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Wolves in the Casentinesi Forests: insights for wolf conservation in Italy from a protected area with a rich wild prey community

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Abstract

The Casentinesi Forests, in the northern Apennines, harbour a rich community of wild ungulates, with the wolf representing the largest predator in the area. Between 1993 and 2000, wolf pack distribution in the area was monitored and estimates of pack size were obtained by wolf-howling surveys, snow-tracking, and occasional observations. Three to five packs were detected yearly, with sizes averaging 4.2 ± 0.9 wolves (maximum 7). The overall density in the area was 4.7 wolves per 100 km^2 with an average distance between adjacent packs of 11.1 km. The high wolf density in the Casentinesi Forests is mostly related to abundance and size of wild prey. In this, like in other areas at low latitudes, wolf density depends mainly on the number of packs, as pack size is rather small and recruitment limited by early dispersal and high mortality. Three homesites used in several years by resident packs were discovered. Homesite fidelity and pack reproductive success were higher in fully protected rather than harvested areas. Establishing a network of protected areas with high ungulate diversity and abundance is proposed as the main factor for allowing a full recovery of the wolf population in Italy.
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1. Introduction

The conservation of wolf (*Canis lupus* Linnaeus, 1758) natural populations represents a priority in several European countries, where the species is endangered or was, in the recent past, severely threatened (Promberger and Schröder, 1993). The Italian wolf population suffered severe persecution till 1971 when wolf hunting was stopped and poison baits banned. This change of attitude was completed in 1976 when the species was given fully protected status, a process stimulated by WWF International, that funded a long-term project including a public educational campaign, scientific works and management solutions to protect wolves. Wolf management at a national scale should not fail to take into account the knowledge of mechanisms regulating population size, territory occupancy by wolf packs, and interactions with prey communities. Such aspects have been well studied in North America, but remain mostly unclear in several ecological contexts. Most studies carried out in Italy investigated small nuclei (Zimen and Boitani, 1975; Ciucci et al., 1997; Ciucci and Boitani, 1999) or resorted to indirect approaches, like interviews (Cagnolaro et al., 1974; Zimen and Boitani, 1975). The main subjects faced in these works were restricted to species distribution, pack/population size, range of pack territories, and reproductive status (presence/absence of a litter).

The present study aimed to collect long-term information over a wide area on the Italian Apennines, where wolves have recovered during the last decades. Wolf density, pack size, and homesite fidelity in the area were evaluated and compared to the abundance of wild prey. The need to know basic wolf biology to provide appropriate management actions was emphasized by Boitani (1992). Our data have a strong relevance to wolf conservation, because our study area represents a wide

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portion of the central and northern Apennines, where presently, because of ungulate reintroduction and the marked decrease in human presence in past decades, relatively pristine conditions occur. There is evidence that this scenario is extending to a wide area of northern and central Italy.

2. Methods

2.1. Study area

The study area lies in the northern Apennines (43°48′N, 11°49′E), between Tuscany and Romagna, and comprises approximately two thirds (223 km^2) of the Foreste Casentinesi National Park, established in 1993 in coincidence with the beginning of the project, plus surrounding zones open to human exploitation. Altitude ranges between 400 and 1658 m a.s.l. Forest cover exceeds 80% and the vegetation comprises species typical of temperate-sub-Mediterranean zones. The number of villages is limited, and human presence, although growing in summer because of tourism, is from low to medium in the rest of the year (resident population density being 21.5 and 60.6 inhabitants per km^2 in Romagna and Tuscany, respectively). During the study, winter temperatures ranged between −13 °C and +25 °C. Snowfalls were occasional from November to April and snow cover lasted on average 56 days (range 33–72) per winter at 1100 m a.s.l., of which only 28 days with a snow depth $\geqslant$ 10 cm.

In this part of the Apennines, wolves declined progressively during the first half of the last century. During the historical minimum of the Italian wolf population (1950–1970), their presence in these areas was debated. Some authors (Cagnolaro et al., 1974) reported a few individuals or packs occasionally recorded in the area, while others (Zimen and Boitani, 1975) considered the wolf population restricted to some ‘islands’ limited to more southern regions. Recent genetic investigations support the former assumption (Scandura et al., 2001). From 1970 on, like in other parts of the peninsula, wolves increased in number following the rise of their prey populations, and an abundant and diversified ungulate community is now present in the Casentinesi Forests. Wild boar (*Sus scrofa*) and roe deer (*Capreolus capreolus*) are ubiquitous; a reintroduced population of red deer (*Cervus elaphus*) is spreading out, whereas fallow deer (*Dama dama*) is restricted to one portion of the area. All these species are protected within the National Park but are hunted outside it in the August–January period. While wild boar collective hunting is widely practised, roe, fallow and, only since 2000, red deer are on the contrary subjected to programmed culling. Local ungulate populations are monitored in the protected and in the exploited areas, and censuses are regularly carried out to estimate species abundance. Reports of unattended or stray dogs within the study area have been rare, and no feral dogs have been reported. Throughout the study, the main prey of wolves were wild boar and roe deer, whereas red deer, fallow deer, hare and livestock represented alternative food sources (Mattioli et al., 1995).

