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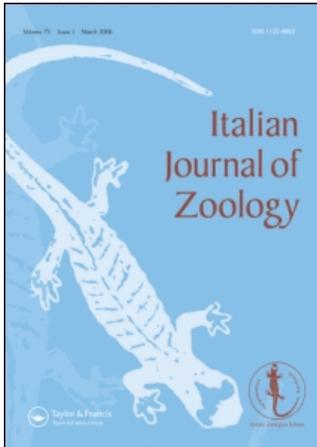
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The role of the wolf in shaping a multi-species ungulate community in the Italian western Alps

A. GAZZOLA¹, E. AVANZINELLI¹, I. BERTELLI¹, A. TOLOSANO², P. BERTOTTO²,
R. MUSSO³ & M. APOLLONIO^{1*}

¹Department of Zoology and Evolutionary Genetics, University of Sassari, Sassari, Italy, ²Provincial Administration of Turin, Turin, Italy, and ³Alpine hunting district CATO2

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Abstract

The impact of predation by wolves on prey populations was analysed in a portion of the western Alps characterized by a rich wild ungulate community. The number of wolves ranged from 7 to 15 (1.7–2.9 wolves/100 km²) during the study period (2000–2001). The diet of wolves mainly consisted of wild ungulates. Red deer and roe deer were the staple prey, while chamois was consumed less despite its high density. From 2000 to 2002, wolves annually removed 20–34 red deer, 21–58 roe deer, and 7–14 chamois per 100 km². These amounts were equivalent to 19–51% of the annual mortality of red deer, 6–28% of roe deer and 6–9% of chamois. Additionally, hunting accounted for 58–94% of the annual mortality of red deer, 18–29% of roe deer and 22–43% of chamois. Other mortality factors (i.e. traffic accidents, disease, poaching) constituted a small percentage of the annual mortality of red deer (5–6%), roe deer (6–9%) and chamois (1%). During the study period, the density of prey animals was stable. Wolf predation did not seriously affect ungulate populations. The role of wolves on wild ungulate populations in the Susa Valley seemed to be compensatory.

Keywords: *Wolf*, *Canis lupus*, *ungulate*, *predation*, *Italy*

Introduction

During the last century, in most countries of Central and Western Europe, the wolf (*Canis lupus* Linneus, 1758) was exterminated. Wolf populations were fragmented and survived in small populations in remote, scarcely populated, hilly or mountainous areas of the Iberian Peninsula, the Balkans and Italy (Boitani & Ciucci 1993; Promberger & Hofer 1994). The Italian wolf population reached a historical minimum around 1970, when it was estimated at about 100 individuals (Boitani & Zimen 1975). Legal protection since 1972, the setting up of protected areas, human abandoning of the countryside, expansion of woodlands, reintroduction and restocking of wild ungulate species are important factors that have led to the reconstruction of a wolf–multiple prey species ecosystem. All this finally contributed to the recolonization by the wolf of its historical range (Apollonio 1992, 2004; Apollonio et al. 2004a, b).

Between 1970 and 1990, the wolf population grew and, in 1990, was estimated at 500–1000 individuals. The re-establishment of good ecological conditions had a big impact on the trophic ecology of the wolves. In fact, they responded to the recovery of wild ungulate populations by a marked shift in feeding habits, that are now based on wild ungulates in most of the northern Italian and French Alps (Mattioli et al. 1995; Meriggi et al. 1996; Poulle et al. 1997; Capitani et al. 2004; Gazzola et al. 2005). However, Italy is characterized by high human population density and activity even in mountainous areas. For this reason, the Italian mountains are constituted by a mosaic of small and medium-sized areas with high abundance and diversity of wild ungulates (Apollonio et al. 2004b). Italian wolf conservation is based on the maintenance of good ecological features in these areas.

Information on the effects of predation by wolves on wild ungulates lends support to wildlife managers in their ensuring a sustainable ungulate hunting bag

*Correspondence: Marco Apollonio, Department of Zoology and Evolutionary Genetics, University of Sassari, Via Muroni 25, I-07100, Sassari, Italy. Tel: +39 079-228667. Fax: +39 079-228665. Email: marcoapo@uniss.it

after wolf recolonization, and it is important to determine this role in the context of conservation and rational management of living natural resources (Głowaciński & Profus 1997). This is even more important in areas of recent recolonization like the Alps, where the wolf's role in ungulate dynamics is an issue among the hunting community.

