



Original research article

Beyond ungulate density: Prey switching and selection by the wolf in a recolonised area

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ABSTRACT

The analysis of mechanisms underlying prey use and selection is crucial for understanding the potential for apex predators to shape ecological processes across trophic levels. Significant implications for the conservation and management of ecosystems can ensue, especially in human-modified landscapes characterised by the recent recovery of apex predators, such as those of Europe. Generalist predators may show frequency-dependent prey selection, leading to prey switching; however, there is no ubiquitous support for positive relationships between prey abundance and prey selection. In a protected area recently recolonised by the wolf *Canis lupus* and hosting abundant wild prey (>20 individuals/km²), we assessed prey use and selection (>3000 wolf scats analysed) throughout 7 years since wolf settlement (April 2016-to-March 2023), during which prey density was relatively stable. Wolf diet was dominated by wild boar *Sus scrofa* and fallow deer *Dama dama* (>70% of occurrences and volume); the roe deer *Capreolus capreolus* and coypu *Myocastor coypus* represented main secondary prey. The wolf showed a clear prey switching throughout the study. In the first two years, the fallow deer was the main prey and was positively selected. Then, wild boar replaced fallow deer as main prey, and was positively selected, with a progressive decrease in the use of fallow deer throughout the years. Selection indices of wild boar were negatively associated with those of fallow deer. The relationship between selection indices and population density was inconsistent across species, being negative for the wild boar and weakly positive for the fallow deer, although the latter showed no sharp decline in the area. Concurrent studies showed increased diurnal activity of fallow deer and a consequent reduced temporal overlap with the wolf throughout years since the settlement of this predator, suggesting temporal avoidance. By supporting a minor role of prey density in mediating prey switching, our results suggest a major role of other factors (e.g., antipredator behavioural responses). Alternative substantial prey are important to buffer apex predators not only towards changes in the

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abundance of main prey, but also towards the effects of other factors potentially reducing prey detectability, e.g., antipredator behaviour.

1. Introduction

According to the 'Optimal Foraging Theory' (Stephens and Krebs, 1986), animals are expected to select food resources to maximise their energy intake and reproductive success while minimizing the risks and effort involved in finding and consuming food (MacArthur and Pianka, 1966; Schoener, 1971; Charnov, 1976). Different factors can influence foragers' choice, including the availability of food resources in terms of abundance, distribution, quality and accessibility, the risk of obtaining that resource, competition with other individuals of the same or different species, and the energy costs of food search and consumption. Thus, food choice is the outcome of a cost-benefit analysis with animals maximizing their energy return by investing their time and energy in cost-effective resources (Krebs and Davies, 2009).

Predator food choice is a major primer of predator-prey dynamics, and its assessment is pivotal for understanding interactions between carnivores and their prey (Mech and Boitani, 2003; Schmitz, 2007). Prey abundance is expected to be a major factor influencing predator food habits, since it influences prey availability. Predators may maximise their foraging efficiency by selecting the most abundant prey, which would lead to a positive frequency-dependent selection (Hughes and Croy, 1993; O'Donoghue et al., 1998; Garrott et al., 2007). A positive frequency-dependent prey selection would elicit prey switching, should the abundance of main food resources decrease (Garrott et al., 2007). Fluctuations in prey abundance can induce changes in prey use and selection by predators, which is also influenced by foraging strategies used by predators to maximize their net rate of energy intake (Garrott et al., 2007). Specialized predators may select for a particular profitable prey irrespective of its abundance (Stephens and Krebs, 1986). Conversely, generalist predators would be expected to respond to numerical fluctuations of their main prey by including a greater variety of food types in their diets and by selecting prey items based on their availability (Schoener, 1971).

Besides direct impact on prey populations through increased mortality (Hebblewhite et al., 2005), predation can trigger indirect effects on prey by eliciting antipredator responses (Kuijper et al., 2013; Esattore et al., 2023). Among antipredator strategies, variation in spatio-temporal activity to avoid areas with high predation risk may influence predator-prey relationships (Kohl et al., 2018; Palmer et al., 2021; Rossa et al., 2021). In multi-prey communities, the adoption of efficient antipredator tactics by main prey may force predators to switch to alternative prey. Hence, antipredator tactics may affect the search effort and the net rate of energy intake by predators. Costs associated with hunting can change in relation to different defence capabilities and antipredator responses of prey (Caro, 2005). If so, changes in prey selection may be driven not only by variations in prey abundance but also by behavioural changes of prey (Huggard, 1993).

The wolf *Canis lupus* is a large predator with a flexible opportunistic feeding strategy, adapted to hunting medium-sized and large ungulates, but capable of adapting to a broad variety of trophic resources according to their availability (Mech and Boitani, 2003; Newsome et al., 2016). Indeed, wolf diet is mainly based on wild ungulates in optimal environments, with anthropogenic food resources (particularly livestock) being used especially in areas with scarce availability of wild ungulates and/or highly anthropized, or where livestock is not properly managed (Meriggi et al., 1991; Patalano and Lovari, 1993; Meriggi and Lovari, 1996; Newsome et al., 2016). In single-prey systems, predator kill rate widely depends on prey density, thus relying primarily on encounter rates. In multiple-prey systems, changes in the relative density of different prey species may influence patterns of prey use and selection. Prey use would be expected to be also driven by seasonal factors: newborn offspring are often primary prey of wolves and are abundant in spring-summer, whereas their availability decreases throughout autumn-winter (Mech and Boitani, 2003; Sand et al., 2008; Bassi et al., 2020). After summer, weaned wolf pups join adult and subadult individuals in hunting, which determines an increase in the number of wolves moving across the territory, thus influencing food requirements and possibly leading to increased use of alternative prey (Mech, 1970). Although the wolf has been typically described as a generalist predator, prey selection has been reported especially in prey-rich communities (Fritts and Mech, 1981; Capitani et al., 2004). The selection of a species is expected to depend on its relative abundance, accessibility, vulnerability, and usability, understood as biomass input, in relation to the energy and time used to obtain it (Huggard, 1993). Some support has been provided to a positive frequency-dependent selection (Ballard et al., 1997; Garrott et al., 2007), although a negative frequency-dependent selection has also been reported (Mattioli et al., 2011; Hoy et al., 2021).