The study area is divided into two parts by the main ridge, corresponding to the regional border. The south western slope (area A – 232 km^2) was monitored continuously from June 1993 until April 2001. On the opposite side (area B – 76 km^2) the study ended in 1995. Preliminary data on resident packs were obtained in 1992. In addition, within area A (Camaldoli Forest) an intensive ca. 130 km^2 study area was selected, corresponding to the assumed territory of a single wolf pack. This was the same area as that of a previous study on wolf food habits (Mattioli et al., 1995).

2.2. Wild prey surveys

Abundance of large prey species was determined every year (1993–1999) within the intensive study area. Drives and vantage point counts were carried out in spring, whereas counts of roaring stags were used in fall to evaluate red deer abundance (Provincial Administration of Arezzo, 1989–1999; Orlandi et al., 2000, unpubl. report; Apollonio et al., 2000; Lovari et al., 2000; Mazzarone et al., 2000). Sex and age class structure were evaluated for every species, on the basis of year-round observations recorded from vantage points and standardised transects. Body weights were measured of animals killed during the hunting season outside the park. Pre-birth densities, referred to late winter, were calculated on the basis of counts and population structure for every species. For fallow deer, due to its scarcity and discontinuous distribution, a constant number was assumed throughout the study period. To estimate total prey biomass available in the area, mean weights were obtained for each age/sex class by weighing samples of killed animals (roe deer: $n = 196$, red deer: $n = 173$, fallow deer: $\underline{n} = 91$, and wild boar: $\underline{n} = 71$).

2.3. Wolf surveys

During the eight-years study period, wolves were monitored by different methods. All direct observations of them within the study area, or in its proximity, were recorded in a database. A specific questionnaire was filled in by the observer for every record and, on the basis of that, the reliability of each observation was evaluated. All records not judged reliable (insufficient description of physical traits, contradictory depiction of the scene) were discarded. From winter 1995–96, wolves were tracked in presence of fresh snow (24–48 h after snowfall). Searching effort was not constant during the study, and it was mostly concentrated within the intensive study area. 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. Every year, from 1993, wolf-howling surveys were carried out in summer to ascertain the presence of wolf packs and their reproductive status (i.e., birth of a litter) and to locate homesites (den or rendezvous sites – Mech, 1981). The approach described as "saturation census" by Harrington and Mech (1982a) was adapted to local requirements, dictated especially by the mountainous topography. Surveys were carried out once or twice per year between late June and early September. A total of 92 sampling sites (0.3 per km^2) were chosen in prominent places, in order to maximize the range of audibility and to minimize sound dispersion. They were placed along routes, each covered by a team of two or more operators. One thousand and eighty-one wolf-howling sessions, (i.e., a continuous period of 15 min during which we attempted to elicit howling from a single site) were carried out during the eight-years monitoring activity. The equipment, artificial stimuli and session protocols have been described elsewhere (Gazzola et al., 2002). The whole census area was divided into 6 sectors, defined on the basis of previous locations of wolf packs, and every night from 2 to 4 adjacent sectors were covered simultaneously by different teams. In the event of no reply, each sector was surveyed for up to three consecutive nights. Homesites used by a pack, when located, were monitored by further howling sessions, for as long as several months. Source direction and approximate distance of responding wolves were evaluated considering factors such as topography, weather conditions, and howl audibility. Therefore, the approximate location of the pack was established and immediately transferred onto a 1:10,000 scale map, with an assumed error $\leqslant 1$ km. In order not to cause any disturbance to the pack in a sensitive part of its biological cycle, we never visited a homesite during the time in which it was used by wolves. As the mere hearing of a reply does not allow one to correctly establish the number of howling wolves, when they are more than two (Harrington and Mech, 1982a), recorded howls were studied by spectral analysis using the Avisoft SAS LAB PRO 3.0 software (Raimund Specht, Berlin). On the basis of fundamental harmonics, it was possible to determine the minimum number of individuals joining the chorus. In good-quality summer recordings, pup vocalizations were recognizable. We arbitrarily assumed the pup/adult discrimination feasible until the end of October. In absence of bioacoustic analysis, choral howls in which the presence of pups was detectable were conservatively interpreted as produced by 4 individuals (2 adults + 2 pups), as in Ciucci and Boitani (1999).

2.4. Parameter estimates

The number of packs was defined by counting different social units, consisting of $\geqslant 2$ individuals, detected in summer throughout the study area. As in past studies on the Italian wolf population, the usual number of wolves in a pack was between two and four (Boitani, 1992), we still considered two adult individuals as a pack. Mech (1981), as well, considered a breeding pair as the most basic element of wolf social organization. In our calculation, wolf packs were assumed to be different if one of the following conditions was satisfied: (1) groups with two or more adults were detected by the same team simultaneously in different valleys; (2) they were located by different teams within the same night in areas >5 km apart; (3) packs, replying in different nights, were located in areas >5 km apart, where different packs had been found during the previous year. Reproductive success of a known pack was determined each year considering the presence/absence of pups in summer-early fall, either on the basis of howling replies or of observed groups. To define areas containing homesites, summer observations and howls of groups including pups were taken into account. Therefore, each area was defined by drawing the minimum convex polygon (MCP) with 95% of all summer locations falling within the presumed territory of a known pack. Homesites frequented by a pack for >2 years were analysed for physical features (vegetation, altitude, slope, exposure).

