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Home ranges of two wolf packs in the Slovak Carpathians

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A b s t r a c t . Movements, home-range size and habitat use of the European wolf (*Canis lupus*) are described in the Slovak Carpathians. The study was carried out in 1994–2002 in two national parks of central Slovakia. In the Tatry National Park we monitored for 11 months an adult male associated with a pack of 7. In the Nízke Tatry National Park we radio-tracked an adult female for 82 months (1995–2002). Over the course of the study the pack size in the Nízke Tatry ranged from 2 to 7 members. In this park the most intensive telemetry was conducted from 1996 to1997 when the radio-tagged female reared her offspring. Home – ranges of radio-collared wolves calculated for the whole period of radio – tracking (MCP with 100 % of observations) were 146 km^2 (male) and 191 km^2 (female), respectively. Extraterritorial forays were not observed. Core areas of the home – ranges estimated by the Kernel method (50 % of locations), were small (21 km^2: male; 28 km^2: female) and overlapped mainly with the forest habitats heavily used by red deer (*Cervus elaphus*). The size of territory used in summer was 24 % – 49 % smaller than in winter.

Key words*:* wolf, home range, habitat use, Slovakia

Introduction

The European wolf (*Canis lupus*) was a permanent member of the fauna of the contiguous forests of Slovakia up until the middle of the 19th Century. The combination of intensive control methods carried out by local people – poisoning, removing pups from the den, shooting and trapping, were probably responsible for wolf absence at the beginning of the 20th Century. After the First World War the wolf population naturally recovered by immigration from the Ukraine and Poland and during the Second World War both the numbers of wolves and their range gradually increased. In the immediate post-war period wolves were rarely hunted. Their control intensified in the 1950s and, as a result of the concept of intensive husbandry of wild ungulates, a government bounty for taking wolves was introduced. Consequently in the 1960s the wolf was again on the verge of extinction and numbers were estimated at about 40 individuals (V o s k á r 1995). Following a half-year protection order, and a ban on poisoning, trapping and removing pups from dens, from 1975 the wolf population rapidly recovered and numbers peaked again in the 1990s. Natural re-colonization of the former range took place, but a lack of knowledge about movements, dispersal and home range size initiated radio-tracking research into wolf behavior.

Recent telemetry studies in central and Eastern Europe have produced the first accurate results on landscape use by wolves. Radio-tracking studies have been carried out in the Białowieża Primeval Forest (Poland) and in the Carpathians (Romania, Slovakia) (F i n ď o 1998, O k a r m a et al. 1998, P r o m b e r g e r - F ü r p a s s et al. 2001).

In northern and southern Europe existing data on wolf home range size has been gradually updated. Various authors have reported home range sizes from 16 km^2 to more than 750 km^2 (C i u c c i & B o i t a n i 1998, H å k a n et al. 2000, K u s a k & H u b e r

2000). Wolf territories up to 30 km^2 are recognized in central and Eastern Europe while in Fennscandia wolf packs occupy much larger areas (O k a r m a et al. 1998).

In Slovakia the only records relating to the home range size of the wolf were reported by V o s k á r (1995). Based on snow-tracking the average size of the wolf's territory in eastern Slovakia ranged from 150 to 200 km^2 and in the Nízke Tatry Mountains 70–100 km^2.

We studied the spatiotemporal behavior of the wolf in central Slovakia in the Tatry National Park and the Nízke Tatry National Park. Both national parks spread over the westernmost section of the continuous geographic range of the wolf in the Carpathians (Fig. 1). The study was carried out from1994–2002 when the wolf population was well established and numbers had peaked. The primary objective of this investigation was to delineate home ranges and territories of individual wolves and packs. Associated objectives were to determine the factors affecting wolf movements and landscape use.

Fig. 1. Location of study areas and wolf distribution in Slovakia.

