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Changes of wolf (*Canis lupus*) diet in Italy in relation to the increase of wild ungulate abundance

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We reviewed 20 studies on wolf diet in Italy, to relate the changes in diet composition to the increase of wild ungulate population in Italy. Researches covered the period from 1976 to 2004 and the whole range of wolves from southern Apennines to western Alps. We used the frequency of occurrence of seven food categories and of the wild ungulate species occurring in the diet. Estimates of wild ungulate populations were obtained from the literature and we extrapolated their trend in the period considered. Differences among geographic areas (south-central Apennines, northern Apennines, and western Alps) were tested by nonparametric multivariate analysis of variance, while the trends of the wild ungulate and livestock use and of diet breadth were analysed by regression and curve-fit analyses. We used the same method to support the relationships between the use and availability of wild ungulates. Wolves preyed on wild herbivores more in the northern Apennines and in the western Alps than in the southern Apennines; the contrary was the case for livestock. Among wild ungulate species, wild boar, roe deer and red deer were the main prey of the wolf. The occurrence of wild ungulates in the wolf diet increased from 1976 to 2004 together with a decrease of livestock; the increase was mainly due to roe deer, red deer and chamois. The results of scat analysis in the province of Genoa showed an increase of the occurrence of wild ungulates from 1987 to 2005, in particular roe deer and fallow deer. Wolves in Italy seem to select wild ungulates over domestic ones where the former are available with rich and diversified guilds and abundant populations.

KEY WORDS: wolf, *Canis lupus*, diet shift, wild prey, livestock, Italy, ungulate abundance.

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INTRODUCTION

The Italian wolf population is at present in an expansion phase that has led to re-colonisation of large areas in the Apennines and in the Alps, from which the species disappeared between the end of the 19th century and the first decades of the 20th (CAGNOLARO et al. 1974; CIUCCI & BOITANI 1991, 1998; MERIGGI et al. 1991; MASSOLO & MERIGGI 1996, 1998; BREITENMOSER 1998). In spite of this apparently positive situation, the wolf should still be considered a threatened species both in Italy and in Europe, because of the conflicts with human activities that are triggered by its predatory behaviour and that lead to illegal persecution. This in turn makes the colonisation of new areas unstable, in particular those where livestock husbandry is an important economic activity (GENOVESI 2002).

The man-wolf conflicts arise both when wolves use domestic prey (livestock) and when they prey on wild ungulates. In the first case wolves cause direct or indirect damage to the livestock husbandry that is often the main economic activity of the human population inhabiting mountain zones; in the second the conflict arises because of the supposed competition with hunting, for which in Italy wild ungulate species are becoming more and more important (GAZZOLA et al. 2007).

Understanding the mechanisms that lead to changes of feeding habits and predatory impact of large carnivores is of great importance in outlining effective strategies for their conservation. One of the cruxes of the management of the conflicts between human activities and large predators lies in understanding to what extent predation is a regulatory or limiting factor acting on wild prey populations, and how it is possible to reduce the impact on domestic prey. Regarding the relationships between wolves and wild ungulates, the main question is whether predation can regulate the populations of these prey species. Usually in a prey-predator system regulation occurs when predation is density dependent and it stabilises prey populations at an equilibrium density. However, if predation is independent of density there is a limiting effect and if it is inversely density dependent there is a depensatory effect. In these cases predation rate increases as prey density declines, causing the population to decline even faster; this situation can occur when there is no switching by predators, there is no refuge for the prey, and predators have an alternative prey source (MESSIER 1991; MARSHAL & BOUTIN 1999; JEDRZEJEWSKI et al. 2002; WITTMER et al. 2005; SINCLAIR et al. 2006).

Predation by wolves on livestock is dependent on the species, age class, rearing methods, and on the availability of wild prey (ROBEL et al. 1981; BLANCO et al. 1990; MERIGGI et al. 1991; BOITANI & CIUCCI 1993; MERIGGI & LOVARI 1996; KACZENSKY 1999; MECH et al. 2000; BRADLEY & PLETSCHER 2005; GAZZOLA et al. 2008). In particular, wolves select sheep and goats, and cattle calves less than 15 days old (MERIGGI et al. 1991, 1996; GAZZOLA et al. 2008). Moreover, attacks occur mainly on free-ranging unguarded livestock and damage is concentrated to a few farms, suggesting that environment is also important in determining the probability of predation (KACZENSKY 1999; SCHENONE et al. 2004; BRADLEY & PLETSCHER 2005; GAZZOLA et al. 2008).

Finally, from an analysis of the diet of wolves in Mediterranean ranges, a close negative correlation was observed between the frequency of occurrence of livestock and that of wild ungulates; this may mean that wolves prefer wild prey, when available, to domestic prey (MERIGGI & LOVARI 1996).

It seems that the diet of wolves in Italy markedly changed from the first studies carried out in the 1970s in the central Apennines to the recent ones performed in the

western Alps; in particular the diet of wolves evolved towards a greater occurrence of large wild herbivores, becoming more and more similar to that of North American and north-eastern European areas (MERIGGI & LOVARI 1996).