Mortality data were collected from wolves found dead in the area. When an individual was partially or completely consumed (only bone remains), age and sex were not diagnosed.

Distances between packs were computed either considering the geometric centres of summer locations attributable to each group or, in the case of just a single location, its coordinates themselves. Every year these values were calculated on the basis of the detected packs and averaged over the whole study area. Wolf density was calculated by the estimated maximum number of counted wolves per year, divided by the extent of the overall investigated area, enlarged in order to include peripheral zones toward which pack territories might easily be extended (no physical barrier, continuity of forest cover, homogeneity of vegetation). Therefore, density values may be underestimated. In calculating annual estimates, years were considered from May to April, following the biological cycle of the species and assuming births to occur in late April–early May. 'Period A' and 'period B' throughout the text refer to the periods May–October and November–April, respectively.

3. Results

3.1. Ungulate biomass

The overall density of wild ungulates was estimated in period B as 19.9 heads/km^2. Roe deer was the most abundant large prey (12.2 heads/km^2) representing 62% of relative density. Wild boar, the main food item found in wolf scats (Mattioli et al., 1995), was less abundant (3.6 heads/km^2, 17% relative density). Red deer, although present at lower density in the area (2.7 per km^2 in period A, 14.8% relative density), was as important in terms of biomass as roe deer. The contribution of fallow deer was instead marginal, being around 6% (1.3 heads/km^2). The overall biomass of wild ungulates in the area was estimated on average at roughly 860 kg/km^2 in period B.

3.2. Wolf packs and density

From June 1992, 104 recorded observations of single wolves or packs were considered reliable. One hundred and thirty-two track lines (up to 9.1 km long) were found in period B, of which 79 in the intensive study area. Out of 1081 wolf-howling sessions, 207 (14%) elicited replies by wolves. Most replies (64%) were obtained in period A (May–October), when pack members were with the litter at the den, or at rendezvous sites. One hundred and five elicited howls (51% of the total) were tape-recorded and 64 of them (61%) had an acceptable quality for making a spectral analysis. The results of annual monitoring carried out in the Casentinesi Forests study area are shown in Fig. 1. In 1992, before starting with the programmed research, two packs (Camaldoli Forest – CF and Falterona – FA) were detected by a sequence of sightings, revealing in both cases the presence of a litter. In particular, within the CF pack, 5 pups were observed in October attended by an adult, and this represents the largest litter seen in the whole study area. Adding these data to those of the study, during a nine-years period a total of 32 packs per year were detected. Between 1993 and 1995, when the study became systematic and concerned the whole area (A + B), 5 packs were present. With the monitoring reduced to area A alone, from 1996 to 2001, the number of detected packs was three.

Maximum pack size was that of the 1992 CF pack, when repeated and prolonged observations enabled us to count an adult pair attending to 5 pups in late summer and fall. Average pack size, computed over all packs and years, was 4.2 ± 0.90 (mean ± SD); the most recurring case was that of 4 wolves in a pack (53%), a figure probably influenced also by the conservative procedure used when treating wolf-howling data. Period A and period B sizes were on average 4.4 ± 1.22 ($n = 14$) and 3.8 ± 1.07 ($n = 19$), respectively, with an average decrease in the cold season of 12%. In 13 cases it was possible to evaluate the minimum number of pups in a pack (sightings or analysis of recorded vocalizations). The resulting estimate of litter size, based on cases in which the number of pups was computable, was on average 2.5 ± 0.88, with a modal value of just two pups. Reproduction was ascertained in 25 (78%) packs/year. The CF pack reproduced every year, except for 1996, when no young were detected, though a high number of contacts was made. For the FA pack, we had no confirmation of reproduction in 1993 and 2000. In Valle Santa (VS), several members of the resident pack were illegally killed between 1996 and 1997, which seemed to be the main factor causing the lack of reproduction in 1997 and 1998, as the area was occupied by just 2–3 wolves.

The overall wolf density, calculated over a 506 km^2 area and taking into account only members of packs, averaged 4.7 wolves/100 km^2 (Table 1). The highest value was obtained in the first year (5.2 wolves/100 km^2 in 1993); then it fluctuated reaching a minimum value in the last year (3.9 wolves/100 km^2). Considering the presence of solitary wolves, the proportion of which was estimated according to Peterson and Page (1988), the average density rose to 5.6 wolves/100 km^2. The distance between adjacent packs was on average 10.8 ± 4.37 km (mean ± SD), ranging between 2.5 and 17.8 km.

3.3. Wolf mortality

Eighteen records of wolf mortality were obtained from 1987 to 2001 in the study area. In 14 cases we could ascertain the cause of death: 3 wolves were poisoned, 5 were shot, 4 were driven, 1 was fired by an electric line, and 1 died because of mange. Males were more represented than females (9 vs. 6), while juveniles and subadults (<2 years) occurred slightly more than adults (7 vs. 5). Three individuals (20%) had black fur, whereas the others had the common grey-reddish coat. The oldest wolf recovered was a female with an estimated age of 8–10 years. In a single case it was possible to analyse the fecundity of a female, found poisoned in November 1995 in a zone close to area B. She was 4–5 years old and had 5 uterine scars.