Study Areas

The Nízke Tatry National Park (NAPANT)

The park, located in central Slovakia extends over an area of 184 km^2. The study area (27 km^2, 48° 50' – 48° 57' N, 19° 23' – 19° 35' E) situated in the central portion of the park is mainly mountainous terrain. The main ridge of the Nízke Tatry Mountains has a large number of side

ridges running from it, which are divided by deep valleys with steep slopes. A dense network of mountain streams and rivers covers the area. Elevations vary up to 2,043 m; however, ungulates and their predators seldom range above 1,500 m. The average annual temperature in the valleys ranges from 4.2 to 6.3 °C and at the top of the mountains can be about 0 °C. The rainfall ranges from 1,020 to 1,400 mm. Snow cover persists in valleys for 70 days, at mid elevations for 140 days and on the ridge and at heads of north facing valleys for more than 200 days.

Forest cover in the study area is 93 %. The main trees are Norway spruce (*Picea abies*), beech (*Fagus sylvatica*) and silver fir (*Abies alba*). Other important trees include sycamore (*Acer pseudoplatanus*), common ash (*Fraxinus excelsior*), European larch (*Larix decidua*) and Scots pine (*Pinus sylvestris*). The upper timberline between 1,400 and 1,500 m is composed of Norway spruce, and in some places beech. At the altitudinal limit of trees is a zone of dwarf pine (*Pinus mugo*), above which lies a zone of alpine meadows and cliffs.

The buffer zone of the park at elevations below 800 m is utilized for forestry and agriculture, especially the grazing of livestock. The whole territory of the national park was divided into a number of hunting grounds with hunting and tourism permitted throughout, including the core area.

The primary prey of wolves is red deer (*Cervus elaphus*), roe deer (*Capreolus capreolus*) are present in substantially lower numbers, along with a small population of wild boar (*Sus scrofa*). Alpine meadows are inhabited by an isolated population of about 85 Tatra chamois (*Rupicapra rupicapra tatrica*), which was reintroduced from the Tatry National Park in 1969–1976. Other large predators besides the wolf are the brown bear (*Ursus arctos*) and lynx (*Lynx lynx*). The wolf was exterminated from the park in the 1960s and re-colonized it again at the end of the 1970s.

Tatry National Park (TANAP; TNP)

The Tatry National Park stretches contiguously across the two states of Slovakia and Poland, of which the Slovak (TANAP) and Polish (TNP) sections have areas of 1,107 km^2 and 202 km^2, respectively. Our study area covered approximately 20 km^2 in the north-central part of the park on both sides of the state border (49° 14’ – 49° 19’ N, 20° 04’ – 20° 20’ E). The Tatry are the highest mountains in the Carpathians ranging from 610 m to 2,654 m a.s.l. and include 25 peaks over 2,500 m. Numerous valleys orientated north and south complicate the relief. The area is rich in rivers and mountain streams as well as glacial lakes.

The average annual temperature ranges from – 3.7 °C (above 2,600 m a.s.l.) to 4.6 °C (around 1,000 m a.s.l.) and annual precipitation from 944 to 1,855 mm. Snow cover in areas above 1,000 m persists for more than 120 days.

Almost two thirds of the national park is covered by coniferous trees and dwarf pines, while the remaining part is covered by rocky terrain, alpine meadows and lakes. The dominant tree is the Norway spruce with intermittent stands of Scots pine, European larch and common silver fir. Carpathian downy birch (*Betula pubescens* spp *carpatica*), rowan (*Sorbus aucuparia*), Silesian willow (*Salix silesiaca*) and especially Swiss stone pine (*Pinus cembra*) occur at higher elevations. The upper timberline is around 1,550 m a.s.l. The lower edge of the forest merges into a zone of foothill vegetation at 700 m a.s.l. This is mostly formed of agricultural land, partly by wetlands and the remainder by peat bogs. Hunting is allowed for red deer, roe deer and wild boar. Above the timberline on both sides of the state border there is an endemic population of Tatra chamois totaling perhaps 300–350 individuals. The large carnivores include the brown bear, lynx and wolf. At the end of the 1960s and in the 1970s the wolf was exterminated; in the 1980s it recolonized the area.

