Prey selection and dietary response by wolves in a high-density multi-species ungulate community

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Prey selection and dietary response by wolves in a high-density multi-species ungulate community

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Abstract Studies on predation by the wolf (*Canis lupus*) have often reported contradictory results about the role of prey density and vulnerability on wolf prey use. We investigated dietary response and prey selection by wolves in a high-density and multi-species ungulate community, analysing scats collected over a period of 11 years in the Casentinesi Forests, Italy. The second most abundant species, wild boar (*Sus scrofa*), was found to be the main wolf prey, and we did not observe any dietary response of wolves to variations in the density of either primary or secondary prey species. Selection patterns were uniform throughout the study period. Wolves strongly selected for wild boar piglets, while roe deer (*Capreolus capreolus*) fawns and adults, red deer (*Cervus elaphus*) adults and fallow deer *(Dama dama)* adults were avoided. Wolf preference for wild boar was inversely density dependent. Within each species, juveniles were preferred to adults. Medium-sized, young individuals of both wild boar and roe deer were optimal prey, although with different selection patterns related to the different anti-predator strategies adopted by each prey species. The results of this study suggest that in productive ecosystems with high density and high renewal rates of prey, selection patterns by wolves are determined by prey vulnerability, which is connected to prey age and body size. The different patterns of wild boar versus cervids use by wolf across Europe seems to be related to their relative abundances, while the strong selection of wild boar in Italian Apennines with respect to the more frequent avoidance in central-eastern Europe is better explained by higher piglet productivity and smaller body size of adults boar in Mediterranean temperate forests.

Keywords Age-specific selection · *Canis lupus* · Prey vulnerability · Wild boar · Wolf diet

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Introduction

Foraging behaviour is a driving factor of predator–prey dynamics, and its understanding is fundamental for proper management and conservation of large carnivore and wild ungulate communities (Huggard 1993; Kunkel et al. 2004; Smith et al. 2004). Opportunistic predators tend to select the most abundant prey (apostatic selection, Yearsley 2003), and their patterns of selection are influenced by changes in prey abundance. When a predator selects abundant prey and avoids rare ones, then it is said to show prey switching behaviour (Murdoch 1969), and in terms of functional response (Holling 1959) it is expected to exhibit a sigmoidal or logistic (type III) functional response (Andersson and Edrlinge 1977, Joly and Patterson 2003).

Conversely, predators that show strong selection for a certain prey type irrespective of its abundance are defined as specialists. As a consequence, specialist predators may

show selection for prey species that are rare or less abundant compared with other potential prey species (antiapostatic selection or negative prey switching). Finally, specialist predators should exhibit an asymptotic or hyperbolic (type II) functional response.

Wolves are generally considered generalist-opportunistic predators (Becker et al. 2008), relying on whatever vulnerable prey are available in their territory (Mech and Peterson 2003). However, in multiple prey systems wolves often show a clear selection for a single prey species (Huggard 1993; Jędrzejewski et al. 2000) even when the preferred prey is less abundant than others (Potvin 1988; Dale et al. 1994; Kunkel et al. 2004).

According to the optimal diet theory (Stephens and Krebs 1986), predators should select the more profitable prey, profitability being the ratio between energy gain and handling time. However, in wolf-ungulate systems, preys are mobile and have effective defence traits, both physical and behavioural. In addition, each prey species is composed of individuals differing in sex, age and size; each prey category provides different biomass and requires a different amount of effort to be killed. In this context, prey profitability, and, consequently, prey use and selection, is the result of several factors affecting searching time, encounter rate, capture success and risk of injury.

Prey abundance significantly influences searching time and encounter rate, and when a prey species increases in abundance, a functional response of the predator population is expected.

Prey vulnerability, i.e. the physical, behavioural and environmental factors that influence the susceptibility to predation (Becker et al. 2008; Lind and Cresswell 2005), is of great importance in prey–predator interactions because it strongly affects capture success, and consequently handling time. Among the physical factors determining vulnerability, particularly in temperate climate ecosystems, age class and body size are the most important, with young-of-the-year and medium-sized individuals generally proving to be the most vulnerable (Mech and Peterson 2003). Accordingly, both population structure and renewal rate of prey can influence prey selection patterns. Moreover, spatial behaviour of prey (habitat selection and predictability) that may be related to various factors such as, for instance, the presence of man, can be decisive in influencing vulnerability: in this context density itself may not be a constant clue for determining predation rate (Theuerkauf and Rouys 2008).

In this study, we analysed the effect of prey density, age and size on wolf predation in a multiple prey and high renewal rate wolf-ungulate system in the Casentinesi Forests, Italy. A rich and diverse community of wild ungulate is present, composed of four species: wild boar (*Sus scrofa*), roe deer (*Capreolus capreolus*), red deer (*Cervus elaphus*) and fallow deer (*Dama dama*). Following

preliminary results on wolf diet (Mattioli et al. 1995), we extended our analysis of predator–prey relationships over an 11-year period. Firstly, we evaluated the response of wolves to wild ungulate density variations, by calculating both dietary response (sensu Jędrzejewska and Jędrzejewski 1998) and the strength of selection. We then applied a multiple-level selection analysis in order to better differentiate the effects of density, age and size on prey selection.

We tested three hypotheses:

1. wolves would change use and selection of the main prey species according to prey density variation;
2. in productive ecosystems where prey populations have high density and high renewal rates, diet composition and prey selection by wolves are more affected by prey age and body size then by their abundance.
3. within the main prey species wolves generally select young of the year, and among them intermediate weight classes are the most profitable and are more strongly selected for.

Materials and methods

Study area

The study was carried out from May 1988 to April 2000 in a 130-km² area located in the north-eastern Apennines, in Tuscany, Italy. This is the same area that was referred to as the intensive study area in previous papers on wolf feeding ecology by Mattioli et al. (1995) and Mattioli et al. (2004), and it is comprised within the wider wolf-monitoring area (308 km²) described by Apollonio et al. (2004).

The area can be divided into two portions along the elevation range. The upper portion (69 km²), above ca. 700 m, is found within the Casentinesi Forests National Park. Hunting is not allowed in this area and logging is limited. In contrast, the lower portion (61 km²) is exploited by extensive logging and hunting. The wild ungulate community included four species, namely, wild boar, roe deer, red deer and fallow deer (Table 1), which amounted to a biomass of 860 kg/km² during the study period (Apollonio et al. 2004).