3.4. Homesite fidelity

Sightings and elicited howls allowed us to define areas (homesites) used by territorial packs for attending to pups in summer and fall. Wolves frequented three of them over several years. In the intensive study area, locations of the CF pack including pups were all concentrated into two restricted zones, 1.5 km apart. In the first of them (HS1), approximately 20 ha, a litter was heard 5 times from June 22nd to August 18th in 1993, 1994, and 1999, whereas on other occasions only adult

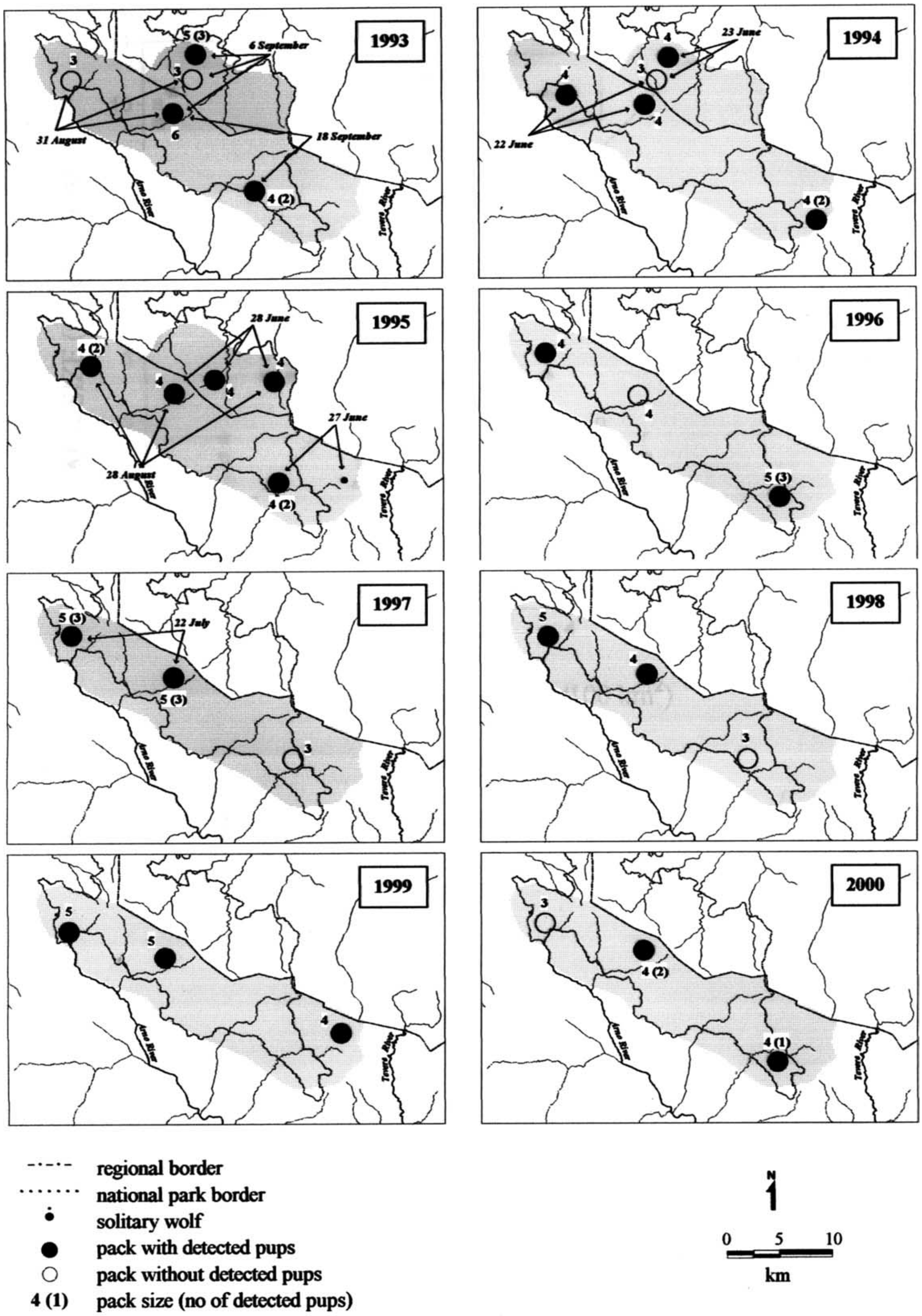

Fig. 1. Wolf packs monitored within the Casentinesi Forests. The study area is shaded. Dates and arrows refer to simultaneous responses (same night) elicited by howling stimulation. Pack sizes refer to the maximum number of wolves detected in the pack during the year.

individuals were present and always in period A. In seven different years (from 1992 to 1994 and from 1997 to 2000 in the time span comprised between August 29th and October 25th) pups were observed or localized by wolf-howling in a second larger area (HS2) within the presumed territory of the CF pack. Moreover, in that

Table 1
Estimates of different parameters for the Casentinesi Forests wolf population in 1993–2000