Material and Methods

We captured wolves in summer with leg-hold traps Newhouse Number 14 OS Woodstream Corporation. Trapping was done in TANAP from July to August 1994 and in NAPANT during September 1995. Traps were set along wolf trails and rivers across the study areas. We checked the traps each morning and tranquilized trapped wolves with an 1.5 ml intramuscular injection of ketamine-xylazine mixture (500 mg of Rompun/Bayer dissolved in 4 ml of 10 % Ketaset/Forth Dodge). Although trapped wolves suffered minor cuts, the travel patterns and gait of the trapped animals usually appeared normal within a few days. The wolves were weighed and standard body measurements and teat characteristics were recorded. Wolves were classified as pup or adult by canine tooth appearance, lower incisor wear providing a relative indicator of adult age. In each study area we trapped and monitored one wolf affiliated to one pack (Table 1).

Both trapped wolves were fitted with radio-transmitter collars without an activity sensor manufactured by Advanced Telemetry Systems, USA and ear-tagged with numbered red tags. Wolves fitted with a transmitter were located by portable receiver (Wagener, Advanced Telemetry Systems and Wildlife Materials Inc.), handheld H-antenna and 3-element Yagi antenna. We attempted to locate radio-collared wolves by ground telemetry once a week during the daytime and at night. We succeeded in locating radio-collared animals in 85–93 % of our attempts to find them. In cases where we failed to locate the wolves, a minimum of one or two bearings were done during the field work that indicated presence of radio-collared animals within or near the pack territory. In addition, sessions of 24 hour continuous ground radio-tracking were conducted every month in 1995 and 1996 (male wolf: 11 sessions, female wolf: 12 sessions). However, we usually failed to follow hunting wolves continuously during 24 hour sessions, due to the high mountain terrain. During fieldwork attempts were always made to count the number of tracked, seen, or heard wolves. Winter snow tracking was used to minimize error in radio-tracking locations especially when close to the home range boundary. The Universal Transverse Mercator (UTM) coordinate, date and time were recorded on data sheets. We determined the biophysical description by plotting the telemetry location on military maps (1: 25,000 and 1: 50,000).

We used the minimum-convex-polygon (MCP) method to estimate total size of home ranges of wolves (White & Garrott 1990) and the adaptive kernel method to delineate core areas of home ranges (Worton 1989). Contours at 50 % probability (grid cell size 50) were used to define the core area of concentrated activity (Shivik et al. 1996, Lawson & Rodgers 1997). All calculations of home-range sizes were made with Calhome software (U.S. Forest Service) and computer images with ArcView 3.2 software. The size of home ranges and core areas were computed as two-dimensional flat surface areas and not derived from a digital terrain model, so that our results would be comparable with other studies.

Table 1. Individual summaries of radio-tracked wolves in Slovakia 1994–2002.

Study area	Pack	Pack size[1]	Sex	Age	Weight Kg	Capture date	Duration of telemetry	No of locations
TANAP	Bialka	7	Male	Adult	37	25 Jul 1994	11 months	180
NAPANT	Struhár	5	Female	Adult	40	14 Sep 1995	82 months	319

[1] Pack size at capture date.

Results and Discussion

Number of wolves in the packs

During the study both national parks, including surrounding areas, were occupied by other wolves, but knowledge of their total numbers and the distribution of packs was lacking. The radio-collared wolves belonged to resident packs.

In July 1994 the Bialka pack (in TANAP) numbered 7–8 members. The size of this pack was confirmed by snow tracking in winter 1994–1995 and by observation of 7 pack members, including the radio-collared wolf, during a hunt of a red deer female on the 3rd March 1995. Based on further observation in May 1995 it was surmised that the number of adult wolves in this pack remained unchanged untill the end of telemetry on 19th June 1995. In July 1995 four pups were observed on the rendezvous site of the Bialka pack.