In this area, the presence of the Camaldoli Forest wolf pack was regularly reported from 1992 to 2000. Mean pack size in late summer was 4.9±0.9 individuals (range, 4–7). The pack showed a high fidelity to pup raising areas and reproduction was observed every year, except for 1996 (Apollonio et al. 2004).

According to the locations of home sites obtained during wolf howling sessions, the spatial distribution detected by snow tracking in winter and the results of genetic analysis on fresh wolf scat samples, the study area was assumed to

Table 1 Mean values of body mass, population structure and density of wild boar, red deer, roe deer and fallow deer in the Casentinesi Forests area, from 1989 to 2000

Sources of data: Lovari et al., 2000; Orlandi, Gualazzi and Bicchi (unpublished report for 1999–2000), Provincial Administration of Arezzo (unpublished annual report for 1989–1999), for ungulate density; Apollonio et al. (2000) for population structure

Parameter	Wild boar	Roe deer	Red deer	Fallow deer	Total
Mean body mass adult (kg)	60	24	115	60	
Mean body mass Juv. (kg)					
In summer	3.8	3.4	13.3	7.5	
In winter	28.5	18.3	60	30.8	
Juvenile/Adult ratio					
In summer	1.44	0.65	0.37	0.38	
In winter	0.75	0.35	0.27	0.38	
Mean density (n/km^2)					
In summer	9.2	20.2	3.7	1.6	34.7
In winter	3.6	12.2	2.7	1.3	19.8

approximately overlap the estimated territory of the CF pack.

Estimating abundance and population structure of the wild ungulate community

Late-winter densities were estimated by means of drive censuses for roe deer and wild boar, following the protocols described in Jędrzejewska et al. (1994). Data were collected every year on 11 permanent sample areas (39.9±17.9 ha of surface) covering a total of 590 ha. The average density of surveyors was 110/100 ha of sampled area. More detail on density calculation from drive census data are described in Mattioli et al. (2004). Red deer numbers were estimated by counting roaring males each year during the rut throughout the whole study area, divided in two sectors. Permanent survey points, with a density of one point per 100 ha were used. In each sector counts were twice replayed during the night from 21:00 to 24:00, using every point of each sector simultaneously. The number of roaring stags was established by recording number, direction (given by compass) and time of all roars heard from each hearing points, and by comparing data of adjacent points. The number of roaring stags was converted in total red deer estimate using the following formula:

$$Population\ estimate = \frac{N\ roaring\ stags}{percentage\ of\ mature\ stags} \times 100.$$

The percentage of mature stags was calculated as the mobile mean over three following years.

Due to the low-density and patchy distribution of fallow deer, and the consequential high variability of drive census estimates across different years, a mean density value for the whole study period was calculated. This was obtained by taking into account drive census data as well as observations from fixed vantage points made in 1998 and 1999 in the lower portion of the study area (see Mattioli et al. 2004). Summer (post-parturition) density was calculated

by adding the estimated percentage of young to the late-winter density (see Mattioli et al. 2004). Annual density was calculated as the mean between each summer density and the following late-winter density, for each species. Data on population structure (age and sex classes) were collected from 1992 to 2000 for each species by observation along 11 permanent transects of 71,3 km of total length and four blinds, distributed in the whole study area and repeated each month. Four classes were distinguished for roe deer: adult male (>2 years), yearling males, females (>1 year) and fawns. Red deer and fallow deer were divided into five classes; adult mature males (>4 years), subadult males (2–4 years), yearling males, females (>1 year) and calves. For wild boar, only piglets (1–12 months) and adults (>1 year) were distinguished.

Prey use

Prey use was studied through the analysis of scat contents. The choice of method for diet analysis is crucial when small-size prey is abundant. Many authors, in fact, emphasize that kill analysis tends to underestimate the importance of smaller prey species in predators' diet, because such individuals are usually completely consumed and, as a consequence, remains of such a kill are more rarely found (Olsson et al. 1997; Jędrzejewski et al. 2002; Nowak et al. 2005; Gula 2004; Sand et al. 2008). Moreover, searching for fresh kills is only possible during winter and in countries with frequent snowfall. Therefore, in our study we found scat analysis a more suitable method for year-round analysis focused on small prey.

Samples were collected from 13 transects established on unpaved forest roads and paths along a total of 53.6 km, ranging from 700 to 1,500 m in elevation, carried out each month from 1992 to 2000. The study also included 240 scats that were collected from the same area between 1988 and 1992, and previously analysed by Mattioli et al. (1995). The total period of scat collection (period A) was divided into one year sections according to the annual biological

cycle of the main prey (wild boar), with each year starting in March and ending the following February. Annual values were calculated from 1989 to1999. A sub-sample of scats collected from 1993 to 1996 (period B) was used for more detailed analyses.

Scat content was analysed following the methods described in Mattioli et al. (1995) and Ciucci et al. (1996).

Operators were tested on their ability to identify prey species, age classes, and relative volume by performing a blind test (see Mattioli et al. 2004).

The utilization rate of each food item was assessed in terms of mean percent volume (MPV). For each scat, a volume value was assigned to each food item, considering a total of 1 volume per scat. Since in previous study (Mattioli et al. 1995), scats contained just one item in 80% of the cases, five fixed volume classes were used: 0% (0–5), 25% (6–25), 50% (26–50), 75% (51–75) and 100% (76–100). For wild ungulates and other wild mammals such as hare (*Lepus europaeus*), badger (*Meles meles*), marten (*Martes foina*) and fox (*Vulpes vulpes*), the relative biomass (BIO) and number of prey (RNP) were calculated by means of the biomass model developed by Floyd et al. (1978): $Y = 0.38 + 0.02X$, where Y represents the biomass (kg) of prey eaten for each collectable scat and X is the live weight of prey. This model was chosen because it was developed using prey which are comparable in size to those available in our study area. However, in order to be confident that the biomass estimates were not affected by our choice of model, results were also calculated using alternative models, such as Weaver's model (1993, $Y = 0.439 + 0.008X$) and the model 1 by Ruehe et al. (2003, $Y = 0.00554 + 0.00457X$), and then compared with our preferred model. Significant differences were not found between the model developed by Floyd et al. (1978) and the alternative models described above, with respect to both the consumed relative biomass and the relative number of prey.