The aims of this study were to document the diet changes of wolves in Italy and to identify if such variations could be related to the use of wild ungulate species.

METHODS

We carried out an analysis of the scientific papers about the feeding habits of wolves in Italy and we took into consideration the studies carried out by analysis of scats because they were more numerous than those that had used predations. We considered studies published in scientific journals, degree, masters and PhD theses, and unpublished reports. If a study summarised results from more than one study site, these were analysed separately, i.e. per site. For each study we first considered the absolute percentage of occurrence (ratio between the number of times that a prey occurs in the sample and the sample size) of seven food categories (Wild ungulates, Livestock, Small mammals, Other vertebrates, Fruits, Other vegetables, Garbage) in which we pooled the items found in each study to make them comparable, and then the percentage of occurrence calculated for each wild ungulate species. Moreover we calculated diet breadth by the normalised Levins' B index on food categories (FEISINGER et al. 1981). At a local level we considered the data on wolf diet from the Genoa province (northern Apennines) from 1987 to 2005, computing for each year the frequency of occurrence of pooled wild ungulates, and of each species that occurred in scats.

We obtained population estimates of the different species of wild ungulates in Italy from PAVAN & BERRETTA BOERA (1981), PEDROTTI et al. (2001), and APOLLONIO (2004); the trend at national level was obtained by extrapolation, assuming a constant numeric increase between time intervals, thus obtaining a rate of increase that decreases linearly with the increase in population.

We compared the diet composition of wolves among geographic areas by nonparametric multivariate analysis of variance (NPMANOVA; ANDERSON 2001; HAMMER 2010) with permutation (10,000 replicates) and pairwise comparisons with Bonferroni's correction; furthermore we tested each variable with the Kruskal–Wallis test. For this aim we assigned the examined studies to the following geographic areas: southern-central Apennines (Region administrations: Umbria, Abruzzo, Calabria), northern Apennines (Region administrations: Piedmont, Lombardy, Liguria, Emilia-Romagna, Tuscany), and western Alps (Region administration: Piedmont) (Fig. 1). To show significant trends of wild ungulate and livestock use and of diet breadth we used curve-fit analyses with the time as independent variable; for these analyses we considered for each study the last year of data collection. The same type of analysis was used to show the type of relationships between wild prey usage and their abundance.

RESULTS

Differences among geographic areas

We found 20 studies on the wolf diet in Italy for a total of 28 different study areas, 4 of them carried out in the western Alps, 9 in the northern Apennines, and 7 in the south-central Apennines (Table 1). Wolf diet was significantly different among geographic areas both when considering food categories ($F = 7.16$, $P = 0.0002$), and the species of wild ungulate prey ($F = 7.08$, $P < 0.0001$). Considering food categories, pairwise comparisons showed significant differences between south-central and northern Apennines ($P = 0.001$) and between south-central Apennines and western Alps