In NAPANT from September 1995 we monitored the movements of an alfa female affiliated to the Struhár pack. The size of the Struhár pack during the 8 years ranged from 2 to 7 wolves. The average number of wolves in this pack at the end of winter was 4.2 and in autumn 5.4 individuals respectively. Hunting by humans was the main reason for mortality. Within the Struhár pack territory over the course of eight years up to 14 wolves were shot, 7 adults and 7 pups of less than one year old. Average annual number of the wolves shot from this pack was 1.74 individuals (Table 2).

Table 2. Size changes of the Struhár pack and known human-caused mortality. Data from snow-tracking and direct observations have been pooled.

Demographic parameter	Year 1995	1996	1997	1998	1999	2000	2001	2002	Mean ± SD
Pack size in winter–spring	7	2	4	6	6	3	3	3	4.25 ± 1.71
Pack size in late autumn	5	4	7	7	6	4	3	7	5.38 ± 1.49
Number of adults shot	1	0	1	2	2	1	0	0	0.87 ± 0.78
Number of young shot	2	0	1	0	1	1	0	2	0.87 ± 0.78

The mean annual pack size in Slovakia, 5.7 members (N=82) in winters 1979–1989 without distinguishing early and late winter period, was reported by Voskár (1995). In the southeastern part of the Polish Carpathians (the Bieszczady Mountains) bordering Slovakia, the mean size of three packs over a period of five years averaged 5.6 and 3.9 members in early and late winter respectively (Śmietana & Wajda 1997). The mean size of the Struhár pack in the Nízke Tatry (5.4 and 4.2 members, Table 2) was similar to that reported by Śmietana & Wajda (1997). The size of packs observed in this study (Bialka pack 7 and Struhár pack 2–7 members) fell within the range of 2–14 reported from the western Carpathians (Voskár 1995, Śmietana & Wajda 1997).

Size and use of home ranges

The size of the territory used by the radio-collared male wolf from the Bialka pack increased during 86 days of telemetry (11 months, 180 locations) (Fig. 2). The home range size of the female wolf affiliated to the Struhár pack increased rapidly during the first 35 days of radio-tracking (5 months, 52 locations). From the 5th to the 16th month of telemetry the female wolf used only the southern part of the Nízke Tatry up to the main ridge while the territory size

was almost the same (Figs 2 and 4). From the 16th month of radio-tracking onward the size of this territory had increased again due to expansion of landscape use northward beyond the main ridge of the Nízke Tatry (Figs 2 and 4). Thus, a reliable estimation of home-range size of wolves in the high mountain terrain required more than 16 months of ground radio-tracking. Based on an intensive radio-tracking study of wolves in the lowland habitat of Białowieża Primival Forest (eastern Poland) a duration of telemetry of 9–12 months was recommended (O k a r m a et al. 1998).

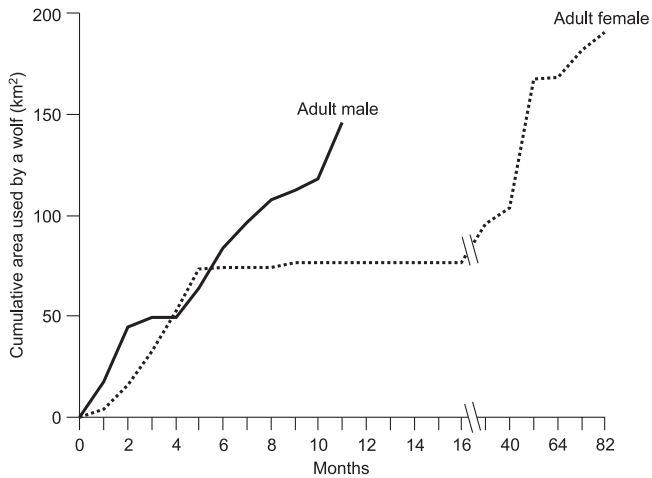

Fig. 2. Increase in the estimated size of home ranges (100 % MCP) of two radio-collared wolves relative to length of radio-tracking. The male was radio-tracked for 11 months (1994–1995) and the female for 82 months (1995–2002).