We evaluated the effect of wolf predation over three years in an area of a western Alpine region (the Upper Susa Valley) recently recolonized by wolves and characterized by a rich wild ungulate community. The mortality induced by wolves was compared with densities of ungulates and mortality factors, such as harvesting by hunters and other natural/human mortality aspects.

Materials and methods

The study area is located in an Alpine region in the western part of Turin province (45°05'N, 7°00'E), and extends over 523 km² from 800 to 3300 m a.s.l. The landscape at lower altitude is a mixture of mixed woods of beech (*Fagus sylvatica*), maple (*Acer platanoides*) and birch (*Betula pubescens*) and fields, while from 1100 to 2300 m a.s.l., coniferous forests comprised of pine (*Pinus sylvestris*), spruce (*Picea abies*), and larch (*Larix decidua*) are dominant. Above 2300 m, alpine meadows and rocky areas are the main habitats.

From 1850 to 1970, the wild ungulate community of Susa Valley was poor: cervids were rare after the end of the 19th century and became extinct during World War II. Although the chamois never disappeared, it fell to a low density. Since 1962, reintroduction and restocking of wild ungulates was the task of hunting associations and the Turin Province Administration (Luccarini & Mauri 2000; Demeneghi et al. 1987). Thanks to these operations, rapidly growing wild ungulate populations have been restored in Susa Valley, and in 1985 hunting was again permitted (Demeneghi et al. 1987). Currently, a rich wild ungulate community lives in Alta Valle di Susa constituted by six species: chamois (*Rupicapra rupicapra*), roe deer (*Capreolus capreolus*), red deer (*Cervus elaphus*), wild boar (*Sus scrofa*), alpine ibex (*Capra ibex*) and moufflon (*Ovis orientalis musimon*). The first four ungulate species are annually harvested by hunters.

Flocks of sheep and goats and herds of cows are free-ranging on high pastures from May to October and are stabled in the valley during the rest of the year. During the study period, the presence of two stable wolf packs (Bardonecchia pack; Gran Bosco pack) was verified in the study area. The climate is continental with prolonged snow cover in winter from October–November to April–May, depending on altitude.

Wolf status

To evaluate wolf status, we used snow-tracking and wolf-howling techniques. The largest number of wolves of each wolf pack was accepted as the size of the wolf pack in a given season (following Jędrzejewski et al. 2000). Two seasons were considered: May–October (summer); November–April (winter).

During the winter season, wolves were tracked in presence of fresh snow (24–48 h after snowfall). When a wolf trail was found, it was followed until the number of individuals travelling along it became distinguishable. The largest number of wolves travelling together within a considered area was used as an estimate of winter pack size.

Wolf-howling surveys were carried out, only in summer from late June to end October, to ascertain the presence of wolf packs and their reproductive status (i.e. birth of a litter). The approach described as 'saturation census' by Harrington and Mech (1982) was adapted to local requirements, dictated especially by the mountainous topography.

Sampling sites were located in prominent places, in order to maximize the range of audibility and to minimize sound dispersion. The equipment, artificial stimuli, and session protocols have been described elsewhere (Gazzola et al. 2002). The whole census area was divided into two sectors, defined on the basis of hypothetical activities range of wolf packs, and for every working night, two adjacent sectors were covered simultaneously by different teams. Home sites, when located, were monitored by further howling sessions once a week. Home sites were never visited by researchers during their use by wolves, and the number of howling wolves (pup/adult) was determined when possible. Each reply by packs to wolf-howling stimulus was recorded. Pack size was determined by maximum number of pups and adults heard in all replies collected during each summer.