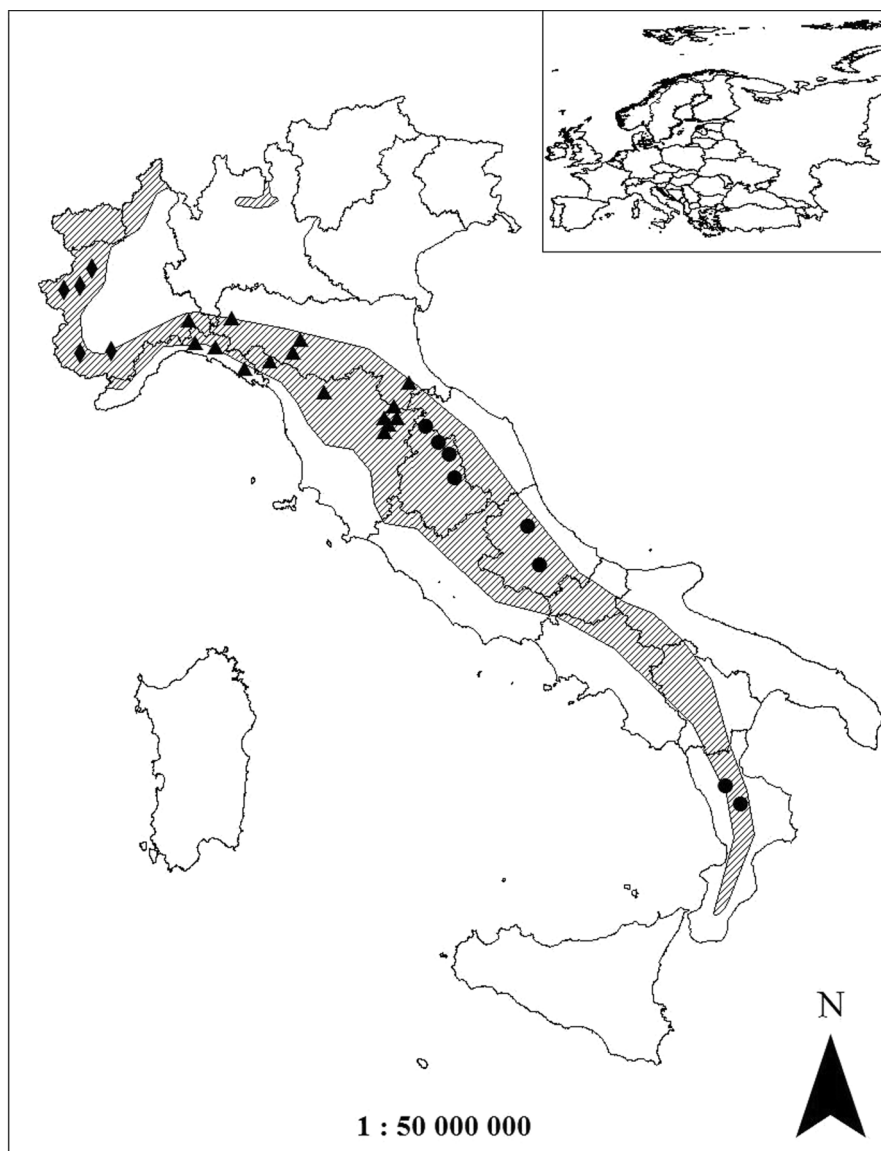


Fig. 1. — Distribution of analysed studies on wolf diet in Italy carried out from 1976 to 2004 (circles, south-central Apennines; triangles, northern Apennines; diamonds, western Alps; shaded area, wolf range).

($P = 0.003$); considering wild ungulate species instead significant differences resulted for all comparisons ($P \leq 0.0005$ in all cases). Conversely, diet breadth was not significantly different among geographic areas ($H = 0.77$, $df = 2$, $P = 0.679$).

Regarding food categories, the frequency of occurrence of wild ungulates and livestock differed significantly among geographic areas (Table 2). In particular, the

Table 1.

Frequency of occurrence (%) of wild ungulates and livestock and B index of diet breadth in the studies on wolf diet in Italy (small letters in brackets indicate different study areas or periods in the same study).

Geographic area	<i>n</i>	Wild ungulates	Livestock	Levins' B	Source
Western Alps	290	93.1	4.1	0.15	AVANZINELLI et al. 2003 (a)
	118	87.3	9.3	0.19	AVANZINELLI et al. 2003 (b)
	494	89.7	11.7	0.21	RICCI 2003
	568	66.9	28.3	0.30	MARUCCO 2003
	848	87.2	9.7	0.20	GAZZOLA et al. 2005
Northern Apennines	38	62.5	0.0	0.27	MATTEUCCI 1992
	100	20.0	34.0	0.70	MERIGGI et al. 1991
	229	92.0	7.1	0.18	MATTIOLI et al. 1995
	292	16.1	23.0	0.72	MERIGGI et al. 1996 (a)
	71	35.2	56.0	0.61	MERIGGI et al. 1996 (b)
	156	94.2	4.0	0.20	MERIGGI et al. 1996 (c)
	263	60.8	14.8	0.34	CIUCCI et al. 1996
	537	73.4	9.0	0.37	GILIO 2001
	1862	90.2	4.9	0.17	MATTIOLI et al. 2004 (a)
	?	94.1	1.2	0.15	MATTIOLI et al. 2004 (b)
	?	88.8	7.4	0.17	MATTIOLI et al. 2004 (c)
	?	91.3	1.2	0.17	MATTIOLI et al. 2004 (d)
	?	85.4	7.8	0.19	MATTIOLI et al. 2004 (e)
	868	74.4	14.6	0.14	REGGIONI 2004
	190	23.7	59.5	0.43	SCHENONE et al. 2004
South-central Apennines	220	0.0	49.0	0.42	MACDONALD et al. 1980
	?	0.0	84.0	0.26	RAGNI et al. 1996 (a)
	94	2.0	64.0	0.15	GAMBARO 1984
	131	0.0	71.0	0.14	RAGNI et al. 1985
	294	26.0	51.0	0.26	RAGNI et al. 1996 (b)
	165	39.4	13.0	0.51	PATALANO & LOVARI 1993
	116	16.0	74.5	0.37	BORELLI 1999
	1162	60.4	13.7	0.22	CIUCCI et al. 2004

frequency of occurrence of wild ungulates was significantly lower in the south-central Apennines than in the northern Apennines and western Alps ($P = 0.005$ and $P = 0.007$ respectively), whereas the frequency of occurrence of livestock was significantly greater in the south-central Apennines than in the northern Apennines ($P = 0.004$). Significant differences among geographic areas resulted for wild boar, roe deer, fallow deer, red deer, and chamois (Table 2). Wild boar was more used in the northern Apennines than in the south-central range ($P = 0.016$) and the western Alps ($P = 0.004$). The frequency of occurrence of roe deer was lower in the south-central Apennines than in the northern

Table 2.

Average frequency of occurrence (SD) of food categories and of wild ungulate species found in the three geographic areas, and significance of the differences (Kruskal–Wallis test).

