

## Density and demography of wolf, *Canis lupus* population in the western-most part of the Polish Carpathian Mountains, 1996–2003

Sabina NOWAK<sup>1</sup>\*, Robert W. MYŚLAJEK<sup>1</sup> and Bogumiła JĘDRZEJEWSKA<sup>2</sup>

<sup>1</sup> Association for Nature “Wolf”, Twardorzeczka 229, 34-324 Lipowa, Poland; e-mail: sdnwilk@vp.pl

<sup>2</sup> Mammal Research Institute, Polish Academy of Sciences, ul. Waszkiewicza 1c, 17-230 Białowieża, Poland; e-mail: bjedrzej@zbs.bialowieza.pl

Received 20 October 2007, Accepted 15 September 2008

**A b s t r a c t.** In Central Europe, where most wolf populations persist in habitats altered by humans, the dynamics of these populations are significantly influenced by human activities. Our studies in the western-most part of the Polish Carpathian Mts, 1996–2003, revealed that the winter density of wolves varied in the region from 1.3–1.9 wolves/100 km<sup>2</sup> (on average 1.6, SE=0.13). In late summer, the average number of wolves in a pack was 4.7 wolves (n=21, range 2–9, SE=0.4), while an average pack in winter consisted of 4.0 wolves (n=25, range 2–7, SE=0.3). The mean wolf territory covered an area of 158 km<sup>2</sup> (SE=26.7, range 98–227 km<sup>2</sup>). In the Silesian Beskid Mountains, where no human hunting pressure occurred, the wolf population increased during the study period at a mean rate of 28% per year. However, in the Żywiecki Beskid Mountains, where wolves were subject to hunting management in the Slovakian parts of their territories, the population did not increase. The mean rate of increase of the wolf population in the entire study area was 8% per year. Wolf mating seasons began on February 13<sup>th</sup> and lasted until March 7<sup>th</sup>, with pups being born during the first ten days of May. Pup rearing places were located between 880 and 1290 m a.s.l. (average = 1009 m a.s.l., SE=34.5, n=11), in dense thickets or under roots of fallen trees and stumps. We did not find excavated dens. In late summer, we recorded an average of 1.9 pups per pack, but counted only 1.3 pups per pack the following winter. Reasons for death (n=18) included culls (83%), collisions with motor vehicles (11%), and sarcoptic mange (6%). In the Żywiecki Beskid Mountains we estimated the minimum mortality rate of 1.5 individuals/pack/year.

**Key words:** reproduction, mortality, territory size, pack size, denning sites

### Introduction

In Europe, wolves *Canis lupus* have begun to recover in areas where they had been persecuted years ago. However, many of these areas have already been significantly altered by humans (Wabakken et al. 2001, Boitani 2003, Valiére et al. 2003, Ansorge et al. 2006). Thus, local wolf populations are likely to be influenced by different kinds of human activities, such as intensive logging, hunting, tourism, recreation, motor traffic, and development of transportation networks.

This study was conducted in the western-most range of the Polish Carpathian Mountains (Southern Poland), situated near the Polish-Slovakian and the Polish-Czech borders (49°23'–49°53'N, 18°45'–19°48'E). The area is densely populated by people (Nowak & Myśłajek 2002). Part of the region was spontaneously re-colonized by wolves (in 1996), while wolves were never fully eradicated from another area (Wolsan et al. 1992, Nowak & Myśłajek 2003). Within the study area, wolves have been protected since 1994, one year earlier than in adjacent provinces in Poland. Wolves are also protected in the Czech Republic, while in Slovakia, after several years of protection, the wolf has been

---

\* Corresponding author

classified as a game species since 1999 and hunted for 2.5 months each year. Hunting influences all wolf packs that occupy transborder territories in the Polish Carpathian Mts. The goal of our study was to find out the dynamics, demography, density and territory sizes of wolves living on the edge of their continuous range, in an environment heavily altered by humans and being subjected to different management practices.

## Study Area

We conducted our study in the Silesian Beskid Mountains and the Żywiecki Beskid Mountains, within two landscape parks separated by the Soła River valley: the Landscape Park of the Silesian Beskid Mountains (SBM) and the Żywiecki Landscape Park (ZLP). Their total area is 745 km<sup>2</sup>. Altitude ranges from 300 to 1557 m a.s.l. The majority of the area is covered by forest dominated with Norway spruce *Picea abies* with admixtures of beech *Fagus sylvatica* and fir *Abies alba*. Woodlands occur also on the Slovakian and Czech sides of the border, creating a contiguous forest complex. The average July temperature varies from 12°C (mountains) to 16°C (basins). The respective mean temperatures of January are –6°C and –3°C. Snow cover persists from 80 days per year in basins to 160 days on northern slopes and tops (H e s s 1965).

The region is densely but irregularly inhabited by humans (on average, 150 person/km<sup>2</sup>). Numerous towns and villages are located mostly in river valleys and on lower, deforested slopes (up to 600 m a.s.l.). Agriculture and livestock farming occur in the area, with small flocks of sheep and goats being the most common. The majority of forests are exploited, with only 1% of the forest area protected in nature reserves. Large meadows are located within the forests and some of them are still used as pastures. The remaining meadows have been overgrown with young spruce, beech, and birch trees. There is a large number of weekend cabins and recreation centers along forest peripheries, and many ski lifts, ski routes, and tourist paths located in the forest. Human penetration of the forest is intense during weekends and holidays (N o w a k & M y s ł a j e k 2002). The mean density of public roads within the study area is 1.3 km/km<sup>2</sup>.

