Research

Territory size of wolves *Canis lupus*: linking local (Białowieża Primeval Forest, Poland) and Holarctic-scale patterns

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Factors affecting territory size in wolves *Canis lupus* were studied at 2 scales, the local population (Białowieża Primeval Forest (BPF), eastern Poland) and the geographic range of species (literature review from 14 localities in the Holarctic). Four packs of wolves were studied by radio-tracking in BPF from 1994 to 1999. The annual territories of packs (Minimum convex polygons with 95% of locations) averaged 201 km^2 (SD 63, range 116–310). Core areas of territories (50% MCP) covered from 14 to 78 km^2 (mean 35). Territory sizes and core areas both were negatively correlated to the encounter rates of ungulates (mean number of ungulates seen per unit time spent in the forest by human observers). Pack size (3–8 wolves) did not influence territory size. Home ranges of individual wolves from the same pack varied with season as well as the age, sex, and reproductive status of the wolf. Review of literature from North America and Europe (42–66°N), showed that latitude and prey biomass were essential factors shaping the biogeographic variation in wolf territory size. Territories increased with latitude and declined with growing biomass of prey. The analysis showed that latitude acted partly independently of the south–north gradient in prey abundance. At similar standing crop of ungulate biomass (100 kg km^{-2}), wolf territories would average 140 km^2 at 40°N, 370 km^2 at 50°N, and 950 km^2 at 60°N. Pack size was larger at northern latitudes, but the increase did not keep pace with enlargement of territories. Within-territory density of wolves declined from 2.5–3 wolves 100 km^{-2} at 40–45°N to 0.7 wolves 100 km^{-2} at 60°N. Our analyses documented similarities regarding the role of prey resources in shaping wolf territoriality at the different scales. Furthermore, a macroecological approach revealed additional factors affecting wolf territory size that were not emergent from knowledge of local population.

Understanding the links between large-scale abundance and local dynamics is of fundamental importance for in situ conservation of species (Gaston and Blackburn 2003). However, the scaling from local- to large-scale population size is not simple, as it is highly dependent on the form of the area occupancy – abundance relationship (Watkinson et al. 2003). In Carnivora, home ranges generally increase with body mass of species and increasing share of meat in their diet (Gittleman and Harvey 1982, Goszczyński 1986). Intraspecific variation in home range size of carnivores is dependent on latitude and individual body mass. Home ranges of bobcats *Felis rufus*, coyotes *Canis latrans*, and black bears *Ursus americanus* are signifi-

cantly larger at higher latitudes (Gompper and Gittleman 1991). In bobcat, the most carnivorous of these species, home range size correlated positively with body mass. Latitude usually is accepted as a proxy for ecological and dietary productivity (i.e. availability and distribution of food resources). However, as emphasized by Gompper and Gittleman (1991), this underlying assumption needs to be verified and tested.

In social carnivorous mammals, most of which are strictly territorial, large-scale patterns of abundance are shaped primarily by territory size and group size. Across the latitudinal range of the wolf *Canis lupus*, these 2 parameters exhibit substantial geographic variation. Territories held by wolf packs cover from less than a

hundred to a few thousand square kilometers (Ballard et al. 1987, 1997, Fuller and Snow 1988, Fuller 1989), with the largest ones in the northern parts of their geographic range. Indeed, a positive correlation was found between latitude and wolf territory size in Europe (Okarma et al. 1998) and the latitude was interpreted to reflect a gradient in dietary productivity. Concordant with this finding is a positive correlation in North America between wolf densities and abundance of ungulates at a geographic scale (Keith 1983, Fuller 1989, Gasaway et al. 1992, Fuller and Murray 1998, Fuller et al. 2003).

However, the role of prey abundance in shaping wolf territory size at a local scale is not clear. For instance, in Quebec, Canada, Messier (1985) found that larger wolf packs had larger territories, but this was independent of the densities of moose *Alces alces*. Temporal variation in space use by wolves in relation to the annual cycle of reproductive activities has been studied in one locality in Europe. Packs curtailed their movements and daily ranges in May−June, when new-born pups stayed in a den, and expanded them in winter (Jędrzejewski et al. 2001). Social groups of wolves may include from 2 to over 20 individuals (Thurber and Peterson 1993, Schmidt and Mech 1997, Okarma et al. 1998, Mech 2000) and increase in pack size has been interpreted as an adaptation to easier acquisition of large prey. The aspect of individual differences in space use by wolves belonging to the same pack has so far received little attention.