Categories and species	South-central Apennines	Northern Apennines	Western Alps	<i>H</i>	<i>P</i>
Wild ungulates	18.0 (22.52)	67.2 (29.50)	84.9 (10.34)	12.83	0.002
Livestock	52.5 (26.81)	15.5 (19.46)	12.8 (9.08)	10.76	0.005
Small mammals	2.2 (2.68)	6.2 (8.27)	1.2 (1.24)	0.31	0.859
Other vertebrates	16.6 (22.91)	13.2 (21.34)	4.4 (4.09)	0.77	0.680
Fruits	1.0 (2.67)	9.2 (17.71)	0.0 (0.00)	5.23	0.073
Other vegetables	13.5 (27.26)	7.2 (10.67)	0.9 (0.88)	0.21	0.901
Garbage	3.5 (6.40)	1.2 (2.20)	0.0 (0.00)	2.45	0.293
Wild boar	12.4 (20.20)	39.2 (21.15)	1.6 (2.02)	14.08	0.001
Roe deer	2.0 (3.27)	18.8 (16.53)	32.3 (10.43)	12.28	0.002
Fallow deer	0.0 (0.00)	5.4 (11.75)	0.0 (0.00)	7.59	0.022
Red deer	2.6 (7.28)	2.0 (4.17)	22.6 (19.58)	11.35	0.003
Mouflon	0.0 (0.00)	2.1 (4.29)	0.3 (0.61)	2.96	0.228
Chamois *	0.2 (0.43)	0.0 (0.00)	25.3 (24.67)	26.67	<0.0001

* Alpine and Apennine chamois pooled.

Apennines ($P = 0.017$) and the western Alps ($P = 0.004$). For fallow deer a borderline significance resulted between south-central and northern Apennines ($P = 0.051$). Red deer showed greater frequency of occurrence in western Alps than in south-central and northern Apennines ($P = 0.004$ and $P = 0.009$ respectively). Finally chamois occurred in wolf diet only in Alpine study areas with the exception of one study in the Abruzzo National Park (central Italy; PATALANO & LOVARI 1993) ($P < 0.0001$ for all pairwise comparisons).

Changes of wolf diet in time

The occurrence of wild ungulates in wolf diet showed an increasing trend following a logarithmic model ($R^2 = 0.439$, $SE = 26.41$, $F = 22.93$, $P < 0.0001$) (Fig. 2). We recorded significant trends of the frequency of occurrence of wild boars, roe deer, red deer, and chamois during the period covered by the analysed studies (Fig. 3). The frequency of occurrence of wild boars increased until the middle of the study period whereupon it then decreased following a second-order polynomial model ($R^2 = 0.441$, $SE = 18.64$, $F = 10.27$, $P = 0.001$). The frequency of occurrence of roe deer clearly increased in accordance with a linear model ($R^2 = 0.303$, $SE = 14.02$, $F = 11.29$, $P = 0.002$). Red deer and chamois occurred in the wolf diet in Italy only after the middle of the study period, reaching high frequencies of occurrence; for both species the best model was a second-order polynomial one (red deer: $y = 7.7 - 1.4t + 0.1t^2$; $R^2 = 0.246$, $SE = 10.79$, $F = 4.07$, $P = 0.030$; chamois: $y = 1.6 - 0.7t + 0.1t^2$; $R^2 = 0.230$, $SE = 12.48$, $F = 3.74$, $P = 0.038$).

Both for the frequency of occurrence of livestock and for diet breadth negative and significant relationships with the frequency of occurrence of wild ungulates

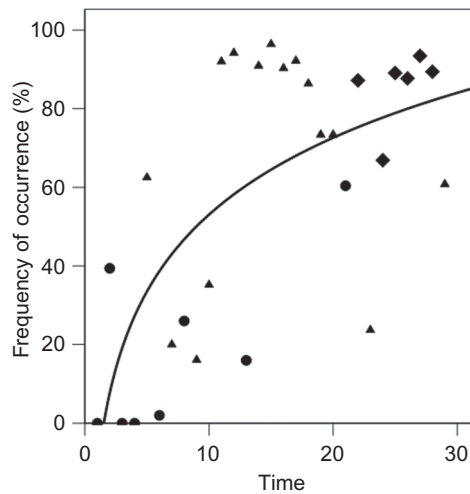


Fig. 2. — Trend of frequency of occurrence of wild ungulates in wolf diet in Italy from 1976 to 2004 (circles, south-central Apennines; triangles, northern Apennines; diamonds, western Alps; $y = -11.9 + 28.2 \ln(t)$).

resulted; in particular for livestock the best model was a linear one ($R^2 = 0.756$, $SE = 12.88$, $F = 87.93$, $P < 0.0001$), whereas for diet breadth a second-order polynomial model was selected ($R^2 = 0.421$, $SE = 0.13$, $F = 10.83$, $P < 0.0001$). In accordance with this model the B index increased until intermediate values of the frequency of occurrence of wild ungulates and then decreased (Figs 4–5).