After being almost eradicated from Europe, in recent decades wolves are spreading again across most countries (Chapron et al., 2014). This process is expected to generate ecological consequences through the restoration of trophic webs but is also triggering management implications through the potentially ensuing conflicts with human activities in anthropized areas (Ripple et al., 2014; van Eeden et al., 2018). Thus, it is particularly important to investigate the prey-predator dynamics in recently restored areas of Europe, because there is growing support to the context-dependent nature of wolf-prey interactions (Kuijper et al., 2016; Sand et al., 2021), which could differ from what has been reported in relatively untouched ecosystems like those of North America.

We have assessed wolf food habits and prey selection in an area recently recolonised by this predator, in relation to inter-annual variations of prey abundance and time elapsed from wolf settlement. We worked in a prey-rich area of central Italy (Maremma Regional Park), holding three species of wild ungulates (the wild boar *Sus scrofa*, the fallow deer *Dama dama*, and the roe deer *Capreolus capreolus*: c. 20–30 individuals/km², overall). Previous studies in the same area showed that, in the first two years after wolf settlement, the wolf diet was dominated by wild ungulates (> 80 % of occurrences and volume): the fallow deer was the main and selected prey, although the wild boar (i.e., the second most used prey) was the most abundant ungulate (Ferretti et al., 2019). Fallow deer and wild boar were used especially in spring-summer, with increasing use of alternative wild prey such as roe deer and medium-sized mammals

in autumn-winter (Ferretti et al., 2019). Studies conducted through camera trapping showed that fallow deer increased their diurnal activity throughout years and increased their vigilance in sites more used by wolves, indicating an antipredator response based on temporal avoidance and increased vigilance (Rossa et al., 2021, Esattore et al., 2023; Lazzeri et al., 2024). The same response was not detected in the wild boar, whereas the wolf showed consistently nocturnal behaviour throughout years (Ferretti et al., 2023a), which would suggest increased overlap with this suid.

In this study, we aimed to assess wolf food habits and prey selection in a recently recolonised area using multi-year data. We evaluated how these aspects changed with inter-annual variations in prey abundance and time elapsed since wolf settlement. Consistently with previous work, we expected seasonal variations in wolf diet because of increased use of alternative prey in autumn-winter (Ferretti et al., 2019), and inter-annual variations of wolf prey use and selection, with decreased predation on fallow deer and increased predation on wild boar, in response to the temporal avoidance of fallow deer (Rossa et al., 2021; Esattore et al., 2023). Thus, we predicted that (i) the wolf used fallow deer and wild boar especially in spring-summer, with a decreasing use in autumn-winter, whereas the use of roe deer would show the opposite pattern (Ferretti et al., 2019); (ii) the wolf decreased its use of fallow deer and increased that of wild boar throughout years, with no significant change for the roe deer; (iii) prey selection occurred, because of the high availability of wild, large prey; (iv) selection of fallow deer decreased and that of wild boar increased over the years; (v) prey selection was not correlated with prey density.

2. Materials and methods

2.1. Study area

Our research was conducted in the Maremma Regional Park (MRP; Central Italy: 42°39'N, 11°05'E; ~90 km²; Fig. 1). The local climate is Mediterranean, with dry summers and wet winters. The vegetation primarily consists of Mediterranean sclerophyllous scrub wood.

The wolf was stably reported in our study area since 2015 with a first pack; then the number of packs increased to two since 2017 and to three since 2019–2020 (Ferretti et al., 2021a, 2023a). Wild ungulate species include the wild boar, the fallow deer, and the roe deer.

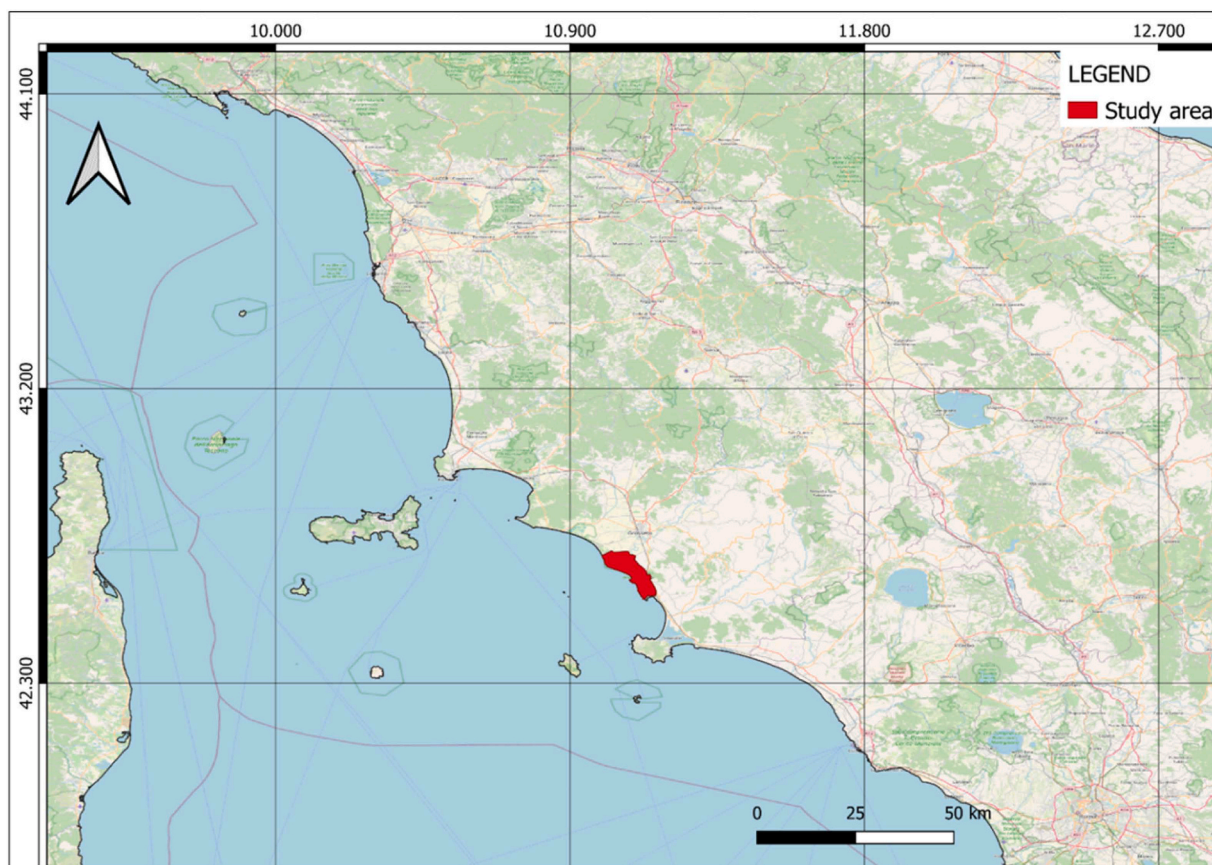


Fig. 1. Map of our study area. Red polygon indicates the Maremma Regional Park. Coordinates are in the WGS 84 Reference System. Maps created using the Free and Open Source QGIS 3.22.0 'Białowieża' (<https://www.qgis.org>).