The ungulate community is dominated by roe deer *Capreolus capreolus* (74% of all wild ungulate numbers), followed by red deer *Cervus elaphus* (21%), and wild boar *Sus scrofa* (5%) (N o w a k et al. 2005). The guild of large predators includes the wolf, the lynx *Lynx lynx* (J ę d r z e j e w s k i et al. 2002a), and the brown bear *Ursus arctos* (J a k u b i e c 2001). In the Silesian Beskid Mountains, wolves were eradicated in the mid-1970s (W o l s a n et al. 1992). During the 1980s, there were sporadic records of a few immigrant wolves in the area, but these individuals were immediately shot by hunters. Finally, SBM was repopulated by a pair of wolves in 1996. In the Żywiecki Beskid Mountains, prior to the introduction of protection, wolves occurred in small numbers, mostly in refuges along the Polish-Slovakian border. From 1987–1994, only 1–2 wolves were killed by hunters annually (N o w a k & M y s ł a j e k 2002, 2003).

## Materials and Methods

Data on wolf occurrence and numbers were collected from 1996–2003 in SBM, and from 1998–2003 in ŻLP. We conducted regular snow tracking surveys in winter (in total approximately 2 250 km) in order to locate wolf tracks and scats. During these efforts, we

attempted to distinguish between packs, estimate the number of wolves, and search for resting places in order to count their lairs. At the beginning of winter we estimated the number of pups which had survived until winter in each group. The pups were recognised based on the difference in track size compared to adults, and on “playful” behaviour which is frequent in 7–8 months old pups. During the mating season (February–March), we recorded evidence of oestrus in dominant females and the typical mating behaviour of pairs, in order to estimate the minimum number of reproductive pairs within the study area.

During other (snow free) seasons of the year we walked established transects along forest roads and tourist paths to detect wolf tracks and scats (in total about 3 600 km of transects, 560 scats). Tracks were measured to distinguish between adults and pups in summer and autumn. According to results of studies conducted by Zub et al. (2002), wolves mark with scats most intensively within core areas of their territories. Thus, we regularly checked different parts of every wolf pack territory and recorded locations of wolf scats with GPS units (Garmin eTrex), then we computed scats coordinates using MapInfo software (MapInfo Professional 6.0, MapInfo Corporation, USA). Since scats were collected for diet analyses (Nowak et al. 2005), only new scats were recorded during consecutive visits. We then checked the areas of the highest accumulation of scats using howling stimulation (Harrington & Mech 1982, Gazzola et al. 2002, Nowak et al. 2007). We also howled in other parts of territories to discover every possible location of wolves.

When the weather allowed (calm nights without rain), we howled from higher parts of forest roads, clearcuts, and mountain summits using human-emitted howl imitation, primarily with a single stimulus. For all replies ( $n=68$ ), we estimated the number of replying adult wolves and the presence and number of pups (in June–September), based on live aural analysis of the replies as the wolves howled, or subsequent analysis of recordings of the replies (Harrington 1986, Nowak et al. 2007). We measured the directions of replies containing pup voices to find places of pup rearing, which enabled us to estimate the number of packs in the study area. We then checked the adjacent area for fresh scats and tracks again, to finally assess the number of pups. After the abandonment of the area by wolves, we attempted to confirm their presence in these sites based on lairs, scats, hair and prey remains ( $n=11$ ).

Furthermore, we gathered reports on wolf tracks ( $n=140$ ), howling ( $n=4$ ), prey remains ( $n=90$ ), wolf sightings ( $n=40$ ), dead wolves (1), wolves hit by vehicles (2), and wolf-derived damage to livestock (45 cases). These reports were compiled from local foresters, border guards, hunters, and livestock owners, and were verified in the field. After wolf attacks on domestic animals, we searched wolf core areas for wolf scats containing sheep wool or cattle hair. As those cases were relatively rare and most of borders of the wolf territories lie along villages and busy roads preventing wolf movement, we could assume with a high probability which pack was responsible for the damage. This aided us in mapping the most distant points in pack territories. We also collected information on wolves shot in the Slovakian part of the Żywiecki Beskid Mountains (the Horna Orava Landscape Park and the Kysuce Landscape Park) from Slovakian hunters and staff of landscape parks ( $n=15$  records).

We computed coordinates of all findings, using GIS techniques with MapInfo software. Based on the largest accumulation of tracks, fresh scats, elicited howls, places of rearing pups, and wolf resting places in consecutive years, we attempted to determine the locations of core areas of each pack. The territory of each pack was estimated as Minimum Convex Polygons with 100% of all information which we could attribute to separate packs, during the whole study period.

Tracking, recording of other wolf signs and sightings, as well as howling stimulation were earlier used for wolf pack censusing, estimation of the wolf territory sizes, finding core areas and distinguishing between adults and pups (e.g. Joslin 1967, Harrington & Mech 1982, Harrington 1986, Šmietana & Wajda 1997, Jędrzejewski et al. 2002a, Gazzola et al. 2002). However, all those methods have some limitations, which allow to assess only the approximate size of packs' territories and make it difficult to determine their possible overlaps. Furthermore, they mostly let to record only the minimum number of wolves in packs, so the wolf densities could be underestimated to some degree.