Finally, for each species, the mean individual weight of consumed prey was calculated by dividing the total ingested biomass by the number of consumed individuals, both of which were obtained from the biomass model.

Evaluation of age and weight classes of prey consumed

Age-species classes of 517 out of 1,091 scats collected during period B were identified Deer remains found in scats were classified into two groups: <1-year-old individuals and >1-year-old individuals. Such distinction was made on the basis of the characteristics of their fur (roe deer, $n=15$; red deer, $n=31$; and fallow deer, $n=4$) and the ossification extent of bones (roe deer, $n=101$; red deer, $n=38$; and fallow deer, $n=10$); <1-year-old individuals were grouped into seven weight classes, according to the month when the scat was collected and to juvenile body-growth curves

estimate from their birth month, set in June, to the following May. For each species, the body-growth curve was derived from the weight of juveniles which were shot in the exploited area between August, 11 and March, 15. In contrast, only one weight class was adopted for adults of each species; this was calculated as the mean weight of each sex and age class multiplied by their frequency in the population. In respect of roe and fallow deer, both > and <1-year-old individuals could be distinguished throughout the year. For red deer, the same two age classes could be discriminated with some certainty only from May to October, according to differing characteristics of their fur. For every species, samples which could not be aged were presumed to fall into adult and young classes with the same relative proportions as in the aged samples.

Wild boar samples ($n=318$) were aged primarily by analysing bone remains (89.3%), and secondarily by analysing hair (10.7%). For wild boar, weight classes of young cannot be determined on the basis of the time of scat deposition, because births are scattered over a long period. For this reason, distinct regression functions relating bone dimensions and body weight were calculated for approximately 250 morphological measurements obtained from nine individuals of known weights. Only those measurements that were correlated with weight at the significance level of $p<0.005$ were taken into account. From the regression equations, we calculated the limits of the intervals for 5-kg wide classes (nine classes from 1–5 to 30–35 and >40 kg). Samples containing bone remains that could be measured were grouped into one of these nine classes, while samples standing on the threshold between two classes were distributed pro-rata.

The likelihood of finding recognisable wild boar bone fragments in wolf scats appeared to be inversely correlated to individual boar size, which led to a slight overestimation of young individuals. To avoid difficulties related to this bias, all scats containing only boar hair were also analysed, and three weight clusters were subsequently identified (<10, 10–35 and >35 kg) which could be recognised on the basis of the size and colour of the hair. In order to ascertain the right classification of wild boar hair into these clusters, a blind test was carried out on 61 hair samples belonging to different boars of known weight. All individuals falling into the <10 kg ($n=5$) and >35 kg ($n=31$) clusters were correctly classified, although two individuals actually belonging to the 11–35 kg cluster ($n=25$) were misclassified as falling into the >35 kg cluster. Thus, samples falling into either the <10 or >35 kg clusters were grouped into the extreme classes (1–5, 6–10 and >35 kg), while the remainder were assigned to the 11–15, 16–20, 21–25, 26–30, 31–35 kg weight classes, according to their relative occurrence among the samples identified by bone dimensions.

Analysing the frequency of weights in an independent sample of 71 wild boar of known ages and weight, we set a threshold of 35 kg for distinguishing between individuals younger or older than 1 year. Accordingly, all scat samples attributed to weight classes below 35 kg, were assigned to the <1-year-old age class, whereas the ones attributed to weight classes ≥35 kg were assigned to the adult age class.

Prey selection

In this paper, we used the term 'selection' in the same sense as Taylor's (1984) 'black box' definition of preference, reported by Becker et al. (2008), 'when a predator selects a prey type disproportionately to its occurrence in the environment'. For each prey category i, the selection ratio $w_i = o_i / \pi_i$, was calculated, where o_i is the proportion of used individuals and π_i is the proportion of available individuals in the ungulate community (Manly et al. 2002). When all resources are used proportionately to their availability, w_i equals 1, while $w_i > 1$ suggests a selection and $w_i < 1$ an avoidance. In addition, as a proxy of the strength of selection, the standardised selection ratio was calculated, as $\beta = \left(\frac{o_i}{\pi_i} \right) / \left(\sum_{j=1}^{n} \frac{o_i}{\pi_i} \right)$ (Manly et al. 2002).

Prey selection was analysed at three different levels only in relation to wild ungulate species. Firstly, selection of prey species was calculated using annual data from 1989 to 1999 and by comparing the relative use of prey, expressed as mean percent volume, with the percentage of prey in the population calculated by mean annual density. To evaluate the potential effects of density estimate inaccuracies, simulation of selection ratio was performed taking into account the upper and lower values of 95% confidence intervals of wild boar and roe deer late-winter densities (Fig. 1) and w_i was recalculated for each of eight possible combinations between different estimates of density (Appendix). In order to test the influence of variations in prey density on the strength of selection, a regression analysis was carried out for each prey species between the standardised selection ratio, β, and the mean annual density.

Secondly, age-related selection patterns of all prey species were analysed according to each species' classification into two age classes: <1-year-old individuals and adults (Höner et al. 2002). This analysis was performed using only data from 1993 to 1996 for which the annual sample size was >100 scats. The proportion of used individuals was expressed by RNP.