Medium-sized mammals include the red fox *Vulpes vulpes*, the European badger *Meles meles*, the stone marten *Martes foina*, the pine marten *Martes martes*, the European polecat *Mustela putorius*, the wildcat *Felis silvestris*, the crested porcupine *Hystrix cristata*, the coypu *Myocastor coypus* (a non-native species of South American origin), the European brown hare *Lepus europaeus*, and several smaller mammal species (Ferretti et al., 2019). Livestock (c. 20 heads/100 ha) includes free-ranging cattle and horses (approximately 1000 heads in total) and sheep. Cattle are moved seasonally through selected pastures and sections of pinewood/scrubwood. Calf births mainly occur during winter and early spring, with calves remaining with their mothers until 6–8 months of age (Ferretti et al., 2019). Typically, adult cows actively protect their calves from predators (Meriggi et al., 1991, 1996; Smit and Kuijper, 2024). Farming practices tend to promote herd cohesion, minimizing separation between mothers and offspring, particularly until the weaning period in October. No targeted measures for calf protection were undertaken until late summer 2020, when an antipredator fence was constructed in the northern sector of the Park to protect calves during birth and weaning periods. Two sheep herds (totalling ~800 heads) are present, with preventive measures including direct shepherd supervision during daylight hours, livestock guarding dogs, and/or fencing.

Efforts to control populations of wild boar and fallow deer involve culling (both species) and trapping (wild boar) implemented by the Park Agency. The culling intensity has decreased over our study period, with 538 wild boars removed in 2017 and ~150–220/year in 2018–2021, along with 135 fallow deer in 2017, ~70–90/year in 2018–2019, and ~20–40/year in 2020–2021 (Maremma Regional Park Archive). Ungulate densities were estimated annually through pellet group counts in summer, repeatedly described in previous studies (Fattorini et al., 2011; Ferretti et al., 2016, 2019, 2021b, 2023b; Fattorini and Ferretti, 2020; Ferretti and Fattorini, 2021). During our study, counts indicated density estimates of 10.4–15 individuals/km² and 6.8–9.1 individuals/km² for the wild boar and the fallow deer, respectively, whereas roe deer density estimates declined from 6.9 to 2.9 individuals/km² over the same timeframe (Fattorini and Ferretti, 2020; Ferretti and Fattorini, 2021; Ferretti et al., 2022, 2023c; Fig. 4a–b–c). Thus, each year the wild boar was 1.15–1.67 times more abundant than the fallow deer. Combined density of major wolf prey (fallow deer and wild boar) was 17–24 individuals/km² during the study period.

2.2. Scat collection

Wolf scats were collected monthly between April 2016 and March 2023 along itineraries located to homogeneously cover the Park (with increasing effort in relation to wolf expansion, from ~60 km in the first and second year to up to ~120 km/month in the following years, i.e., ~8.6 km on average per itinerary, for a total of 14 itineraries), as well as opportunistically during usual activities of territory patrolling by Park wardens. We categorised study years as ranging from April to March of the following calendar year, i.e., the first year included April 2016–March 2017, etc. A previous work showed a stabilisation of wolf dietary diversity over 61 scats, indicating that the sample was adequate (Ferretti et al., 2019). We adopted a conservative multi-criteria approach to select wolf scats from those of other canids (Ciucci et al., 1996) i.e., size, shape, scent, position (Asa et al., 1985). Scats were collected in plastic bags, labelled (using a permanent marker) with date, univocal alphanumeric code, location and georeferenced with a handheld Global Positioning System. Then the scats were frozen (-20°C) before analyses.

2.3. Scat analyses

The scats were stored, then were put in an oven at 80° Celsius for at least four hours to destroy the possible pathogens harmful to humans. All data recorded on the plastic bags were copied on forms. Faeces were processed according to Lovari et al. (2009), (2015). Scats were washed with running water to separate the components; a fine mesh strainer (size from 1 to 3 mm) was used for this procedure. Undigested components (i.e., hairs, hooves, bones, claws, fruits, seeds, feathers, grass, etc.) were separated and we estimated the percentage volume of each of them. All the remains ingested involuntarily by the wolf (e.g., leaves, soil, stones, etc.), were excluded from the subsequent analysis (Ciucci et al., 1996). Hairs and other undigested remains, useful for the identification of prey were left to dry ready for subsequent microscopic analysis. Mammalian hairs were identified by comparison with identification keys of the structure of the cuticula and medulla of hair of potential prey species (cf. Teerink, 2004; De Marinis and Asprea, 2006a–b), at magnifications of 100–400× with optical microscope. A blind test was performed to test the skills of the observer 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 ≥ 95 % of reference samples correctly (Ferretti et al., 2019, 2021a). Food items of wolves were categorised at the specific level for meso-large wild mammals (i.e., ungulates, carnivores, meso-mammals). Additionally, we considered the following categories: livestock, small mammals (i.e., other rodents); other vertebrates (i.e., birds); invertebrates; fruits. The diet of wolves was described considering the whole study period (April 2016–March 2023), and each single study year (from April to March) in order to compare the use of different ungulate species with the relevant density estimated annually.