Due to substantial differences in altitudes, which reach 1200 m in the study area, the area values of wolf territories estimated from a topographic map differ from their true surface area. Thus we attempted to estimate the actual surface area of wolf territories. Using MapInfo software, we randomly chose 36 circular sampling plots, each measuring 0.9852 km<sup>2</sup> within territories of wolf packs, on a digital map with a scale of 1: 50,000. For each plot, we counted the total length of contour lines  $L$ , for which a drop ( $d_s$ ) is 10 m. We then calculated the true area of each sampling plot using Pythagoras' formula:  $a^2 + b^2 = c^2$ , where  $c^2$  is the plot area that we searched,  $a^2 = L \times d_s$ , and  $b^2 = 0.9852 \text{ km}^2$  – the area of a sampling plot. We then calculated a ratio of the actual surface area of a plot to its area on the map. The mean from 36 values, counted using this method, was 1.32 (SE = 0.01). We used this value as a ratio to calculate the true sizes of wolf territories in the study area. The wolf density was referred both to the forested area of SBM and ŽLP and adjacent forests on the Slovakian side of the border (817 km<sup>2</sup>), and to the true surface of the study area calculated with the ratio 1.32 (1078 km<sup>2</sup>).

We estimated the trends in wolf numbers using linear regression analyses, with the explanatory variable being years and the dependent variable being number of wolves (Sokal & Rohlf 1994).

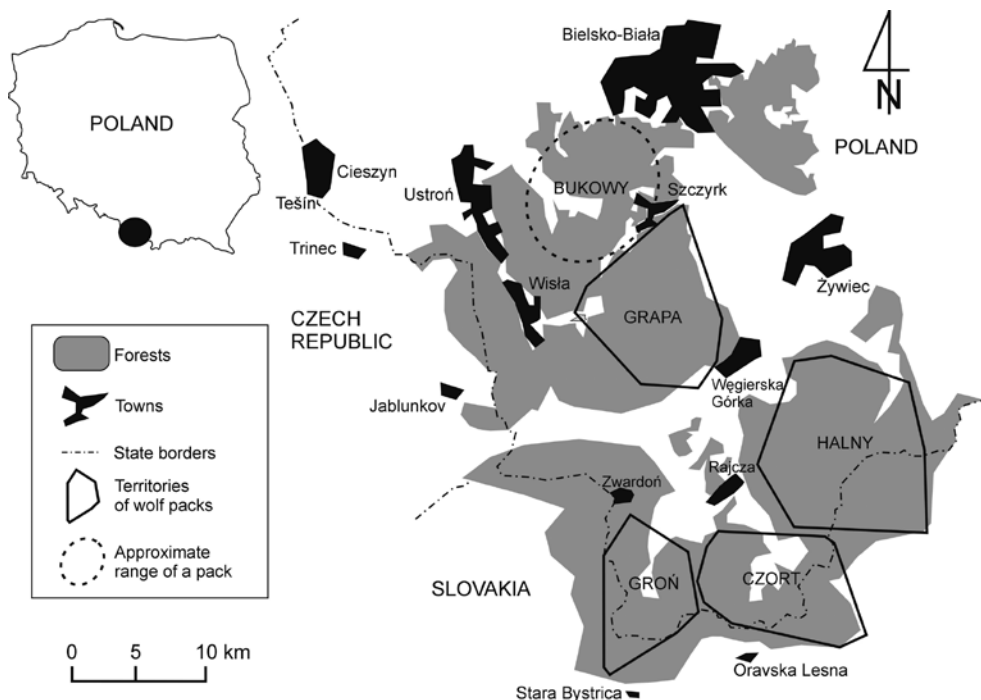
## Results

### Development of the population

From 1998–2001, we recorded 4 resident wolf packs within the study area: 3 packs in the ŽLP and one pack in the SBM. Since 2002, we have also recorded a fifth resident pack in SBM (Fig. 1).

In ŽLP, the number of wolves varied between years, but with no significant temporal trend in the population size (Table 1). From 1998–2003, there was an average of 11.2 wolves (range 9–13, SE=0.7) during winter and 13 wolves (11–14, SE=0.7) during summer. Pack size ranged from 2–6 wolves (mean 3.9, SE=0.3) during winter and 3–7 wolves (mean 4.4, SE=0.3) in summer.

In SBM wolf number significantly increased during the study period ( $N \text{ wolves} = -2208.46 + 1.11 \text{ Year}$ ,  $R^2 = 0.9625$ ,  $p=0.00006$ , Table 1). The region was repopulated by a pair of wolves in 1996 (Grapa pack). The first successful reproduction was recorded in 1998, when one pup survived until the winter season. Over the following summer seasons we observed regular reproduction and a steady increase in the pack size until it reached 9 individuals in summer 2001. From 1996 to the winter of 2001/2002, the average size of the Grapa pack was 4.3 wolves in winter, and 5.5 wolves in summer (Table 1). In early spring 2002, the Grapa pack split into two groups. The parental group stayed within its old



**Fig. 1.** Distribution of wolf packs within the study area, 1996–2003. Names of wolf packs: Groń, Halny and Czort (Żywiecki Landscape Park); Grapa and Bukowy (Landscape Park of the Silesian Beskid Mts.).

territory. The second smaller pack (Bukowy), which included 3 individuals, occupied a part of SBM adjacent to a main town in the region – Bielsko-Biała. From 1996 to the winter of 2002/2003, the number of wolves in SBM increased at a mean rate of 28% per year (annual finite rate of increase of the wolf population in SBM was 1.28).

