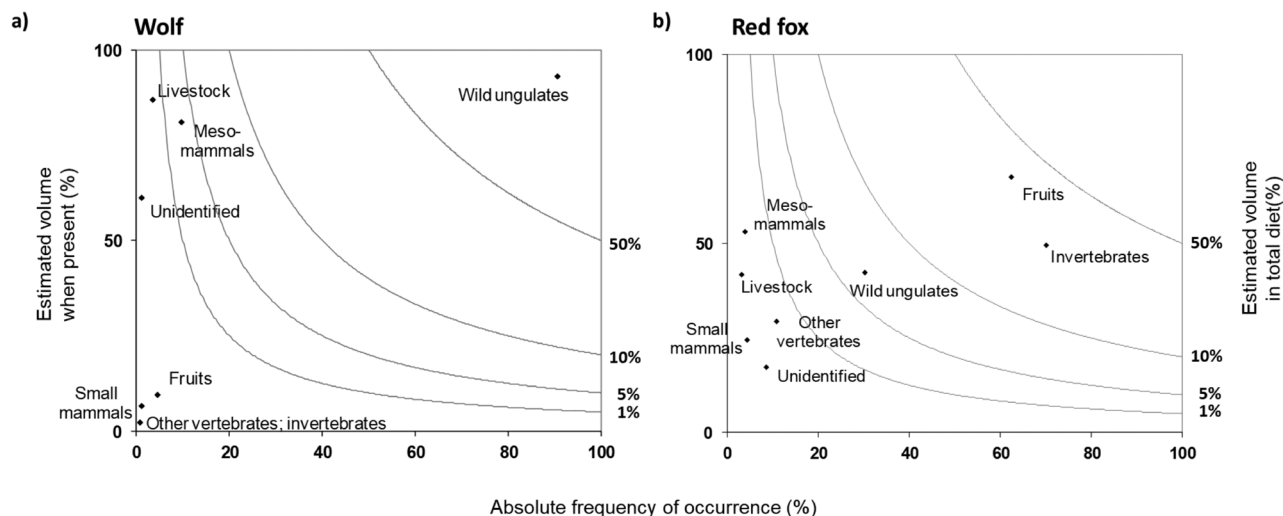


Figure 2. Food habits of the wolf (A) and the red fox (B) in the Maremma Regional Park (November 2017–October 2018; $N = 292$ wolf scats and $N = 665$ red fox scats). The estimated volume when present and the estimated volume in the total diet are shown in relationship to the absolute frequency of occurrence.

substantial alternative food category (AOcc: 30%; EV: 13%) and other mammals and vertebrates together making up ~8–11% of the diet (Table 1; Fig. 2). The fox diet differed significantly between 6-month periods (NPMANOVA: $F = 31.297$, $P < 0.001$). Fruits were the main food item in the cold period, whereas invertebrates predominated in the warm period, with the importance of wild ungulates increasing from the warm period (ROcc: 12%; EV: 10%) to the cold one (ROcc: 18%; EV: 16%) (Table 1; Fig. 2).

With regard to vertebrates, wild boar and fallow deer were the main food resources for both canids (wolf, ROcc = 43% and 39%, respectively, among vertebrates; fox, ROcc = 29% and 28%, respectively, Fig. 3A). Large mammals made up 66% ROcc of vertebrates in the diet of the fox (Fig. 3A). Occurrences of vertebrate categories in the diets of the two canids were correlated ($r = 0.76$ – 0.92 , $P < 0.03$, depending on the temporal scale). Red fox hair was found in only one out of 292 wolf scats (AOcc, 0.3%).

Considering all food categories, the trophic niche of the fox was approximately five to ten times broader than that of the wolf, depending on the temporal scale, with an interspecific dietary overlap of 0.23 (Pianka index: Fig. 3B). In particular, interspecific dietary overlap and the absolute frequency of occurrence of wild ungulates in the diet of the red fox were approximately two times larger in the cold period compared with the warm one (Table 1; Fig. 3C). Restricting the analysis to vertebrates, the dietary breadth of the fox was ~1.5–1.8 times broader than that of the wolf (Fig. 3B). Interspecific overlap was almost complete (Pianka

index: 0.86–0.89, depending on the temporal scale; Fig. 3C).

