Journal of Zoology
Journal of Zoology. Print ISSN 0952-8369

ORIGINAL RESEARCH

Spatiotemporal plasticity of prey selection in the wolf

I. Belardi[1], J. Borkowski[2,†], L. Lazzeri[1], R. Banul[3], G. Pacini[1], A. Poerling[3] & F. Ferretti[1,4,†]

[1]Research Unit of Behavioural Ecology, Ethology and Wildlife Management, Department of Life Sciences, University of Siena, Siena, Italy
[2]Department of Forestry and Forest Ecology, University of Warmia and Mazury, Olsztyn, Poland
[3]Słowiński National Park, Smołdzino, Poland
[4]National Biodiversity Future Center, NBFC, Palermo, Italy

Keywords
deer; wolf diet; predator–prey relationships; prey selection; ungulates; wild boar; *Canis lupus*.

Correspondence
Jakub Borkowski, Department of Forestry and Forest Ecology, University of Warmia and Mazury, Pl. Łódzki 2, Olsztyn 10-727, Poland.
Email: jakub.borkowski@uwm.edu.pl
Francesco Ferretti, Research Unit of Behavioural Ecology, Ethology and Wildlife Management, Department of Life Sciences, University of Siena, Via P.A. Mattioli 4, Siena 53100, Italy.
Email: francesco.ferretti@unisi.it

†Contributed equally as senior authors.

Editor: Matthew Hayward
Associate Editor: Emerson Vieira

Received 4 July 2023; revised 29 June 2024; accepted 16 July 2024

doi:10.1111/jzo.13205

Abstract

Under an optimal foraging scenario, prey selection would be expected to occur when food resources are abundant. A positive frequency-dependent prey selection would elicit prey switching when the abundance of main food resources decreases, potentially favouring community resilience to the effects of intensive, selective predation on a single prey. We assessed whether a positive frequency-dependent prey selection by the wolf *Canis lupus* occurred in two areas hosting abundant populations of wild ungulates, one in northern (Słowiński National Park, Poland) and the other one in southern (Maremma Regional Park, Italy) Europe, throughout a cold semester. In Słowiński, ungulate community was dominated by red deer *Cervus elaphus* (57% availability) over wild boar *Sus scrofa* (35%) and roe deer *Capreolus capreolus* (8%); wild boar and fallow deer *Dama dama* (43–37%) were more abundant than roe deer (20%) in Maremma. In both areas, wolf diet was dominated by wild ungulates, with a major use of red deer in Słowiński and wild boar in Maremma. Prey selection occurred in both areas, and it was addressed towards the most abundant prey in Słowiński, that is, the red deer, but only towards the wild boar in Maremma, where the fallow deer was used according to availability. In Slowinski, high red deer density may have driven wolf prey selection, while the shifting of activity rhythms of the fallow deer in the Maremma as antipredator response to wolf presence may have reduced predation. Despite its comparable densities between the two areas, the wild boar was selected in Maremma and under-used in Słowiński. Results provide partial support to positive frequency-dependent selection, emphasising the spatiotemporal plasticity of wolf–prey relationships. The relative role of prey density and other factors (e.g., antipredator behavioural responses) should be assessed at longer temporal scales.

Introduction

The dynamics of species interactions are influenced by patterns of resource use and selection, and animals usually select resources providing the best trade-off between benefits and costs (Charnov, 1976; Pulliam, 1974). Ecological and evolutionary theories suggest that prey selection can be triggered by ultimate factors, such as energetic benefits and costs involved in prey searching, capture and utilisation, and by proximate mechanisms, such as development of search image or prey vulnerability (Karanth & Sunquist, 1995; Stephens & Krebs, 1986). Accordingly, the trade-off between benefits and costs is influenced by factors such as prey detectability, catchability or size. Prey abundance is expected to be a major factor influencing prey selection: predators may maximise their foraging efficiency by selecting for the most abundant prey. If so, predators would show a positive frequency-dependent selection (Garrott et al., 2007; Hughes & Croy, 1993; O'Donoghue et al., 1998). Alternatively, predators may show a negative frequency-dependent selection, when their predation is not concentrated on the most abundant prey but, rather, on the least abundant ones which are particularly attractive (Edenius et al., 2002; Hoy et al., 2019, 2021). In multi-prey systems, a positive frequency-dependent selection should be expected to promote prey switching, that is, the potential for predators to consistently address their selection to the most currently abundant prey. In turn, prey switching would enhance community resilience to the potential effects of differential predation on prey abundances.

The ongoing recolonisation of European ecosystems by large predators, especially the wolf *Canis lupus*, is expected to generate significant ecological consequences, because of the re-established predator–prey interactions (Chapron et al., 2014). Most European countries host abundant and increasing populations of large herbivores, which can trigger significant management issues, especially in protected areas (Apollonio et al., 2017; Carpio et al., 2021; van Beeck Calkoen et al., 2020). Selective and/or intensive predation may determine direct effects on prey numbers (Hebblewhite et al., 2005) or indirect effects through eliciting antipredator responses (Esattore et al., 2023; Kuijper et al., 2013). The use of anthropogenic food resources may tone down the ecological role of predators by decreasing their use of wild prey (Ciucci et al., 2020; Kuijper et al., 2016; Mech, 2012). Accordingly, there is growing evidence that the nature of predator–prey interactions is highly context-dependent (e.g., Bubnicki et al., 2019; Esattore et al., 2023; Kuijper et al., 2016; Samelius et al., 2013; Sand et al., 2021), suggesting a sharp variation of patterns of predator food habits and prey selection across areas. The knowledge of factors driving prey selection especially for areas recently recolonised by predators helps make predictions of the potential impacts of predation on prey populations, as well as wolf–livestock interactions (Chapron et al., 2014).

We have considered the main predator of European ecosystems, that is, the wolf. This ecologically flexible carnivore is typically considered a cursorial hunter of medium-sized and large ungulates (Mech, 1970; Mech & Boitani, 2003; Newsome et al., 2016; Peterson & Ciucci, 2003). Some studies provided support to a positive frequency-dependent selection (Ballard et al., 1997; Garrott et al., 2007), but a negative frequency-dependent selection has been also reported (Hoy et al., 2021; Mattioli et al., 2011). We tested for the occurrence of prey selection by wolves in two European areas characterised by a rich community of wild ungulates (Słowiński National Park, Poland, and Maremma Regional Park, Italy). The high abundance of wild prey (>20 individuals/km^2, see Study Area 1; Study Area 2) leads to the expectation that prey selection by wolves would occur in both of them, under an 'optimal foraging' scenario (Charnov, 1976; Pulliam, 1974). Prey composition is similar between the two areas, including two deer species and a suid species. Both study sites include the wild boar *Sus scrofa* and the roe deer *Capreolus capreolus*, that are among the most used prey by wolves in Europe (Meriggi & Lovari, 1996; Mori et al., 2017), whereas red deer *Cervus elaphus* occur in Słowiński and fallow deer *Dama dama* occur in Maremma. However, the densities of prey differ across the two sites, which gives the opportunity to test for the occurrence of frequency-dependent selection towards the most abundant prey in each area. In fact, while the ungulate community is numerically dominated by a single species in Słowiński, that is, the red deer, two ungulates dominate the prey assemblage in Maremma, that is, the fallow deer and the wild boar. Moreover, if prey selection is driven by prey abundance, we would expect a selection towards the red deer in Słowiński and towards the wild boar and the fallow deer in Maremma.