Wolf feeding habits and energy requirements

Wolf food habits were assessed by scat analysis. Prey remains (hairs and bones), fruit and grasses, found in every scat, were dried at 50°C for 24 h. Prey remains were identified on the basis of a reference collection of mammal hairs. Moreover, the age of the ungulates recovered from wolf scats was determined through the analysis of recognizable bone fragments, teeth, and macroscopic comparison of hairs (see Materials and methods in Mattioli et al. 1995). We distinguished two age classes for cervids and chamois: juveniles (<1 year of age) and adults (>1 year). When

a component at a specific taxonomic group could not be recognized, it was considered to be undetermined.

On the basis of 716 scats collected from May 2000 to April 2003, we calculated the relative biomass (Bio) of ungulate species and other mammals. Using the volume values, we applied the biomass model of Ciucci et al. (2001): $y=0.274+0.011x$, where y represents the biomass (kg) of prey for each collectable scat and x is the live weight of prey. For wolf diet analysis two seasons were considered: May–October (summer), November–April (winter).

Daily food consumption by wolves was calculated through the field metabolic rate (FMR) for all eutherian mammals (Głowaciński & Profus 1997). The equation, derived from Nagy’s formula (1987), is closely correlated with body mass: $FMR (kJ/d)=2.58 W^{0.862}$, where W is body weight in g. This allows indirect estimates of total daily energy expenditure of a free-living animal. Since food consumption is affected by body mass, the wolf pack age structure was taken into account, but for summer only, because wolves reach adult body mass in midwinter.

Data from Italy give an average body weight of 32 kg for an adult wolf (>1 year old). The average body mass of young individuals was considered to be 16 kg in summer. Calculations based on FMR yielded 2.6 kg of meat per day for an adult wolf and 1.4 kg for a young one.

On the basis of the number of wolves and structure of packs (young/adults), we calculated the seasonal body mass required by wolves. Moreover, we took into account a second method to evaluate the impact of wolves on a wild ungulate community. On the basis of the kill rate by wolves in eastern Poland (Jędrzejewski et al. 2002), it was determined that a wolf over six months old needs 5.6 kg of meat each day (PW), while 2.8 kg are necessary for a young wolf (<six months) (Kojola et al. 2004).

Average body weight of prey

Table I reports the average body mass of each wolf food item. That for staple prey (cervids and chamois) was based on local data from hunting bags. Sex and age of prey consumed by wolves were taken into account. Moreover, values of average body mass of ungulates, taken for calculations, were reduced by 10% for juveniles and 25% for adults (Fuller 1989; Okarma 1992; Głowaciński & Profus 1997) on account of inedible and indigestible parts of their bodies (large bones, hair and stomach).

On the basis of consumption rates for each wild ungulate, we calculated the effective usage of carcasses by wolves. Based on the mass of 112 carcass remnants, wolves consumed 55% of their live

Table I. Mean body mass of wolf prey items.

Prey items	Body mass (kg)		
	Adult or mean value	Young (in winter)	Young (in summer)
Red deer	110.4	57.8	26.5
Roe deer	25.0	15.4	8.0
Chamois	30.2	14.2	11.0
Mouflon	29.5	–	–
Wild boar	20.3	–	–
Hare	3.0	–	–
Marmot	4.5	–	–
Rodent	0.03	–	–
Sheep	66.8	–	–
Goat	44.9	–	–
Cattle	110.0	–	–

mass in red deer, 85% in roe deer and 73% in chamois. It was assumed that young individuals were completely consumed by wolves in summer.

Live weights of the wild prey species quantitatively unimportant in wolf diet were taken from previous studies (Bassano et al. 1999; Mattioli et al. unpublished). The mean body weight of different domestic ungulates was based on data from species bred in the study area. Moreover, sex, age and use of livestock carcass by wolves in the study area were taken into account (Dalmaso 2003 unpublished).

Surveys and mortality of the ungulate community

Surveys of cervids were performed each April from 2000 to 2002. Chamois census was carried out each year in June. Data on wild ungulates were obtained by observations from vantage points to estimate number of individuals, sex, and age structure of each species. Summer abundance of ungulates was calculated on the basis of their late winter counts, on the percentage of adult females in the population and on female fertility. The latter data were obtained by counts of foetuses found in females shot by hunters and found dead in the study area (Ferroglio, personal communication).