In 1998–2003, the wolf population as a whole in the study area increased from 14–18 individuals in 1999–2000 to 20–23 wolves in 2002–2003 ( $N \text{ wolves} = -3183.00 + 1.60 \text{ year}$ ,  $R^2 = 0.7333$ ,  $p=0.04$ , Table 1). The mean rate of increase of the wolf population in the entire study area was 8% per year (annual finite rate of increase of the wolf population = 1.08). In late summer, the average number of wolves in a pack was 4.8 wolves (range 3–9), while in winter, there was an average of 4.1 wolves per pack (range 2–8) (Table 1).

### Population density and territory size

In ŻLP, we recorded a regular bi-directional crossing of the Polish-Slovakian border by wolves. Snow tracking showed that home ranges of packs were established along both sides of the border, as only a narrow belt of continuous forest, 1–6 km in width, was available for wolves (on average 3 km), both in Poland and Slovakia. Thus, population density was calculated in the forested area of SBM and ŻLP, and also adjacent forests on the Slovakian side of the border (817 km<sup>2</sup>). It varied from 1.7 to 2.5 wolves/100 km<sup>2</sup>, on average 2.1, with reference to the map area. When the mountainous character of the study area was taken into consideration (see Methods) to determine the true surface of the forested area (1078 km<sup>2</sup>, Table 2), the population density varied from 1.3–1.9 wolves/100 km<sup>2</sup>, with an average of 1.6.

**Table 1.** Wolf pack size and number of wolves in the western-most part of the Polish Carpathian Mountains in 1996-2003. Packs from the Żywiecki Landscape Park: Groń, Halny and Czort; packs from the Landscape Park of the Silesian Beskid Mts: Grapa and Bukowy. See Fig. 1 for the pack distribution.

Season	Packs					Average size of pack (SE)	Number of wolves		
	Groń	Halny	Czort	Grapa	Bukowy		Silesian Beskid Mts	Żywiecki Landscape Park	Whole study area
1996/97	?	?	?	2	-	-	?	2	?
1997	?	7	?	2	-	4.5 (2.5)	?	2	?
1997/98	6	5	?	2	-	4.3 (1.2)	?	2	?
1998	?	3	?	3	-	3.0 (0.0)	?	3	?
1998/99	6	3	3	3	-	3.8 (0.8)	12	3	15
1999	5	3	5	5	-	4.5 (0.5)	13	5	18
1999/2000	3	4	2	5	-	3.5 (0.6)	9	5	14
2000	4	4	3	8	-	4.8 (1.1)	11	8	19
2000/01	4	4	2	6	-	4.0 (0.8)	10	6	16
2001	5	5	4	9	-	5.8 (1.1)	14	9	23
2001/02	4	5	4	7	-	5.0 (0.7)	13	7	20
2002	5	5	4	6	3	4.6 (0.5)	14	9	23
2002/2003	4	5	3	5	3	4.0 (0.4)	12	8	20
Winter seasons									
Mean	4.5	4.3	2.8	4.3	3	4.0	11.2	4.7	17.0
(SE)	(0.5)	(0.3)	(0.4)	(0.7)	-	(0.3)	(0.7)	(0.9)	(1.3)
<i>N</i> seasons	6	6	5	7	1	25	5	7	5
Summer seasons									
Mean	4.8	4.5	4.0	5.5	3	4.7	13.0	6.0	20.8
(SE)	(0.3)	(0.6)	(0.4)	(1.1)	-	(0.4)	(0.7)	(1.3)	(1.3)
<i>N</i> seasons	4	6	4	6	1	21	4	6	4

Using Minimum Convex Polygons (MCP) with 100% of all observations prescribed to each group, we estimated that wolf territory size averaged 120 km<sup>2</sup> (SE 20.3), when calculated as the vertical projection on a map. The true surface area of wolf territory averaged 158 km<sup>2</sup> (SE 26.7) (Table 2).

## Reproduction and mortality

Snow tracks of copulating pairs were recorded from February 13 to March 7, and pups were born in the first 10 days of May. Pup rearing places (*n*=11) were located between 880 and 1290 m a.s.l. (on average 1009 m a.s.l., SE 34.5). No excavated dens were recorded. Females gave birth and reared their young under tree stumps and roots or in lairs located in dense spruce thickets. We never found wolf litters in caves, which are numerous within the study area. Based on the howling stimulation and observations, we estimated number of pups in 12 pack-seasons (end of July – end of September) from 1997–2002 (Table 3). On average, we recorded 1.9 pups per pack in late summer, and 1.3 pups in early winter (Table 3). This indicated 32% mortality of pups from late summer until early winter.