RED FOX FOOD HABITS IN PRESENCE VS. ABSENCE OF THE WOLF

In 1985–1986, fruits and invertebrates together made up > 90% of the estimated volume of the red fox diet, with large mammals (i.e. wild and domestic ungulates) occurring in ~7% of samples, for a total estimated volume of 3% (Fig. 4A). In 2017–2018, fruits and invertebrates together made up ~84% of the total estimated volume. The absolute frequency of occurrence of large mammals was ~24%, significantly greater than in 1985–1986 ($G = 97.986$, d.f. = 1, $P < 0.001$), for a total volume of ~10% (Fig. 4B). The volume of other mammals/vertebrates was ~5–6% in the two periods (Fig. 4A).

SPATIOTEMPORAL OVERLAP

Both species were active especially at night and at dawn/dusk, with temporal activity patterns significantly different from homogeneity ($U = 21.32$ – 80.91 , $P < 0.01$; Fig. 5). Interspecific temporal overlap was extensive in both periods ($\Delta_4 \geq 0.90$; Figs 5, 6), with no significant difference between activity patterns of the two species ($U^2 = 0.14$ – 0.16 , $P > 0.05$). Passage rates of the two canids were correlated at the yearly scale ($r = 0.84$, $P < 0.001$) and in the cold period ($r = 0.96$, $P < 0.001$), but not in the warm period ($r = 0.27$, $P = 0.254$). Accordingly, interspecific spatial overlap was 0.84 at the yearly scale, 0.92 in the cold period and 0.52 in the warm period (Fig. 6).