Data on ungulate mortality of the study area were given by the Provincial Administration of Turin (Servizio Tutela della Flora e della Fauna). Species, age (juvenile or adult), sex, and condition of ungulate carcasses found in the whole study area were determined, and the cause of death was recorded. That for ungulates was evaluated by the veterinary staff of Turin University. Data on annual hunting harvests were provided by the Game Alpine Department (CATO2) and by Gran Bosco Natural Park Administration.

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Results

Wolf dynamics

During 2000–2003, we monitored two wolf packs: the Bardonecchia pack (2–9 wolves) and the Gran Bosco pack (3–6 wolves). The total number of wolves ranged from 7 to 15 (Table II).

During May 2000–April 2001, the Bardonecchia pack was composed of 2–3 wolves, but after summer 2001, it grew in size (7–9 wolves). Data about pack reproduction are available for summers 2001 and 2002, but not for summer 2000.

The size of the Gran Bosco pack was stable from summer 2000 to winter 2001/02 (5–6 wolves) but decreased (3 individuals) during the last year. Reproduction was confirmed only in summer 2000.

Direct observations and wolf-howling technique provided an estimate of the number of pups in each pack. During summer 2000, the Gran Bosco pack was composed of 2 adult wolves and 3 pups. During summer 2001, two pups were heard in the Bardonecchia pack, but we hypothesised a litter size of 6 pups on the basis of snow-tracking data. In summer 2002, the wolf pack was constituted by 4 adults and 3 pups.

Wild ungulate dynamics

Roe deer and chamois were the most abundant species in the ungulate community, followed by red deer (Table III). Wild boar was scarce and was not censused. Ibex had been recently reintroduced (1994–1996), and 75 individuals were present. Moufflon was present on the edge of the study area with about 50 individuals. Data of density and

Table II. Wolf population dynamics.

	2000–2001		2001–2002		2002–2003	
	Summer	Winter	Summer	Winter	Summer	Winter
Bardonecchia pack	2	3	3 (+6*)	9	4 (+3)	8
Gran Bosco pack	2 (+3)	6	6	6	3	3
Number of wolves	7	9	15	15	10	11

(+) litter size, * number of pups hypothesized.

population increases of main wolf prey species were calculated for each year (Table III).

Wolf diet

The most important prey of wolves was wild ungulates (Table IV), which constituted 51.5–98.9% of the biomass consumed (summer: 51.5–77.7%; winter: 95.3–98.9%). Cervids represented 43.3–65.9% of total biomass eaten by wolves in summer and 87.4–92.3% in winter. Livestock was an important food item only in summer (summer: 20.7–45.6%; winter: 0.0–4.1%) while chamois was the third most important prey in winter (summer: 4.4–15.2%; winter: 4.0–10.9%).

The impact on the wild ungulate population of wolves, hunting harvests and other causes of mortality

On the basis of the field metabolism rate (FMR) an adult wolf (32 kg) needs 2.56 kg of meat per day, while a young wolf (<6 months old; weight: 16 kg)

Table III. Population dynamics of staple wolf preys in Alta Valle di Susa (2000–2002).

Parameters (no. of individuals/100 km ²)	Years (late winter to late winter)			Mean ± SD
	2000–01	2001–02	2002–03	
Red deer (<i>Cervus elaphus</i>)				
Density in late winter	218	218	223	219 ± 2.7
Juveniles born in spring	83	66	78	76 ± 8.7
Density in summer	327	284	296	302 ± 22.0
Annual mortality	109	66	73	83 ± 22.8
Roe deer (<i>Capreolus capreolus</i>)				
Density in late winter	251	234	232	239 ± 10.4
Juveniles born in spring	299	236	201	245 ± 49.4
Density in summer	613	487	435	512 ± 91.6
Annual mortality	363	253	204	273 ± 81.4
Chamois (<i>Rupicapra rupicapra</i>)				
Density in late winter	350	355	341	349 ± 7.1
Juveniles born in spring	150	108	105	121 ± 24.9
Density in summer	568	458	461	495 ± 62.7
Annual mortality	218	102	119	147 ± 62.6

Table IV. Wolf diet (% of biomass).