No method for the assessment of food habits from scats is free from potential biases and ideally, several methods should be used at the same time to show an approximate picture of the diet (e.g., Meriggi et al., 1996; Ciucci et al., 1996, 2018; Lovari et al., 2013, 2015). Previous work showed high consistency between different estimators in our study area, including absolute and relative frequencies of occurrence, estimated volume and biomass (Ferretti et al., 2019). For each category, we calculated initially the absolute and relative occurrence in diet (Lucherini and Crema, 1995). For each *i*-th prey category, the absolute frequency of occurrence (AO_{*i*}) was obtained through the ratio between the number of occurrences of that category (n_{*i*}) and the total number of scats analysed (N), expressed as a percentage: AO_{*i*} = (n_{*i*} / N) × 100 (Kruuk and Parish, 1981; Lucherini and Crema, 1995). The relative frequency of occurrence of each *i*-th category (RO_{*i*}) resulted from the ratio between the number of occurrences of that category (n_{*i*}) and the total number of occurrences of all categories (N_{tot}), expressed as percentage: RO_{*i*} = (n_{*i*} / N_{tot}) × 100. For each sample, we also estimated the relative volume (Vol) of

each food category, that was first estimated visually and then scored on a scale of seven categories: Absent, $\leq 5\%$, 6–25%, 26–50%, 51–75%, 76–95% and $> 95\%$ (Kruuk and Parish, 1981). The median values of these categories were used in subsequent calculations, according to the method described by Kruuk and Parish (1981): 2.5%, 15.5%, 38%, 63%, 85.5% and 98%, respectively. We initially estimated the volume of each category when it was present, i.e., the mean volume across all scats where that category was found (VP_i). Then, we calculated the estimated volume as $Vol_i = (VP_i \times AO_i) / 100$ (Kruuk and Parish, 1981), and then standardised it on a percentage scale. For each indicator of wolf diet, we estimated the relevant uncertainty (Davis et al., 2012) by computing 95% bootstrap confidence intervals, through 1000 resampling.

Furthermore, we evaluated the potential seasonal variations in the use of main prey by wolves throughout the years. Thus, for each considered ungulate species (wild boar, fallow deer, roe deer), we created a dichotomous dependent variable, i.e., we coded each scat with '1' if it included that focal prey, and with '0' if it did not include it. We performed species-specific generalized linear models with binomial errors (link function: logit) where the presence/absence of each ungulate in each scat was modeled against the season (categorical predictor; "autumn": October-December; "winter": January-March; "spring": April-June; "summer": July-September), the numbers of years elapsed from the wolf recolonization (numeric predictor; with 2015 = 0 years from recolonization), and their interactive effect. Model coefficients and their 95% confidence intervals were estimated through the 'lme4' package (Bates et al., 2015), whereas models were validated through visual inspection of residuals with the 'DHARMA' package (Hartig, 2022), in RStudio 2022.02.1 (R Core Team, 2022). We initially inserted all the predictors in global models; then we used the model selection to identify the best model, i.e., the one having the lowest AICc. Moreover, we selected for inference all models with $AICc \leq 2$ and among these, those which were not more complex versions of any simpler model to avoid retaining overly complex models ('nesting rule': Harrison et al., 2018).

2.4. Prey selection

We assessed the selection patterns of wild ungulates using yearly April-to-March timeframes. We used data on summer density estimates of wild ungulates (Fattorini et al., 2011; Ferretti et al., 2016, 2021b; Fattorini and Ferretti, 2020; see *Study Area*) to calculate, for each year, the relative availability of each ungulate species, as the ratio of species' density to the total density of all wild ungulates. In each study year, prey selection was estimated using the Jacobs' Index (Jacobs, 1974), for each ungulate species. The formula for this index is: $J_i = (U_i - A_i) / [(U_i + A_i) - (2 \times U_i \times A_i)]$, where U_i (i.e., the "use") represents the ratio of the number of wolf scats including the i -th prey species over the total number of wolf scats including wild ungulates, and A_i represents the proportion of availability of each i -th prey species, calculated as above. The Jacobs' Index ranges from 1 to -1, with positive values indicating positive selection for a food type, and negative values indicating negative selection. Values close to zero suggest no selection of the food item, implying that the predator utilizes it in proportion to its availability in the area. To assess support to positive/negative selection, we calculated 95% confidence intervals for prey use through bootstrap resampling (1000 replicates), and calculated selection indices consequently. We considered as indicative of prey use according to availability those intervals including '0'; values with the lower bound > 0 were

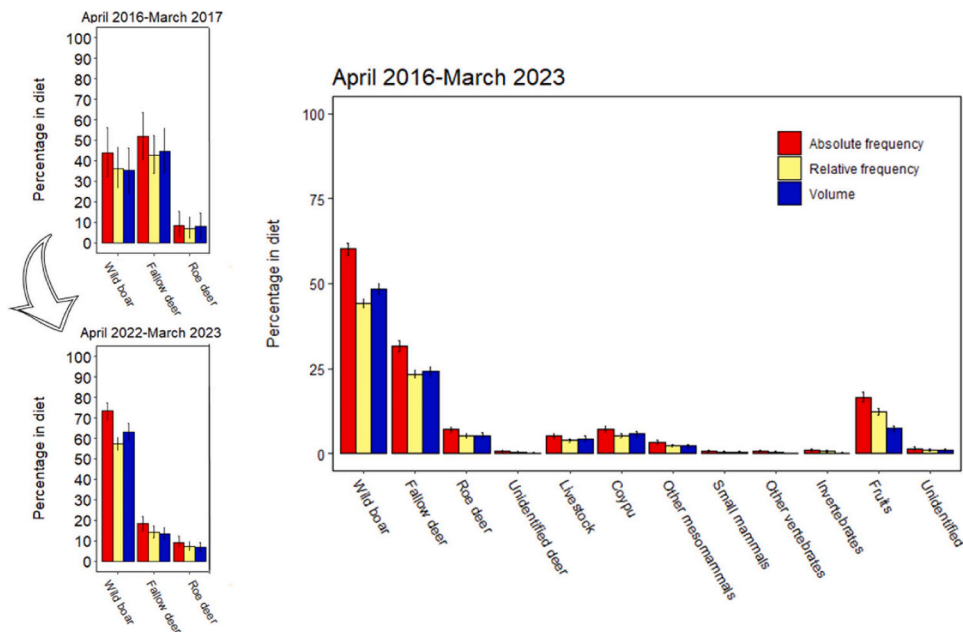


Fig. 2. Absolute frequencies, relative frequencies and volumes of the different food categories found in wolf faecal samples in Maremma Regional Park (2016–2023), with a focus on wild ungulates in the first and last year, as an example, on the left. Error bars indicate 95% confidence intervals estimated through bootstrap with 1000 resamplings.

considered as indicative of positive selection; values with the upper bound < 0 were considered as indicative of negative selection (Werhahn et al., 2019). Then, for each wild ungulate species we fitted linear models where we entered the yearly Jacobs' index as the response variable and (a) the density estimates of each species or (b) the number of years from the wolf settlement, as predictors. We also tested (c) the correlation (Pearson correlation coefficient) between the yearly ratio of the wild boar over fallow deer density estimates with the ratio of their occurrences in the wolf diet, and (d) the correlation (Pearson correlation coefficient) between Jacobs' selection indices of the wild boar and fallow deer.