Home range sizes of radio-collared adult wolves calculated for the whole period of radio-tracking (MCP with 100 % of observations) were 146 km² for the male in TANAP (Bialka pack) and 191 km² for the female in NAPANT (Struhár pack) respectively (Table 3). The 95 % MCP (excluding outliers) covered 60 % (male) and 55 % (female) of their total home ranges. Core areas of the home ranges of radio-collared wolves comprising 50 % of locations, calculated by the Kernel method. For both wolves, 50 % of the radiolocations fell into small core areas of 21 km² (male) and 28 km² (female), or 14 % and 15 % of their total home ranges (Table 3).

Thus, wolves used their home ranges unevenly (Figs 3, 4). Core areas overlapped mainly with the habitats used all year by red deer, including their wintering yards. In these areas we observed both pups and signs of wolf activity (rendezvous sites, tracks in the mud, howling). The wolves used the less accessible side ridges and vast forest tracts for daily resting, where they retreated after hunting at night. Core areas were free of villages but included individual forest lodges, chalets and small settlements. The most important human activities in the areas included all year round logging and summer tourism. In both packs, rivers and streams delimited core areas.

Packs hunted both in core areas and peripheral parts of their home ranges. Locations of the male wolf in TANAP ranged from 700 to 1,600 m a.s.l. and the female in NAPANT from 518 to 1,680 m a.s.l. Based on analysis of scats collected between 1992–1999 (F i n ď o 2002) the diet of wolf in TANAP and NAPANT was composed of free-living red deer and to a lesser extent wild boar, the entrails of animals killed by hunters (autumn-early winter),

Table 3. Home ranges of two radio-collared wolves in Tatra Mountains in Slovakia. Numbers of locations were 180 and 319 respectively.

Wolf/pack	Home-range estimate (km^2)		
	MCP 100 %	MCP 95 %	Kernel 50 %
Adult male (Bialka pack)	146	87	21
Adult female (Struhár pack)	191	105	28

bear baits (late winter-early spring) and sheep on summer ranges (May–October). Red deer was the preferred prey of wolves. In two wolf scats chamois remains were found. However, in our study no wolf attacks on chamois were observed.

Home-range estimates can yield very different results as a consequence of the research methods adopted, and this should be taken into account when comparing data from different studies in Europe. Apparent variation emerged from the duration of radio-tracking (O k a r m a et al. 1998). Another important source of variation may be caused by the use of different home-range estimators. Furthermore home-range sizes computed by different computer software packages can produce different values (L a w s o n & R o d g e r s 1997). In this study we compare only values of home-range size which fulfilled the following criteria: a) radio-tracked wolves belonged to resident packs, b) radio-tracking was carried out for longer than 6 months, c) minimum convex polygon 100 % was used as home-range estimator. Telemetry techniques produce sets of data hardly comparable with other type of information (B o i t a n i & C i u c c i 1995), so we did not take into consideration home-range sizes estimated from snow-tracking.