Area	Year	N packs	N wolves	Average pack size	Wolves/100 km^2	Packs/100 km^2	Average distance between adjacent packs (km)
A + B 407 km^2	1993	5	21	4.2	5.16	1.23	7.8
	1994	5	19	3.8	4.67	1.23	9.2
	1995	5	20	4.0	4.91	1.23	10.3
A 283 km^2	1996	3	13	4.3	4.59	1.06	14.1
	1997	3	13	4.3	4.59	1.06	11.9
	1998	3	12	4.0	4.24	1.06	10.7
	1999	3	14	4.7	4.95	1.06	14.1
	2000	3	11	3.7	3.89	1.06	–
Mean				4.2	4.73	1.12	11.1

portion of the territory several adults were detected without young throughout the year, often in a group. A similar situation was obtained for the FA pack, which in five years from July 22nd to October 26th was found with pups at the same site (HS3). On the contrary, the VS litters had different locations during the period of study; an area was used as homesite for a maximum of two years and was then changed.

Use by wolves and habitat characteristics of the three above-mentioned homesites are listed in Table 2. Use of the two areas by the CF pack differed over time: 4 locations out of 5, falling in HS1, referred to the period June–July, while all 20 records of the HS2 were dated August–October (Fisher exact test $p < 0.001$). The only time pups were localized in HS1 after the end of July (in summer 1999) was on August 18th, and ten days later the pack was with its litter in HS2, where it was heard howling twice in September. HS1 and HS2 lie in adjacent valleys, both densely forested and rich in streams. Altitude and slope differ between HS1 and HS2, the former being more elevated and steeper than the latter. Rendezvous sites were documented only for HS2; in 1992 a small bush area was used from September until March 1993, at first as a place for looking after the pups, then as the meeting place to which pack members periodically came back. Another similar site was discovered in 1999. Several late summer-early fall locations fell in a restricted area, where in November a rendezvous site was discovered. Both the sites had similar characteristics: they were stretches of bush surrounded by forest, with evident signs of prolonged wolf activities (resting places, tracks, scats and remains of eaten prey). HS3 lies within the presumed territory of the FA pack; in 6 cases out of 7 pups were detected there in late summer-fall (August–October). MPC with 95% of locations covered an area of about 70 ha. The main part of HS3 was dense forest, but large bush areas were also present.

4. Discussion

4.1. Pack and litter size

Pack size ranged between 2 and 7 individuals, as reported for several European wolf populations (Boitani, 1992; Ciucci and Boitani, 1999; Okarma et al., 1998; Poulle et al., 1999). It should be stressed that numbers reported in this work are minimum estimates, so actual

Table 2
Features of three homesites discovered within the Casentinesi Forests study area in 1992–2000

	HS1	HS2	HS3
No. locations	5	20	7
– June–July	4	0	1
– August–October	1	20	6
No. of years	3	7	5
Surface (ha)	21	194	70
Altitude range (m a.s.l.)	1120–1380	820–1250	780–1050
Mean slope (°)	46	46	35
Exposure	SO	SSE	SE
Vegetation			
– Dense hardwood	47%	67%	28%
– Dense pinewood or firwood	43%	17%	24%
– Bush	–	7%	28%

HS1 was frequented by the CF pack in 1993, 1994, and 1999. HS2 was frequented by the CF pack in 1992–1994 and in 1997–2000. HS3 was frequented by the FA pack in 1993 and in 1996–1999. Locations were obtained by acoustic stimulation (wolf-howling) and/or visual observation.

pack size may be underestimated. Nevertheless, the mean value obtained in the Casentinesi Forests between May and October (4.4) is comparable to other values reported in forested regions of central and southern Europe. For example in the Bialowieza Primeval Forest (BPF), wolf packs ranged in size on average between 4.0 and 5.3 (Jedrzejewska et al., 1996; Okarma et al., 1998; Jedrzejewski et al., 2000). In a different area of the Italian Apennines, approximately 100 km from our study area, average pack size calculated over nine years for a single group was 3.7 (Ciucci and Boitani, 1999). In a colonizing wolf population on the French Alps the mean value, calculated for the six years following the first settlement, amounted to 4.9 (Poulle et al., 1999). A higher variability is reported for North American populations: minimum values were estimated in Quebec (3.7 – low prey density area in Messier, 1985) and Minnesota (4.3 – Fritts and Mech, 1981) whereas the highest values are reported for Alaska (12.7 – Van Ballenberghe, 1983a; 15.3 – Peterson et al., 1984), where packs may reach 25 or more members (National Research Council, 1997).

More than a single litter per pack, although sometimes elsewhere reported (Van Ballenberghe, 1983b), was never observed in this study. The number of pups in a pack depends greetly on the period at which the count is made, as mortality within the first year of life may be as high as 85% (Jedrzejewska and Jedrzejewski, 1998), mostly concentrated between April and December (Harrington et al., 1983). For this reason the reported data on litter size are not easily compared. In our case, the estimate referred to summer-early fall, when on average 2.5 pups were present in a pack. Jedrzejewska et al. (1996) reported for BPF average litter sizes comprised between 2.2 (exploited areas) and 3.1 (protected areas), calculated three months after the births. Summer estimates were obtained also by Mech (1977) and amounted to 3.0–3.4 pups per pack. We were unable to count pups at birth, which in different studies averaged 5.3–6.5 (Rausch, 1967; Potvin, 1987; Bibikov, 1990; Jedrzejewska et al., 1996; Smietana and Wajda, 1997), but inferred their number just in one case from the five uterine scars of an adult female.