3. Results

3.1. General food habits

Overall, we gathered $N=3129$ scats. The number of scats in each study year was $N=71$ (1st year); $N=346$ (2nd year); $N=586$ (3rd year); $N=588$ (4th year); $N=601$ (5th year); $N=484$ (6th year); $N=453$ (7th year).

During the study period (2016–2023), the overall wolf diet underlined that the wild boar was the main prey (~60 % of scats, i.e., AO, and 44–48 % of diet, i.e., RO and Vol), followed by the fallow deer (~32 % scats; 23–24 % of diet; Fig. 2). Roe deer occurred in 7 % scats and built-up ~5 % of total diet (Fig. 2). Coypu occurred in 7.1 % scats and built up 5–8 % of the diet (Fig. 2). Fruits were present in ~16–17 % wolf scats, but their volume in the diet was ~7 %; conversely, livestock represented ~4–6 % of diet, depending on the indicator (Fig. 2). Other meso-mammals appeared in 3 % of scats; all the other categories built up minor percentages of wolf diet (i.e., frequencies and volumes ~2 %; Fig. 2).

During the first two study years, the fallow deer was the first prey (AO: 51–52 %; Vol: 41–45 %, yearly) followed by the wild boar (AO: 44–55 %; Vol: 35–39 %, yearly; Fig. 1S). From the third study year, we detected a clear switching of the main prey, with the wild boar showing 49–73 % occurrences and 36–63 % volume in diet and fallow deer having 18–35 % occurrences and 14–27 % volume, yearly (Fig. 1S). Occurrence and volume of roe deer and coypu remained stable throughout years (i.e., frequencies and volumes ≤ 10 %; Fig. 1S). The use of livestock peaked irregularly in the fourth and seventh years (8–12 % occurrences, 7–10 % volume), being 0–4 % in the other years (Fig. 1S). The use of fruits increased throughout the fourth-to-sixth year (~22–33 % occurrences; 10–18 % volume), being ~0–8 % occurrences and 0–2 % volume in diet in the other years (Fig. 1S).

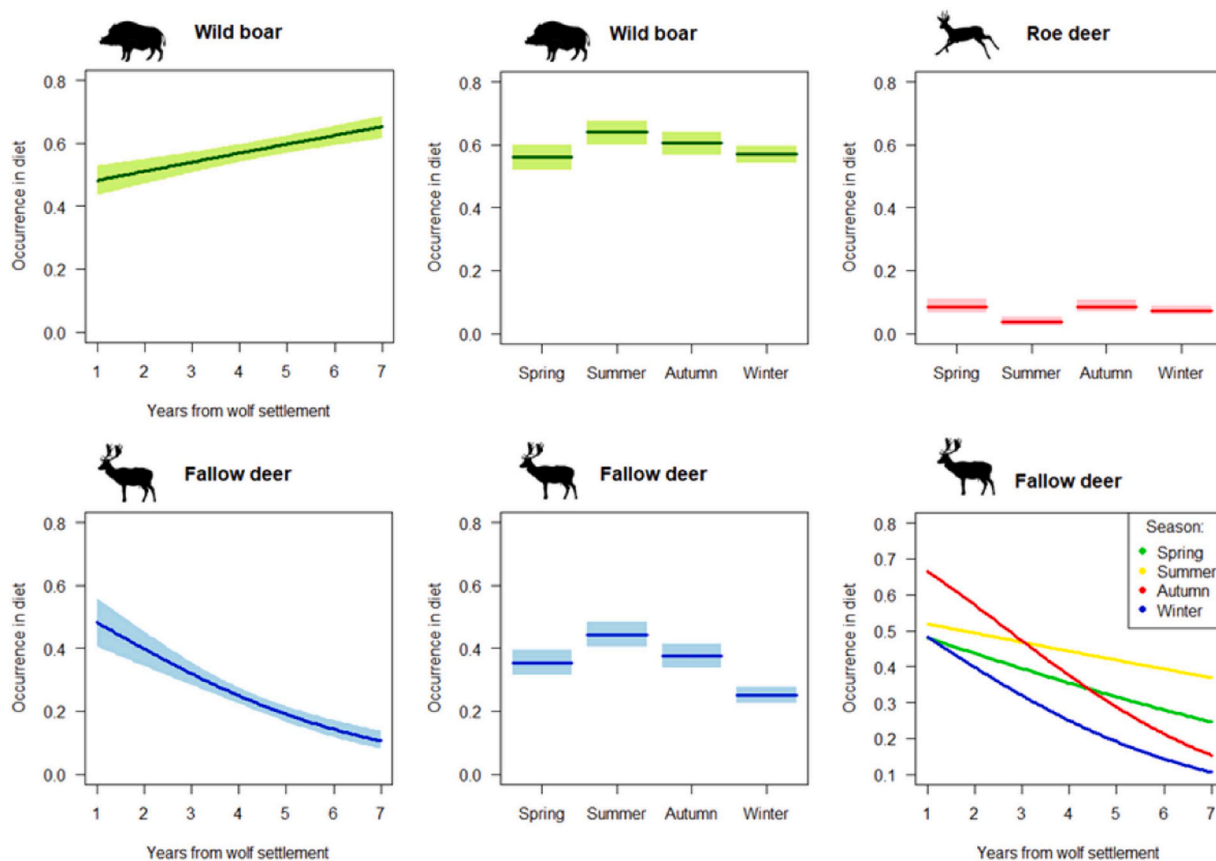


Fig. 3. Seasonal and inter-annual variations of occurrence of wild ungulates in the wolf diet, between April 2016 and March 2023. Relationships estimated through generalized linear models and relevant 95% confidence intervals are shown.