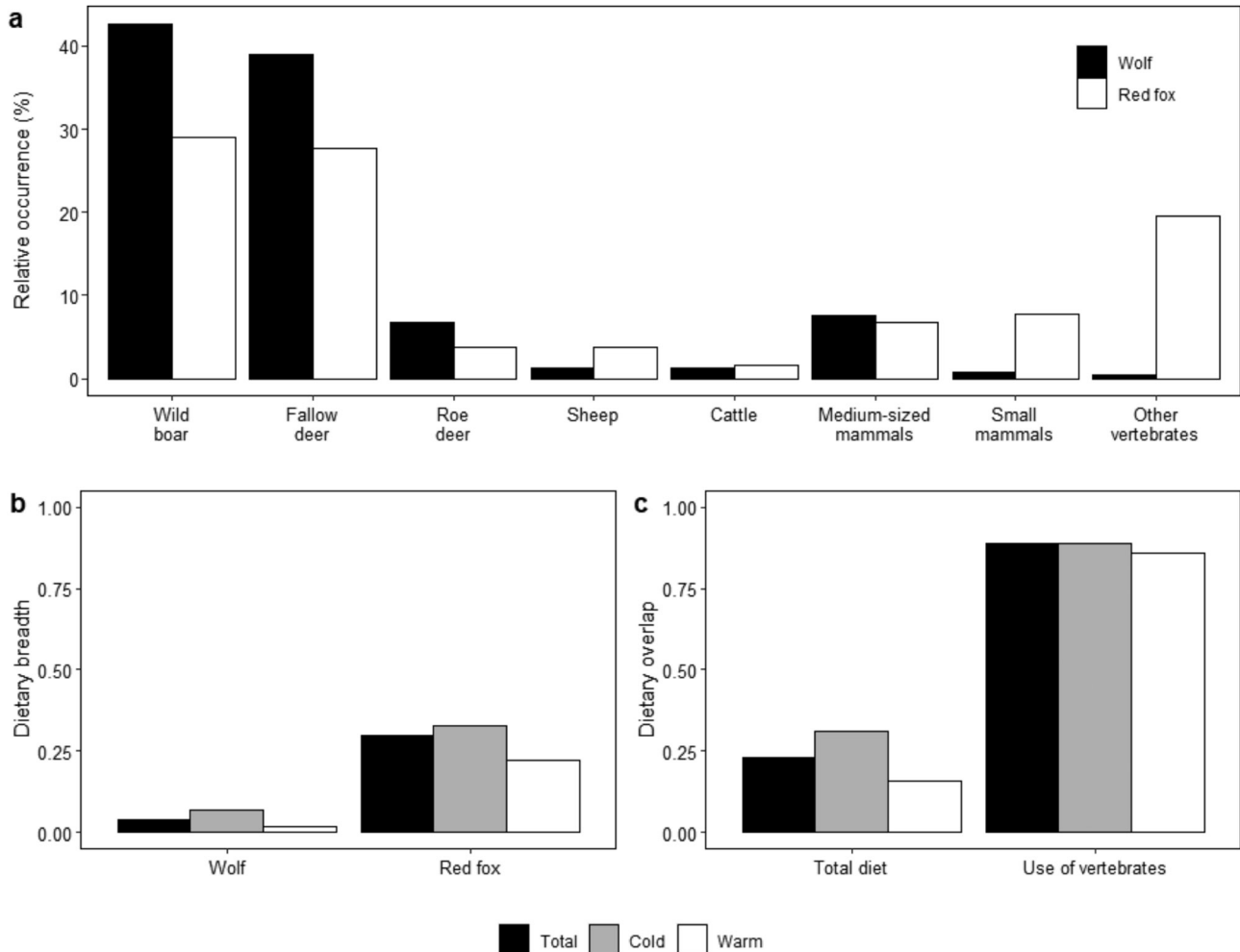


Figure 3. (A) use of vertebrates by the wolf and the red fox, shown as the relative frequency of occurrence, calculated as a percentage of the total number of vertebrate items found in the diet. Dietary breadth (B) and interspecific dietary overlap (C) of the wolf and the red fox (cold period, November 2017–April 2018; warm period, May–October 2018; and total, November 2017–October 2018).

DISCUSSION

Interspecific overlap in the use of resources, e.g. carcasses, can lead to non-neutral interactions ranging from facilitation to competition (Palomares & Caro, 1999; Donadio & Buskirk, 2006; Ritchie & Johnson, 2009; Prugh & Sivy, 2020). Here we show, for an apex predator (the wolf) and a mesocarnivore (the red fox): (1) significant interspecific spatiotemporal overlap; (2) an interspecific partitioning of diet, with the wolf mainly exploiting wild ungulates and the fox feeding mainly on fruits and invertebrates; and (3) a substantial use of large mammals by the fox, with ungulates occurring in its diet much more than they were reported to do when the wolf was not present. Red fox occurrence in the wolf diet was negligible. Studies conducted in 1980s through radio-tracking reported nocturnal activity patterns of foxes (Cavallini & Lovari, 1994; Lovari

et al., 1994; Lucherini *et al.*, 1995), which have been confirmed by our data. Thus, the presence of wolves did not seem to affect the activity patterns of foxes. In our study area, foxes avoided the wolves neither temporally nor spatially; thus the ‘avoidance hypothesis’ was not supported. Conversely, our results are in agreement with the ‘facilitation hypothesis’, strongly suggesting that foxes benefit from increased foraging opportunities provided by carcasses left by wolves.

The results of our comparison are consistent with those of studies conducted in 1980s in the main habitats of our study area. Mammals (mainly rodents and lagomorphs) were reported in ~21–22% fox scats collected in 1982–1983 in the ecotone between sand dune, pinewood and scrubwood (Ciampalini & Lovari, 1985; Calisti *et al.*, 1990). The occurrence of large mammals in the diet of foxes radio-tracked in a rural