In this paper, we focus on explaining the variation in wolf territory size at 2 spatial scales: 1) the local population, based on our long-term field study; and 2) the geographic range of the species in the Holarctic, based on a literature review. The field research was conducted in Białowieża Primeval Forest, eastern Poland, one of the best preserved lowland temperate forests in Europe, where wolves coexist with 5 species of wild ungulates. The aims of our 5-yr study, based on radio-tracking of wolves, were to: 1) assess the individual and seasonal differences in home range sizes and core areas utilized by wolves belonging to the same packs, and 2) determine how changes in ungulate abundance and pack size affect the size and core areas of wolf pack territories. Throughout the text we use the term "territory" for the area used by a pack of wolves, and the term "home range" to refer to the areas used by individual wolves.

We reviewed and analyzed the literature on wolf territory size, pack size, and ungulate densities in the Holarctic region in order to: 1) describe latitudinal variation in wolf territories, and 2) explain the roles of prey density and pack size in shaping territory size. By combining micro- and macroecological approaches, we aimed at finding whether the same factors affect wolf territory sizes at different scales.

Material and methods

Study area

The study was conducted in the Polish part of Białowieża Primeval Forest (=BPF, 595 km^2, 52°45′N, 24°00′E). BPF covers a total of 1450 km^2 and is located on the Polish-Belarussian borderland (595 km^2 in Poland and 855 km^2 in the Belarus Republic). It is the best preserved woodland of its size in temperate Europe. The Polish part of BPF consisted of exploited stands (495 km^2) and a protected part (100 km^2). The exploited part (average age of tree stands 72 yr) had timber harvest, reforestation, and game hunting. In the protected area (Białowieża National Park = BNP), most of tree stands were of natural origin (average age >100 yr). Neither exploitation of timber nor game hunting is allowed in BNP, which has been a Man and Biosphere Reserve of UNESCO since 1977 and a World Heritage Site since 1979.

The most characteristic association in BPF is oak-lime-hornbeam forest (*Quercus robur, Tilia cordata, Carpinus betulus*) with admixtures of maple *Acer platanoides* and spruce *Picea abies* growing on brown and podzolic soil. Drier sandy soils are overgrown with coniferous and mixed coniferous forest dominated by pine *Pinus silvestris* and spruce with admixtures of oak. Wet places with stagnated water are covered by black alder *Alnus glutinosa*. Vicinities of small forest rivers and brooks are habitats of river-side forests of alder, ash *Fraxinus excelsior*, and elm *Ulmus glabra*. The terrain is flat (134−186 m a.s.l.). The only open areas within the woodland are marshes of sedge *Carex* and reed *Phragmites* in narrow river valleys (width 0.1−1 km) and several glades with small villages and traditional agriculture (2−14 km^2). There are 5 public roads of a total length ca 50 km in the Polish part of BPF. Towards the north and south, the Polish part of BPF adjoins other woodlands and forests (also inhabited by wolves), but along its western border there are extensive open agricultural areas and a town (Hajnówka, ca 15 000 inhabitants). During the study (1994−1999), the mean temperature was −2.9°C in January and 19.7°C in July. Annual precipitation averaged 611 mm, and snow cover (maximal depth 10−63 cm) persisted for an average of 87 d yr^{-1}. More information on BPF was given by Jędrzejewska and Jędrzejewski (1998).

BPF harbors 5 species of ungulates. The most numerous are red deer *Cervus elaphus* and wild boar *Sus scrofa*; less common are roe deer *Capreolus capreolus*, European bison *Bison bonasus*, and moose (Jędrzejewska et al. 1997). Wolves have been protected in the Polish part of BPF since 1989, but poaching does occur. In the Belarussian part, wolves are still heavily hunted. In 1996−1999, from 5 to 16 wolves yr^{-1} were shot, constituting 10−64% of their estimated winter

numbers. In 1981, a wire fence was constructed in BPF on the Polish-Soviet state border, but wolves are known to cross it in some places.

Estimation of wolf territory size and ungulate abundance

In 1994−1999, 12 wolves belonging to 4 packs were live-trapped and radio-collared (Appendix 1). Data collected on 11 wolves (9 females and 2 males) were sufficient for analysis. Wolves were captured in nets (Okarma and Jędrzejewski 1997) or with footsnare traps (Aldrich footsnare traps for black bears, modified by authors). Footsnare traps were equipped with a radio-alarm system (A. Wagener, Köln, Germany), which allowed us to release animals within 1−2 h of capture. Wolves were immobilized with 1.2−1.8 ml of a xylazine-ketamine mixture (583 mg of Bayer's Rompun dissolved in 4 ml of Parke−Davis Ketavet 100 mg ml^{-1}) and were fitted with radio-collars (Telonics, AVM Instrument Company, Telemetry Systems, and Advanced Telemetry Systems). Five radio-collars were equipped with head position activity sensor, which helped identifying if wolves were feeding, resting, or travelling. Radio-collared wolves were located by triangulation 2−5 d per week by following forest roads with vehicle or bicycle. In addition to daily locations, sessions of 2−9 d (usually 4−6) of continuous radio-tracking were conducted (total of 584 d). From March 1994 to August 1997, we mapped locations of wolves on forest maps with a 533 × 533 m square grid. Depending on the estimated location of wolves, their position was mapped as in the center of a square, in the middle of a side of 2 adjacent squares, or in the corner between 4 adjacent squares. From September 1997 to September 1999, we used a metric system on topographic maps and increased the precision of wolf mapping to 10 m. The accuracy of radio-locations was, on average, 291 and 194 m, respectively in the 2 study periods (Theuerkauf and Jędrzejewski 2002).