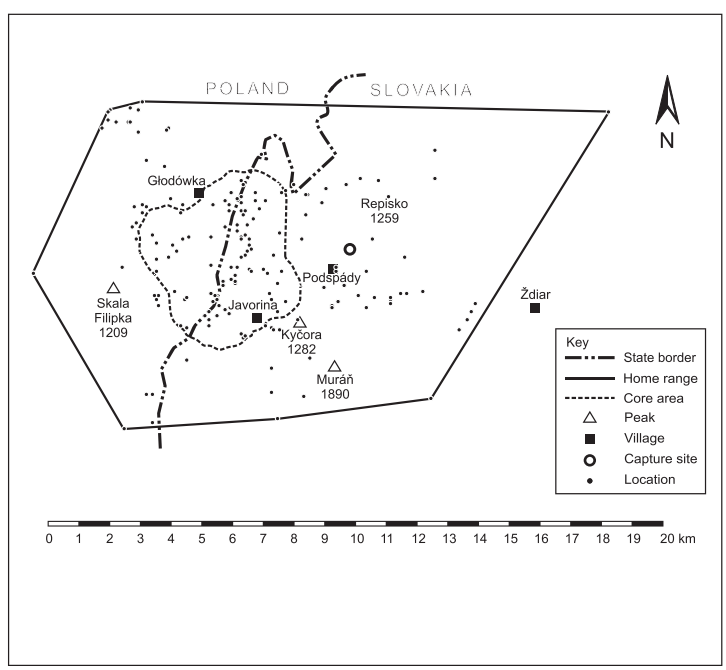

Fig. 3. Home range (MCP 100 %) and core area (Kernel 50 %) of the radio-collared male wolf in Tatry National Park (1994–1995).

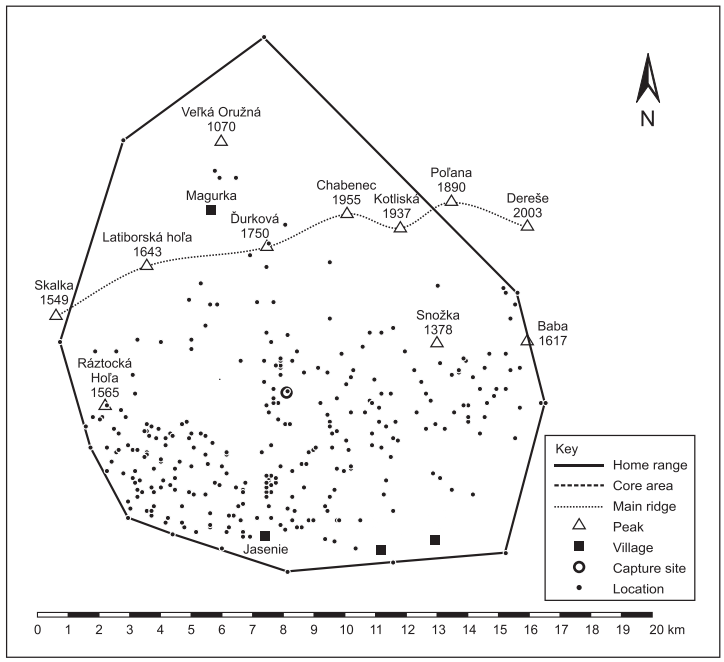

Fig. 4. Home range (MCP 100 %) and core area (Kernel 50 %) of the radio-collared female wolf in Nízke Tatry National Park (1995–2002).

Much of the observed natural variation in territory size has been explained as dependent on several factors, among which the most relevant appear to be pack size, prey density, and wolf population density (F r i t t s & M e c h 1981, P e t e r s o n et al. 1984, L i c h a c k i j 1995). The influence of all these factors on territory size appears to be dependent also on the level of human exploitation of the local wolf population (P e t e r s o n et al. 1984) and the social status of individual wolves in a pack (O k a r m a et al. 1998). The movements of both territorial wolves, studied in Slovakia throughout the year, were obviously influenced by seasonal changes in population density and distribution of red deer. Based on the occurrence of red deer remains in the wolf scats (Nízke Tatry 62 %, N = 97; Tatry 69 %, N = 65, F i n ď o 2002) and red deer killed by wolves within the Struhár pack territory (41 recorded during the this study) (F i n ď o unpublished data), it is possible to conclude that the movements of both territorial wolves studied in Slovakia throughout the year were basically influenced by seasonal changes in distribution of red deer. Furthermore, topography also played an important role. It is likely that combination of these factors, including social status of studied wolves, explains much of the variation in home-range size. Over the course of the study no extraterritorial forays were observed.