Finally, selection of young in comparison to adults was analysed separately for each prey species. In investigating this, data relating to period 1993–1996 were used together with the cumulative data from the period 1988–1992. Different annual periods, however, were identified for each species according to their birth season: from March to the
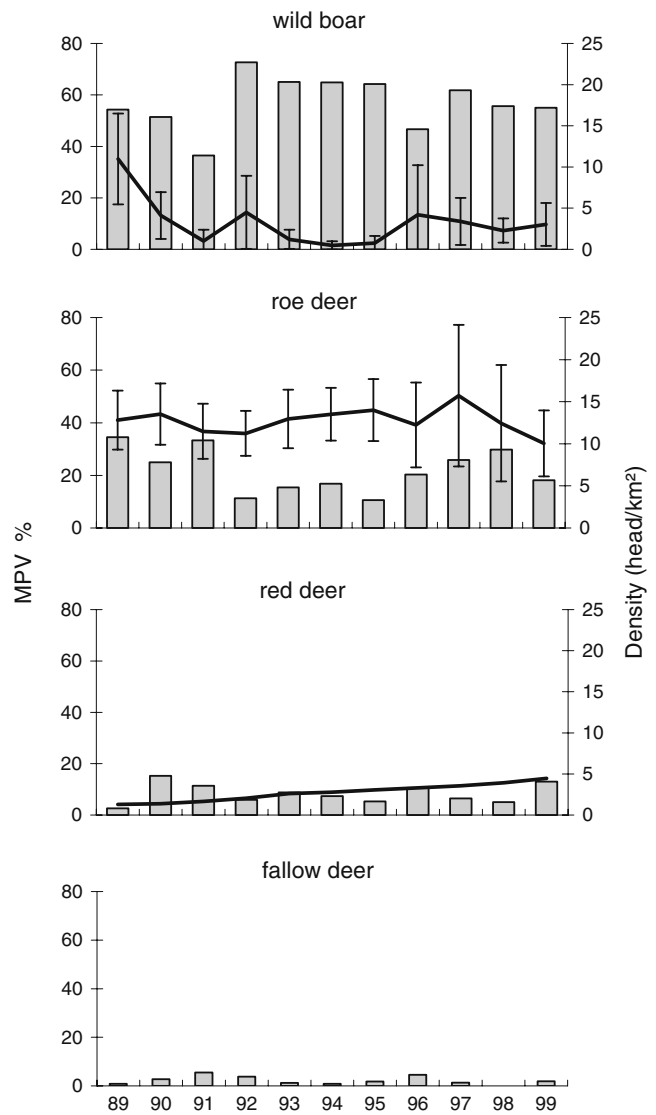

Fig. 1 Late-winter (before prey parturition) density of wild ungulates (*bold lines* with confidence intervals at 95%) and prey use (*bars*, mean percent volume in scats) by the wolf pack in the Casentinesi Forests, from 1989–1999. Confidence intervals were calculated only for drive census data of wild boar and roe deer. Each year runs from March to the following February. Scat sample size: 1989=29; 1990=36; 1991=77; 1992=106; 1993=334; 1994=309; 1995=261; 1996=187; 1997=93; 1998=84; 1999=208

following February for wild boar and from May to the following April for roe deer. For red deer, only 6-month periods (May–October) were adopted while for fallow deer, only one analysis using the cumulative data from all years was carried out due to the small sample size available. The RNP was used as the utilization index. For wild boar and roe deer, selection indices were also calculated for bimonthly time periods, by pooling data from all years. This aimed to evaluate variations in the strength of selection for young during their first year in relation to their body growth stage, which was expressed as the

number of bimonthly time periods that had elapsed since their birth.

Statistics

Selection was assessed by calculating confidence intervals (CI) for w_i through the following formula, including Bonferroni correction for multiple comparisons: $CI = \pm Z_{\alpha/2k} \times SE(w)$ where Z is the upper value of the normal standard for $\alpha/2k$, α is the significance threshold, set to $\alpha = 0.01$, k is the number of categories, and SE is the standard error. The selection was considered not significant if confidence intervals included 1 (Manly et al. 2002). Furthermore, confidence intervals ($\alpha = 0.01$) were calculated using the Bonferroni correction and used to test differences in biomass models by Weaver (1993), Ruehe et al. (2003) and Floyd et al. (1978). Statistical analyses were performed using SPSS 13.0 software package.

Results

Wild ungulate availability

During period A, the mean density of wild ungulates in the study area was estimated to be approximately 19.9 heads/km^2, before parturition, and 34.7 heads/km^2 after parturi-

tion (Table 1). Roe deer was the most abundant species throughout the period, except for 1989 (Fig. 1), and wild boar was the second most abundant. Density of red deer increased threefold over the study period, thus showing a significantly positive trend ($Y = 1.154 + 3.723*X$, $R^2 = 0.994$, $F = 1235.7$, $p < 0.0001$). A uniform density of 1.4 heads/km^2 was calculated for fallow deer. Wild boar showed the highest juvenile/adult ratio, being <1-year-old individuals approximately 51% of the average population, while 32.8% of roe deer were fawns and 24.1% of red deer were calves. Observed group size was larger for wild boar (mean=6.5; $n = 566$) than for red deer (mean=3.1; $n = 846$), fallow deer (mean=3.7; $n = 366$), and particularly roe deer (mean=2.0; $n = 828$). All these data come from observations performed along transects and from blinds, for a total of 4,425 boars, 5,868 roe deer and 3,805 red deer recorded.

Prey use and dietary response

The analysis of 1,862 scats collected during period A showed that the diet of the wolf pack was based almost exclusively on wild ungulates, with domestic ungulates and other prey items representing approximately 10% of volume in the scats (Table 2). The percentage of scats composed of one item (78.9%), two items (19.3%) or three items (1.5%) were very close to those found by Mattioli et al. (1995) (80.0%, 18.3% and 1.3%, respectively). Wild boar proved to be the most

Table 2 Wolf diet in the Casentinesi Forests area

Food items	Period A (1988–2000) n=1,862	Period B (1993–1996) n=1,091		
	MPV%	MPV%	BIO%	RPN%
Wild boar	58.7	67.9	65.1	66.5
Roe deer	19.1	17.1	14.0	18.9
Red deer	8.7	8.6	13.9	6.0
Fallow deer	1.9	2.0	2.3	1.6
Unidentified Cervidae	2.5	2.9	3.9	2.1
Total Wild Ungulates	90.9	98.5	99.2	95.1
Sheep and Goats	3.3	–	–	–
Cattle or Horse	0.6	–	–	–
Pig	0.5	–	–	–
Dog	0.1	–	–	–
Total livestock	4.5	–	–	–
Carnivora[a]	0.4	0.7	0.4	2.1
Hare	1.2	0.8	0.4	2.7
Small rodents[b]	1.0	–	–	–
Unidentified mammals	0.5	–	–	–
Fruit	0.2	–	–	–
Vegetable	0.5	–	–	–
Unidentified material	0.7	–	–	–
Total	100	100	100	100

[a] Carnivora include fox (*Vulpes vulpes*), badger (*Meles meles*) and undetermined Mustelidae

[b] Small rodents include dormouse (*Glis glis*) and undetermined mice and voles

abundant prey species taken, while roe deer and red deer were secondary prey. During period 1993–1996 (*n*=1,091), wild boar represented about two thirds of the total wild prey species taken. Roe deer were the second most important species in terms of RNP although they had the same importance as red deer in terms of BIO. Fallow deer represented a small proportion of the wolves' diet at ca. 1.6% of RNP. Despite yearly variations in the density of wild boar (from 1.3 to 12.5 boar/km²) and red deer (which increased threefold, from 1.6 to 4.6 deer/km²), there was no correlation between MPV and density variations of the main prey species (linear regression analysis—wild boar: R^2= 0.02, *n*=11, *p*=0.70, roe deer: R^2=0.04, *n*=11, *p*=0.56; red deer: R^2=0.01, *n*=11, *p*=0.81).