In the province of Genoa, the frequency of occurrence of wild ungulates in the wolf diet increased linearly and significantly from 1987 until 2005 ($R^2 = 0.444$, $SE = 12.65$, $F = 11.40$, $P = 0.006$) (Fig. 6). Significant trends resulted for roe deer ($y = -0.5 + 0.3 t$, $R^2 = 0.281$, $SE = 3.17$, $F = 6.07$, $P = 0.030$) and for fallow deer ($y = -3.0 + 1.0 t$, $R^2 = 0.254$, $SE = 9.75$, $F = 5.43$, $P = 0.038$), whereas for wild boar no trend resulted.

Abundance of wild ungulates in Italy and their use by wolves

The overall abundance of wild ungulates in Italy increased from about 188,000 heads in 1977 to 1,383,000 in 2004; the increase was mainly because of a dramatic recovery of wild boar (1900–667,000 individuals) and roe deer populations (102,000–464,000 individuals), while the other species, even if with marked increases, scarcely contributed to the overall trend, because of their low numbers and narrow distributions (Fig. 7).

A positive and significant relationship resulted between the frequency of occurrence of wild ungulate in the wolf diet and their overall abundance in Italy, in accordance with a logarithmic model ($y = -446.6 + 38.0 \ln(x)$, $R^2 = 0.470$, $SE = 25.73$, $F = 24.96$, $P < 0.0001$). Considering the different species of wild ungulates, significant and positive relationships resulted only for wild boars ($y = -6.7 + 2.6 x - 2.4 x^2$, $R^2 = 0.247$, $SE = 21.42$, $F = 5.42$, $P = 0.011$) and for roe deer ($y = -10.2 + 0.0001 x$, $R^2 = 0.371$, $SE = 13.07$, $F = 16.91$, $P < 0.0001$).

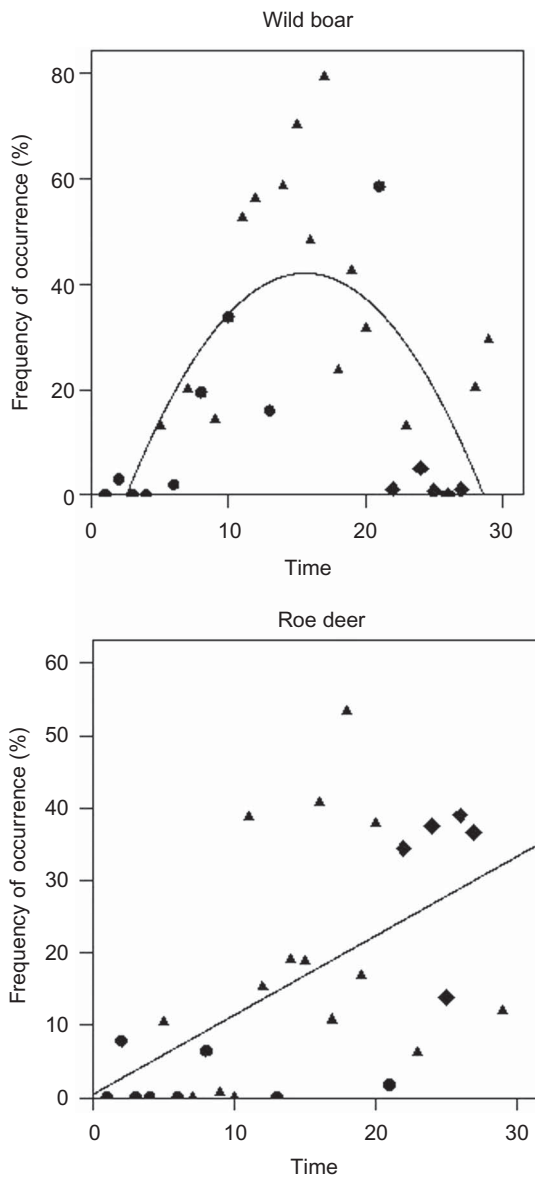


Fig. 3. — Trend of frequency of occurrence of wild boar and roe deer in wolf diet in Italy from 1976 to 2004 (circles, south-central Apennines; triangles, northern Apennines; diamonds, western Alps; wild boar: $y = -18.2 + 7.7t - 0.3t^2$; roe deer: $y = 0.5 + 1.1t$).

DISCUSSION

Wolf diet was markedly different between geographic areas, in particular for wild ungulates and livestock. The studies carried out in the south-central Apennines showed an important use of livestock, whereas in the northern Apennines wild ungulate occurrence increases and in the western Alps the use of livestock was negligible and the diet was characterised by large wild herbivores. These differences agree with