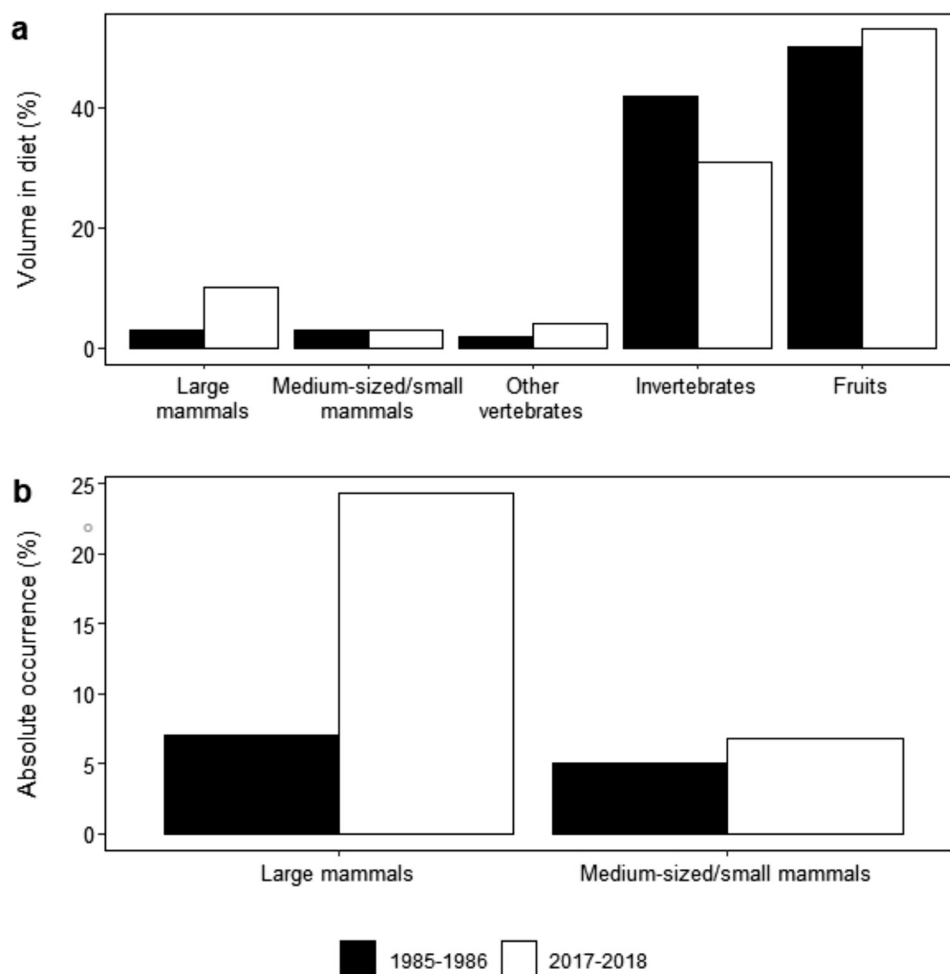


Figure 4. Food habits of the red fox in 1985–1986 (wolf absent, $n = 1180$ scats, November 1985–December 1986; Cavallini & Lovari, 1991) and 2017–2018 (present study, wolf present, $n = 576$ scats, November 2017–December 2018). A, estimated volume in the diet of different food categories. B, absolute occurrence of mammals.

area and in the pinewood was low (1987–1989: ~0–40% per individual, $N = 8$ foxes monitored for 4–12 months per individual; Lovari *et al.*, 1994; Lucherini *et al.*, 1995). Conversely, remains of mammals occurred in 34% of scats analysed throughout our study, and ~80% of them included ungulates. In the 1980s–1990s, culling of wild boar and fallow deer had been implemented by the MRP Agency to limit their negative effects on biodiversity and agriculture, suggesting that the densities of these ungulates were not low, and their availability to foxes may have not increased with respect to wolf-free times (see Material and Methods subsection ‘Study area’). Red fox predation on wild ungulates has been reported to be restricted mainly to newborn offspring (Aanes & Andersen, 1996; Jarnemo *et al.*, 2004; Panzacchi *et al.*, 2008, for predation on roe deer fawns). Thus, predation by foxes on ungulates should be expected in spring to early summer. We reported the presence of wild ungulates in the fox diet all year round, which

is consistent with wolves providing foxes with an increased availability of ungulate leftovers.

