

Original investigation

A comparative analysis of wolf (*Canis lupus*) diet in three different Italian ecosystems

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Abstract

To verify food habit flexibility of wolf populations under different ecological conditions, scats collected year round were analysed in three study areas and diet composition of resident packs was compared. The three study areas, representing Alpine (SV), Apennine (PM) and Mediterranean (CV) ecosystems, are rich in wild ungulates, which differ in number of species and relative abundance; livestock is also present. Wild ungulates were the main source of food, accounting for 89.4%–95.1% of the diet. Livestock, instead, scarcely reached 8% of annual mean percent volume in any one area, and only in the Alps did they play a major role in autumn. Other food items constituted less than 5% of annual mean percent volume. Variations in the proportions of use of wild ungulate categories were observed among the study areas, although some patterns of intraspecific selection emerged in each area. Finally, differences both in the relationships between utilisation and availability of preys, and in trophic niche breadth were discussed in relation to environmental features and colonization patterns.

Key words: *Canis lupus*, diet, wild preys, Italy

Introduction

Recent expansion of wolf populations in Italy, due to a general improvement of environmental conditions and legal protection, has given rise to a debate on the interactions of this species both with human activity and with wild ungulate communities.

In the past few years, most studies on the Italian wolf population have focused on diet composition and revealed a strong relationship between food habits and ecological features such as wild prey availability, presence

of livestock, and human activity (MERIGGI et al. 1991, 1996; PATALANO and LOVARI 1993; MATTIOLI et al. 1995; MERIGGI and LOVARI 1996; CIUCCI et al. 1996). According to these authors, Italian wolves usually consume wild ungulates, as observed for North American and eastern European wolf populations (VOIGT et al. 1976; FRITTS and MECH 1981; PETERSON et al. 1984; BALLARD et al. 1987; PETERS 1993; BOYD et al. 1994; OKARMA et al. 1995; OKARMA 1995; OLSSON et al. 1997; BERGERUD and ELLIOTT 1998; JEDRZE-

JEWSKI et al. 2000); however, where these preys are not sufficiently available or are absent, wolves show great flexibility and adaptation to local conditions. In this case, livestock, small mammals, or garbage may play the main role in their diet (MERIGGI et al. 1991; PETERS 1993; HEPTNER and NAUMOV 1998; Vos 2000).

The aim of this study is a comparison of wolf food habits in three Italian ecosystems characterized by specific climatic and vegetation features: an area in the Alps recently colonized by wolves, a mountain area on the northern Apennines, and a hill Mediterranean area, close to the Tyrrhenian coast, which wolves occasionally settled in the last few decades.

Material and methods

Study areas

Study areas were located in central and northern Italy (Fig. 1). The Susa Valley (SV) is a 120 km² area in the Alpine region near Turin, including

the Gran Bosco di Salbertrand Regional Park. Altitudes range between 600 and 2700 m a.s.l.; landscape is dominated by coniferous woodlands, but above 2300 m alpine meadows are widespread. Snowfalls occur from October to April, and snow cover lasts for more than 50 days. After eradication, in last century the first reproduction of wolves in the area was documented in 1997. Four species of wild ungulates are present (Tab. 1), whereas livestock is free ranging on high pastures from June to September and is kept in stables in the valley during the other months. Further relevant potential preys are hares (*Lepus* spp.) and marmot (*Marmota marmota*).

The second study area, Pratomagno (PM), is part of the homonym massif departing from the main ridge of the Apennines towards the Arezzo plain. The study refers to 110 km², half of which are represented by the Pratomagno Natural Reserve, ranging in altitude between 300 and 1600 m a.s.l. Deciduous forests dominate this area, while meadows are present only at the top. The climate is continental and winters are characterised by snowfalls alternating with melting (snow cover is present on average for <50 days per winter). Wild ungulates are mostly represented by wild boar (*Sus scrofa*), roe deer (*Capreolus capreolus*) and fallow deer (*Dama dama*) as showed in table 1.