Thus, we predicted first that (1) in both study areas, wolves show prey selection. Then, we evaluated the direction of selectivity and tested for a positive frequency-dependent selection (Ballard et al., 1997; Garrott et al., 2007) driven by the relatively greater abundance of red deer or wild boar and fallow deer in Słowiński and Maremma, respectively. If so, we would expect (2) a selection of the red deer in Słowiński and a selection of wild boar and fallow deer in Maremma.

Materials and methods

Study area 1: Słowiński National Park

In November 2019–April 2020, we studied the wolf diet in Słowiński National Park (SNP, northern Poland, 54°45′ N, 17°30′ E; 327.4 km^2; Fig. 1). SNP is a World Biosphere Reserve located along the Polish coast edging with the Baltic Sea (Koprowski et al., 2010). The area includes pine forests, deciduous forests, meadows and grasslands, sand dunes, cultivated fields and large lakes (Łebsko Lake: 71.7 km^2; Gardno Lake: 24.7 km^2; Borkowski et al., 2021). The maximum altitude reaches 115 m a.s.l. in Rowokół hill (Kolendowicz & Bednorz, 2010).

It is characterised by a sub-continental maritime climate with cold and humid winters, cool and relatively dry springs, as well as moderately warm and wet summers (Koprowski et al., 2010), with an average annual precipitation of *c.* 700 mm (Matuszkiewicz, 2022). The Scots pine *Pinus silvestris* was the main tree species; other common tree species were the birch *Betula pendula* and black alder *Alnus glutinosa*.

The wolf was the only apex predator, and according to the park managers, there are 2–3 packs using the SNP area (Borkowski et al., 2021). Wild ungulates included the red deer, the roe deer and the wild boar, while the elk *Alces alces* was only transient. The densities of resident ungulates were 13.9 individuals/km^2 (wild boar), 22.9 individuals/km^2 (red deer) and 3.4 individuals/km^2 (roe deer), as estimated through pellet group counts covering the entire Park area, performed in March 2020, that is, in the transition period between winter and spring, and whose methods have been described in previous papers (Borkowski et al., 2019, 2021). These values were used to calculate the relevant prey availability for wolves (see following sections). Medium-sized mammals included the red fox *Vulpes vulpes*, the raccoon dog *Nyctereutes procyonoides* (alien), the European badger *Meles meles*, the mink *Mustela lutreola*, the pine marten *Martes martes*, the stone marten *Martes foina*, the ermine *Mustela erminea*, the European brown hare *Lepus europaeus* and the Eurasian beaver *Castor fiber*. Livestock occurred with *c.* 600 cattle heads (about 1.8 heads/km^2: Słowiński National Park data). SNP is visited by over 300 000 people annually, with the majority of visitors coming during the summer months.

Study area 2: Maremma Regional Park

In November 2018 – April 2019, we studied the wolf diet in the Maremma Regional Park (MRP, central Italy, 42°39′ N, 11°05′ E; 89 km^2; Fig. 1). MRP is located along the coast of the Tyrrhenian sea in southern Tuscany. The landscape is characterised by hilly ground (maximum altitude: 417 m a.s.l.) covered with Mediterranean sclerophyllic forests dominated by oak tree *Quercus ilex*. Shrubby plants include rosemary *Rosmarinus officinalis*, juniper *Juniperus* spp., cistus *Cistus salvifolius* and heather *Erica*

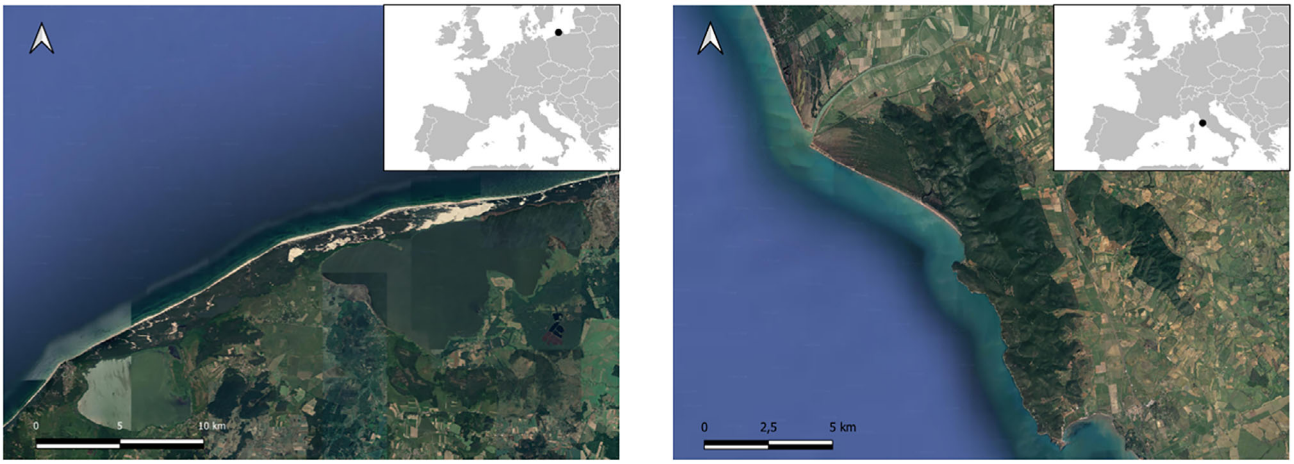

Figure 1 Satellite images of the study areas. Słowiński National Park with a 1:500 000 scale (left) and Maremma Regional Park with a 1:250 000 scale (right).

arborea. The domestic pine *Pinus pinea* and maritime pine *Pinus pinaster* characterise a coastal pinewood of anthropogenic origin. Coastal wetlands, open meadows, abandoned olive groves and cultivated fields are also present (Melini et al., 2019; Sforzi et al., 2013). The climate is Mediterranean, with wet winters and dry summers, mean daily temperature ranging from 9°C (January) to 24°C (August), monthly rainfall from 9.3 mm (July) to 81.8 mm (November) (Ferretti et al., 2021).

Two wolf packs were present (Ferretti et al., 2021). Wild ungulates included the wild boar, the fallow deer and the roe deer; their densities in summer 2018 were 10.5 individuals/km^2 (wild boar), 9.1 individuals/km^2 (fallow deer) and 5.0 individuals/km^2 (roe deer), as estimated through pellet group counts conducted on the whole Park area (Ferretti, Machetti, et al., 2019), whose sampling design has been repeatedly described (Fattorini et al., 2011; Fattorini & Ferretti, 2020; Ferretti & Fattorini, 2021). These values were used to calculate prey availability (see following sections). Medium-sized mammals were the red fox, the wildcat *Felis silvestris*, the stone marten, the pine marten, the European badger, the crested porcupine *Hystrix cristata*, the coypu *Myocastor coypus* (alien) and the European brown hare. Livestock was also present locally (~20 heads/km^2), including free-ranging cattle and horses, in addition to two sheep herds (Ferretti, Lovari, et al., 2019). Population control of wild boar and fallow deer is implemented by the Park Authority to reduce their densities and their potential negative impacts on habitats and agriculture (Ferretti et al., 2016). Fallow deer culling has occurred for several decades, with a recent decreasing intensity (*c*. 223 individuals per year in 2011–2015 and *c*. 104 individuals per year in 2016–2020, Maremma Regional Park data) and no major changes in the relevant procedures. The carcasses of culled animals are collected by Park wardens and removed from the environment, thus avoiding the feeding facilitation for scavenger species. Coypu were also culled by the Park Agency for eradication purposes. The anthropogenic disturbance in the park is mainly limited to touristic areas close to the main beach and some touristic trails (Rossa et al., 2021).