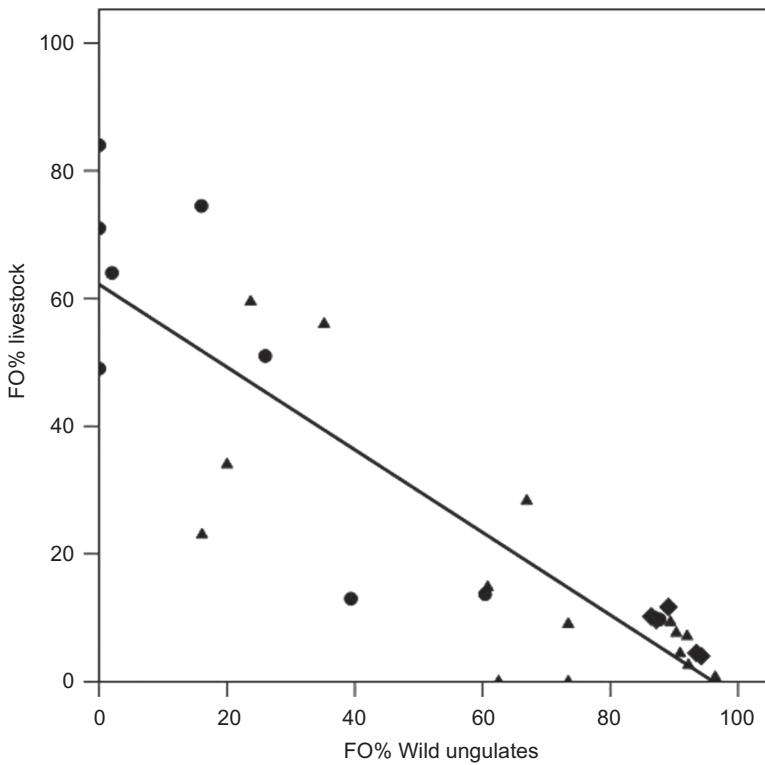


Fig. 4. — Relationship between frequency of occurrence of livestock and wild ungulates in wolf diet in Italy ($y = 62.2 - 0.7x$).

changes of abundance and density of wild ungulate populations in the Italian peninsula. As a matter of fact the richness and abundance of wild ungulate communities in Italy follow a north-south gradient, from the Alps to the southern Apennines, where some species (i.e. red and roe deer) are localised and at low densities (PEDROTTI et al. 2001; APOLLONIO 2004). Moreover livestock abundance and husbandry methods, as well as the proportions of different species, show great differences from the Alps to the Apennines and in the different parts of the Apennine chain, with consequences on domestic prey availability and in turn on wolf feeding habits (ISTAT 2003).

Wolf diet in the three geographic areas differed also in the specific composition of the wild ungulate component; in particular, differences were recorded for wild boar, roe deer, red deer, and chamois. The use of wild boars increased from the south-central to the northern Apennines and decreased markedly in the western Alps; the occurrence of roe and red deer in wolf diet increased in a regular fashion from south to north, reaching the maximum in the western Alps study areas. Finally chamois occurred in the wolf diet only in the Alps if we exclude a limited occurrence of Apennine chamois (*Rupicapra pyrenaica ornata*) in a study carried out in the Abruzzo National Park (PATALANO & LOVARI 1993); this was because of the lack of chamois population in the Apennines, apart from a few areas in which no studies have been carried out. The use of wild ungulate species by wolves seems related to their availability at range level, but locally there can be exceptions because of behavioural characteristics and accessibility of the different species (HUGGARD 1993; MERIGGI et al. 1996; MERIGGI & LOVARI 1996). In

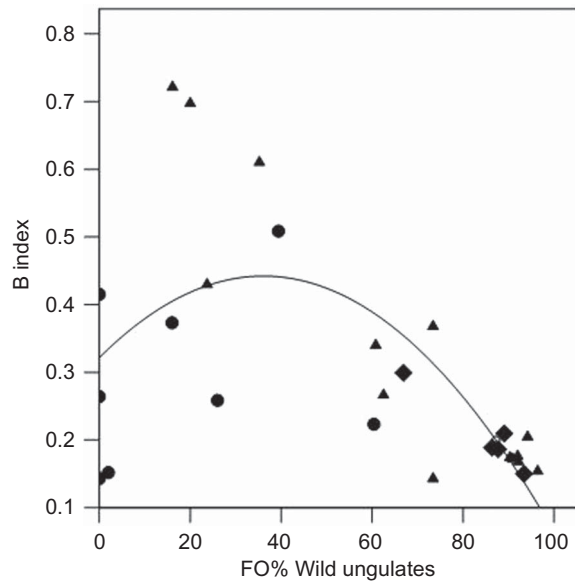


Fig. 5. — Relationship between wolf diet breadth (Levins' B index) and frequency of occurrence of wild ungulates ($y = 0.3 + 0.1 x - 0.0001 x^2$).

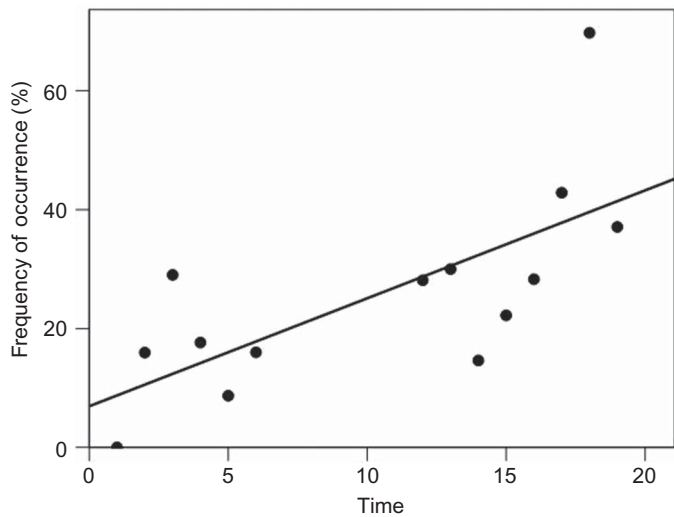


Fig. 6. — Trend of frequency of occurrence of wild ungulates in wolf diet in the Genoa province from 1987 to 2005 ($y = 6.9 + 1.8 t$).