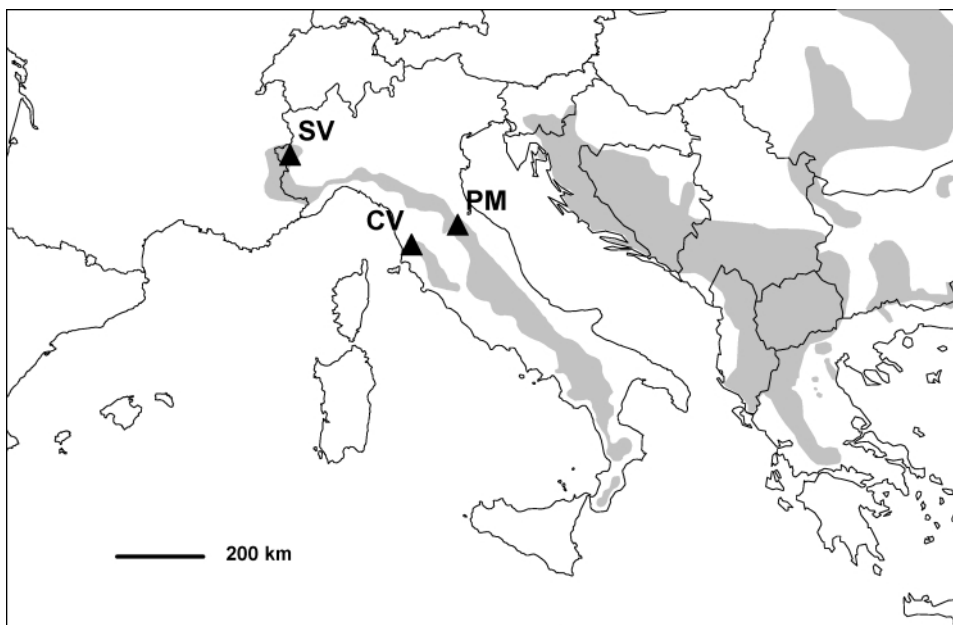


Fig. 1. Geographical location of the three study areas in north and central Italy. Wolf range is hatched (SV – Susa Valley, PM – Pratomagno, CV – Cecina Valley).

Table 1. Distribution and density of wolf (*Canis lupus*) main preys in the three study areas. Ungulate abundances were estimated by drive censuses ^(a), vantage point counts ^(b) and hunting rate ^(c).

Species	Susa Valley	Pratomagno	Cecina Valley
Roe deer <i>Capreolus capreolus</i>	below 2000 m a.s.l. 3.6/100 ha ^b	widespread 22.5/100 ha ^{a,b}	widespread 16/100 ha ^a
Wild boar <i>Sus scrofa</i>	below 2000 m a.s.l. 1.0/100 ha ^b	widespread 5.1/100 ha ^{a,b}	widespread 15/100 ha ^c
Fallow deer <i>Dama dama</i>	absent	limited to about 1/3 of the area 0.6 /100 ha ^{a,b}	widespread about 6/100 ha ^b
Red deer <i>Cervus elaphus</i>	widespread 5.9 /100 ha ^b	absent	absent
Mouflon <i>Ovis ammon musimon</i>	present close to the study area	an isolated herd of a few individuals	widespread about 4/100 ha ^b
Chamois <i>Rupicapra rupicapra</i>	widespread 7.0–8.0 /100 ha ^b	absent	absent

Hare and porcupine (*Hystrix cristata*) are also present. Cattle and horses are free ranging on the main ridges from June to September, while sheep and goats are present throughout the year at lower altitudes.

Finally, a 25 km² area close to the Tyrrhenian coast of Tuscany, the Cecina Valley (CV), was investigated. The area has low altitudes (100–600 m a.s.l.) and it includes wooded hills, composed of deciduous and evergreen oak forest of *Quercus pubescens*, *Q. robur* and *Q. ilex*. Climatic conditions are typically Mediterranean, with rare snowfalls. Among wild ungulates, fallow deer, mouflon (*Ovis ammon musimon*), roe deer, and wild boar are present; small mammals are also common, as in PM. Sheep and goats are present in open areas throughout the year. A few large herds of cattle and horses are present in small number and close to farms and villages.