O k a r m a et al. (1998) compared the home ranges of wolves derived from radio-tracking and snow-tracking data from various regions in Europe. They found two other sources of variation in the size of home ranges of wolves: latitude and status of population. We assume, agreeing with B o i t a n i & C i u c c i (1995), that both methods of tracking of wolves produce usually incomparable home range sizes. Therefore we refer only to home ranges of wolves achieved by radio-tracking (Table 4). Average wolf territory sizes in Europe, estimated by telemetry, may range from 87 km^2 to 1,000 km^2 (Table 4). Within the range of latitudes of 42°–53° N, where the main prey species are red deer, wild boar and roe

deer the home range size varied from 87 km² to 243 km². Wolves apparently use much larger territories at higher latitudes in Scandinavia (750 km² and 1,000 km²) where European elk (*Alces alces*) and reindeer (*Rangifer tarandus*) are the main prey (see also Okarma et al. 1998). Based on recent studies in Romania and Slovakia the home-range size in the Carpathians may vary from 87 km² to 191 km² (Table 4).

Table 4. Summary of home ranges of individual wolves and packs in Europe studied by radio-tracking.

Country (Region)	Latitude (N)	Home-range Size km²	References
Italy (Apennines)	42°	120–200	Ciucci & Boitani (1998)
Spain (Leon, Zamora)	42°	195	Vila et al. (1990)
		243	
Croatia (Dalmatia)	45°	151	Kusak & Huber (2000)
Romania (southern Carpathians)	46°	87	Promberger-Fürpass et al. (2001)
		170	
Slovakia (western Carpathians)	48°	146	This study
		191	
Poland (Białowieża)	53°	167	Okarma et al. (1998)
		170	
Sweden, Norway (Scandinavia)	62°	750	Håkan et al. (2000)
		1,000	

Temporal variation in size of wolf home ranges

We compared spring – summer (April–September) and autumn–winter (October–March) home range sizes of radio-collared wolves calculated from the locations gathered in 1994–1997 (Table 5). The seasonal pattern of territory utilization observed in our radio-collared wolves corresponds with the shifts in the use of internal parts of wolf territories reported by various authors (e.g. Vyrypaev & Vorobev 1983, Filonov 1989, Jędrzejewski et al. 2001). The landscape use was heavily reduced in summer as a result of pup presence at the den and at rendezvous sites, and in winter increased to enhance effectiveness of prey exploitation (Fritts & Mech 1981).

Table 5. Seasonal changes in the area (100 % MCP) used by wolves in TANAP and NAPANT.

Wolf/Pack	Spring – Summer range		Autumn – Winter range	
	Year	(km²)	Year	(km²)
Adult male, Bialka pack	1994	44	1994–1995	86
	1996	47	1995–1996	74
Adult female, Struhár pack	1997	34	1996–1997	45
Mean ± SD		42.7 ± 5.6		68.3 ± 17.2

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LITERATURE

BOITANI L. & CIUCCI P. 1995: Comparative social ecology of feral dogs and wolves. *Ethology Ecology & Evolution 7: 49–72.*

CIUCCI P. & BOITANI L. 1998: Il lupo. Elementi di biologia, gestione, ricerca. *Istituto Nazionale per la Fauna Selvatica "Alessandro Ghigi", Bologna, Documenti Tecnici 23, 114 pp.*

FILONOV K. P. 1989: Kopytnye zhivotnye i krupnye chishniki na zapovednych territoriach (Ungulates and large predators in wildlife reserves). *Nauka, Moscow (in Russian with English summary).*

FINĎO S. 1998: Priestorová aktivita a domovské okrsky vlka (*Canis lupus*) v Slovenských Karpatoch (Wolf (*Canis lupus*) movements and home ranges in the Slovak Carpathians). In: Urban P. (ed.), Výskum a ochrana cicavcov na Slovensku III. *Slovenská agentúra životného prostredia, Banská Bystrica: 25–30 (in Slovak with English summary).*

FINĎO S. 2002: Potravná ekológia vlka (*Canis lupus*) v Slovenských Karpatoch (Feeding ecology of the European Grey Wolf (*Canis lupus*) in the Slovak Carpathians). In: Urban P. (ed.), Výskum a ochrana cicavcov na Slovensku V. *Štátna ochrana prírody, Centrum ochrany prírody a krajiny, Banská Bystrica: 43–55 (in Slovak with English summary).*

FRITTS S. H. & MECH L. D. 1981: Dynamics, movements, and feeding ecology of a newly protected wolf population in northwestern Minnesota. *Wildlife Monographs 80: 1–79*.