4.2. Wolf density

The estimated wolf density in the area averaged 4.7 wolves per 100 km^2, based on the number of pack members. This value is high, compared to estimates obtained for other North American and European areas. The lowest densities were found in the tundra and taiga habitats of Alaska, Canada, and Eurasia, where common prey are moose (*Alces alces*) and caribou (*Rangifer tarandus caribou*). In those areas, wolf density is usually comprised between 0.1 and 2.0 animals per 100 km^2 (Gasaway et al., 1983; Peterson et al., 1984; Messier, 1985; Bergerud and Elliot, 1986; Bibikov, 1990; Dale et al., 1994; Boertje et al., 1996; Ballard et al., 1997; Larivière et al., 2000; Wabakken et al., 2001). At lower latitude, in forested areas where wolves prey mostly upon deer, their density is much higher (Mech, 1977; Harrington et al., 1983; Potvin, 1987; Kunkel and Mech, 1994; Forbes and Theberge, 1995; Smietana and Wajda, 1997; Okarma et al., 1998). A single exception is represented by Isle Royale, where wolves reached in the past a density of up to 9.2 individuals/100 km^2 (Peterson and Page, 1988). Isle Royale is a quasi-closed ecosystem, in which wolf presence is strictly related to the abundance of moose, the only large prey inhabiting the island. Following an increase in moose availability, local wolf density may thus become unusually high.

There seems to exist a different relationship between pack size and density of wolves at different latitudes (Fig. 2). Considering values reported in other studies in which both parameters were determined, two tendencies are seen. In northern regions, where moose and caribou are major prey, wolves gather in large packs (on average 4–10 members), defend vast territories, their density is low (0.1–2.0 per 100 km^2) and they may become nomadic. On the contrary, at lower latitudes, where wolves prey mostly upon deer and wild pigs, they live in

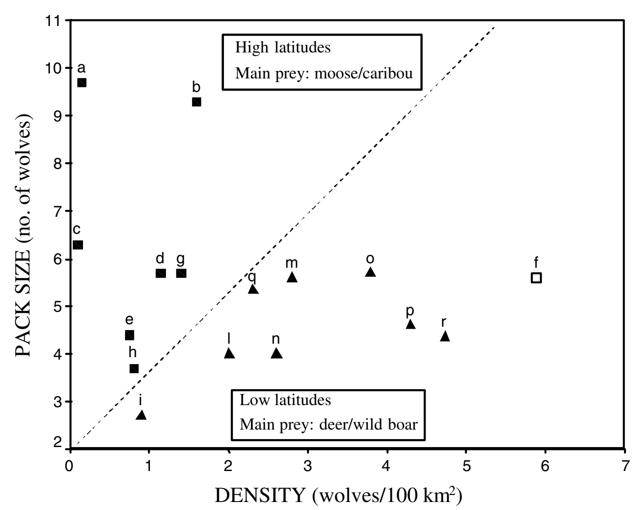

Fig. 2. Relationship between pack size and wolf density, referred to latitude and main prey species. Filled squares refer to northern regions, where moose and/or caribou are the main prey. Triangles refer to southern areas where wolves prey mostly upon deer and/or wild boar. The case of Isle Royale (empty square) is treated separately. The values used are minimal estimates reported in the following studies: (a) Ballard et al. (1997) – North-West Alaska, (b) Gasaway et al. (1983) – Interior Alaska, (c) Wabakken et al. (2001) – Scandinavia, (d) Peterson et al. (1984) – Kenai peninsula, Alaska, (e) Dale et al. (1994) – Northern Alaska, (f) Peterson and Page (1988) – Isle Royale, (g) and (h) Messier (1985) – Quebec, (i) and (l) Okarma et al. (1998) – BPF, Poland, (m) Potvin (1987) – Quebec, (n) Jedrzejewska et al. (1996) – BPF, Poland, (o) Mech (1977) – Minnesota, (p) Smietana and Wajda (1997) – Bieszczady Mountains, Poland, (q) Jedrzejewski et al. (2000) – BPF, Poland, (r) present study.

small packs (on average 3–6 members), occupy smaller territories and may reach high values of density (2.0–6.0 per 100 km^2), depending on prey availability and level of harvesting. Prey abundance is without doubt a crucial variable in this context. In moose–wolf systems, pack size is positively related to moose density (Messier, 1985) and territory size seems to be mostly influenced by pack size (Peterson et al., 1984; Messier, 1985). In fact, at high moose densities, pack recruitment and pup survival increase, whereas the dispersal rate decreases, thus favouring the enlargement of local packs (Messier, 1985). As a consequence, wolf density depends mostly on pack size rather than on the number of packs.

Alternatively, where the main wolf prey is caribou, its patchy distribution forces wolves to become nomadic and to move across vast territories (Mech, 1981; Bergerud and Elliot, 1986; Dale et al., 1994). In such circumstances, large packs temporarily concentrate their foraging in areas with abundant prey (Dale et al., 1994), and therefore, the effect on wolf density is expected to be the same as in moose–wolf systems.