Early-winter size of the monitored wolf packs in SV, PM and CV was 6, 5 and 4–5 respectively; estimates were obtained by wolf-howling and snow-tracking (only in SV and PM).

Feral and stray dogs have been observed occasionally in SV, whereas in the other areas the presence of stray dogs is limited to the hunting season (from September to January).

Data on population density of wild ungulates (Tab. 1) were obtained by different methods: in SV, the number of ungulates was estimated from vantage point counts in early spring (Gran Bosco di Salbertrand Regional Park, unpubl. data). In PM, drive censuses and vantage point counts were carried out in April and May (Provincial Administration of Arezzo, unpubl. data). In CV, the rela-

tive density of ungulate species was estimated by drive censuses and vantage point counts in early spring and from winter hunting rates.

The data here presented were collected from February 2000 to March 2001 in SV, from February 1999 to March 2000 in PM, and from September 2000 to August 2001 in CV.

Scat analysis

Wolf scats were collected on standard transects, travelled every month for a whole year, for a total of 75.9 km in SV, 90.0 km in PM and 22.8 km in CV. Scat content was analysed to assess diet composition, as in previous studies (MERIGGI et al. 1991; MATTIOLI et al. 1995; CIUCCI et al. 1996; MERIGGI et al. 1996). The small amount of scats containing >1 item allowed us to reduce to five the number of volume classes (0%, 25%, 50%, 75% and 100%). All authors involved in the laboratory analysis (C.C., I.B. and P.V.) were previously checked for their ability in discriminating hairs at a specific level. Items in the blind test included almost all prey species present in the study areas. Moreover, authors were tested for their capacity to identify wild boar weight classes by hairs. In both tests, errors were below the threshold of 5%.

In most cases, hairs were identified by comparison with a collection of mammal hairs, after examining their length, thickness, shape and colour through a 10x lens. Occasionally microscopy was needed for hair analysis; features of cortex and medulla were compared with a specific atlas

(DEBROT et al. 1982). In this way, almost every item was recognised at a specific level, and only few of them remained undetermined (<1%). Young (<1 year) cervids and chamois were discriminated from adult (>1 year) by hairs, which allowed newborns to be distinguished from adults only in summer, and by bone remains, where the closure of the epiphyses is not complete in the first year of life in these species. For wild boar, we assigned individuals to three weight classes, <10 kg, 10–35 kg, and >35 kg, identified by diameter, colour and wear of hairs on the basis of a reference collection.

In order to compare wolf diet among the three study areas, all the components were then grouped into five conventional categories, namely: wild boar, cervids (roe, red, and fallow deer), bovids (mouflon and chamois), livestock (horses, cattle, sheep and goats) and other (small mammals, rodents, lagomorphs, fruit, and grass).

The degree of utilisation by wolves of different categories was evaluated by calculating the following indices: mean percent volume (V_{MP}) = sum of the volumes of each category/total number of scats $\times 100$; absolute frequency of occurrence (F_O) = number of scats containing a category/total number of scats $\times 100$. For seasonal comparisons of mpv values, months were pooled as follows: March–May = Spring (spr); June–August = Summer (sum); September–November = Autumn (aut); December–February = Winter (win). Moreover, diet breadth within each sampled areas was evaluated by the standardized Levins index (B_a , range: 0–1) according to HURLBERT (1978), whereas an index (O) of trophic niche overlap among areas was estimated as in PIANKA (1973).

Since census methods of ungulates (wild and domestic) differed among our study areas, we could not directly compare the degree of selection for each prey category. Nevertheless, the proportions of utilisation and availability of the five categories were ranked and then ranks compared (U_r = utilisation rank, A_r = availability rank).

Since a strong positive correlation between V_{MP} and F_O was found (SV, $r_s = 1$, $n = 5$, $p < 0.01$; PM, $r_s = 1$, $n = 5$, $p < 0.01$; CV, $r_s = 0.975$, $n = 5$, $p < 0.01$), statistical analysis was applied exclusively to V_{MP} values. Differences in the distribution of V_{MP} values among areas were estimated by replicated goodness-of-fit test (G-statistic). Non-parametric tests were used to evaluate significance in seasonal changes in the use of different food categories. In case of multiple comparisons among data, the threshold of significance (α) was lowered according to Bonferroni's method (SIEGEL 1956). Finally the correlation between

two variables was evaluated by calculating the Spearman's Rank correlation coefficient, r_s (SIEGEL 1956).