3.2. Seasonal and inter-annual variation of wild ungulate use

For each prey species, only one model was selected (see Tab. 2 S). Wild boar occurrence in the wolf diet increased across years from the wolf resettlement and peaked in summer (Fig. 3; Tab. 1 and Tab. 2 S). Conversely, the use of fallow deer decreased throughout years, with peaks in summer (Fig. 3; Tab. 1 and Tab. 2 S). The interactive effect of year and season was supported: the use of this cervid by the wolf decreased throughout years especially in autumn and winter (Fig. 3; Tab. 1 and Tab. 2 S). The roe deer was the least used in summer, with no variations throughout years (Fig. 3; Tab. 1 and Tab. 2 S).

3.3. Selection of wild ungulates

Jacobs' index supported a selection for the fallow deer during the first two study years and for the wild boar during the third-to-seventh year (Fig. 4). In the 3rd-5th years, the fallow deer was used according to availability then in the last two years was negatively selected, whereas the wild boar was used according to availability in the 1st-2nd years (Fig. 4). The roe deer was under-utilised throughout all study years (Fig. 4f).

The selection of wild boar was negatively associated with estimates of wild boar density ($B = -0.105$, 95% CIs: $[-0.173, -0.038]$, $p = 0.01$) (Fig. 4g; the result pertains to the linear regression). The selection of wild boar increased throughout years from wolf settlement ($B = 0.076$, 95% CIs: $[0.005, 0.147]$, $p = 0.041$). The selection of fallow deer was positively associated with the density estimates of this cervid (linear regression: $B = 0.279$, 95% CIs: $[0.012, 0.546]$, $p = 0.043$) (Fig. 4h). The selection of the fallow deer decreased throughout years from wolf settlement (linear regression: $B = -0.129$, 95% CIs: $[-0.190, -0.069]$, $p = 0.003$).

The correlation between the wild boar and fallow deer selection indices was negative ($r = -0.938$, $p = 0.002$). We found no support for a correlation between the ratio of wild boar over fallow deer density estimates and the ratio of wild boar over fallow deer occurrences in the wolf diet ($r = 0.006$; $p = 0.989$).

We found support for the selection of roe deer being negatively associated with roe deer density estimates ($B = -0.081$, 95% CIs: $[-0.142, -0.020]$, $p = 0.019$) (Fig. 4i). The selection index of the roe deer increased slightly throughout years from wolf settlement ($B = 0.062$, 95% CIs: $[0.005, 0.119]$, $p = 0.038$).

4. Discussion

In ecosystems with multiple prey species, predator food habits would be expected to show variations according to fluctuations in prey density and vulnerability over time and space (Hughes and Croy, 1993; O'Donoghue et al., 1998; Garrott et al., 2007). Assessing temporal variation of food habits and prey selection is especially important in European areas recently recolonised by predators, where human presence may influence interspecific relationships (Kuijper et al., 2016; Ciucci et al., 2020; Prugh, 2023). In a prey-rich area of central Italy recently recolonised by the wolf, and where the predator diet was dominated by wild ungulates (see also Ferretti et al., 2019), we reported seasonal variations of prey use throughout seven years since wolf settlement, with the occurrence of wild boar and fallow deer peaking in summer, and inter-annual variations in use and selection of wild ungulates throughout years. A switch from fallow deer to wild boar as main prey was reported, with selection indices decreasing for the former and increasing for the latter, throughout the years. Relationships between selection indices and prey density were inconsistent across species, being negative for the wild boar and the roe deer, and weakly positive for the fallow deer. Results suggest that factors driving prey selection were not simply related to prey density.

Table 1

Factors influencing seasonal and inter-annual variations of occurrence of wild ungulates in the wolf diet estimated through generalized linear models. Estimates of model coefficients (B), their standard errors (SE) and 95 % confidence intervals (95 % CIs), as well as P-values are shown for selected models. In bold, variables for which an effect was statistically supported. See Table 1S for the selection model results and Table 2 S for the post-hoc analyses.

Species	Variables	B	SE	95 % CIs	P
Wild boar	(Intercept)	-0.228	0.127	[-0.48, 0.02]	0.074
	Season [Summer]	0.333	0.120	[0.10, 0.57]	0.005
	Season [Autumn]	0.185	0.115	[-0.04, 0.41]	0.106
	Season [Winter]	0.040	0.103	[-0.16, 0.24]	0.702
	Years from wolf settlement	0.117	0.022	[0.07, 0.16]	< 0.001
Fallow deer	(Intercept)	-0.68	0.09	[-0.86, -0.50]	< 0.001
	Season [Summer]	0.40	0.12	[0.16, 0.64]	< 0.001
	Season [Autumn]	-0.02	0.12	[-0.26, 0.23]	0.902
	Season [Winter]	-0.58	0.12	[-0.81, -0.35]	< 0.001
	Years from wolf settlement	-0.29	0.09	[-0.46, -0.12]	< 0.001
	Season [Summer] × Years from wolf settlement	0.12	0.12	[-0.11, 0.35]	0.312
	Season [Autumn] × Years from wolf settlement	-0.37	0.12	[-0.61, -0.13]	0.002
	Season [Winter] × Years from wolf settlement	-0.28	0.12	[-0.51, -0.06]	0.015
Roe deer	(Intercept)	-2.383	0.151	[-2.68, -2.09]	< 0.001
	Season [Spring]	-0.920	0.264	[-1.44, -0.40]	< 0.001
	Season [Summer]	0.017	0.200	[-0.38, 0.41]	0.932
	Season [Winter]	-0.185	0.188	[-0.55, 0.18]	0.325