Scat collection and content analyses

In both areas, scats were collected along itineraries walked monthly and covering all the sectors of the areas and, opportunistically, during usual activities of territory patrolling conducted by Park wardens. The identification of scats in the field was based on several characteristics such as scat size, shape, texture, content, position and, especially, their characteristic odour (Lovari et al., 2009, 2013, 2015). In Maremma, field identification of scats was confirmed through genetic analyses of a subsample of fresh putative wolf scats collected during our study period, thus supporting our field criteria ($N = 12$ successful samples out of 30 analysed ones, i.e., a success rate of 40%; Istituto Superiore per la Protezione e la Ricerca Ambientale, unpublished). A concurrent study with camera trapping did not report free-ranging and feral dogs (Ferretti et al., 2021; Rossa et al., 2021).

Analyses were based on $n = 363$ scats collected from November 2019 to April 2020 for Słowiński and on $n = 334$ scats collected between November 2018 and April 2019 for Maremma. In both areas, each sample was collected, put in a plastic bag and identified through the date of collection, a numerical code and the geographic coordinates of the location. Samples were stored in a freezer (−20°C) until they were put into an oven at 80°C for at least 4 h, to inactivate potential parasites. Dried scats were put in water, examined using tweezers and then washed through a 1–3 mm mesh sieve. Undigested remains (e.g., hair, bones, feathers and seeds) were collected for the subsequent identification (e.g., Ciucci et al., 1996; Ferretti et al., 2021; Kruuk & Parish, 1981). Hair were assigned to prey species through visual assessment of hair morphology, shape, length and colour, as well as comparison of the cell pattern of their medulla and cuticula with reference collections of hair of potential prey in study areas, with photographic atlases and with identification keys, through an optic microscope (100–400×; De Marinis & Asprea, 2006a, 2006b; Teerink, 1991). Operators ($n = 2$) were allowed to identify prey species after an accuracy blind test, when they correctly identified at least 95% out of 75 samples of known origin (Ferretti & Fattorini, 2021; Ferretti, Lovari, et al., 2019).

Estimates of diet composition

Different indicators, usually adopted to quantify the diet of carnivore species, were used to describe the wolf food habits (e.g., Cavallini & Lovari, 1991; Ferretti, Lovari, et al., 2019). Wild ungulates (i.e., red deer, roe deer, fallow deer and wild boar, depending on the area) and medium-sized mammals (i.e., coypu, beaver, hare, porcupine, red fox, badger) were considered as food categories at the specific level. Other food categories were livestock (pooling cattle, sheep, goats and horses), other mustelids (*Martes* spp.), felids (*Felis* spp.), small mammals (i.e., small rodents and insectivores), birds, invertebrates and fruits. No method to estimate the diet of carnivores is free from potential limitations, and the use of several estimators is usually recommended (Ciucci et al., 1996; Klare et al., 2011; Reynolds & Aebischer, 2008). First, for each i-th category we considered the absolute frequency of occurrence ($AOcc_i$), that was calculated as: $AOcc_i = (n_i/N) \times 100$, where n_i was the number of scats including that category and N was the total sample size (i.e., the number of analysed scats). Second, we estimated the relative frequency of occurrence of each i-th category ($ROcc_i$) as: $ROcc_i = (n_i/n_{tot}) \times 100$, where n_{tot} is the sum of all occurrences of all i-th categories. Third, we estimated the volume of each i-th food category visually, considering the volumetric classes 1–5, 6–25, 26–50, 51–75, 76–95 and >95% and taking the relevant median point (Kruuk, 1989; Kruuk & Parish, 1981). We initially estimated the volume of each category when it was present, that is, the mean volume across all scats where that category was found (VP_i). Then, we estimated the volume of each i-th food category in the total diet as Vol_i = (total estimated volume of each prey species/ total estimated volume of all prey species) × 100 (Kruuk & Parish, 1981; Lovari et al., 2015; Lucherini & Crema, 1995). We estimated the uncertainty for each indicator of wolf diet by computing 0.95 bootstrap confidence intervals, through 1000 resamplings (Davis et al., 2012). Analyses were conducted through RStudio 2022.02.1 (R Core Team, 2022).

Prey selection

For each study area, we estimated the degree of selection of ungulate prey by the wolf through the Jacobs' index (Jacobs, 1974). This index was calculated as $J = (U{-}A)/[(U + A){-}(2 \times U \times A)]$, with U and A indicating the relative use and availability of each ungulate species, respectively. The use of each ungulate was calculated as the ratio of the number of scats including it over the total number of ungulate occurrences. To calculate prey availability, we used ungulate density estimates obtained through pellet group counts (see Methods and relevant references). The availability of each ungulate prey was calculated as the ratio of the density of it and the sum of the densities of all the ungulate species in the area, thus being expressed on a 0–1 scale. The Jacobs' index expresses values ranging between −1 (negatively selected prey) and 1 (positively selected prey), while values close to zero indicated a comparable use of the prey regarding its availability. To assess support to positive/negative selection, we computed 0.95 confidence intervals for the estimated prey use and calculated selection indices consequently. Intervals including '0' were considered as indicative of prey use according to availability; values with the lower bound greater than 0 were considered as indicative of positive selection, whereas values with the upper bound lower than 0 were considered as indicative of negative selection (Werhahn et al., 2019).

Results

Wolf diet composition

Wild ungulates dominated the diet of wolves in both areas (Fig. 2, Table S1). In Słowiński, the red deer was the staple prey (AOcc: 75.9%; ROcc: 67%; Vol: 70.3%; Fig. 2, Table S1). Beaver, roe deer and wild boar were secondary prey (AOcc: *c.* 10–14%; ROcc: *c.* 5–10%; Vol: *c.* 6–13%; Fig. 2). All the other categories occurred with frequencies and volumes <2% (Fig. 2, Table S1).

In Maremma, the wild boar was the main prey (AOcc: 67.3%; ROcc: 56.5%; Vol: 59.5%), followed by the fallow deer (AOcc: 32.9%; ROcc: 27.6%; Vol: 26.4%; Fig. 2). Roe deer and coypu built up *c.* 4–6% of diet, each, depending on the indicator (Fig. 2). Fruit occurred in *c.* 3% wolf scats, but its volume in diet was <1%; all the other categories occurred with frequencies and volumes <2% (Fig. 2, Table S1).

Wolf prey availability and selection

In Słowiński, red deer was the most available ungulate (availability = 0.57), followed by wild boar (0.35) and roe deer (0.08). The red deer was selected by wolves, while the wild boar was under-utilised; the roe deer was used according to availability (Fig. 3).