Inter-species selection

During period A, wild boar were significantly selected by the wolf pack every year, except during 1989, when boar density was at its highest. Conversely, significant avoidance of roe deer was observed every year except during 1989. Avoidance of red deer proved to be significant in only 4 out of 11 years (1994, 1995, 1997 and 1998), and avoidance of fallow deer was significant in only 1993 and 1994. In the remaining years, the use of roe, red and fallow deer was proportionate to their availability. In order to consider variability in population densities estimate we took into account the 95% confidence interval range of population estimates of the two dominant ungulate species, roe deer and wild boar, then we calculated selectivity with all possible combinations of the extreme values: no change in the direction of selectivity was recorded as only the number of years with significant results changed (Appendix).

The strength of selection, expressed by *β* index, proved to be inversely density dependent (Fig. 2) for wild boar (R^2= 0.536, *n*=11, *p*=0.011), but not for roe deer (R^2=0.079, *n*= 11, *p*=0.401) and for red deer (R^2=0.272, *n*=11, *p*=0.100).

Age-class selection of all species

Wolf selection at the age-species level was found to be significant only for wild boar juveniles, which were strongly selected over any other category. Wild boar adults and red and fallow deer calves were taken according to their availability, while all adult cervids and roe deer fawns were actually avoided. This pattern was uniform during every year of period 1993–1996, except during 1996 when the use of fallow deer adults and roe deer fawns was observed not to differ from what was expected (Table 3). Likewise, when using cumulative data for the period 1988–1992, positive selection of wild boar piglets and proportionate use of the other classes was observed.
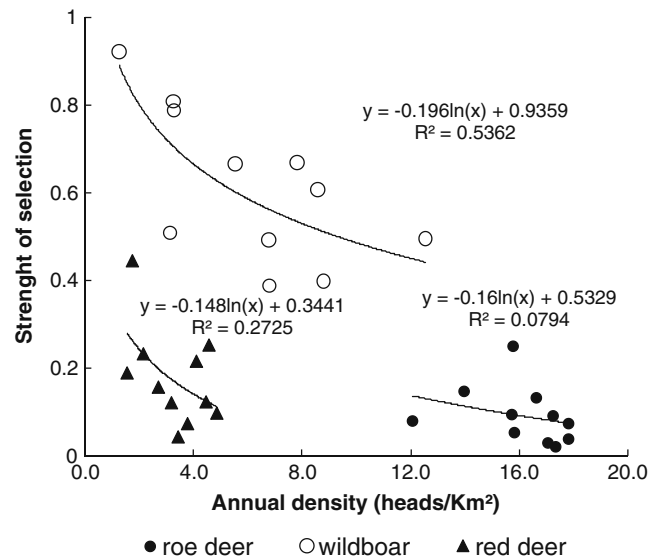

Fig. 2 Strength of selection by wolf of wild boar, roe deer, and red deer, measured by standardized selection index (*β*) and plotted against the density of prey in the ungulate community, from 1989 to 1999

Intra-species selection

For wild boar, <1-year-old individuals represented 89.5% of MPV and 93.2% of RNP. This age class proved to be selected every year in comparison to adults (Table 4). Likewise, roe deer fawns averaged 55.2% and 67.9% of MPV and RNP, respectively, and a significant selection of fawns was observed every year (Table 4). Moreover, within the sample of 60 scats attributed to the period May–October, red deer calves represented 76.1% of MPV and 82.9% of RNP. Selection of red deer calves was always found to be significant, except during 1995 when they were taken in proportion to their availability (Table 4). Also for fallow deer, <1-year-old individuals were the most represented class: 71.8% of MPV and 78.9% of RNP. Assuming an observed mean percentage of fawns of ca. 38% of the total population, <1-year-old individuals were found to be selected.

Wolf selection of <1-year-old wild boar was compared with that of adult boar and was observed to change during their first year of life. In March–April, piglets were significantly avoided by wolves, while in May–June their use was proportionate to their availability. Juveniles were then selected from July–August to January–February (Fig. 3). The selection pattern of roe deer fawns was different: they were selected only after reaching a few months in age, with the relative strength of selection found to be at its highest from September to December. From January to April, their use did not differ significantly from that of adults (Fig. 3).

Table 3 Age-species prey selection by wolf expressed by standardized selection ratio, *ß*

1993–1996	Proportion in the population (SD)	Proportion in scats (SD)	Standardized selection ratio (SD)	Type of selection
Wild boar juvenile (3–33 kg)	0.082 (0.06)	0.635 (0.11)	0.610 (0.25)	+
Wild boar adult (>33 kg)	0.065 (0.04)	0.047 (0.01)	0.060 (0.04)	
Roe deer juvenile	0.226 (0.03)	0.139 (0.04)	0.043 (0.03)	−
Roe deer adult	0.435 (0.05)	0.071 (0.02)	0.011 (0.01)	−
Red deer juvenile	0.034 (0.00)	0.058 (0.03)	0.124 (0.10)	
Red deer adult	0.103 (0.01)	0.019 (0.01)	0.012 (0.00)	−
Fallow deer juvenile	0.013 (0.00)	0.021 (0.01)	0.122 (0.12)	
Fallow deer adult	0.042 (0.01)	0.010 (0.01)	0.018 (0.02)	−