Occurrence of wild ungulates in the fox diet was approximately twice as high in the cold period than in the warm one. Water availability is a major limiting factor for wild mammals in Mediterranean habitats, with summer drought usually making the warm season a bottleneck for herbivores (for our study area, see Massei *et al.*, 1997a). During a dry autumn–winter (i.e. with only 15 rainy days and 132 mm of rainfall), red foxes made use of carcasses of wild boar that died of starvation in late winter (Lovari *et al.*, 1994). During our study, 73 days with rain and 287 mm of rainfall were reported in autumn–winter (<https://sir.toscana.it>), indicating no drought. An increase of carcasses available because of natural mortality in winter is unlikely to have occurred. Although our results need confirmation, we suggest two potential (not mutually exclusive) explanations for the increase of ungulates

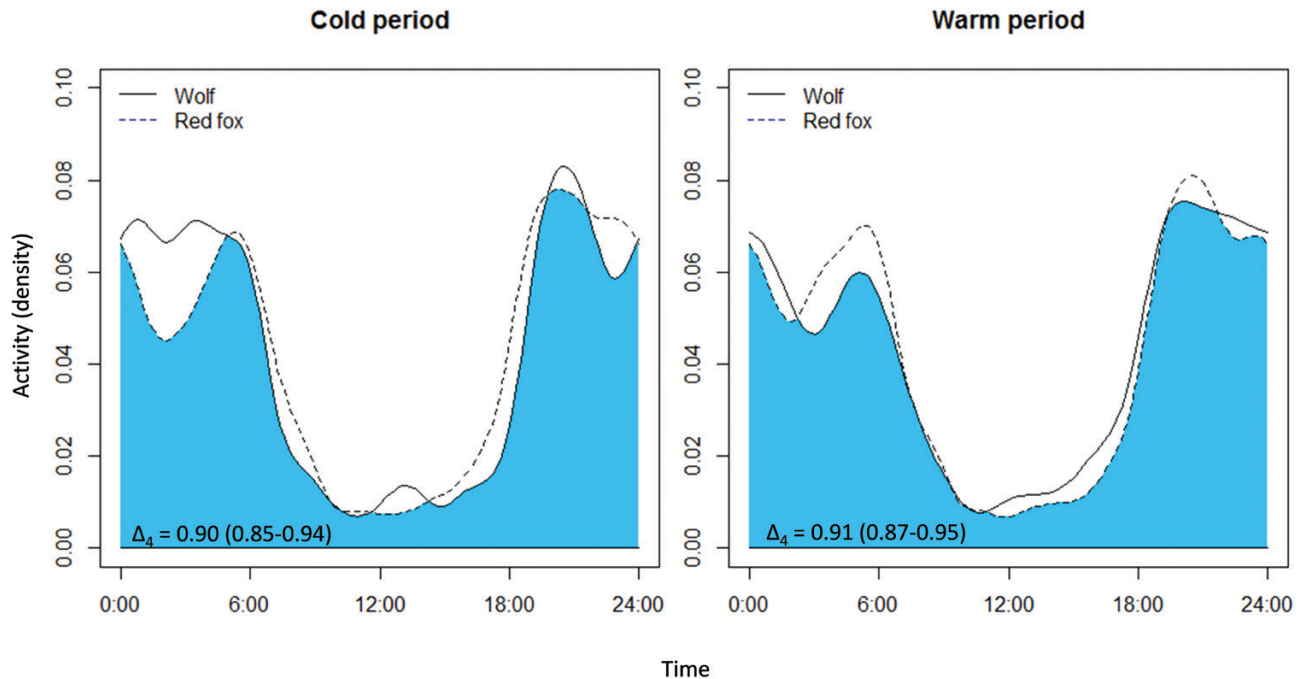


Figure 5. Interspecific overlap of temporal activity between the wolf and the red fox. Cold period, November 2017–April 2018 ($n = 227$ wolf videos and $n = 633$ red fox videos); warm period, May–October 2018 ($n = 112$ wolf videos and $n = 382$ red fox videos). Indices of temporal overlap with bootstrapped 95% confidence intervals are given; the blue area denotes the area of overlap.