Results

One hundred and ninety-four scats were collected in SV, 355 in PM and 118 in CV. The percentage of scats containing more than one item was 12.2% in SV, 15.8% in PM, and 18.6% in CV. Analysis of scat composition showed that wild ungulates were the most commonly used prey in all study areas, reaching 91.4% of V_{MP} in SV, 95.1% in PM and 89.4% in CV. Domestic ungulates and other food categories (small mammals, vegetables, garbage) played a secondary role in wolf diet (Tab. 2). The proportion of use of food categories (V_{MP}) was significantly different among the three areas (G-Test, $G = 25.8$, $p < 0.05$) and changed seasonally in a different way (Fig. 2).

The average V_{MP} of livestock was less than 8% in each area. In SV, the V_{MP} value of livestock for autumn (34.6%) was significantly higher than in other seasons, (Mann-Whitney U test, spr-aut, sum-aut, win-aut, $p < 0.001$). Livestock and cervids V_{MP} values, in SV, were inversely correlated ($r_s = -0.671$, $p < 0.05$).

Cervids were the main prey in SV and in CV (Tab. 2) and seasonal changes in their use proved significant only in SV (Kruskal-Wallis test, $H = 42.4$, $p < 0.001$). Cervids showed the highest values of V_{MP} in sum-

Table 2. Annual frequency of occurrence (F_O) and mean percent volume (V_{MP}) of food categories in the three study areas, Susa Valley (Western Alps), Pratomagno (North-eastern Apennines) and Cecina Valley (coastal Mediterranean Tuscany).

	Susa Valley		Pratomagno		Cecina Valley	
	F_O	V_{MP}	F_O	V_{MP}	F_O	V_{MP}
Wild boar	2.1	1.7	87.3	80.8	20.3	15.9
Cervids	74.7	69.7	20.6	14.1	45.8	40.5
Bovids	20.6	20.0	0.3	0.2	34.7	33.0
Livestock	5.7	5.7	0.8	0.3	9.3	7.6
Other	5.1	3.0	8.4	4.5	9.3	3.0