Food items	2000–01		2001–02		2002–03	
	Summer	Winter	Summer	Winter	Summer	Winter
Red deer	39.6	64.5	22.0	71.5	36.1	41.2
Roe deer	14.4	23.0	17.4	18.7	27.4	51.1
Chamois	18.5	10.9	4.0	4.0	9.7	6.4
Mouflon	0.0	0.5	1.4	0.0	0.0	0.0
Wild Boar	0.6	0.1	1.1	0.3	0.9	0.0
Alpine Ibex	0.0	0.0	0.0	0.0	0.0	0.0
Hare	0.5	0.8	0.2	0.5	1.6	1.2
Marmot	2.9	0.2	2.0	0.0	0.0	0.0
Rodents	0.1	0.1	0.5	0.0	0.0	0.1
Sheep	9.8	0.0	43.6	4.5	24.4	0.0
Goats	4.0	0.0	7.4	0.5	0.0	0.0
Cattle	9.6	0.0	0.0	0.0	0.0	0.0
Total	100.0	100.0	100.0	100.0	100.0	100.0

needs 1.40 kg. Consequently, the mean daily consumed rate was 0.11 prey items per wolf per day, a food requirement amounting to 41.0 ungulates per adult wolf per year (based on the sum of the number of individuals of each species preyed upon by the wolves in the study area) (Table V). Considering cervids only, the average consumed rate by wolves was 0.08 prey per wolf per day. Taking into account the second method, i.e. that of 5.60 kg of meat per day per adult wolf (Jędrzejewski et al. 2002) and 2.8 kg per young wolf (Kojola et al. 2004), we obtained an average of consumed rate of 0.24 prey items per wolf per day. Food requirements per wolf yearly amounted, then, to 87 ungulates (Table V). The average consumption rate by wolves was 0.17 prey item per wolf per day.

Six reports values of predation impact of wolves on staple prey (cervids and chamois) in relation to densities and the annual increase due to reproduction (estimated number of young born annually). Considering wolf food expenditure calculated according to Nagy's formula (FMR), from summer 2000 to winter 2002/03, wolves annually killed 25 ± 8.1 ungulates/100 km² (mean \pm SD). The highest predation was on cervids (41–78 individuals/100 km²), followed by chamois (7–14 individuals/100 km²). The numbers of red deer and roe deer consumed by wolves were similar during 2000–2001 (red deer: 20–34 individuals/100 km²; roe deer: 21–38 individuals/100 km²), but markedly different in the last year (red deer: 20 individuals/100 km²; roe deer: 58 individuals/100 km²).

Table V. Food requirement per adult wolf (32 kg) estimated by FMR formula (Nagy 1987) and based on mean daily food intake by eastern Poland wolves (Jędrzejewski et al. 2002).

Food items	% biomass	Daily consumption rate per adult wolf (kg/d/wolf)		Annual consumption rate per adult wolf (no. of individuals/a/wolf)	
		(2.56 kg/d/wolf)	(5.6 kg/d/wolf)	(2.56 kg/d/wolf)	(5.6 kg/d/wolf)
Red deer	55.3	1.42	3.10	12.4	26.8
Roe deer	22.6	0.58	1.27	20.0	43.1
Chamois	8.6	0.22	0.48	6.7	14.4
Mouflon	0.2	0.01	0.01	0.1	0.3
Wild Boar	0.4	0.01	0.02	0.4	0.8
Alpine Ibex	0.0	0.00	0.00	0.0	0.0
Hare	0.6	0.01	0.03	1.8	3.9
Marmot	0.8	0.02	0.04	2.6	5.6
Rodents	0.1	0.00	0.01	46.4	99.8
Sheep	8.6	0.22	0.48	4.5	9.8
Goats	1.4	0.04	0.08	1.0	2.1
Cattle	1.4	0.04	0.08	0.2	0.4
Total	100.0	2.56	5.60		

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Wolf predation on red deer, expressed as a percentage of deer consumed out of the total deer counted, constituted $8 \pm 3.2\%$ of deer censused in summer. The maximum value (12%) was recorded during 2001. During the study period, the impact of wolf predation on roe deer population increased from 3 to 13% (mean value: $8 \pm 5.0\%$), while on chamois the percentage was 2% and stayed stable over the years.