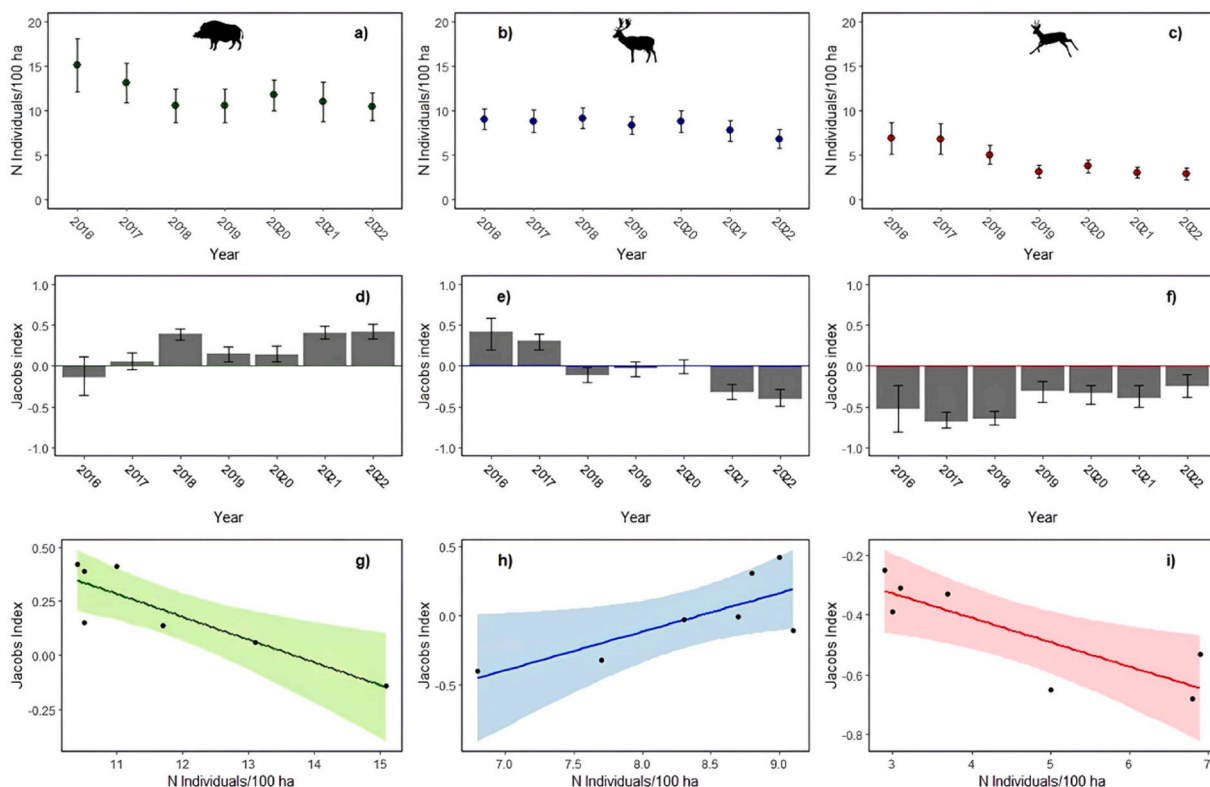


Fig. 4. a) Wild boar density estimates, b) fallow deer density estimates, c) roe deer density estimates over the study years, with their error bars indicating standard errors. Jacobs' indices across the study years referred to d) wild boar, e) fallow deer, f) roe deer; error bars for Jacobs' indices indicate 95 % confidence intervals computed through bootstrap applied to the estimate of prey use (1000 resamplings). Relation estimated through linear models between the selection index and ungulate density estimates in reference to g) wild boar, h) fallow deer, i) roe deer.

The wolf typically focused on wild ungulates, with an interest directed towards larger species with more marked grouping behaviour, i.e., the wild boar and the fallow deer (occurrences and volumes >70 % in the wolf diet, together), whereas the roe deer was used with low percentages (i.e., <10 %). Among alternative food resources, the coypu was regularly used throughout the years, whereas the use of livestock and fruits was irregular, with some occasional peaks. Large semi-aquatic rodents (e.g., beaver *Castor* spp.) have been reported as significant alternative resources for wolves, especially during times when there is an increased energy demand for wolf packs or when the availability of ungulates is reduced (Sidorovich et al., 2017; Gable et al., 2018; Ferretti et al., 2019). Local management strategies of livestock, preventive measures against predation, the capability of cattle to actively defend calves against predators, together with great availability of wild prey, have been suggested as factors to explain the small importance of livestock in the wolf diet, in our study area (Ferretti et al., 2019; see also Meriggi and Lovari, 1996; Sidorovich et al., 2003; Kuijper et al., 2019, for other ecological contexts).

Wild boar and fallow deer are gregarious, have considerable body mass, and are expected to be more remunerative prey than smaller-sized roe deer. Occurrence in large groups can increase detectability by predators (Huggard, 1993; Hebblewhite and Pletscher, 2002). Not surprisingly, the spatial variation of wolf detection rates has been found as associated with those of wild boar and fallow deer, rather than roe deer (Lazzeri et al., 2024). The wild boar has been frequently reported as the most used prey by the wolf in southern Europe (Meriggi et al., 1996; Capitani et al., 2004; Mattioli et al., 2004; Stahlberg et al., 2016; Mori et al., 2017). Conversely, differential use of fallow deer has been reported across Mediterranean contexts, ranging from relatively low (Mattioli et al., 2004, 2011) to significant percentages in the wolf diet (Stahlberg et al., 2016; Ferretti et al., 2019; Del Frate et al., 2023). While it is often a major prey to wolves (e.g., Mattioli et al., 2004; Mori et al., 2017), the roe deer was confirmed as a secondary, minor prey in our study site (Ferretti et al., 2019). Its tendency to live in small groups or to show solitary habits, emphasised by male territoriality in spring-summer (Hewison et al., 1998), selection of concealed habitats such as forest or scrub wood, where predation could be more difficult (Mattioli et al., 2004), as well as avoidance of sites with high densities of fallow deer (Ferretti et al., 2011; Ferretti and Fattorini, 2021), could explain this result (Ferretti et al., 2019). Moreover, roe deer tend to have bimodal activity rhythms, with peaks at dusk and dawn (Cederlund, 1989; Pagon et al., 2013; Mori et al., 2020; for our study area: Rossa et al., 2021; Lazzeri et al., 2024), leading to a low temporal overlap with the wolf, that was predominantly nocturnal in our study area (Lazzeri et al., 2024).

Although the wild boar and the fallow deer were consistently the main prey of wolves throughout the year, their use peaked in summer, which could be probably related to increased availability/vulnerability associated with the presence of newborn offspring, suggesting a positive selection towards the juvenile classes (Meriggi et al., 1996; Mech and Boitani, 2003; Mattioli et al., 2004).