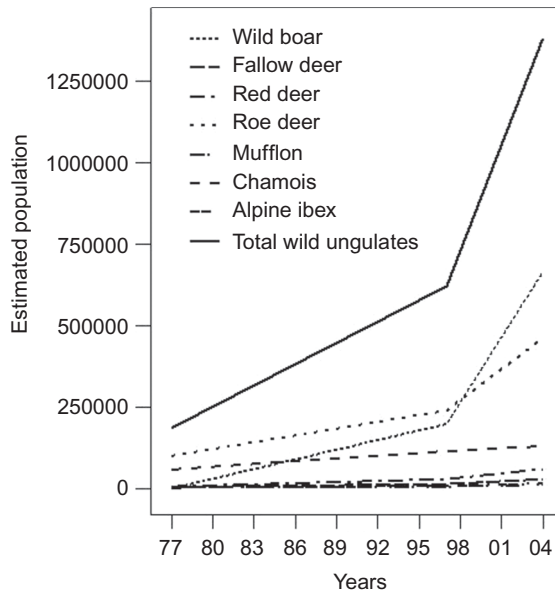


Fig. 7. — Population trend of wild ungulates in Italy from 1977 to 2004.

particular, in some areas wolves select species that live in large groups, are easy to detect and on which the predator can carry out targeted hunting, as opposed to other solitary species for which predation rates mainly depend on encounter rate (HUGGARD 1993; MERIGGI et al. 1996; JEDRZEJEWSKI et al. 2002). In Italy, wild boar is the most important prey species, unlike other Palearctic areas where red deer is the key species for wolves and wild boar is usually the second species (REIG & JEDRZEJEWSKI 1988; JEDRZEJEWSKI et al. 1992; SMIETANA & KLIMEK 1993; JEDRZEJEWSKA et al. 1994; OKARMA 1995; MERIGGI & LOVARI 1996; GULA 2004). The high use of wild boar in Italy can be explained as follows: (i) the species lives in large groups easily detectable by a predator; (ii) births occur all year round, particularly in spring–summer (MERIGGI et al. 1988), and (iii) sub-adults leave matriarchal groups in coincidence with the new births, thus becoming easier to prey upon (HECK & RASCHKE 1980; MAUGET et al. 1984).

The second species in terms of importance in wolf diets in Italy was the roe deer, which is widespread and abundant particularly in the northern Apennines and in the Alps; roe deer, when present at high density, can be a profitable prey for wolves because of the high encounter rate and low handling time (CURIO 1976; HUGGARD 1993; MERIGGI et al. 1996; MERIGGI & LOVARI 1996; JEDRZEJEWSKI et al. 2002). Moreover, from north American and European studies it has been noted that the size of wolf prey is related to the pack size (THURBER & PETERSON 1993; SCHMIDT & MECH 1997; HAYES et al. 2000; JEDRZEJEWSKI et al. 2002); in Europe and particularly in the Mediterranean region, wolf packs are family groups of few individuals, usually from two to four, and rarely do they exceed six members (BOITANI 1992; BOITANI & CIUCCI 1993; MERIGGI et al. 1996; SCHENONE et al. 2004). As a consequence, predation upon roe deer can satisfy the food requirements of small packs, also allowing complete consumption of prey in a short time (JEDRZEJEWSKI et al. 2002).

Red deer was the third species in order of importance in the wolf diet and the fourth after fallow deer in the northern Apennines. Also in the western Alps, where

37.4% of the Italian population of red deer is present and where wild boar is limited to small and fragmented populations, red deer is the third most used species after roe deer and chamois. In the western Alps chamois is the most abundant ungulate; nevertheless, it represents the second species in wolf diet. This can be due to a better adaptation to snow conditions and steeper topography of Alpine valley leading to a low profitability of this prey species. Moreover the presence of pastures interspersed with conifer forests at low altitude in western Alps could contribute to an easy approach by wolves to their main prey (roe deer and red deer) during the winter season (GAZZOLA et al. 2007).

In Italy wild ungulate communities have more species with higher population densities than other North European and North American situations; this leads to a greater flexibility in prey choice by wolves to satisfy food requirements of pack members in different seasons (OKARMA 1995; JEDRZEJEWSKI et al. 2002; PETERSON & CIUCCI 2003; MELIS et al. 2006, 2009).