From 1999–2003, we collected data on 18 cases of wolf mortality in the study area. Reasons for death included: culls in the Slovakian parts of territories – 15 wolves (83%), collisions with motor vehicles – 2 wolves (11%), and parasites (sarcoptic mange) – 1 wolf

**Table 2.** Territory size and population density of wolves (individuals/100 km<sup>2</sup>) in the study area, 1998–2003. Territory size calculated for the following packs: Groń, Halny, Czort, Grapa. See Fig. 1 for the pack distribution. Map area (817 km<sup>2</sup>) – the forested area of the Landscape Park of the Silesian Beskid Mts and the Żywiecki Landscape Park and adjacent forests on the Slovakian side of the border. The true surface area (1078 km<sup>2</sup>) – the map area recalculated with the ratio 1.32, for details see Materials and Methods.

Territory size or density	Map area (817 km <sup>2</sup> )		True surface area (1078 km <sup>2</sup> )	
	Mean (SE)	Min-Max	Mean (SE)	Min-Max
Territory size (km <sup>2</sup> )	120 (20.3)	74–172	158 (26.7)	98–227
Population density in summer (n=4 seasons)	2.5 (0.2)	2.2–2.8	1.9 (0.1)	1.7–2.1
Population density in winter (n=5 seasons)	2.1 (0.2)	1.7–2.5	1.6 (0.1)	1.3–1.9

(6%). All deaths occurred in ŻLP. No dead wolves have been found in SBM. Based on the recorded cases of deaths, we estimated the minimum mortality rate as 1.5 individuals per pack per year in ŻLP. Thus, the average reproduction rate (1.3 pups per pack per year) and the mortality rate were well balanced.

**Table 3.** Number of pups recorded in late summer and early winters in the western-most part of Polish Carpathians, 1997–2003.

Number of pups in a packs	Number of seasons	
	Late summer	Early winter
0	0	1
1	5	6
2	3	4
3	4	0
Mean (SE)	1.9 (0.3)	1.3 (0.2)

**Discussion**

The wolf population in the ŻLP and SBM, showed different dynamics, despite sufficient food sources in both areas (Nowak et al. 2005). The area of ŻLP was saturated with wolf pack territories, and the number of packs did not increase. Contrarily, SBM region was recently recolonised by wolves and the development of that population was significant.

The entire study area, with an average density of 150 people/km<sup>2</sup> and a mean public road density of 1.3 km/km<sup>2</sup>, is the most densely inhabited area of the Polish Carpathian Mountains. Due to expansion of recreation and tourism infrastructure, built-up areas, increasing motor traffic, and the construction of new roads, the local wolf population is forced to cope with a number of factors affecting their number, distribution, and territory use. Also, the region is becoming more and more ecologically isolated from the rest of the Carpathians. As surveys in other parts of Poland and other European countries show, road traffic poses an increasing threat to small populations of wolves by hampering dispersal and migration (Blanco et al. 1992, Huber et al. 1993, Jędrzejewski et al. 2004a, 2005).

In ŻLP, core areas of wolf territories were mostly located near the border, similar to the situation in Tatra Mountains National Park (Slovakia), where a radiotracked resident wolf pack had part of its home range on the Polish side of the border (Fiňo & Chovancová 2004). Transborder wolf territories have been reported from many other montane areas (Genov 1992, Huber et al. 1993, Voskár 1994, Fiňo 1995, Adamič et al. 1998), as well as lowland borderlands (Pulliainen 1980, Okarma



et al. 1998, Wabakken et al. 2001, Jędrzejewski et al. 2007). Thus border areas, as less urbanized and less accessible for humans, serve as good refuges for wolves. However, conservation and management of such populations is often difficult due to different levels of protection afforded to them by neighbouring countries (Jędrzejewska et al. 1996, Wabakken et al. 2001). This is also true for the transborder wolf populations recorded in our study area.

Sizes of mapped territories of wolf packs in our study area were similar to those reported from other parts of the Carpathian Mountains (Voskár 1994, Śmietana & Wajda 1997, Promberger et al. 1998, Findo & Chovancová 2004), as well as from other European mountain ranges (Boitani 1982, Vyrpaeu & Vorobev 1983, Ciucci et al. 1997, Kusak et al. 2005). Bibikov (1985) claimed that territories of wolf packs inhabiting well-forested mountains were significantly smaller than territories in lowlands. However, none of the above cited studies calculated the true surface area of wolf territories, taking into account differences in altitudes and inclination of slopes within study areas. Our accurate sizes of territories calculated using the ratio 1.32 appeared comparable to territories of wolves in Central Europe, where the main prey of wolves is red deer (Okarma 1995, Okarma et al. 1998).

Densities of wolves in our study area were similar to those reported from the Białowieża Primeval Forest (NE Poland, Okarma et al. 1998), but lower than in Tatra Mountains National Park (central part of Polish Carpathian Mountains, Zięba et al. 1996) and in the Bieszczady Mountains (Eastern part of Polish Carpathians, Śmietana & Wajda 1997). The population density of wolves in the study area did not differ substantially from wolf densities reported from other European mountain regions (Ionescu 1992, Genov 1992, Genov & Kostava 1993), but were higher than those reported in heavily exploited wolf populations in Belarus and Ukraine (Jakiwczuk 1996, Okarma et al. 1998).