In Maremma, the wild boar was the most available ungulate (0.43), followed by fallow deer (0.37) and roe deer (0.20) (Fig. 4). The Jacobs' index supported a selection of wild boar, with fallow deer being used according to its availability and roe deer being under-utilised (Fig. 3).

Discussion

Our results have shown that (1) red deer and wild boar were the most used prey by wolves in Słowiński and in Maremma, respectively, (2) prey selection occurred in both areas, supporting our first prediction, and (3) selection was addressed towards the single most abundant prey species in each area, that is, the red deer in Słowiński and the wild boar – but not the fallow deer – in Maremma. Our results provide a partial support to a positive frequency-dependent selection in both study areas (Garrott et al., 2007; Hughes & Croy, 1993;

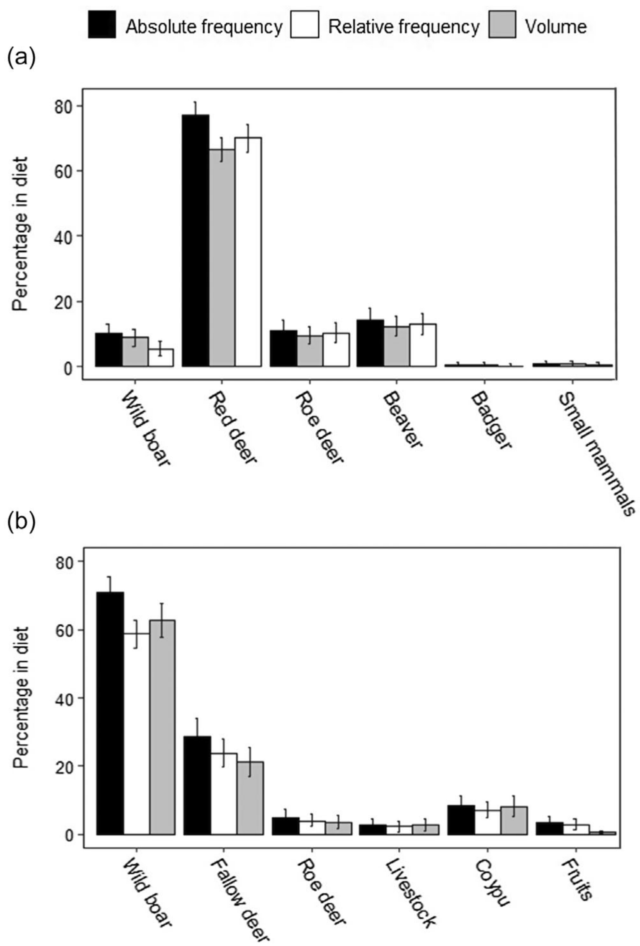

Figure 2 Absolute frequencies, relative frequencies and volumes in the wolf diet of the six most used food categories in (a) Słowiński National Park (November 2019 – April 2020) and (b) in the Maremma Regional Park (November 2018 – April 2019). Sample size: $N = 363$ samples, Słowiński; $N = 334$, Maremma. Error bars indicate 95% confidence intervals estimated through bootstrap ($n = 1000$ resamplings).

O'Donoghue et al., 1998). Previous work in Maremma reported a diet dominated by fallow deer and wild boar (Ferretti, Lovari, et al., 2019). The great availability of large, wild prey (i.e., densities >20–30 individuals/km^2) and a less accessible livestock were probably the key factors allowing wolves to concentrate on wild ungulates (Ferretti, Lovari, et al., 2019; Meriggi & Lovari, 1996; Newsome et al., 2016).

Under an optimal foraging scenario, a great availability of food resources would be expected to stimulate foragers to select the most profitable ones (MacArthur & Pianka, 1966). The patterns of selection towards specific ungulates were different between the two sites, even if the wolf selected the most abundant wild prey in both areas. However, the fallow deer was not selected in Maremma, although it dominated the local ungulate community together with the wild boar. This suid was selected in Maremma and under-utilised in Słowiński. These results emphasise the context-dependent nature of wolf-prey relationships, with the use of a particular prey being probably influenced also by the availability and accessibility of other, large and remunerative prey (Okarma, 1995; Peterson & Ciucci, 2003).

A clear selection for the red deer was found in Słowiński, where the density of this cervid was greater than 20 individuals/km^2. Red deer are large and remunerative prey, live in large groups especially in cold periods, when the snow cover tends to limit their movements and makes them easily locatable by predators (Jędrzejewski et al., 2006). Moreover, red deer lack efficient defence tools against predators, except for adult males, whose antlers may be used as defensive weapons (Lincoln, 1972). The wild boar was the second most abundant prey in Słowiński, but it was negatively selected by wolves. Although this suid has been frequently reported as the main prey to wolves in Mediterranean ecosystems (e.g., Barja, 2009; Bassi et al., 2012; Meriggi & Lovari, 1996; Mori et al., 2017), it has been generally avoided by these predators in central-eastern and northern Europe (Okarma, 1995). Active defence against predators, presence of effective weapons in adults (i.e., the lower canine teeth of wild boar males;

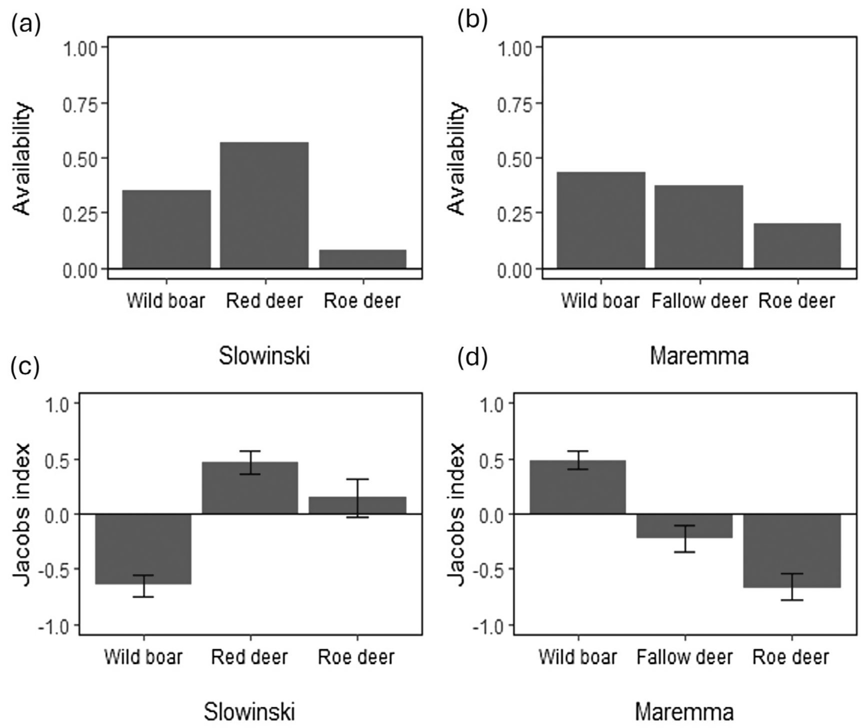

Figure 3 Availability of wild ungulates (expressed on a 0–1 scale) in Słowiński National Park (2020: a) and Maremma Regional Park (2018: b). Selection of wild ungulates by the wolf estimated through the Jacobs' index (values ranging from −1 to +1), in (c) Słowiński National Park (November 2019 – April 2020) and (d) in the Maremma Regional Park (November 2018 – April 2019) Sample size: $N = 363$ samples, Słowiński; $N = 334$, Maremma. Error bars for Jacobs' indices indicate 95% confidence intervals computed through bootstrap applied to the estimate of prey use (1000 resamplings).