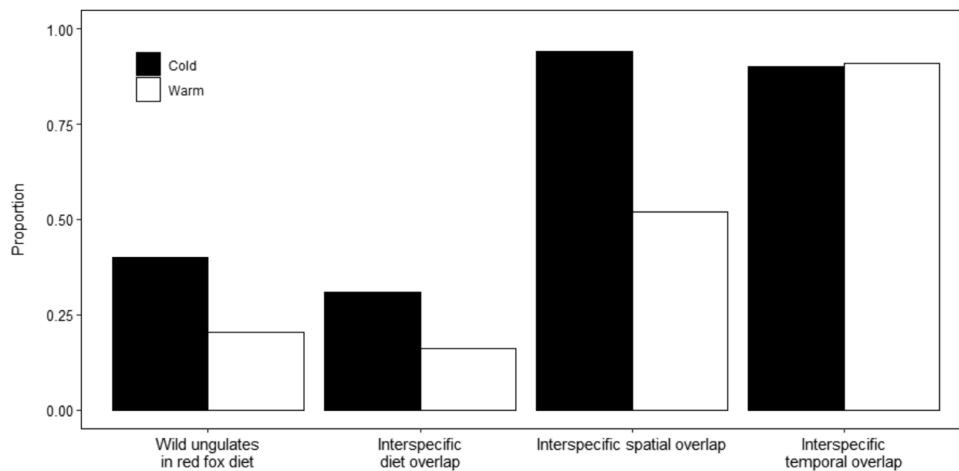


Figure 6. Spatiotemporal and dietary relationships between the wolf and the red fox (cold period, November 2017–April 2018; warm period, May–October 2018).

in the fox diet during the cold period. First, during the warm period invertebrates, especially Orthoptera, are abundant (i.e. major local food resources for foxes; Ciampalini & Lovari, 1985; Calisti *et al.*, 1990; Cavallini & Lovari, 1991; our unpublished data, for 2017–2018). Second, during the warm period wolf pups are kept in the den and in rendezvous sites,

where other pack members provide them with prey; from autumn onwards, they increase their ranging movements and pups join pack members in hunting (Jedrzejewski *et al.*, 2001; Mech & Boitani, 2003). Thus, the availability of prey carcasses on the ground would be expected to be lower in spring–summer than in autumn–winter.

In North American temperate ecosystems, wolves have been shown to limit the abundance of coyotes *Canis latrans* (Smith *et al.*, 2003; Berger & Gese, 2007; Sivy *et al.*, 2017). The mechanisms for coexistence with the fox are less clear (Pasanen-Mortensen *et al.*, 2013; Wikenros *et al.*, 2017). In American ecosystems, where coyotes are also present, a three-level interaction can occur, with wolves suppressing coyotes, thus releasing foxes and other smaller carnivores from competition with this larger canid (Wilmers *et al.*, 2003). Moreover, the availability of carcasses of wolf prey can lead coyotes to increase scavenging and limit their predation on smaller prey, thus facilitating resource partitioning and coexistence with the fox (Sivy *et al.*, 2018). In ecosystems which lack carnivores intermediate in size between apex predators and the red fox, for example in Europe, a greater potential for a direct relationships between the two might be expected. The Eurasian lynx *Lynx lynx* is known to kill red foxes (Sunde *et al.*, 1999; Helldin *et al.*, 2006), with potential effects at the population level (Pasanen-Mortensen *et al.*, 2013; Jiménez *et al.*, 2019; but see Wikenros *et al.*, 2017). Conversely, the impact of wolf abundance on fox populations is unclear (Pasanen-Mortensen *et al.*, 2013; Wikenros *et al.*, 2017). Negative effects have been recorded at the pack territory scale at higher latitudes (Wikenros *et al.*, 2017), although general conclusions cannot be drawn (Prugh & Sivy, 2020).