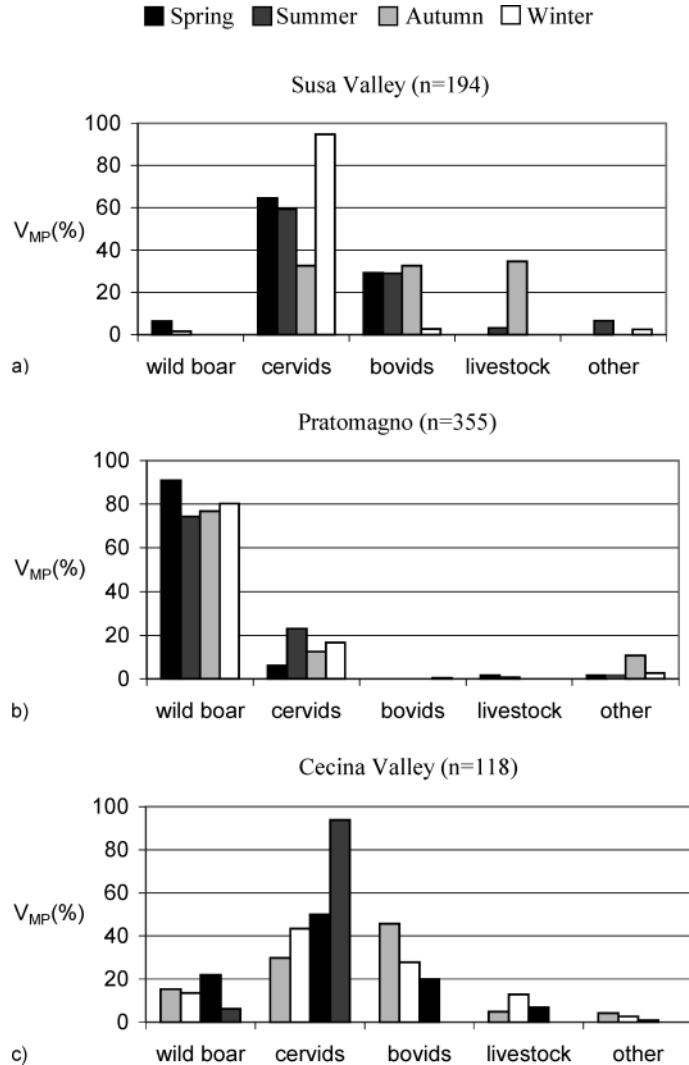


Fig. 2. Seasonal variations of scat contents. In Cecina Valley, where the study started in September, seasons are shifted in order to respect the actual temporal sequence. In Pratomagno, hairs of mouflon (bovids) were found only in one scat collected in winter.

mer in PM and in CV, whereas in SV they were mainly used in winter (Mann-Whitney U test: spr-win, sum-win, aut-win, $p < 0.001$).

The use of bovids proved also significantly different among seasons in SV (Kruskal-Wallis test, $H = 21.6$, $p < 0.001$). The use of chamois, the only wild bovid, in this area significantly decreased in winter (Mann-

Whitney U test, aut-win, sum-win, spr-win, $p < 0.001$). Analysing year-round variations of V_{MP} values, a significant negative correlation was observed between bovids and cervids in SV ($r_s = -0.924$, $p < 0.001$) and in CV ($r_s = -0.695$, $p < 0.05$). Wild boar was the bulk of wolf diet in PM (Tab. 2), with weakly significant seasonal variations (Kruskal-Wallis test, $H = 8.2$, $p < 0.05$).

Spring values were the highest both in PM (91%) and CV (22%).

Concerning the use of different classes within species, in SV and PM it was found that juveniles, in bovids and cervids, represented more than 80% of summer V_{MP} (Tab. 3). Moreover, differences in the proportion of use of wild boar weight classes were found both in CV and in PM (Tab. 4), where they showed the same pattern. Seasonal variations of V_{MP} for the >35 kg class were not significant and piglets were found only in spring and summer scats.

No relationship was found between number of different ungulate species and trophic niche breadth. Standardized Levins' indices exhibited variability among the study areas, particularly between those (SV and CV) with the same number of wild ungulate species. On the contrary, trophic niche overlap was high between SV and CV, intermediate between PM and CV, and markedly low between PM and SV (Tab. 5).

As regards the comparison between diet composition and availability ranks, it was found that in SV the order of the two series coincides, whereas in PM it was found $U_r > A_r$ for wild boar and $U_r < A_r$ for cervids, contrary to CV with $U_r < A_r$ for wild boar and $U_r > A_r$ for bovids.

Discussion

Our results demonstrate that, even in the presence of the same categories of prey, wolves tend to differentiate their diet in relation to local environmental features, relative abundance and vulnerability of preys, and stage of colonization. Thus, these factors could explain the differences in the proportion of use of wild ungulates observed in the three Italian study areas, as found in other studies (BJARVALL and ISAKSSON 1982; FRITTS and MECH 1981; BOYD et al. 1994; POULLE et al. 1997; HUGGARD 1993; HEPTNER and NAUMOV 1998; KUNKEL and PLETSCHER 1999).

In all study areas, the use of livestock was temporarily limited, which is consistent with wolf preference for large wild ungu-

Table 3. Mean percent volume of young (<1 year) and adult (>1 year) cervids and bovids in wolf summer diet in Susa Valley and Pratomagno. N is the number of analysed scats.

	Young	Adults	N
Susa Valley			
Cervids	81.6	18.4	35
Bovids	81.0	19.0	16
Pratomagno			
Cervids	90.1	9.9	11

Table 4. Relative use (V_{MP}) of different weight classes of wild boar (*Sus scrofa*) by wolves in Pratomagno and Cecina Valley, referred to the whole year of study. N is the number of analysed scats.