Wolf predation, expressed as a percentage of kills of annual increase, constituted $34 \pm 14.7\%$ in red deer, $17 \pm 1.1\%$ in roe deer, $9 \pm 1.5\%$ in chamois; however, with respect to the total annual mortality (the difference between summer and subsequent late winter densities), it amounted for red deer to $32 \pm 16.7\%$; for roe deer to $16 \pm 11.1\%$, and for chamois to $7 \pm 1.5\%$.

On the basis of mean daily food consumption by Polish wolves (5.6 kg/day/wolf), the wolf impact clearly doubled with respect to the previous method (Table VI). The annual number of red deer consumed by wolves was 53 ± 16.5 individuals/100 km², while for roe deer it was 83 ± 40 individuals/100 km² and for chamois 23 ± 7 individuals/100 km². The annual predation on ungulates did not exceed 28% of spring density in any one prey. Red deer, however, suffered much more wolf predation than did roe deer and chamois (Table VI).

In the same period, hunters (Table VII) annually harvested 156–175 ungulates/100 km² (red deer: 61 ± 0.6 head/100 km²; roe deer: 57 ± 7.6 head/100 km²; chamois: 44 ± 3.0 head/100 km²). Moreover, a supplement of ungulates dying from other mortality factors was annually found by rangers (19–41 ungulates/100 km²). Hunting harvest on red deer compared with annual mortality amounted to $77 \pm 18.1\%$, a value much higher than those for roe deer and chamois, respectively, $22 \pm 6.1\%$ and $33 \pm 10.5\%$. On the contrary, considering the influence of 'other causes' of death, roe deer yielded the highest percentage of annual mortality ($8 \pm 1.8\%$). Low values were recorded for red deer ($5 \pm 0.7\%$) and for chamois ($1 \pm 0.5\%$).

Harvest by hunters appeared a more important factor on red deer mortality than did wolf predation, and together they played a relevant role in the annual mortality (FMR: 77–145%; PW: 107–208%). Instead, wolf predation on roe deer played a small part in the annual mortality, while the major impact was represented by hunting pressure together with 'other causes' (27–37%). Hunting harvest seemed to be the most important mortality factor for chamois (22–43%).

Discussion

In the Alps, the abundance and richness of the wild ungulate community is actually much higher now

than at the time of wolf eradication, 150 years ago, when chamois only survived in small numbers, while other wild ungulates became extinct.

Wolf restoration produced a new level of complexity in the ecosystem, but its influence on prey population is difficult to determine. Under certain circumstances, wolves can reduce, or even locally eradicate, some prey species (Mech & Karns 1977). At other times, wolf predation may only be compensatory for other mortality causes that occur in the absence of wolves (Ballard et al. 1987). Klein (1995) reported that the black-tailed deer population of Coronation Island was wiped out by wolves after their introduction. On the contrary, on Isle Royale wolves coexist with the world's highest density of moose (Peterson et al. 1998).

The influence of wolves on ungulate populations is very difficult to evaluate, especially in complex European biocenoses. In fact, in North America often only one ungulate species dominates (moose, *Alces alces*; white-tailed deer, *Odocoileus virginianus*; or caribou, *Rangifer tarandus caribou*); instead, most European countries are characterized by richer communities of ungulates (Okarma 1985).

Numerous studies on the effect of wolves on ungulates have been conducted mainly in North America (Peterson et al. 1984; Mech et al. 1987; Gasaway et al. 1992; White & Garrott 2005), but none have yet been made in European countries, except for Poland, Finland, and Scandinavia (Jędrzejewski et al. 2000, 2002; Kojola et al. 2004; Sand et al. 2005). The estimated daily food consumption revealed in 18 North American studies ranged from 0.14 kg to 5.4 kg/wolf/day (Peterson & Ciucci 2003). The estimates of daily food consumption ranged from a minimum of 0.06 kg/wolf/day (Fuller 1989) to a maximum of 0.29 kg/wolf/day (Hayes 1995). The highest values referred to wolves that killed mainly ungulates with large body mass (bison, *Bison bison*; moose), while the lowest to smaller prey (Dall sheep, *Ovis dalli*; white-tailed deer). Considering the latter studies, where body size of prey items was comparable to that of European prey species, the mean food consumption was <3.0 kg/wolf/day (Mech & Boitani 2003).