Wolf pack size has been suggested as an important factor influencing wolf–fox interactions, with red fox abundance decreasing with wolf pack size (Wikenros *et al.*, 2017). Large packs (i.e. six to nine individuals) are expected to leave a smaller amount of biomass available to scavengers than would smaller ones (Zimmermann *et al.*, 2015). The presence of carcasses can attract meso-carnivores, increasing the probability of encounters with superior competitors, ultimately triggering interspecific killing ('fatal attraction hypothesis'; Sivy *et al.*, 2017; Prugh & Sivy, 2020). The probability of encounters between foxes and wolves should increase with pack size, thereby triggering interference. The pack size in our study area was large, especially in winter (seven or eight individuals), but predation on foxes was negligible. Interspecific killing is not always followed by the consumption of the victim by the killer species (Palomares & Caro, 1999). If so, wolves might not feed on the carcasses of killed foxes, potentially leading to an underestimate of competition-related mortality of the latter through analyses of scat contents. We found no evidence of behavioural avoidance of wolves by foxes, suggesting that interference was not a major primer of interactions between these carnivores. A concurrent study has shown that interspecific temporal overlap was greater in sites with high wolf activity than in sites less attended by wolves, suggesting that foxes can

adjust their activity patterns to match those of the wolf (M. Rossa, S. Lovari and F. Ferretti, unpublished data).

It has been suggested that interspecific interference is favoured by taxonomic relatedness and dietary overlap; this extreme mechanism of competition has probably evolved for the rapid elimination of a potential competitor and/or killer of cubs (Palomares & Caro, 1999; Donadio & Buskirk, 2006). Not surprisingly, adaptive mechanisms of coexistence among species of carnivore are largely based on avoidance of interference (Palomares & Caro, 1999; Donadio & Buskirk, 2006, for reviews). Competition is triggered by overlap in the use of scarce resources (de Boer & Prins, 1990). Accordingly, where prey availability is low, interference can be more frequent (Palomares & Caro, 1999; Prugh & Sivy, 2020). Moreover, meso-carnivores might then exhibit increased attraction to carcasses, and will be more likely to be killed by larger carnivores (Prugh & Sivy, 2020). The availability of wild ungulates was remarkably high in our study area (~30 individuals/100 ha, after births; see Fuller *et al.*, 2003, for a review of population densities of wolf prey in other study areas), indicating favourable foraging conditions and a low potential for interspecific competition. Therefore, the motivation to kill foxes approaching a carcass might have been low for wolves; if so, high availability of wild ungulates may be the key to coexistence between these two carnivores. Suggestively, in spring and summer the use of ungulates by foxes decreased, but their temporal overlap with the wolf remained high. Activity when the probability of encounters with wolves is high might even benefit foxes, although our results require confirmation. Future work should assess the spatial and temporal variation of resource overlap between these carnivores according to spatiotemporal variation of wolf pack size and ungulate density.

There is a wide debate on the role of the wolf in shaping communities through top-down cascading effects (Ripple *et al.*, 2014; Martin *et al.*, 2020; but see Mech, 2012; Barber-Meyer, 2015). The potential for a regulatory role of wolves on other components of communities has been questioned for ecosystems greatly modified by human action (Kuijper *et al.*, 2016), where reliance on abundant livestock carcasses may alter their predatory behaviour (Ciucci *et al.*, 2020). Conversely, in more natural ecological communities, the action of wolves could be expected to play an important role in shaping behaviour and ecology, in addition to the genetic structure (Frati *et al.*, 2000) of mesocarnivores. Variation in key factors, such as climate, resource availability and competitor numbers, is expected to play a major role in influencing the potential for facilitation vs. competition (Palomares & Caro, 1999; Ritchie & Johnson, 2009; Prugh & Sivy, 2020). If so, suitable foraging conditions may promote a facilitative role. The spontaneous recovery of wolves

in European ecosystems (Chapron *et al.*, 2014) would probably provide the opportunity to test short- and long-term effects of the presence of this apex predator on organisms belonging to lower trophic levels, further clarifying eco-evolutionary determinants of multispecies interactions among different components of ecosystems.

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