Spìchal, 2020), large body size (e.g., *c*. 70 and 100 kg carcass mass, for females and males, respectively, in north-western Poland, with up to *c*. 300 kg for adults, in eastern and northern Europe: Scandura et al., 2022) and high availability and accessibility of alternative, substantial prey probably concurred to the negative selection of wild boar by wolves, in Słowiński.

The positive selection of wild boar in Maremma was the most striking difference in prey selection patterns of wolf between our study sites. The high overlap of wild boar's temporal activity patterns with those of wolves in the Maremma, as well as its smaller size than populations in northern Europe (Rossa et al., 2021; Scandura et al., 2022; for Maremma: *c*. 25 kg for >6 months old individuals, Ferretti, Lovari, et al., 2019, and up to *c*. 120 kg for adult males, MRP archive), makes the wild boar in the mediterranean area easier to detect and manipulate by the wolf.

Both the red deer and the fallow deer would be predicted to be substantial prey for the wolf, because of their body size, detectability emphasised by group living and habitat use, as well as absence of defensive weapons in females and young individuals (Ferretti, Lovari, et al., 2019; Okarma, 1995). We predicted a positive selection towards the fallow deer over our study period in Maremma. In fact, in an earlier stage of wolf establishment in the area, this deer was the most used and selected prey by the wolf (Ferretti, Lovari, et al., 2019). Despite the relatively high and constant density of this cervid (*c*. 9 individuals/km^2, throughout 2016–2018: Ferretti, Lovari, et al., 2019; Ferretti & Fattorini, 2021), no evidence of selection occurred during the present study. At the same time, wild boar density did not increase (Fattorini & Ferretti, 2020), suggesting that changes in prey selection were not driven by variations in ungulate abundance (Lazzeri et al., 2024). A concurrent study based on camera trapping documented an antipredator response of the fallow deer, based on temporal avoidance through increased diurnal activity, along with the stabilisation of wolf presence in the area, that showed nocturnal activity (Esattore et al., 2023; Lazzeri et al., 2024; Rossa et al., 2021). If so, in Maremma fallow deer would be less selected than red deer was in Słowiński because of its reduced detectability by the wolf and the concurrent availability of a significant alternative prey, that is, the wild boar.

Wolf selection of roe deer was different between our study areas, with this deer species being used according to its availability in Słowiński and under-used in Maremma. Roe deer are often important prey to wolves (Mori et al., 2017; Okarma, 1995), with predation increasing with roe deer density (Meriggi et al., 2015) and with decreasing forest cover (Mattioli et al., 2004). Both our study areas are forested and this deer occurred at relatively low densities, making it less detectable by the wolf. Besides, both areas included larger, gregarious, more abundant and more remunerative prey, that is, the fallow deer (Maremma), the red deer (Słowiński) and the wild boar (both sites), that tend to use large open habitats such as grasslands, small clearings, open woods and marshes (Apollonio et al., 2006; Del Frate et al., 2023; Ferretti, Bertoldi, et al., 2011). The density of the roe deer was also negatively influenced by that of the fallow deer in the Maremma and that of the red deer in Słowiński, which have been suggested to have an impact on food availability for the roe deer (e.g., Borkowski et al., 2021; Ferretti & Fattorini, 2021; Ferretti, Sforzi, et al., 2011).

In both our ecosystems, the wolf selected the most abundant prey, which provides support to a positive frequency-dependent selection (Ballard et al., 1997; Garrott et al., 2007), although the fallow deer - whose abundance was similar to that of the wild boar - was not selected in Maremma. The major caveat of our interpretation is related to the short-term duration of our study, that was based on a single cold period. Multiple-year and multidimensional studies would be necessary to evaluate the relative role of prey abundance and antipredator tactics (e.g., spatiotemporal avoidance) in influencing interannual variations in wolf prey use and selection. Furthermore, we could not associate scats to specific packs in both study areas, which prevented us from conducting analyses at the scale of single packs.

In systems with several prey, a positive frequency-dependent selection has been suggested to favour community resilience towards sharp decreases of prey abundance (Garrott et al., 2007; Hughes & Croy, 1993; O'Donoghue et al., 1998). However, abundance of the main prey may trigger negative effects on secondary prey by supporting high predator densities, in turn emphasising predation on other species through apparent competition (Holt, 1977). Negative frequency-dependent selection could also occur towards highly profitable prey, which may affect prey resilience to predation (Hoy et al., 2021). Knowledge on the frequency-dependent prey selection by wolves can also be helpful in shaping ungulate management strategies (setting the hunting quotas of respective species).

Acknowledgements

We are indebted to E. Giunta, S. Rusci and L. Venturi for continuously supporting the work in the Maremma Regional Park. We thank the Maremma Regional Park Authority, Ente Terre Regionali Toscane and many landowners who authorised us to collect samples in Maremma. We greatly thank Lucia Burrini, Niccolò Fattorini and the many students and collaborators of University of Siena, as well as all the wardens of the Maremma Regional Park, for their support in scat collection. We thank A. Meriggi, S. Lovari and an anonymous reviewer for improving an earlier draft of our paper with their comments, as well as A. Pastorelli for providing a wolf picture for the graphical abstract. Open access publishing facilitated by Universita degli Studi di Siena, as part of the Wiley - CRUI-CARE agreement.

Funding

Funding to study wolf food habits in Maremma Regional Park was provided by the Maremma Regional Park Agency to FF.

Author contributions

Conceptualisation: IB, JB and FF; Data collection in Maremma: IB, LL, GP and FF; Data collection in Słowiński: RB, AP and JB; Scat analyses: IB, LL and GP; Data analyses: IB and FF; Writing: IB, JB and FF; and Review and editing: all authors.

Data availability statement

Data analysed in this study are available from the corresponding authors upon reasonable request.