Our lower estimate of annual predation by wolves on ungulates was based on the field metabolism rate, while the upper one considered the average of meat consumption per wolf per day observed by Jędrzejewski et al. (2002) in Poland. Species, age, sex, and consumption rates (to evaluate the degree of unconsumed portions) of carcasses used by wolves were considered in wolf impact calculations. Moreover, a relatively high value (25% for adult ungulates) of inedible biomass was taken in order to

Table VI. Wolf impact on red deer, roe deer and chamois in Alta Valle di Susa in relation to population densities and increase of prey.

Year	Food requirement per wolf estimated by FMR formula (Nagy 1987)				Mean daily food intake by wolves in eastern Poland (Jędrzejewski et al. 2002)			
	Annual predation (no. killed/100 km ²)	Annual predation on ungulates (%)			Annual predation (no. killed/100 km ²)	Annual predation on ungulates (%)		
		Spring density	Annual increase	Annual mortality		Spring density	Annual increase	Annual mortality
<i>Red deer (Cervus elaphus)</i>								
2000–01	20	6	25	19	44	13	53	40
2001–02	34	12	51	51	72	25	109	109
2002–03	20	7	26	27	43	14	55	59
2000–03	25±8.1	8±3.2	34±14.7	32±16.7	53±16.5	17±6.7	72±31.8	69±35.6
<i>Roe deer (Capreolus capreolus)</i>								
2000–01	21	3	7	6	44	7	15	12
2001–02	38	8	16	15	81	17	34	32
2002–03	58	13	29	28	124	28	62	61
2000–03	39±18.5	8±5.0	17±11.1	16±11.1	83±40.0	17±10.5	37±23.6	35±24.6
<i>Chamois (Rupicapra rupicapra)</i>								
2000–01	14	2	9	6	30	5	20	14
2001–02	7	2	7	7	16	4	15	16
2002–03	11	2	10	9	23	5	22	19
2000–03	11±3.5	2±0.0	9±1.5	7±1.5	23±7.0	5±0.6	19±3.6	16±2.5

Table VII. Impact of hunting harvests and other causes of mortality on the wild ungulate population in Alta Valle di Susa (2000–2002).

Year	Hunters				Other causes of mortality			
	Annual hunting harvest on ungulates (%)				Annual losses (%)			
	Annual hunting harvest on ungulates (%)	Spring density	Annual increase	Annual mortality	Annual mortality (no. killed/100 km ²)	Spring density	Annual increase	Annual mortality
<i>Red deer (Cervus elaphus)</i>								
2000–01	63	19	76	58	5	2	6	5
2001–02	62	22	94	94	3	1	5	5
2002–03	58	20	75	80	5	2	6	6
2000–03	61 ± 2.6	20 ± 1.5	82 ± 10.7	77 ± 18.1	4 ± 1.2	2 ± 0.6	6 ± 0.6	5 ± 0.7
<i>Roe deer (Capreolus capreolus)</i>								
2000–01	64	10	21	18	34	6	12	9
2001–02	49	10	21	19	15	3	6	6
2002–03	54	14	29	29	16	4	8	8
2000–03	57 ± 7.6	11 ± 2.3	24 ± 4.6	22 ± 6.1	22 ± 10.7	4 ± 1.5	9 ± 3.1	8 ± 1.8
<i>Chamois (Rupicapra rupicapra)</i>								
2000–01	47	8	32	22	1	0.2	1	1
2001–02	44	10	41	43	1	0.1	1	1
2002–03	41	9	39	34	2	0.4	2	1
2000–03	44 ± 3.0	9 ± 1.0	37 ± 4.7	33 ± 10.5	1 ± 0.6	0.2 ± 0.2	1 ± 0.6	1 ± 0.5

avoid underestimating the consumption rate. This approach probably leads, however, to a slight discrepancy between the hypothesized and the effective impact of wolves on ungulate populations. The estimate of daily food requirement per 32 kg wolf was 2.6 kg (FMR) (based on Nagy's 1987 metabolic model) (3.2 kg/wolf/day taking into account that 25% of carcass biomass is inedible). However, results from intensive radio-tracking yielded 5.6 kg/wolf/day in Poland where adult wolves are somewhat heavier (about 45 kg) (Jędrzejewski et al. 2002). However, most of the variation could be due to methodological aspects and local context variations from one study to another, so we decided to consider the consequences of adopting different models to evaluate their suitability.