	0–10 kg	10–35 kg	> 35 kg	N
Pratomagno	10.8	65.7	23.5	310
Cecina Valley	11.6	63.2	23.3	23

Table 5. Standardized Levins' index of trophic niche breadth (B_a) compared to the number of species of wild ungulates for each study area, and Pianka's index of trophic niche overlap (O) across areas (SV – Susa Valley, PM – Pratomagno, CV – Cecina Valley). Mean percent volume was used to estimate both indices.

	SV	PM	CV
B_a	0.2	0.1	0.6
Nr. of species	4	3	4
	PM-SV	SV-CV	PM-CV
O	0.2	0.9	0.4

lates observed here, like in other regions (MECH 1970; FRITTS and MECH 1981; PETERSON et al. 1984; BALLARD et al. 1987; JEDRZEJEWSKI et al. 1992; PETERS 1993; BOYD et al. 1994; MATTIOLI et al. 1995; OKARMA et al. 1995; OKARMA 1995; MERIGGI et al. 1996; CIUCCI et al. 1996; OLSSON et al. 1997; HEPTNER and NAUMOV 1998; JEDRZEJEWSKI et al. 2000). Unlike what happens for other packs inhabiting exploited or newly recovered areas, which recur to livestock particularly in summer (MERIGGI et al. 1991;

POULLE et al. 1997; SALVADOR and ABAD 1987), in SV, i.e. the only area we investigated where seasonal use of this food item exceeded 20%, its presence in the diet was concentrated in autumn. Probably fawns represent a more accessible prey than livestock in summer, whereas in autumn they are able to escape predators more successfully and consequently livestock becomes more "advantageous, to prey upon. In CV a low level of consumption of livestock was found from autumn to spring, due to the local climate, which allows breeders to leave animals on pastures throughout winter. In PM, instead, livestock represented an irrelevant portion of diet, although in summer cattle and horses are free ranging on the main ridge, frequently travelled by wolves. This result may be the consequence of the high density of wild preys in the area and of the defensive behaviour and body size of these domestic ungulates, but long-standing interactions between wolves, livestock and men have to be considered.

Habitat features may have conditioned the opposite use of wild boar observed in PM and in CV. In a study on wild ungulates of a Polish lowland forest (OKARMA et al. 1995), the mortality of wild boar was strongly affected by snow depth and acorn crop. In our study areas, this category was less used than available in CV, an area characterised by mild winters and rare snow falls and by the presence of vast Mediterranean woods that provide a stable food resource. In contrast, in PM, more severe climatic conditions, with the occurrence of snowfalls in winter, and consequent fluctuations of trophic resource availability may have enhanced wild boar susceptibility to wolf predation. However, a lesser use of cervids in this area, in comparison to the other two, may be partly due to the fact that only roe deer is widespread, fallow deer being present only in one third of the area. On the contrary, two cervid species are widely diffused both in SV and in CV.

As emerged for wild boar and cervids in several European studies (SALVADOR and ABAD 1987; MATTIOLI et al. 1995; MERIGGI et al. 1996; OLSSON et al. 1997; JEDRZEJEWSKI

et al. 2000; JEDRZEJEWSKI et al. 2002), we found wolves using age/weight classes of the main preys with similar patterns, in spite of ecological differences among areas. A high summer consumption of cervids was observed both in PM and SV, attributable to a positive selection of fawns.

Moreover, a similar use of wild boar weight classes was found both in PM and in CV, being more than 75% in both areas. In fact, in PM, the percentage of individuals <40 kg harvested during the 1999–2000 hunting season was 21.8% (Provincial Administration of Arezzo, unpubl. report), whereas in CV individuals between 5 and 12 months (average weight = 26.8 kg) represented 42% of wild boars killed in 1990 and 1991 (D.R.E.A.M., unpubl. data). In northern Apennines, MERIGGI et al. (1996) and MATTIOLI et al. (1995) reported that wild boars <30 kg were positively selected by wolves, being more readily hunted than adults. Similar results were found by SALVADOR and ABAD (1987) in Spain and by JEDRZEJEWSKI et al. (1992) in Białowieża Primeval Forest. In the latter area, the mean body mass of wild boar killed by wolves was 23 kg (JEDRZEJEWSKI et al. 2002). We assume that the highest values of V_{MP} observed in spring both in PM and in CV, depended on both the occurrence of new births and the consequent increase in vulnerability of subadults. During this period, in fact, yearlings lose parental protection because females can no longer take care of them, and they begin to disperse from the family group, exposing themselves to the risk of predation.