HÅKAN S., ANDRÉN H., LIBERG O. & AHLQVIST P. 2000: Telemetry studies of wolves (*Canis lupus*) in Scandinavia: A new research project. In: Beyond 2000 Realities of Global Wolf Restoration, Program & Abstracts. *University of Minnesota, Duluth: 66–67.*

JĘDRZEJEWSKI W., SCHMIDT K., THEUERKAUF J., JĘDRZEJEWSKA B. & OKARMA H. 2001: Daily movements and territory use by radio-collared wolves (*Canis lupus*) in Białowieża Primival Forest in Poland. *Can. J. Zool. 79: 1993–2004*.

KUSAK J. & HUBER D. 2000: Tracking a wolf pack in livestock-raising areas of Dalmatia, southern Croatia. In: Beyond 2000 Realities of Global Wolf Restoration, Program & Abstracts. *University of Minnesota, Duluth: 32.*

LAWSON E. J. G. & RODGERS A. R. 1997: Differences in home-range size computed in commonly used software programs. *Wildlife Society Bulletin 25: 721–729.*

LICHACKIJ J. P., BIBIKOV D. I. & RJABOV L. C. 1995: Volk (*Canis lupus*) i blagorodnyj olen (*Cervus elaphus*) vo Voronezhskom Zapovednike (Wolf (*Canis lupus*) and red deer (*Cervus elaphus*) in Voronezh State Reserve). *Zoologicheskij Zhurnal 74: 110–120 (in Russian with English summary).*

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.*

PETERSON R. O., WOOLINGTON J. D. & BAILEY T. N. 1984: Wolves of the Kenai Peninsula, Alaska. *Wildlife Monogrs. 88: 1–52.*

PROMBERGER-FÜRPASS B., SÜRTH P. & PREDOIU G. 2001: Carpathian Large Carnivore Project. *Annual report, Zarnesti, Romania, 77 pp.*

SHIVIK J. A., JAEGER M. M. & BARRET R. H. 1996: Coyote movements in relation to the spatial distribution of sheep. *J. Wildl. Manage. 60: 422–430.*

ŚMIETANA W. & WAJDA J. 1997: Wolf number changes in Bieszczady National Park, Poland. *Acta Theriol. 42: 241–252.*

VILA C., URIOS V. & CASTROVIEJO J. 1990: Ecologia del Lobo en la Cabrera (Leon) y la Carballeda (Zamora). In: Blanco J. C., Cuesta L. & Reig S. (eds), El Lobo *(Canis lupus)* en España: situacion, problematica y apuntes sobre su ecologia. *Instituto para la Conservacion de la Natureza, Madrid: 95–108.*

VOSKÁR J. 1995: Ekológia vlka obyčajného (*Canis lupus)* a jeho podiel na formovaní a stabilite karpatských ekosystémov na Slovensku (The ecology of wolf (*Canis lupus*) and its share on the formalization and stability of the Carpathian ecosystems in Slovakia). *Ochrana prírody 12: 241–276 (in Slovak with English and German summaries).*

VYRYPAEV V. A. & VOROBEV G. G. 1983: Volk v Kirgizii [The wolf in Kirgizia]. *Ilim, Frunze (in Russian).*

WHITE G. C. & GARROT R. A. 1990: Analysis of wildlife radio-tracking data. *Academic Press, New York.*

WORTON B. J. 1989: Kernel methods for estimating the utilization distribution in home-range studies. *Ecology 70: 164–168.*