Average value calculated from 4 years of the period B (1993–1996) and standard deviation (in brackets) for each parameter are given in the table. Proportion in the population is obtained from census data and population structure. Proportion in scats is expressed as relative number of prey. Significance, assessed by calculating the confidence intervals for $p=0.01$ and type of selection (positive sign, selection and negative sign, avoidance) were consistent throughout the period, except for roe deer juveniles and fallow deer adults in 1996 (α)

Prey size

Wolves fed almost exclusively on prey whose body mass was smaller or equal to their own (ca. 85% of the total number of prey), while prey over 60 kg accounted for only 6% of the total number of prey (Fig. 4). The mean individual weight of wild prey consumed by wolves was 20.5 kg and corresponded to a prey to predator body mass ratio of 0.71. Wild boar used by wolf during period 1993–1996 weighed 19.5 (SD=11.70; $N=292$) kg, with minimum values recorded in July–August (12.4 kg) and maximum values recorded in January–February (26.6 kg). Mean weight of cervids consumed by wolves in period 1993–1996 was 14.6 (SD 8.03; $N=116$) kg for roe deer, 45.6 (SD 32.77; $N=70$) kg for red deer, and 29.0 (SD 16.82; $N=14$) kg for fallow deer.

Discussion

Prey use and dietary response

The pack we studied relied almost exclusively on wild ungulates and fed on every available species, but the main prey was wild boar. Apart from the Italian Apennines (Mattioli et al. 1995; Ciucci et al. 1996; Meriggi et al. 1996, Capitani et al. 2004; Mattioli et al. 2004), a similar result was found only in a few other locations of Eastern Europe like Estonia (Kübarsepp and Valdmann 2003), Russia (Rusakov and Timofeeva 1984 in Okarma 1995) and Belarus (Sidorovich et al. 2003).

Comparing the results on multiple prey–predator systems referred to other 13 study areas where wild boar, red deer and roe deer are present (Western Alps, Capitani et al. 2004;

Table 4 Intra-species prey selection of <1-year-old individuals in comparison to adults for the three main prey species, estimated by selection ratio, *w*

Years	1988–1992	1993	1994	1995	1996
Wild boar					
juveniles in diet	0.83	0.94	0.92	0.95	0.91
n (scats)	77	98	89	73	32
juveniles in population	0.67	0.57	0.61	0.53	0.61
Type of selection	+	+	+	+	+
Roe deer					
juveniles in diet	0.71	0.68	0.70	0.69	0.64
n (scats)	57	28	36	23	29
juveniles in population	0.35	0.31	0.29	0.30	0.29
Type of selection	+	+	+	+	+
Red deer					
juveniles in diet	0.77	0.91	0.88	0.57	0.91
n (scats)	11	21	11	11	14
juveniles in population	0.25	0.25	0.25	0.24	0.22
Type of selection	+	+	+		+

Data were analysed separately for each year of period B (1993–1996) and pooled for the period 1988–1992. Significance of selection ratio (w_i) was assessed by calculating the confidence intervals for $p=0.01$ (positive sign, selection and negative sign, avoidance)
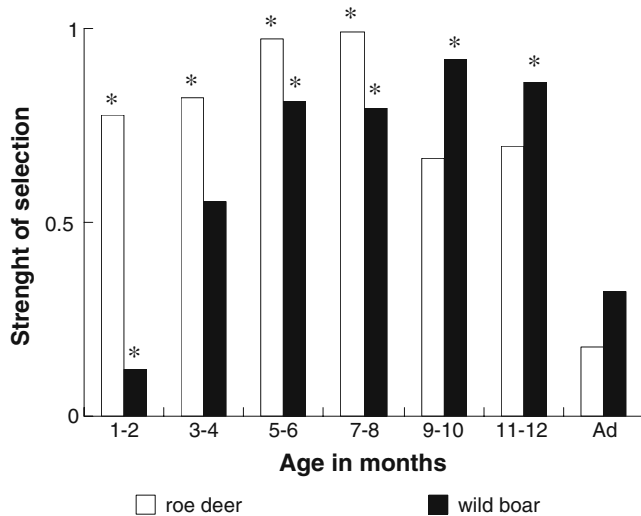
Fig. 3 Intra-species strength of selection of both roe deer fawns and wild boar piglets in relation to prey size in their first year of life, as expressed by the numbers of 2-month periods starting from their birth. Mean values for adults (Ad) are shown for comparison. The strength of selection is measured by standardized selection index (β), and the birth time is taken to be May for roe deer and March for wild boar, according to data collected in this study. Data on period B (1993–1996) were pooled for calculating the selection index (*asterisk*, significant selection at $p<0.01$)

Gazzola et al. 2005; Białowieża Primeval Forest, Jędrzejewski et al. 1992, 2000, 2002; Bieszczady Mountains, Smietana and Klimek 1993; Gula 2004; Carpathian Mountains, Nowak et al. 2005; Latvia, Andersone and Ozolins 2004; Saxony, Ansorge et al. 2006; Western Russia, Filonov 1989 in
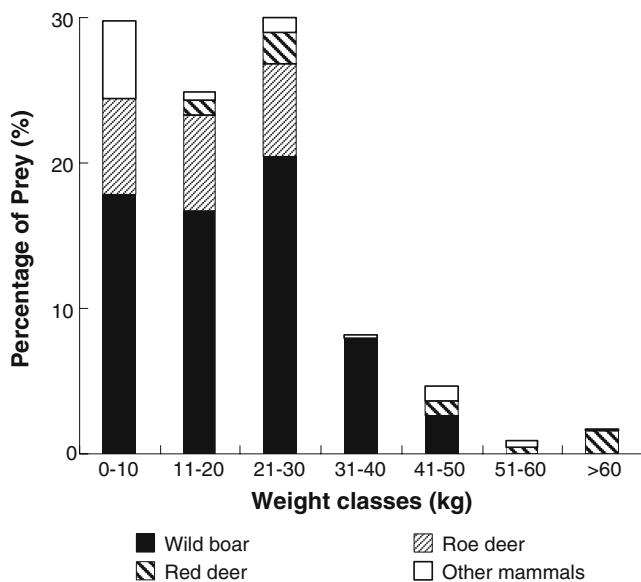

Fig. 4 Occurrence of each species-weight class in wolf diet, as expressed by the proportion of prey. The class 'other mammals' includes fox (*Vulpes vulpes*), badger (*Meles meles*), hare (*Lepus europaeus*), martens (*Martes* sp.), fallow deer and undetermined cervids

Jędrzejewski et al. 1992), we found that the percentage of wild boar in wolf diet was related to both the percentage of wild boar in the ungulate community ($R^2=0.515$, $n=13$, $p=0.006$) and the ratio between late-winter density of wild boar and red deer ($R^2=0.560$, $n=13$, $p=0.003$). With respect to this picture, Casentinesi Forests represent an outlier, as wild boar use was double that expected by its abundance in the ungulate community.