The average pack size (4.1 individuals) in the western-most part of the Polish Carpathian Mountains was similar to pack sizes in other parts of Poland (Śmietana & Wajda 1997, Jędrzejewski et al. 2002a) and central Europe (Genov & Kostava 1993, Huber et al. 1993, Voskár 1994, Adamič et al. 1998, Findo & Chovancová 2004). Jędrzejewski et al. (2002b) suggested that pack size was determined by the size of the main wolf prey and for red deer, the optimal pack size would be 4–5 individuals. In our study area, the main wolf prey was also red deer, mainly calves and females, followed by roe deer (Nowak et al. 2005), which confirms that hypothesis. After reaching the maximal recorded pack size (9 individuals), the Grapa pack split into two packs. A similar phenomenon occurred in the Białowieża Forest in eastern Poland (Jędrzejewski et al. 2004b), where a large pack of 7 wolves split in two.

Data on pup survival in European wolf populations is very scarce. Numbers of pups recorded in our study area in late summers and early winters were slightly smaller than in the Białowieża Primeval Forest, where on average 1.8 pups per pack survived until winter (Jędrzejewska et al. 1996). In the whole Polish population of wolves, the average number of pups per pack was 2.6 in May–August (Jędrzejewski et al. 2002a). The low number and survival of pups within the study area might be a result of severe mountain conditions and human-caused mortality. As we found, pup-rearing places were located, on average, at 1009 m a.s.l. Due to thin soil (about 30 cm) on sandstone, wolves could not excavate regular dens. Thus, newborn pups were exposed to frost, rain, and snowfall, all of which are common at that elevation in the beginning of May (Hess 1965).



Compared to other newly protected or recovering wolf populations (Fuller et al. 2003), the mean rate of population growth in our study area was quite low (8%), despite sufficient food resources (Nowak et al. 2005). However, the population growth rate in the SBM was significantly higher (28%), comparable to wolf populations in North America which inhabited areas of high prey density and had good possibilities for dispersal of young (Fuller & Keith 1980, Fritts & Mech 1981, Wydeven et al. 1995, Hayes & Harestad 2000). A population growth rate of 28% was also reported for a recovering population of Swedish wolves from 1990–1997 (Boman et al. 2000)

The observed lack of population growth in ŽLP was caused by much higher human-related mortality, such as culls in Slovakia and vehicle collisions, which could not be compensated by low pup survival (1.3 pups per pack per year). Moreover, wolf packs in ZLP might have served as a source of dispersing individuals to adjacent and more distant parts of the Slovakian Carpathians, where wolves were also hunted (Voskár 1994, Findo 1995).

In conclusion, our study has provided evidence that, when legally protected, wolves can survive and even increase in numbers in areas both densely inhabited by humans and characterized by high road densities, as long as sufficient food resources exist. However, if the wolves are subject to intense hunting management, the combined effect of human-related and natural mortality factors can significantly lower wolf numbers and hamper their population growth.

#### Acknowledgements

This study was financed by the budget of the Association for Nature ‘Wolf’, the Polish State Committee for Scientific Research (grant 6 PO4F 01420), European Natural Heritage Fund EURONATUR (Germany), International Fund for Animal Welfare (USA) and the Wolves and Humans Foundation (UK). We thank Mr L. Wiśniewski, and the personnel of Forest Districts of Bielsko, Jeleśnia, Ujsoty, Ustroń, Węgierska Górká, and Wisła, as well as CHKO Beskydy and CHKO Horná Orava, who provided information on wolves. We are also grateful to Dr Matthew W. Hayward and Nathan Owens for the English correction.

#### LITERATURE

- Adamič M., Kobler A. & Berce M. 1998: The return of the wolf (*Canis lupus*) into its historic range in Slovenia – is there any place left and how to reach it? *Zbornik gozdarstva in lesarstva* 57: 235–254.
- Ansorge H., Kluth G. & Hahne S. 2006: Feeding ecology of wolves *Canis lupus* returning to Germany. *Acta Theriol.* 51: 99–106.
- Bibikov D.I. 1985: [Wolf]. *Izdatestvo Nauka, Moskva (in Russian)*.
- Blanco J.C., Reig S. & de la Cuesta L. 1992: Distribution, status and conservation problems of the wolf *Canis lupus* in Spain. *Biol. Conserv.* 60: 73–80.
- Boitani L. 1982: Wolf management in intensively used areas of Italy. In: Harrington F.H. & Paquet P.C. (eds), *Wolves of the World. Noyes Publications, Park Ridge, New Jersey*: 158–172.
- Boitani L. 2003: Wolf conservation and recovery. In: Mech L. D. & Boitani L. (eds), *Wolves: Behaviour, Ecology and Conservation. University of Chicago Press, Chicago-London*: 317–340.
- Boman M., Postedt G. & Persson J. 2000: The bioeconomics of the spatial distribution of an endangered species – the case of the Swedish wolf population. *Arbetsrapport 294, Institutionen för Skogsekonomi, Umeå*.
- Ciucci P., Boitani L., Francisci F. & Andreoli G. 1997: Home range, activity and movements of a wolf pack in central Italy. *J. Zool. (London)* 243: 803–819.
- Findo S. 1995: (Present situation and perspectives on conservation of the gray wolf (*Canis lupus*) in Slovakia). *Výskum a ochrana cicavcov na Slovensku* 2: 37–46 (in Slovakian with English abstract).
- Findo S. & Chovancová B. 2004: Home ranges of two wolf packs in the Slovak Carpathians. *Folia Zool.* 53: 17–26.