On the other hand, where prey species are smaller in size and homogeneously distributed, their availability seems to have a different effect on pack size and distribution. In presence of vacant territories, as happens in newly protected and recovering populations, wolves may choose to disperse early in their life, to form new social units (Fritts and Mech, 1981; Gese and Mech, 1991). A self-enforcing mechanism may be established, in which a major dispersal increases the chance to find a partner for mating. Precocious abandonment of the family group by some pack members (mostly pups and yearlings) leads to the extreme situation in which the pack is represented only by the alpha pair and its last litter. Therefore, a reduction in pack size may negatively influence pup survival, due to the absence of non-parental care, again limiting the consistency of the social unit (Harrington et al., 1983; Jedrzejewska et al., 1996). Small packs are only able to defend small territories, but, in presence of trophic abundance, this may not represent a great handicap.

The combination of high dispersal rate, small territories, and large availability of medium-sized prey may promote the formation of new social units. All these considerations lead us to expect that local wolf density is mostly influenced by the number of wolf packs rather than by pack size.

In the investigated area of the Italian Apennines, a rich community of wild ungulates is present, with post-birth overall densities of up to 19.9 heads/km^2, corresponding to an average overall biomass of 860 kg/km^2. As shown in Table 3, these values are very high compared with other wolf areas. In particular, the Bialowieza Primeval Forest represents the closest situation: total biomass per square kilometer is similar but with half the cumulative density of prey (Jedrzejewski et al., 2000). In this part of Poland, red deer is the main prey, whereas roe deer and wild boar are the main prey in our study area. The mean prey size killed by wolves reported for the former region was 55 kg, in comparison with the 20.5 kg obtained in this study for the Casentinesi Forests. In short, the wolf population we studied has at its disposal the same biomass of ungulates present in a rich temperate lowland forest like Bialowieza, but subdivided into a higher number of potential prey of smaller size. As mentioned above, average pack size was similar in both areas (4.2 CF vs. 4.0–5.3 BPF), whereas wolf density in BPF was about half that estimated for the

Table 3
Comparison of pack size and wolf density among different areas in relation to prey abundance and biomass availability

	Area size (km^2)	Main prey	Pack size	Wolves/100 km^2	Cumulative density of wild ungulates	Ungulate biomass (kg/km^2)
Italy (Casentinesi Forests)[a]	130	Wild boar	4.2	4.7	19.9	860
Poland (Bialowieza P.F.)[b]	520	Red deer	5.3	2.3	11.6	809
Ontario – Algonquin P.P. (region C)[c]	2869	Moose	–	5.2	0.37–0.42	125–139
Quebec – La Verendrye Reserve[d]	3000	Moose	5.7	1.4	0.37	130
Quebec – Papineau-Labelle Reserve[e]	1667	w-t deer	5.6	2.8	3.6	450
Michigan – Isle Royale[f]	544	Moose	8.8	5.9	1–2.5	350–875
Alaska[g]	17060	Moose	9.3	1.6	0.61	90

Cumulative density of wild ungulates (number of head/km^2) was obtained by adding census values reported for each species. Biomass density was calculated using average body mass reported by Authors, or, in case weight data were not mentioned throughout the paper, the following average values were assumed: white-tailed deer (*Odocoileus virginianus*) 80 kg and adult moose 350 kg.

[a] Present study.
[b] Jedrzejewski et al. (2000).
[c] Forbes and Theberge (1995).
[d] Messier (1985).
[e] Potvin (1987).
[f] Peterson and Page (1988).
[g] Gasaway et al. (1983).

Casentinesi Forests (2.3–2.7 vs. 4.7). Due to local abundance of prey, wolf packs in CF need to occupy smaller territories than in BPF, thus reducing the distances between each other (on average 11.1 km between adjacent core areas). This local concentration of medium-sized prey, typical of some regions of Western Europe, may be the key to explain the high wolf density discovered here.

4.3. Mortality

Mortality seems to be high considering also that what we collected was just a subsample of the actual figure. Human-caused mortality was markedly prevalent in the sample, and this was consistent with previous studies in Italy (Francisci and Guberti, 1992) and can represent a major threat to population viability. However, we must take into account the high productivity of the studied packs, 78% of which had a litter per year consisting on average of 2.5 pups that apparently was able to dump the negative effect of human-induced deaths.