References

Apollonio, M., Belkin, V. V., Borkowski, J., Borodin, O. I., Borowik, T., Cagnacci, F., Danilkin, A. A., Danilov, P. I., Faybich, A., Ferretti, F., Gaillard, J. M., Hayward, M., Heshtaut, P., Heurich, M., Hurynovich, A., Kashtalyan, A., Kerley, G. I. H., Kjellander, P., Kowalczyk, R., … Yanuta, G. (2017). Challenges and science-based implications for modern management and conservation of European ungulate populations. *Mammal Research*, **62**, 209–217. https://doi.org/10.1007/s13364-017-0321-5

Apollonio, M., Focardi, S., Toso, S., & Nacci, L. (2006). Habitat selection and group formation pattern of fallow deer *Dama dama* in a submediterranean environment. *Ecography*, **21**, 225–234. https://doi.org/10.1111/j.1600-0587.1998.tb00560

Ballard, W. B., Ayres, L. A., Krausman, P. R., Reed, D. J., & Fancy, S. G. (1997). Ecology of wolves in relation to a migratory caribou herd in northwest Alaska. *Wildlife Monographs*, **135**, 1–47. https://www.jstor.org/stable/3830776

Barja, I. (2009). Prey and prey-age preference by the Iberian wolf *Canis lupus signatus* in a multiple-prey ecosystem. *Wildlife Biology*, **15**, 147–154. https://doi.org/10.2981/07-096

Bassi, E., Donaggio, E., Marcon, A., Scandura, M., & 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

Borkowski, J., Banul, R., Jurkiewicz, J., Hołdyński, C., Świeczkowska, J., Nasiadko, M., & Załuski, D. (2019). High density of keystone herbivore vs. conservation of natural resources: Factors affecting red deer distribution and impact on vegetation in Słowiński National Park, Poland. *Forest Ecology and Management*, **450**, 117503. https://doi.org/10.1016/j.foreco.2019.117503

Borkowski, J., Banul, R., Jurkiewicz-Azab, J., Hołdyński, C., Święczkowska, J., Nasiadko, M., & Załuski, D. (2021). There is only one winner: The negative impact of red deer density on roe deer numbers and distribution in the Słowiński National Park and its vicinity. *Ecology and Evolution*, **11**, 6889–6899. https://doi.org/10.1002/ece3.7538

Bubnicki, J. W., Churski, M., Schmidt, K., Diserens, T. A., & Kuijper, D. P. J. (2019). Linking spatial patterns of terrestrial herbivore community structure to trophic interactions. *eLife*, **8**, e44937. https://doi.org/10.7554/eLife.44937

Carpio, A. J., Apollonio, M., & Acevedo, P. (2021). Wild ungulate overabundance in Europe: Contexts, causes, monitoring and management recommendations. *Mammal Review*, **51**, 95–108. https://doi.org/10.1111/mam.12221

Cavallini, P., & 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.14697998.1991.tb04768.x

Chapron, G., Kaczensky, P., Linnell, J. D. C., von Arx, M., Huber, D., Andrén, H., López-Bao, J. V., Adamec, M., Álvares, F., Anders, O., Balčiauskas, L., Balys, V., Bedő, P., Bego, F., Blanco, J. C., Breitenmoser, U., Brøseth, H., Bufka, L., Bunikyte, R., . . . Boitani, L. (2014). Recovery of large carnivores in Europe's modern human-dominated landscapes. *Science*, **346**, 1517–1519. https://doi.org/10.1126/science.1257553

Charnov, E. L. (1976). Optimal foraging, the marginal value theorem. *Theoretical Population Biology*, **9**, 129–136. https://doi.org/10.1016/0040-5809(76)90040-X

Ciucci, P., Boitani, L., Pelliccioni, E. R., Rocco, M., & Guy, I. (1996). A comparison of scat-analysis methods to assess the diet of the wolf *Canis lupus*. *Wildlife Biology*, **2**, 37–48. https://doi.org/10.2981/wb.1996.006

Ciucci, P., Mancinelli, S., Boitani, L., Gallo, O., & Grottoli, L. (2020). Anthropogenic food subsidies hinder the ecological role of wolves: Insights for conservation of apex predators in human-modified 45 landscapes. *Global Ecology and Conservation*, **21**, e00841. https://doi.org/10.1016/j.gecco.2019.e0084

Davis, M. L., Stephens, P. A., Willis, S. G., Bassi, E., Marcon, A., Donaggio, E., Capitani, C., & Apollonio, M. (2012). Prey selection by an apex predator: The importance of sampling uncertainty. *PLoS One*, **7**(10), e47894. https://doi.org/10.1371/journal.pone.0047894

De Marinis, A. M., & Asprea, A. (2006a). Hair identification key of wild and domestic ungulates from southern Europe. *Wildlife Biology*, **12**, 305–320. https://doi.org/10.2981/09096396(2006)12[305:HIKOWA]2.0.CO;2

De Marinis, A. M., & Asprea, A. (2006b). How did domestication change the hair morphology in sheep and goats. *Human Evolution*, **21**, 139–149. https://doi.org/10.1007/s11598-006-9010-0

Del Frate, M., Bongi, P., Tanzillo, L., Russo, C., Benini, O., Sieni, S., Scandura, M., & Apollonio, M. (2023). A predator on the doorstep: Kill site selection by a Lone wolf in a Peri-Urban Park in a Mediterranean area. *Animals*, **13**, 480. https://doi.org/10.3390/ani13030480

Edenius, L., Ericsson, G., & Naslund, P. (2002). Selectivity by moose vs the spatial distribution of aspen: A natural experiment. *Ecography*, **25**, 289–294. https://doi.org/10.1034/j.1600-0587.2002.250305.x

Esattore, B., Rossi, A. C., Bazzoni, F., Riggio, C., Oliveira, R., Leggiero, I., & Ferretti, F. (2023). Same place, different time, head up: Multiple antipredator responses to a recolonizing apex predator. *Current Zoology*, **69**, 703–717. https://doi.org/10.1093/cz/zoac083

Fattorini, L., Ferretti, F., Pisani, C., & Sforzi, A. (2011). Two-stage estimation of ungulate abundance in Mediterranean areas using pellet group count. *Environmental and Ecological Statistics*, **18**, 291–314. https://doi.org/10.1007/s10651-010-0133-0

Fattorini, N., & Ferretti, F. (2020). Estimating wild boar density and rooting activity in a Mediterranean protected area. *Mammalian Biology*, **100**, 241–251. https://doi.org/10.1007/s42991-020-00030-0

Ferretti, F., Bertoldi, G., Sforzi, A., & Fattorini, L. (2011). Roe and fallow deer: Are they compatible neighbours? *European Journal of Wildlife Research*, **57**, 775–783. https://doi.org/10.1007/s10344-010-0487-5

Ferretti, F., Fattorini, L., Sforzi, A., & Pisani, C. (2016). The use of faeces counts to estimate relative densities of wild boar in a Mediterranean area. *Population Ecology*, **58**, 329–334. https://doi.org/10.1007/s10144-016-0536-3

Ferretti, F., & Fattorini, N. (2021). Competitor densities, habitat and weather: Effects on interspecific interactions between wild deer species. *Integrative Zoology*, **16**, 670–684. https://doi.org/10.1111/1749-4877.12470

Ferretti, F., Lovari, S., Mancino, V., Burrini, L., & Rossa, M. (2019). Food habits of wolves and selection of wild ungulates in a prey-rich Mediterranean coastal area. *Mammalian Biology*, **99**, 119–127. https://doi.org/10.1016/j.mambio.2019.10.008

Ferretti, F., Machetti, A., Fattorini, N., Boldorini, U., & Tonini, L. (2019). *Programma per la gestione delle popolazioni di ungulati selvatici del Parco Regionale della Maremma*. Maremma Regional Park Agency, Alberese (GR), Italy. Report.