In PM, seasonal analysis of V_{MP} variations among weight classes revealed that newborns (0–10 kg) were used in a specific period of time (spring-summer), although in this area births may occur from February to August. Major use of 10–35 kg individuals in autumn, instead, could be related to the fact that, as they increase in weight, they become more profitable preys. Considering all wild ungulate categories, our findings suggest that summer selection of young individuals, observed in different areas, may be a common behaviour related to the need to change hunting habits in pre- and post-

parturition periods. In fact, the presence of pups was proven to influence time and extension of movements of the alpha pair (HARRINGTON and MECH 1982). Thus, we suggest that a selection of fawns and piglets, more vulnerable prey and less costly to hunt, might occur also because it allows wolves to chase individually and to reduce hunting time.

The influence of different factors on food habits is confirmed by trophic niche indices and utilisation and availability ranks of ungulate categories, which suggest the presence of three different feeding patterns. In SV wolves tended to hunt prey in proportion to their relative availability, possibly focusing on the few most available species (specialised/availability-dependent pattern). In PM, instead, they seemed to have reached a marked specialisation only for one species, almost independently of its abundance (specialised/availability-independent pattern). Finally, in CV wolves preyed upon a larger number of species, widening their trophic niche, and selecting preys independently of their density (un-specialised/availability-independent pattern). We suggest that also the stage of wolf

colonization may have played a role in generating these patterns, as found in other studies on newly protected (FRITTS and MECH 1981) or colonizing (BOYD et al. 1994) wolves. Moreover, other authors pointed out that, in areas where they had been present for a long time, wolves positively selected preys despite their decreased density (POTVIN et al. 1987; MATTIOLI et al. 1995; SPAULDING et al. 1998), and they showed delay in changing their food habits after a strong decline of their main prey (JEDRZEJEWSKI et al. 2000).

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Zusammenfassung

Vergleichende Untersuchungen zur Nahrungsökologie des Europäischen Wolfes (*Canis lupus*) in drei verschiedenen Ökosystemen Italiens

Um die Flexibilität in den Nahrungsgewohnheiten von Wolfspopulationen unter verschiedenen ökologischen Bedingungen erfassen zu können, wurden im Jahresverlauf gesammelte Kotproben von drei, in unterschiedlichen Studiengengebieten ansässigen Wolfsrudeln auf ihre Nahrungszusammensetzung analysiert. Die drei Untersuchungsgebiete repräsentieren ein alpines (Susa Tal), ein apenninisches (Pratomagno) und ein mediterranes Ökosystem (Cecina Tal). Alle Habitate sind reich an wilden Huftieren, unterscheiden sich aber hinsichtlich der Artenvielfalt und ihrer prozentualen Zusammensetzung. Hinzu kommt ein gewisser Bestand an Schafen, Ziegen und Rindern in allen untersuchten Gebieten. Mit einem Anteil von 89 bis 95 Prozent waren wilde Huftiere die Hauptnahrungsquelle der Wölfe. Das Hausvieh machte in den untersuchten Gebieten im Jahresmittel maximal 8 Prozent der Nahrung aus. Lediglich in den Alpen und dort nur im Herbst wurde es kurzzeitig die Hauptnahrungsquelle der Wölfe. Andere Nahrungsquellen erreichten einen mittleren Anteil an der Nahrungszusammensetzung von weniger als 5 Prozent. Obwohl sich die Muster innerartlicher Selektion in den verschiedenen Gebieten nicht grundlegend unterscheiden, beobachteten wir Unterschiede in der Beutenutzung der Wölfe. Letzteres wird in der Variation der Beuteverfügbarkeit und der Breite des Beutespektrums in Bezug auf Umweltbedingungen und Niveau der Kolonisierung diskutiert.

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