A drastic decline of red deer population should have been observed during the period of study, if the average daily consumption rate of the Polish wolves were adopted, but that was not the case. We therefore think that the impact of wolves can be better expressed using the value obtained with the FMR method than that based on the consumption rate estimated for Eastern Europe.

Our study seems to be in line with other cases in which prey populations were not influenced by the presence of wolves (Mech 1986; Adams & Dale 1998; Mech et al. 1998; Peterson et al. 1998; Nelson & Mech 2000). Wild ungulate densities did not change before or after arrivals of wolves in Susa Valley (census data of CATO2). Even if red deer was the prey species most influenced by wolf presence, wolf predation alone was a poor predictor of its population dynamics. In fact, wolf predation, as a percentage of annual mortality, yielded a higher value in red deer (32%) than roe deer and chamois (respectively, 16% and 7%). A similar phenomenon was found for Białowieża Primeval Forest (Poland) where 40% of annual red deer mortality was due to wolves, as compared with 24% for wild boar and 7% for roe deer (Jędrzejewski et al. 2002). The high susceptibility of red deer, in the Susa Valley, could be a result of the close overlap of habitat and altitude use with the wolf, and to their more conspicuous herding. On the contrary, the lowest wolf predation, that on chamois, was mainly due to the scarce accessibility of this prey. The high use of wide-rocky and high altitude areas by chamois and their being well adapted to snow conditions makes it difficult for wolves to catch them in Susa Valley (Gazzola et al. 2005).

Numerous studies (Fritts & Mech 1981; Peterson et al. 1984; Jędrzejewski et al. 1992; Mattioli et al. 1995) indicated that young ungulates proved to be an important fraction of the wolf diet. Thus, the

greatest demographic effects on ungulate population by wolves should be due to predation on young of the year (Pimlott 1967; Mech 1970). In our study area, wolves take up to 21% of annual production of red deer, 11% of roe deer and 5% of chamois. These low values may be partially explained by the wide use of domestic ungulates by wolf in summer. The share of wolf predation among cervids, chamois and livestock seems to guarantee the reproduction and stability of wild ungulate populations.

Moreover, numerous papers report that wolf predation tends to focus primarily on the youngest and debilitated members of prey herds (Mech 1966; Schwartz et al. 1992). Thus such herds, given the predation of wolves, tend to be constituted by individuals in good physical and health conditions, and therefore of high productivity. In Susa Valley, most of the red deer killed by wolves were suffering from heavy malnutrition, while in roe deer, femur fat levels of wolf kills were high and did not differ from those of the population (Gazzola et al. unpublished). The viability of the red deer population was evidenced by their high reproduction rate (Meneguz et al. 2005).

Some evidence for the partially compensatory role of predation was provided in central Europe, as wolves in winter selected the weakest deer with very low fat reserves (Jędrzejewski 2005).

Thus we believe that the wolf recolonization of the western Alps should not determine the decline of the ungulate population but, quite the contrary, it will be a driving force of change in prey distribution, behaviour, and movements, and will determine a change in the population structure of prey species.

Hunting harvests by humans and wolf predation together could be important factors, limiting red deer population size in Susa Valley. The effects of these two factors were likely additive and could explain the 109% of red deer annual mortality estimated on the basis of census results. This result shows that cervid censuses can lead to underestimation, but they are important for evaluating the order of magnitude of the effects of hunting and predation.

On the contrary, wolf predation was the lowest mortality factor for roe deer, while traffic accidents were the main cause of mortality (37%) followed by hunting harvests (22%). Harvesting by hunters seemed to be the only important cause of death of chamois, but it must be emphasized that the low value of causes such as malnutrition, disease and avalanches (3%) is clearly underestimated, due to the difficulties of reaching and monitoring the winter quarters of this species and of collecting carcasses.

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