- Fritts S.H. & Mech L.D. 1981: Dynamics, movements, and feeding ecology of a newly protected wolf population in northwestern Minnesota. *Wildl. Monogr.* 80: 1–79.
- Fuller T.K. & Keith L.B. 1980: Wolf population dynamics and prey relationships in north-eastern Alberta. *J. Wildl. Manage.* 44: 583–602.
- Fuller T.K., Mech L.D. & Cochrane J.F. 2003: Wolf population dynamics. In: Mech L.D. & Boitani L. (eds), *Wolves: Behaviour, Ecology and Conservation*. University of Chicago Press, Chicago-London: 161–191.
- Gazzola A., Avanzinelli E., Mauri L., Scandura M. & Apollonio M. 2002: Temporal variation of howling in South European wolf pack. *Ital. J. Zool.* 69: 157–161.
- Genov P. 1992: The wolf *Canis lupus* L. in south-western Bulgaria. In: Bobek B., Perzanowski K. & Regelin W. (eds), *Global trends in wildlife management*. Trans. 18th IUGB Congress, Kraków 1987. *Świat Press, Kraków-Warszawa*: 359–362.
- Genov P.W. & Kostava V. 1993: Untersuchungen zur zahlenmäßigen Stärke des Wolfes und seiner Einwirkung auf die Haustierbestände in Bulgarien. *Z. Jagdwiss.* 39: 217–223.
- Harrington F.H. 1986: Timber wolf howling playback studies: discrimination of pup from adult howls. *Anim. Behav.* 34: 1575–1577.
- Harrington F.H. & Mech L.D. 1982: An analysis of howling response parameters useful for wolf pack censusing. *J. Wildl. Manage.* 46: 686–693.
- Hayes R.D. & Harestad A.S. 2000: Wolf functional response and regulation of moose in the Yukon. *Can. J. Zool.* 78: 60–66.
- Hess M. 1965: [Climatic zones in the Polish Western Carpathians]. *Zeszyty Naukowe Uniwersytetu Jagiellońskiego* 115, *Prace Geograficzne* 11: 1–267 (in Polish).
- Huber D., Frkovic A. & Kuhar D. 1993: Status of wolves in Croatia. Simposio Internacional sobre El Lobo, 19–23 Octubre 1993. Resúmenes. *IUCN/SSC, León*: 24–26.
- Ionescu O. 1992: Current status and prospects for the wolf in Romania. In: Promberger C. & Schröder W. (eds), *Wolves in Europe. Status and perspectives*. Proceedings of workshop “Wolves in Europe – current status and prospects”, Oberammergau, Germany April 2–5, 1992. *Wildbiologische Gesellschaft München e.V., München*: 51–56.
- Jakiwczuk I. 1996: [Wolf *Canis lupus* problem in the Carpathian National Park]. *Rocznik Przemyski* 32 (2): 103–108 (in Polish).
- Jakubiec Z. 2001: (The brown bear *Ursus arctos* L. in the Polish part of the Carpathians). *Studia Naturae* 47: 1–108 (in Polish with English summary).
- Jędrzejewska, B., Jędrzejewski W., Bunevich A.N., Miłkowski L. & Okarma H. 1996: Population dynamics of wolves *Canis lupus* in Białowieża Primeval Forest (Poland and Belarus) in relation to hunting by humans, 1847–1993. *Mammal Rev.* 26: 103–126.
- Jędrzejewski W., Nowak S., Schmidt K. & Jędrzejewska B. 2002a: (The wolf and the lynx in Poland – results of a census conducted in 2001). *Kosmos* 51: 491–499 (in Polish with English summary).
- Jędrzejewski W., Schmidt K., Theuerkauf J., Jędrzejewska B., Selva N., Zub K. & Szymura L. 2002b: Kill rates and predation by wolves on ungulate populations in Białowieża Primeval Forest (Poland). *Ecology* 83: 1341–1356.
- Jędrzejewski W., Niedziałkowska M., Nowak S. & Jędrzejewska B. 2004a: Habitat variables associated with wolf (*Canis lupus*) distribution and abundance in northern Poland. *Diver. Distrib.* 10: 225–233.
- Jędrzejewski W., Schmidt K., Jędrzejewska B., Theuerkauf J., Kowalczyk R. & Zub K. 2004b: The process of a wolf pack splitting in Białowieża Primeval Forest, Poland. *Acta Theriol.* 49: 275–280.
- Jędrzejewski W., Niedziałkowska M., Mysłajek R.W., Nowak S. & Jędrzejewska B. 2005: Habitat selection by wolves *Canis lupus* in the uplands and mountains of southern Poland. *Acta Theriol.* 50: 417–428.
- Jędrzejewski W., Schmidt K., Theuerkauf J., Jędrzejewska B. & Kowalczyk R. 2007: Territory size of wolves *Canis lupus*: linking local (Białowieża Primeval Forest, Poland) and Holarctic-scale patterns. *Ecography* 30: 66–76.
- Joslin P.W.B. 1967: Movements and home site of timber wolves in Algonquin Park. *Am. Zool.* 7: 279–288.
- Kusak J., Skrbinek A.M. & Huber D. 2005: Home ranges, movements, and activity of wolves (*Canis lupus*) in the Dalmatian part of Dinarids, Croatia. *Eur. J. Wildl. Res.* 51: 245–262.
- Nowak S. & Mysłajek R.W. 2002: (To prevent conflicts – a comprehensive programme of wolf *Canis lupus* protection in the Western Carpathians). *Przegląd Przyrodniczy* 13 (4): 169–180 (in Polish with English abstract).
- Nowak S. & Mysłajek R.W. 2003: [Problems of the wolf *Canis lupus* protection in landscape parks of the Western Beskidy Mountains]. In: Broda M. & Mastaj J. (eds), *Wybrane gatunki zagrożonych zwierząt na terenie*