In a multiple prey–predator system, we expected an opportunistic predator to respond to variations in prey densities by changing its relative use of prey. However, we did not observe any dietary response of wolves to variations in the density of either the main or the secondary prey species. In addition, the strength of selection of the primary prey, wild boar, measured by β index, was inversely related to variations in the density of the species. In the Białowieża Primeval Forest, in Eastern Poland, Jędrzejewski et al. (2000) reported dietary response of wolves to variations in the density of the main prey, red deer, and also found that red deer density determined the proportion of other ungulates in the wolves' diet. In North America, the functional response was analysed in terms of per capita kill rate rather than relative proportion in diet, and some studies reported functional responses only with very low prey densities, while, when a wider range of densities was considered, no relationship was reported to occur (Dale et al. 1994; Eberhardt 1997). In reviewing these studies, Mech and Peterson (2003) argued that kill rates of a specific prey species could depend more on pack size and prey vulnerability than prey density. In addition, in Yellowstone National Park, Smith et al. (2004) reported no functional response to variations in elk density, thus suggesting that wolves had adopted a minimum kill rate strategy so as to reduce the risk of injury during predation.

As regards this study, it is our suggestion that the high density of wild ungulates in the area mainly accounted for the lack of dietary response. The ratio of wild ungulates to predators in the study area averaged from 740 heads/wolf in summer to 421 heads/wolf in winter, so that variations in the density of prey species could have little if any influence on predation rates.

Another factor affecting dietary response is the wolf's strong selection for wild boar over roe deer. During the study period, wild boar proved to be selected every year except one, suggesting that wild boar was the most profitable prey species regardless of their actual abundance. Despite their profitability, the annual relative use of wild boar did not exceed 77% and on average 30% of the wolf diet consisted of the other three ungulate species. We argue that this effect was caused by the temporary availability of more profitable prey, such as deer newborns in summer, which accounted for a seasonal shift in prey selection (Mattioli et al. 2004) that was less evident in the annual analysis.

Prey selection

Among wild ungulate species, only wild boar was observed to be selected. The strong selection of young wild boar in comparison to other age-species classes by the wolf pack suggests that the high number of vulnerable individuals in wild boar populations could be the most important factor accounting for the general preference for this species. In fact, in wild boar populations the percentage of young is higher than in other ungulates and births are scattered over a longer period. As a consequence, wolves are more likely to encounter vulnerable individuals of this species and the relative capture success is likely to increase.

The effect of group size and distribution pattern of prey species on encounter rate could have strengthened the selection of <1-year-old boar. Several studies have reported encounter rates to be higher for larger groups of prey (Hebblewhite and Pletscher 2002; Creel and JAJr 2005), probably because of their increased detectability. In the Casentinesi Forests, wild boars live in larger groups than the other ungulate species, particularly the roe deer. Moreover in Northern Apennines, wild boar groups seem to exhibit more predictable distribution patterns, which are affected by their frequent and customary use of resting sites with dense vegetation (Bertolotto 2010).

The selection pattern observed in the Casentinesi Forests is consistent with that observed in other Apennine areas where wild boar proved to be selected (Meriggi et al. 1996; Capitani et al. 2004, Mattioli et al. 2004). In contrast, red deer was generally positively selected in central-eastern Europe (Okarma 1995; Jędrzejewski et al. 2000; Andersone and Ozolins 2004; Nowak et al. 2005) and in the western Alps (Gazzola et al. 2005), on the contrary roe deer was selected in fewer locations of Sweden (Olsson et al. 1997), Saxony (Ansorge et al. 2006), Russia and Belarus (Okarma 1995). Apart from Italy, wild boar was selected as secondary prey in the Bieszczady Mountains, Poland, during winter (Smietana and Klimek 1993; Gula 2004), in two locations of central Russia and Caucasus (Okarma 1995), and as main prey only in Estonia (Valdmann et al. 1998).

Wild boar population density in Europe differs according to different ecological conditions. Melis et al. (2006) found that wild boar density on a continental scale was strongly affected by winter temperature, vegetation and, consequently, acorn productivity, with a 1,000-fold decrease in their north-eastern range when compared with their south-western Eurasian range. Wild boar density at a local scale also depends on hunting and forest exploitation (see e.g. Theuerkauf and Rouys 2008). This pattern probably accounts for the variability in wild boar use by wolves in different European areas. Nevertheless, the high use and strong selection of wild boar by wolf in Casentinesi Forests may be related to factors other than density such as the high wild boar productivity in our study area. We observed a 1.4 piglets/adult boar ratio and

a 5.5 piglets/red deer calf ratio which differ from the 0.8 piglets/adult ratio and the 1.2 piglets/calf ratio reported by Jędrzejewski et al. (2000) in Białowieża Primeval Forest. Furthermore, the differences in the weight ratio between prey and predators can also play an important role. In Casentinesi Forests, the wild boar/wolf weight ratio for adult is half that in red deer (1.9 vs 3.7), while in Białowieża Forest the ratio is similar, 2.2 and 2.7, respectively (Jędrzejewska et al. 1996; Jędrzejewska and Jędrzejewski 1998). Thus, the larger body size of adult boar, and consequently the greater possibility to successfully defend offspring from predation, might be another reason why wild boars are not often selected in northern regions.