Ferretti, F., Pacini, G., Belardi, I., Ten Cate, B., Sensi, M., Oliveira, R., Rossa, M., Burrini, L., & Lovari, S. (2021). Recolonizing wolves and opportunistic foxes: Interference or facilitation? *Biological Journal of the Linnean Society*, **132**, 196–210. https://doi.org/10.1007/s00265-020-02956-4

Ferretti, F., Sforzi, A., & Lovari, S. (2011). Behavioural interference between ungulate species: Roe deer are not velvet with fallow deer. *Behavioral Ecology and Sociobiology*, **65**, 875–887. https://doi.org/10.1007/s00265-010-1088-8

Garrott, R. A., Bruggeman, J. E., Becker, M. S., Kalinowski, S. T., & White, P. J. (2007). Evaluating prey switching in wolf-ungulate systems. *Ecological Applications*, **17**, 1588–1597. https://www.jstor.org/stable/40062059

Hebblewhite, M., White, C. A., Nietvelt, C. G., Mckenzie, J. A., Hurd, T. E., Fryxell, J. M., Bayley, S. E., & Paquet, P. C. (2005). Human activity mediates a trophic Cascade caused by wolves. *Ecology*, **86**, 2135–2144. https://doi.org/10.1890/04-1269

Holt, R. D. (1977). Predation, apparent competition, and the structure of prey communities. *Theoretical Population Biology*, **12**, 197–229. https://doi.org/10.1016/0040-5809(77)90042-9

Hoy, S. R., MacNulty, D. R., Metz, M. C., Smith, D. W., Stahler, D. R., Peterson, R. O., & Vucetich, J. A. (2021).

Negative frequency-dependent prey selection by wolves and its implications on predator-prey dynamics. *Animal Behaviour*, **179**, 247–265. https://doi.org/10.1016/j.anbehav.2021.06.025

Hoy, S. R., Vucetich, J. A., Liu, R., DeAngelis, D. L., Peterson, R. O., Vucetich, L. M., & Henderson, J. J. (2019). Negative frequency-dependent foraging behaviour in a generalist herbivore (*Alces alces*) and its stabilizing influence on food web dynamics. *The Journal of Animal Ecology*, **88**, 1291–1304. https://doi.org/10.1111/1365-2656.13031

Hughes, R. N., & Croy, M. I. (1993). An experimental analysis of frequency dependent predation (switching) in the 15-spined stickleback, *Spinachia spinachia*. *The Journal of Animal Ecology*, **62**, 341–352. https://doi.org/10.2307/5365

Jacobs, J. (1974). Quantitative measurement of food selection. *Oecologia*, **14**, 413–417. https://doi.org/10.1007/BF00384581

Jędrzejewski, W., Spaedtke, H., Kamler, J. F., Jędrzejewska, B., & Stenkewitz, U. (2006). Group size dynamics of Red Deer in Białowieża primeval Forest, Poland. *Journal of Wildlife Management*, **70**, 1054–1059. https://doi.org/10.2193/0022-541X(2006)70[1054:GSDORD]2.0.CO;2

Karanth, K. U., & Sunquist, M. E. (1995). Prey selection by tiger, leopard and dhole in tropical forests. *The Journal of Animal Ecology*, **64**, 439–450. https://doi.org/10.2307/5647

Klare, U., Kamler, F., & MacDonald, D. W. (2011). A comparison and critique of different scat-analysis methods for determining carnivore diet. *Mammal Review*, **41**, 294–312. https://doi.org/10.1111/j.1365-2907.2011.00183.x

Kolendowicz, L., & Bednorz, E. (2010). Topoclimatic differentiation of the area of the Słowiński National Park, northern Poland. *Quaestiones Geographicae*, **29**, 49–56. https://doi.org/10.2478/v10117-010-0005-6

Koprowski, M., Winchester, V., & Zielski, A. (2010). Tree reactions and dune movements: Slowiński National Park, Poland. *Catena*, **81**, 55–65. https://doi.org/10.1016/j.catena.2010.01.004

Kruuk, H. (1989). *The social badger: Ecology and behaviour of a group-living carnivore (Meles Meles)*. Oxford University Press.

Kruuk, H., & Parish, T. (1981). Feeding specialization of the European badger *Meles meles* in Scotland. *The Journal of Animal Ecology*, **50**, 773–788. https://doi.org/10.2307/4136

Kuijper, D. P. J., de Kleine, C., Churski, M., Van Hooft, P., Bubnicki, J., & Jędrzejewska, B. (2013). Landscape of fear in Europe: Wolves affect spatial patterns of ungulate browsing in Białowieża primeval Forest, Poland. *Ecography*, **36**, 1263–1275. https://doi.org/10.1111/j.1600-0587.2013.00266.x

Kuijper, D. P. J., Sahlén, E., Elmhagen, B., Chamaillé-Jammes, S., Sand, H., Lone, K., & Cromsigt, J. P. G. M. (2016). Paws without claws? Ecological effects of large carnivores in anthropogenic landscapes. *Proceedings of the Royal Society of London, Series B: Biological Sciences*, **283**(1841), 20161625. https://doi.org/10.1098/rspb.2016.1625

Lazzeri, L., Belardi, I., Pacini, G., Fattorini, N., & Ferretti, F. (2024). Beyond ungulate density: Prey switching and selection by the wolf in a recolonised area. *Glob. Ecol. Conserv.*, e03069.

Lazzeri, L., Pacini, G., Belardi, I., Fini, G., De Lillo, C., & Ferretti, F. (2024). Switch or perish? Prey-predator interactions in a Mediterranean area. *Anim. Conserv.*. https://doi.org/10.1111/acv.12973

Lincoln, G. A. (1972). The role of antlers in the behaviour of red deer. *The Journal of Experimental Zoology*, **182**, 233–249. https://doi.org/10.1002/jez.1401820208

Lovari, S., Boesi, R., Minder, I., Mucci, N., Randi, E., Dematteis, A., & Ale, S. B. (2009). Restoring a keystone predator may endanger a prey species in a human-altered ecosystem: The return of the snow leopard to Sagarmatha National Park. *Animal Conservation*, **12**, 559–570. https://doi.org/10.1111/j.1469-1795.2009.00285.x

Lovari, S., Minder, I., Ferretti, F., Mucci, N., Randi, E., & Pellizzi, B. (2013). Common and snow leopards share prey, but not habitats: Competition avoidance by large predators? *Journal of Zoology*, **291**, 127–135. https://doi.org/10.1111/jzo.12053

Lovari, S., Pokheral, C. P., Jnawali, S. R., Fusani, L., & Ferretti, F. (2015). Coexistence of the tiger and the common leopard in a prey-rich area: The role of prey partitioning. *Journal of Zoology*, **295**, 122–131. https://hdl.handle.net/11392/2334267

Lucherini, M., & Crema, G. (1995). Seasonal variation in the food habits of badgers in an alpine valley. *Hystrix*, **7**, 165-171. https://doi.org/10.4404/hystrix-7.1-2-4067

MacArthur, R. H., & Pianka, E. R. (1966). On optimal use of a patchy environment. *The American Naturalist*, **100**, 603–609. https://www.jstor.org/stable/2459298

Mattioli, L., Capitani, C., Avanzinelli, E., Bertelli, I., Gazzola, A., & Apollonio, M. (2004). Predation by wolf (*Canis lupus*) on roe deer (*Capreolus capreolus*) in north-eastern Apennines. *The Italian Journal of Zoology*, **264**, 1–10. https://doi.org/10.1017/S095283690400576X

Mattioli, L., Capitani, C., Gazzola, A., Scandura, M., & Apollonio, M. (2011). Prey selection and dietary response by wolves in a high-density multi-species ungulate community. *European Journal of Wildlife Research*, **57**, 909–922. https://doi.org/10.1007/s10344-011-0503-4

Matuszkiewicz, J. M. (2022). *Polish woodland ecosystems*. PWN.