4.4. Territory and use of homesites

Considering three of the monitored packs, we observed a high constancy of summer – early fall locations throughout the whole period of study. Some packs appeared to have stable territories, and this may be related to protection level and presence of prey. The location of two packs (CF and FA) was especially predictable in period A, as a consequence of their fidelity to specific areas. From spring to early fall, wolves concentrate their activities in core areas, where the pack homesites lie (Joslin, 1967; Harrington and Mech, 1982b,c). Harrington and Mech exhaustively described the pattern of homesite use by two wolf packs in northern Minnesota (Harrington and Mech, 1982b,c). During period A, wolves of those packs frequented one or more homesites, which were progressively abandoned within the first week of October. Then they revisited those sites intermittently during fall and winter, often after temporary pack separation (Harrington and Mech, 1982b). A study carried out in Poland–Belarus reported that pups were taken away from the den from late April to early July (Jedrzejewska et al., 1996). In our study, the summer-early fall location of pup-containing packs covered three areas frequented by wolves in several years. Two of them fell within the territory of the CF pack, while the third was used by the FA pack. Temporal patterns of use and physical features of the two sites located within the CF territory led us to believe that HS1 might contain the den, while HS2 had one or more rendezvous sites (two of them were discovered in different years). Similarly, the FA pack was detected several times in a small valley, which we identified as a homesite (HS3). The fidelity of the two packs to the same areas over the years may be explained considering the particularly favourable features of these sites: they lie inside the National Park, are mostly covered by dense forest and are relatively undisturbed. In particular, the HS1 was in a strictly preserved area, where also human access was limited. Further, the high availability of prey (ungulate hunting was not permitted there) may be a key factor, as it has been observed to influence stability of den use (Ciucci and Mech, 1992).

A third pack VS, continuously monitored from 1993 to 2000, appeared not to be associated with a particular site, but was found during the research in different areas within a range of 8 km in a peripheral zone of the National Park. A possible explanation was that the territory of this pack fell in a more exploited area, where human impact was stronger. The mean size of the VS pack over the years was the lowest detected in our study, as was its reproductive success. On the basis of our results, both pack fidelity to specific core areas and pack size seem to be correlated to the level of protection/exploitation. A similar result was obvious in the newly established Alps population where the same pack moved its home site up to 17 km each year in two consecutive years in an unprotected area (Marucco, 2001). An alternative explanation could be that the pack was replaced by a new one in one or more years after total destruction, even if the total eradication of a pack is quite on improbable event because it would imply the killing of at least four wolves in a small area.

4.5. Guidelines for conservation and conclusions

In the last three decades, the conservation issue for the wolf in Italy has drastically changed. At the beginning of the eighties, Boitani (1982) stressed several critical points for the viability of the species. The most important were the need of a network of protected areas with a sufficient forest cover, the recovery or reintroduction of wild ungulate populations, and the limitation of some human activities (i.e., animal husbandry). In fact, at that time wolves inhabiting the Apennines were present at low density (1 wolf per 85 km^2) and reportedly fed on garbage and livestock (Boitani, 1982; Patalano and Lovari, 1993). Since then, the effects of gradual changes, occurring since the end of World War II, have led to a very different scenario (Apollonio, 1992). Forest cover has increased as consequence of countryside abandonment; the traditional livestock farming has progressively been reduced; wild ungulate populations have been restored in several areas, by reintroduction or restocking. Moreover, a number of protected areas has been created since 1990. All these changes in local ecological conditions had a big impact on wolf consistency and food habits (Mattioli et al., 1995; Meriggi et al., 1996; Poulle et al., 1997; Genovesi, 2002). On a long-term time scale, the maintenance of a viable wolf population is mostly influenced by social structure and prey dynamics, and the number of breeding pairs is what mostly contributes to its viability, rather than wolf density (Vucetich et al., 1997). In our study area a high density of small wolf packs was detected. As reported by two model-based habitat suitability analyses (Massolo and Meriggi, 1998; Corsi et al., 1999), this area is one of the most suitable in the Italian peninsula for wolf presence. In particular, Massolo and Meriggi (1998) found that wild ungulate abundance and diversity were the main factors determining the stable presence of wolves. They even highlighted the avoidance by wolves of areas with high human impact. In these terms, the Casentinesi Forest ecosystem offers important elements, for the calibration of future conservation goals.

The packs we monitored were part of a recovering population occupying the Italian mountain regions, which harbour a rich and abundant community of wild ungulates. Methodological constraints inevitably limited the full understanding of the processes regulating population dynamics; for instance, we had no individual data because we were not in any position to trap and mark wolves. However, evidence from other studies on Italian populations suggests that the pack structure we found, based on an adult pair and their pups, is characterized by the persistence of at least one of the adults and a significant turnover of the younger members of the group (Lucchini et al., 2002; Scandura et al., 2003), and that the high pack site fidelity, shown in most of the cases we analysed, suggests that this can be the case also for the Casentinesi Forests. Nevertheless, the comparison of our data with those published in literature enables us to point out some aspects which wolves seem to share in similar conditions: (1) availability and size of the main prey size ultimately determine the structure of a wolf population (i.e., pack size and density); (2) in densely forested areas with abundant medium-sized prey, wolves may reach high densities even though in presence of significant seasonal human disturbance; (3) in these conditions, pack size is usually maintained smaller than in northern populations and density is mostly influenced by the number of packs and territory size rather than by pack size.

In terms of conservation, the presence of areas with high ungulate density and diversity leads to the persistence of dense, productive wolf populations that guarantee the survival of the species on a medium-size scale, providing a number of young dispersers are able to colonize new favourable areas. The present evolution of the Italian mountains and hills speaks in favour of full of the recovery wolf throughout its historical range, provided that the protected area network continues to act efficiently in providing safe breeding areas. This network should be legally enforced throughout the Italian peninsula, the size and location being established on a local basis. The effectiveness of protection would thus be maximal even in small areas, including possible reproductive sites, which represent a refuge for breeding pairs.

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