In the present study, wolves clearly selected <1-year-old individuals of every ungulate species for each year of analysis. In European studies, wolves were observed to select young wild boar (i.e. <1 year) in many study areas (see Okarma 1995 for a review; Gula 2004; Jędrzejewski et al. 2000) and in particular individuals between 10 and 35 kg (Meriggi et al. 1996; Capitani et al. 2004). Likewise, red deer calves were generally selected (Jędrzejewski et al. 2000; Gazzola et al. 2005; Nowak et al. 2005; Smietana 2005). For roe deer, different studies produced different results. Olsson et al. (1997) and Jędrzejewski et al. (2002) did not find any selection of fawns, which contradicts what was observed in CF and in adjacent mountainous areas (Mattioli et al. 2004). Nowak et al. (2005) found selection of roe deer fawns in scat samples but not in kills. However, these differences may be apparent, due to different diet analysis methodology and the tendency of kill analysis to underestimate the importance of smaller prey in predator diet. Moreover, most kill data are collected in winter and, as a consequence, results could be biased by differences among seasonal selection patterns (Sand et al. 2008).

In this study, selection of young of the two main prey species, wild boar and roe deer, expectedly varied according to their body mass increase. Maximum positive selection was found for roe deer young of 5–8 months and wild boar young of 9–12 months. At these ages, according to the specific growth curves (see Methods), roe deer fawns weighed 12.5 kg and wild boar piglets 29.4 kg, which corresponds to 52% and 49% of the mean adult body mass, respectively (Table 1). Therefore, young in the middle of their body growth seem to be the optimal prey choice for the wolf pack. However, the patterns of selection differed significantly between the two prey species. In fact piglets only became profitable, and were selected, from the age of 5 months, while selection of roe deer fawns was shown from birth. The different anti-predatory strategies adopted by the two species could account for this result. Wild boar piglets are actively defended by females; therefore the advantages connected to their smaller size would not compensate the costs and risks of predation. On

the contrary, roe deer fawns exhibit passive defence, primarily through hiding behaviour, thus becoming more profitable prey when they are abundant.

Prey to predator body mass ratio

The wolves' strong preference for ungulate juveniles in our study area resulted in their feeding upon prey which weighed less than the predators themselves. Although average weight of roe deer adults correspond to the estimated mean prey weight for the wolf pack, this prey class was significantly avoided by the wolves, suggesting that roe deer adults are a difficult prey item for this particular predator (Jędrzejewski et al. 2000; Mattioli et al. 2004). The estimated body-weight ratio of prey to wolf in this study was lower than that observed in other study areas (Jędrzejewski et al. 2002) or for other coursing predators, such as the African wild dog (*Lycaon pictus*) in South Africa (Radloff and Du Toit 2004). Furthermore, the ratio was lower than expected according to the general prey to predator mass relationships reported by Jędrzejewska and Jędrzejewski (1998), and Carbone et al. (1999).

Conclusions

The results of this study confirm wild boar as an important prey for wolf in Italy. Considering the wide distribution range and the actual rate of increase of this ungulate in many European countries (Apollonio et al. 2010), we can expect that this species could contribute in the process of recovery and conservation of the wolf, particularly in Mediterranean temperate ecosystems. In multiple species - high density ungulate systems, use and selection patterns by wolf are not so much determined by prey abundance as by prey vulnerability, as confirmed by selection of more profitable medium-sized young individuals. A complex prey community may also contribute towards buffering any dietary response to changes in main prey abundance, through the seasonal shift in prey preference. Actual differences in wild boar selection patterns by wolf across Europe need further investigation for a better understanding of the importance of demographic against behavioural factors. In consideration of the large amount of juvenile ungulates in wolf diet, the study on wolf prey selection should be performed year round integrating different methods such as scat analysis and search of kills to optimize the different information provided by each method.

Appendix

Table 5 Comparison of the significant results assessed for $p=0.01$ of selection ratio w_i calculated for the eight possible calculations (columns 1–8) performed taking into account the upper and lower values of 95% confidence intervals (CIs) of wild boar and roe deer late-winter density (positive sign, selection and negative sign, avoidance)

Prey	Year	Upper Cls roe deer 1	Lower Cls roe deer 2	Upper Cls wild boar 3	Lower Cls wild boar 4	Upper Cls roe deer and wild boar 5	Lower Cls roe deer and wild boar 6	Upper Cls roe deer and lower Cls wild boar 7	Upper Cls wild boar and lower Cls roe deer 8	Late-winter density 9
Wild boar	1989				+			+		
	1990	+	+		+	+	+	+		+
	1991	+	+	+	+	+	+	+	+	+
	1992	+	+	+	+	+	+	+	+	+
	1993	+	+	+	+	+	+	+	+	+
	1994	+	+	+	+	+	+	+	+	+
	1995	+	+	+	+	+	+	+	+	+
	1996	+	+	+	+	+	+	+		+
	1997	+	+	+	+	+	+	+	+	+
	1998	+	+	+	+	+	+	+	+	+
	1999	+	+	+	+	+	+	+	+	+

Table 5 (continued)

Prey	Year	Upper Cls roe deer 1	Lower Cls roe deer 2	Upper Cls wild boar 3	Lower Cls wild boar 4	Upper Cls roe deer and wild boar 5	Lower Cls roe deer and wild boar 6	Upper Cls roe deer and lower Cls wild boar 7	Upper Cls wild boar and lower Cls roe deer 8	Late-winter density 9
Roe deer	1989							–		
	1990	–	–	–	–	–	–	–	–	–
	1991	–	–	–	–	–	–	–	–	–
	1992	–	–	–	–	–	–	–	–	–
	1993	–	–	–	–	–	–	–	–	–
	1994	–	–	–	–	–	–	–	–	–
	1995	–	–	–	–	–	–	–	–	–
	1996	–	–	–	–	–	–	–	–	–
	1997	–	–	–	–	–	–	–	–	–
	1998	–	–	–	–	–	–	–	–	–
	1999	–	–	–	–	–	–	–	–	–
Red deer	1989						–			
	1990									
	1991									
	1992			–			–			
	1993		–				–		–	
	1994		–	–	–		–		–	–
	1995	–	–	–	–		–	–	–	–
	1996						–			
	1997		–				–		–	
	1998		–	–			–		–	–
	1999		–		–		–			
Fallow deer	1989						–			
	1990									
	1991									
	1992						–			
	1993	–	–	–	–	–	–	–	–	–
	1994	–	–	–	–	–	–	–	–	–
	1995		–				–		–	
	1996									
	1997		–		–		–		–	–
	1998		–	–			–		–	
	1999						–			

Red deer and fallow deer late-winter densities remained unchanged. In column 9, the results obtained with mean values of late-winter density presented in the results section are shown for comparison

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