parków krajobrazowych w Beskidach. *Zespół Parków Krajobrazowych Województwa Śląskiego, Będzin: 14–19 (in Polish).*

- Nowak S., Mysłajek R.W. & Jędrzejewska B. 2005: Patterns of wolf *Canis lupus* predation on wild and domestic ungulates in the Western Carpathian Mountains (S Poland). *Acta Theriol.* 50: 263–276.
- Nowak S., Jędrzejewski W., Schmidt K., Theuerkauf J., Mysłajek R.W. & Jędrzejewska B. 2007: Howling activity of free-ranging wolves (*Canis lupus*) in the Białowieża Primeval Forest and the Western Beskidy Mountains (Poland). *J. Ethol.* 25: 231–237.
- Okarma H. 1995: The trophic ecology of wolves and their predatory role in ungulate communities of forest ecosystems in Europe. *Acta Theriol.* 40: 335–386.
- Okarma H., Jędrzejewski W., Schmidt K., Śnieżko S., Bunevich A.N. & Jędrzejewska B. 1998: Home ranges of wolves in Białowieża Primeval Forest, Poland, compared with other Eurasian populations. *J. Mammal.* 79: 842–852.
- Promberger C., Ionescu O., Mertens A., Minca M., Predoiu M., Promberger-Fürpass B., Sandor A., Sourtu M. & Sürth P. 1998: Carpathian Large Carnivore Project. Annual Report 1997/98. *Wildbiologische Gesellschaft München e.V., München.*
- Pulliaainen E. 1980: The status, structure and behaviour of populations of the wolf (*Canis l. lupus* L.) along the Fenno-Soviet border. *Ann. Zool. Fenn.* 17: 107–112.
- Sokal R.R. & Rohlf F.J. 1994: Biometry: the principles and practice of statistics in biological research. 3rd Edition. *W.H. Freeman & Co, New York.*
- Śmietana W. & Wajda J. 1997: Wolf number changes in Bieszczady National Park, Poland. *Acta Theriol.* 42: 241–252.
- Valière N., Fumagalli L., Gielly L., Miquel C., Lequette B., Poulle M-L., Weber J-M., Arlettaz R. & Taberlet P. 2003: Long-distance wolf recolonization of France and Switzerland inferred from non-invasive genetic sampling over a period of 10 years. *Animal Conserv.* 6: 83–92.
- Voskár J. 1994: (The ecology of wolf (*Canis lupus*) and its share on the formalization and stability of the Carpathian ecosystems in Slovakia). *Ochrana Prírody* 12: 243–276 (in Slovak with English abstract).
- Vyrypaev V.A. & Vorobev G.G. 1983: [The wolf in Kirgizia]. *Izdatelstvo Ilim, Frunze, Soviet Union (in Russian).*
- Wabakken P., Aronson Å., Sand H., Steinset O.K. & Kojola I. 2001: (The wolf in Scandinavia. Status report of the 2000–2001 winter. Oppdragsrapport nr. 1.) *Høgskolen i Hedmark (in Norwegian with English abstract).*
- Wolsan M., Bieniek M. & Buchalczyk T. 1992: The history of distributional and numerical changes of the wolf *Canis lupus* L. in Poland. In: Bobek B., Perzanowski K. & Regelin W. (eds), Global trends in wildlife management. Trans. 18th IUGB Congress, Kraków 1987. *Świat Press, Kraków-Warszawa: 375–380.*
- Wydeven A.P., Schultz R.N. & Thiel R.P. 1995: Gray wolf (*Canis lupus*) population monitoring in Wisconsin 1979–1991. In: Carbyn L.N., Fritts S.H. & Seip D.R. (eds), Ecology and conservation of wolves in a changing world. *Canadian Circumpolar Institute, University of Alberta, Edmonton, Canada: 147–156.*
- Zięba F., Bodziarczyk J. & Szwagrzyk J. 1996: (The limits to renaturalization: large carnivores in the Tatry Biosphere Reserve). *Przegląd Przyrodniczy* 7 (3–4): 245–256 (in Polish with English abstract).
- Zub K., Theuerkauf J., Jędrzejewski W., Jędrzejewska B., Schmidt K. & Kowalczyk R. 2002: Wolf pack territory marking in the Białowieża Primeval Forest (Poland). *Behaviour* 140: 635–648.