Our analysis evidenced an increasing trend of wild ungulate use by wolves not only at a national, but also at regional and local levels. If the trend had been detected only at national level it could have been the case that it was influenced by the increase in information on wolf feeding ecology in the areas recently re-colonised by the species (i.e. the northern Apennines and the western Alps), where wild ungulate populations are more abundant and communities have a greater richness (APOLLONIO 2004; GAZZOLA et al. 2007). Moreover the use of wild ungulates could be influenced by the difference in livestock availability and husbandry methods among geographic areas. However, the increased occurrence of wild ungulate in wolf diet that we recorded in the same region or study areas in subsequent times is possibly dependent on the increase of prey populations (RAGNI et al. 1985, 1996; MERIGGI et al. 1991, 1996; GILIO 2001; SCHENONE et al. 2004; MERIGGI & SCHENONE 2007). In particular in the study area in the province of Genoa the occurrence of wild ungulates in the wolf diet ranged from 0% in 1987 to 70% in 2004; in the same period the hunting bags of wild boars in the area occupied by wolves increased from 606 to 2067 heads and roe and fallow deer counts showed marked increases of population densities (roe deer: from 21 per km² in 1997 to 53.4 per km² in 2005; fallow deer: from 0.7 per km² in 1994 to 20.2 per km² in 2005; GENOA PROVINCE WILDLIFE SERVICE unpub. data). Likewise, in the Pollino National Park (southern Italy) an initial study on wolf diet found an occurrence of wild ungulates of 16% (BORELLI 1999), whereas afterwards wild ungulates increased up to 60.4% (CIUCCI et al. 2004). Also in the Umbria region (central Italy) the frequency of occurrence of wild ungulates increased in a 10 year period from 0% to 26% (RAGNI et al. 1985, 1996).

The species of wild ungulates for which we found significant trends were wild boar, roe deer, red deer, and chamois. The use of wild boar by wolves increased until the mid nineties, whereupon it decreased; this trend could be due on one hand to the shift of diet studies in the recently colonised areas of the western Alps where population densities of wild boars are lower than in the Apennines (PEDROTTI et al. 2001; APOLLONIO 2004), and on the other hand to the increase of the use of other wild ungulate species such as the roe deer. Roe deer occurrence increased linearly in the diet of wolves, showing that this specie could be a highly profitable prey for wolves. As for red deer and chamois, the marked increase in the wolf diet in recent years is mostly due to the contribution of the studies carried out in Alpine areas.

Together with the increase of wild ungulates, a significant reduction of livestock in the wolf diet resulted; the negative and highly significant relationship between the two frequencies of occurrence suggests that when wolves can choose between the two prey categories, they may prefer wild prey. This result agrees with the findings of MERIGGI & LOVARI (1996) for the Mediterranean area, and it seems a constant of the predatory behavior of wolves in Europe, even if shifts from this model can be seen at a local scale (OKARMA 1995; COZZA et al. 1996; POULLE et al. 1997). According to the Optimal

Foraging theory (STEPHEN & KREBS 1986; HUGHES 1993), wolves would prefer domestic herbivores instead of wild ones because of (i) their highly clumped distribution in few and known pastures (reduction of search time and greater opportunity of prey choice), (ii) their low capability of detecting and avoiding predators due to domestication (greater probability of successfully attacking the prey), and (iii) their low efficiency of escape behavior (reduction of attack failures). However, disturbance by man can make domestic prey less profitable than wild ones; in particular wolves risk being killed and they have a high probability of not exploiting carcasses to the full (MERIGGI et al. 1996).

As with the frequency of occurrence of livestock, diet breadth was also negatively and significantly related to the occurrence of wild ungulates; however, this relationship shows an increase of diet breadth up to medium values of wild ungulate occurrence (40–50%), after which it then drops. This result suggests that when wild herbivores are scarce, wolves are forced to use alternative food sources (e.g. small mammals, lagomorphs, fruits, and garbage). In southern Europe wolves tend to prey upon wild ungulates, but locally they can adopt a less specialised diet, in order to survive in areas with low availability of both wild and domestic large herbivores (OKARMA 1995; MERIGGI et al. 1996; MERIGGI & LOVARI 1996; PETERSON & CIUCCI 2003).

From our analyses it transpired that in Italy wolves use more and more wild ungulates, while contemporaneously the occurrence of livestock decreases, in particular in the Alps. This is certainly positive as regards a solution to the problems of human attitudes towards the wolf in the areas of new colonisation, even if the effects on wild ungulate populations should be studied in depth. In Europe it seems that wolves can have a limiting effect only on red deer, for which predation accounts for up to 40% of the total mortality (32% in the western Alps; GAZZOLA et al. 2007), whereas for the other species of wild ungulates the main limiting factors are habitat, food supply, climate, hunting, and traffic accidents (OKARMA 1995; JEDRZEJEWSKI et al. 2002; MELIS et al. 2006, 2009; GAZZOLA et al. 2007). In Italy, considering the present and potential densities of wild ungulate populations and the specific richness of the guilds, it is not plausible that predation by wolves can be a limiting effect. In fact, in Italy the mild climate and the high productive habitats can reduce the relative impact of predation, possibly because of a better ability of ungulate species to compensate for predation losses by a higher reproduction rate (JEDRZEJEWSKA & JEDRZEJEWSKI 2005; MELIS et al. 2009).

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