Mech, L. D. (1970). *The wolf: The ecology and behavior of an endangered species*. University of Minnesota Press.

Mech, L. D. (2012). Is science in danger of sanctifying the wolf? *Biological Conservation*, **150**, 143–149. https://doi.org/10.1016/j.biocon.2012.03.003

Mech, L. D., & Boitani, L. (2003). *Wolves: Behavior, ecology, and conservation*. University of Chicago Press.

Melini, D., Agrillo, E., Ferretti, F., & Tonelli, L. (2019). *Piano di Gestione della ZSC/ZPS IT51A0016 Monti dell'Uccellina*. Ente Parco Regionale della Maremma.

Meriggi, A., Dagradi, V., Dondina, O., Perversi, M., Milanesi, P., Lombardini, M., Raviglione, S., & Repossi, A. (2015). Short-term responses of wolf feeding habits to changes of wild and domestic ungulate abundance in northern Italy. *Ethology Ecology and Evolution*, **27**, 389–411. https://doi.org/10.1080/03949370.2014.986768

Meriggi, A., & Lovari, S. (1996). A review of wolf predation in southern Europe: Does the wolf prefer wild prey to livestock? *Journal of Applied Ecology*, **33**, 1561–1571. https://doi.org/10.2307/2404794

Mori, E., Benatti, L., Lovari, S., & Ferretti, F. (2017). What does the wild boar mean to the wolf? *European Journal of Wildlife Research*, **63**, 1. https://doi.org/10.1007/s10344-016-1060-7

Newsome, T. M., Boitani, L., Chapron, G., Ciucci, P., Dickman, C. R., Dellinger, J. A., López-Bao, J. V., Peterson, R. O., Wirsing, A. J., & Ripple, W. J. (2016). Food habits of the world's grey wolves. *Mammal Review*, **46**, 255–269. https://doi.org/10.1111/mam.12067

O'Donoghue, M., Boutin, S., Krebs, C. J., Zuleta, G., Murray, D. L., & Hofer, E. J. (1998). Functional responses of coyotes and lynx to the snowshoe hare cycle. *Ecology*, **79**, 1193–1208. https://doi.org/10.1890/0012-9658(1998)079[1193:FROCAL]2.0.CO;2

Okarma, H. (1995). The trophic ecology of wolves and their predatory role in ungulate communities of forest ecosystems in Europe. *Acta Theriologica*, **40**, 335–386. https://doi.org/10.4098/AT.arch.95-35

Peterson, R. O., & Ciucci, P. (2003). The wolf as a carnivore. In L. D. Mech & L. Boitani (Eds.), *Wolves, behaviour, ecology, and conservation* (pp. 104–111). The University of Chicago Press. Vol 4.

Pulliam, H. R. (1974). On the theory of optimal diets. *The American Naturalist*, **108**, 59–74. https://www.jstor.org/stable/2459736

R Core Team. (2022). *R: A language and environment for statistical computing*. R Foundation for Statistical Computing. https://www.R-project.org/

Reynolds, J. C., & Aebischer, N. J. (2008). Comparison and quantification of carnivore diet by faecal analysis: A critique, with recommendations, based on a study of the fox *Vulpes vulpes*. *Mammal Review*, **21**, 97–122. https://doi.org/10.1111/j.1365-2907.1991.tb00113.x

Rossa, M., Lovari, S., & Ferretti, F. (2021). Spatiotemporal patterns of wolf, mesocarnivores and prey in a Mediterranean area. *Behavioral Ecology and Sociobiology*, **75**, 1–13. https://doi.org/10.1007/s00265-020-02956-4

Samelius, G., Andrén, H., Kjellander, P., & Liberg, O. (2013). Habitat selection and risk of predation: Re-colonization by lynx had limited impact on habitat selection by roe deer. *PLoS One*, **8**(9), e75469. https://doi.org/10.1371/journal.pone.0075469

Sand, H., Jamieson, M., Andrén, H., Wikenros, C., Cromsigt, J., & Månsson, J. (2021). Behavioral effects of wolf presence on moose habitat selection: Testing the landscape of fear hypothesis in an anthropogenic landscape. *Oecologia*, **197**, 101–116. https://doi.org/10.1007/s00442-021-04984-x

Scandura, M., Podgórski, T., Vicente, J., & Iacolina, L. (2022). Wild boar *Sus scrofa* Linnaeus, 1758. In L. Corlatti & F. E. Zachos (Eds.), *Terrestrial Cetartiodactyla, Handbook of the mammals of Europe*. Springer Nature. https://doi.org/10.1007/978-3-030-24475-0_17

Sforzi, A., Tonelli, L., Cortés-Selva, F., Mastacchi, R., Lanzi, L., Anselmi, G., Martini, G., & Naviglio, L. (2013). *Piano di Gestione dei SIC/SIR IT51A0039 [SIE 113 e A113(ZPS)] Palude della Trappola e Bocca d'Ombrone, IT51A0014 [SIR 114] Pineta Granducale dell'Uccellina e IT51A0015 [SIR 115] Dune costiere del Parco dell'Uccellina*. Alberese: Ente Parco Regionale della Maremma.

Spìchal, L. (2020). Modeling the shape of tusks of wild boars (*Sus scrofa* L.). In *Miroslav Hrubý, Pavlına Racková. Matematika, informacnı technologie a aplikované vedy.* Univerzita Obrany.

Stephens, D. W., & Krebs, J. R. (1986). *Foraging theory.* Princeton University Press.

Teerink, B. J. (1991). *Hair of west-European mammals- atlas and identification key.* Cambridge University Press.

van Beeck Calkoen, S. T., Mühlbauer, L., Andrén, H., Apollonio, M., Balčiauskas, L., Belotti, E., Carranza, J., Cottam, J., Filli, F., Gatiso, T. T., Hetherington, D., Karamanlidis, A. A., Krofel, M., Kuehl, H. L., Linnell, J. D. C., Müller, J., Ozolins, J., Premier, J., Ranc, N., … Heurich, M. (2020). Ungulate management in European national parks: Why a more integrated European policy is needed. *J. Environ. Manag.*, **260**, 110068

Werhahn, G., Kusi, N., Li, X., Chen, C., Zhi, L., Martín, R. L., Sillero-Zubiri, C., & Macdonald, D. W. (2019). Himalayan wolf foraging ecology and the importance of wild prey. *Glob. Ecol. Conserv.*, **20**, e00780.

Supporting Information

Additional Supporting Information may be found in the online version of this article:

Table S1. Number of occurrences, absolute frequencies, relative frequencies and volumes in the wolf diet Słowiński National Park (November 2019–April 2020) and in the Maremma Regional Park (November 2018–April 2019). Sample size: N = 363 samples, Słowiński; N = 334, Maremma.