Accordingly, a seasonal decrease in the use of roe deer occurred in summer. In autumn-winter, roe deer form mixed-sex groups which may increase their detectability in comparison with spring-summer, when these deer have more solitary habits because of male territoriality and the presence of mother-offspring association (Hewison et al., 1998). Suggestively, previous work showed a seasonal increase in roe deer vigilance in winter, possibly associated with an increased perception of predation risk (Fattorini and Ferretti, 2019).

Our results highlighted a sharp prey switching by the wolf, that changed its main prey from the fallow deer, selected in the first two years after its settlement to our study area, to the wild boar, which became dominant in the wolf diet throughout the years. These results were mirrored by inter-annual variations of selection indices, showing a steady decrease for the fallow deer and an increase for the wild boar. Large body size, group living, selection of ecotone/open habitats with bushy patches potentially favouring ambush predation (Torretta et al., 2018), as well as the absence of effective defensive weapons in females, could potentially explain the initial preference of wolves towards fallow deer rather than wild boar, despite the former were less abundant than the latter (Ferretti et al., 2019). Thus, fallow deer may be perceived as a particularly remunerative prey by wolves. The decrease in fallow deer use occurred especially in autumn-winter. Fallow deer diurnal activity has been reported to increase throughout the years, particularly during the cold seasons (Esattore et al., 2023; Lazzeri et al., 2024), which may have led to reduced interaction with wolves especially in autumn-winter. Furthermore, young fallow deer could acquire experience and skills throughout summer to increase their ability to escape predation. Conversely, selection indices for the wild boar increased throughout the years, mirroring the changes observed for the fallow deer: a negative correlation was observed between the selection indices of the two main prey.

Prey switching has been typically associated with positive frequency-dependent selection, occurring when predators concentrate their action on the most abundant prey and modify their food habits according to inter-annual variations of prey relative abundance (Hughes and Croy, 1993; O'Donoghue et al., 1998; Garrott et al., 2007). Our results showed a clear prey switching by the wolf throughout a seven-year study period. However, results did not support that selection was regularly addressed to the most abundant prey. The switching in the main prey by the wolf did not appear to be mediated by the changing availability of resources over time, as prey densities remained fairly constant over the study period, with only a slight initial numerical decrease in wild boar and roe deer. We found a negative relationship between selection indices and wild boar densities, and a positive – although weak – relationship between selection indices and fallow deer densities. Nevertheless, fallow deer population density remained relatively stable during the study period, whereas the occurrence and volume of this deer in the wolf diet showed a ~65–70 % decrease throughout the study, suggesting that density *per se* may have not been a major driver of changes in wolf food habits. Moreover, no correlation was found between the ratio of the densities of wild boar and fallow deer and their occurrences in the wolf diet, which suggests that wild boar did not become progressively more abundant in the wolf diet compared to fallow deer in relation to an increase the density of the suid compared to that of the cervid. Prey accessibility may not be only influenced by prey abundance since antipredator strategies leading to changes in temporal activity, space/habitat use, and/or grouping patterns could affect prey detectability (Mech and Boitani, 2003). Previous and concurrent work showed a sharp increase in diurnal activity of fallow deer throughout years since wolf settlement as a possible anti-predatory response based on temporal avoidance (Rossa et al., 2021; Esattore et al., 2023; Lazzeri et al., 2024), which may have modified the accessibility of this deer to the wolf. During the same period, wolf activity rhythms remained mainly nocturnal, with an increased overlap with those of the wild boar (Lazzeri et al., 2024), which fits our results showing an increased use of this suid by the predator. Prey switching could have been primed by antipredator behavioural responses of the main prey, rather than changes in prey abundance.

A rich prey community is important to allow predators to switch to alternative prey according to variations in abundance or accessibility of main prey (Mech and Boitani, 2003; van Leeuwen et al., 2013). The abundance of alternative wild prey is fundamental to favour carnivore persistence and, together with appropriate husbandry practices, to limit attraction to livestock. Wild boar populations have shown a significant increase in the last decades (Massei et al., 2015), favoured by anthropogenic and natural factors. This medium-sized, gregarious suid is often the main prey of wolves (Mori et al., 2017). In Italy, the geographic pattern of wolf expansion generally matches that of wild boar (Mori et al., 2017), and the wolf recolonised of large sectors of its previous range (La Morgia et al., 2022; Zanni et al., 2023). Wolves and wild boar may establish complex interactions, ranging from predation to scavenging and kleptoparasitism by wild boar over carcasses of wolf prey (Mattioli et al., 2011; Focardi et al., 2017; Mori et al., 2017). These two mammals can trigger effects on other components of ecosystems that can propagate across trophic levels (e.g., Massei and Genov, 2004; Hebblewhite et al., 2005; Barrios-Garcia and Ballari, 2012; Ripple et al., 2014). Thus, the potential for wolf-wild boar interactions to influence the relevant population dynamics would be expected to determine consequences at the community-to-ecosystem level. Substantial implications can also arise for the management of the relevant interactions with human activities, e.g., hunting (Bassi et al., 2020) or livestock depredation (Meriggi and Lovari, 1996; Mori et al., 2017).

Our findings emphasised that the wolf diet and prey selection were influenced by seasonal variations and antipredator responses (Lazzeri et al., 2024), indicating a dynamic prey switching from fallow deer to wild boar. These results indicated that prey density alone did not drive prey selection. Our results testified to a dynamic interannual variation of interactions between the wolf and the wild boar, as well as to the potential for the latter to buffer the former against temporal variations in accessibility of local main, more remunerative prey. A thorough understanding of the relationships between these two mammals, and their inter-annual variations, is thus important to evaluate not only interspecific interactions but also potential implications for wildlife management, especially in areas recently recolonised by this predator such as it is occurring in many European countries.

Ethics approval

Not applicable.

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Consent for publication

Not applicable.

Consent to participate

Not applicable.

CRedit authorship contribution statement

Conceptualization and Supervision: FF; Data collection: All the authors; Data curation and Formal Analysis: LL, IB, GP, FF; Writing – original draft: LL and FF. Writing – review and editing: All the authors.

Declaration of Competing Interest

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

Data availability

Data will be made available on request.

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Appendix A. Supporting information

Supplementary data associated with this article can be found in the online version at [doi:10.1016/j.gecco.2024.e03069](https://doi.org/10.1016/j.gecco.2024.e03069).

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