During the continuous sessions of radio-tracking, locations were taken at 30-min intervals (March 1994−December 1996) or 15-min intervals (January 1997−September 1999). Observers followed the wolves from a mean distance of 0.94 km (SD 0.58) and the distance between wolf and observer had no effect on wolf activity (Theuerkauf and Jędrzejewski 2002). The size of home ranges of individual wolves and territories of packs were calculated with the program Tracker (A. Angerbjörn, Radio Location Systems, Huddinge, Sweden) as Minimum convex polygons with 100, 95, and 90% of locations (MCP100, MCP95, MCP90). Only asymptotic home ranges (calculated based on 165 to 2834

radio-locations, mean 1170, SD 654) were used for the analysis. In total, 33 seasonal home ranges of 11 individuals (most individuals yielded >1 seasonal home range) were analyzed. Annual territories of each pack (11 territories estimated for 4 packs in various years) were analyzed for the period 1 May−30 April, i.e. the whole annual cycle of wolves' life from the birth of pups till the next breeding season. Core areas of individual home ranges and pack territories were calculated with 50 and 75% of locations (MCP50, MCP75). Other aspects of wolf spatial behaviour (daily movements, territory use) and pattern of activity are presented elsewhere (Jędrzejewski et al. 2001, Theuerkauf et al. 2003).

Winter densities of red deer, roe deer, and wild boar come from drive censuses conducted in the whole Polish part of BPF (595 km^2), where the wolves were studied (details in Jędrzejewska et al. 1994, 1997, Kossak 1997, 1998, 1999, Okarma et al. 1997). Spring-summer numbers of ungulates were calculated based on their densities in late winter, percentage of adult females in the population, and numbers of juveniles per female (details in Jędrzejewski et al. 2000). Also, we obtained the index of ungulate abundance by documenting all observations of animals encountered during our field work conducted both during daylight and night hours. Having recorded the time spent in the forest by human observers, we calculated the encounter rates of ungulates (number of animals seen 1 h^{-1} spent in the forest by a human observer). Only data for autumn-winter seasons (no leaves in deciduous forests) were taken so that differences in visibility did not bias the results. In 1996−1999, a total of 4889 ungulates were seen during 8722 h in the forest. Weather data were obtained from a meteorological station located in Białowieża village, which lies in the centre of BPF.

Review of published data

In the literature review, the criteria for data selection were as follows: territory size was estimated by radio-telemetry (Minimum convex polygon with 95% of locations), based on ≥25 locations, and covering at least one autumn-winter season. Whenever available, all data on between-year and between-pack variation territory and pack size in the same study were considered. If detailed data were not given in the original papers, we used the mean values provided. In total, 120 data points from 14 localities in North America and Europe were analyzed (list of data and sources in Appendix 2). We used multiple regression to evaluate if the observed biogeographic variation in territory size (T, log-transformed) could be explained

by variation in latitude (L), prey biomass (P), and pack size (S), and tested the set of 6 multiple regression models using Akaike's information criterion (AIC; Anderson et al. 2000).

Results

Home ranges of wolves in relation to their age, sex, reproductive status, and season

Though wolves lived in packs of 3–8 individuals, which held a common territory, the ranges utilized by individuals of various age and sex differed markedly. In BPF, the most important factors shaping home ranges of wolves were their reproductive status and season (Table 1). The smallest ranges (Minimum convex polygons with 95% of locations) were those of non-breeding subadult females, on average, 62 km^2 in spring-summer and 125 km^2 in autumn-winter. Somewhat larger ranges were covered by adult breeding females (73 km^2 in spring-summer and 191 km^2 in the cold season), and the largest ones by adult females in years when their reproduction efforts failed (146 and 205 km^2 in the warm and cold seasons, respectively). Data for males are scarce but they suggest that adult breeding males utilize ranges similar in size to those used by breeding females (Table 1).

Generally, spring-summer ranges of all wolves in years when the pack was engaged in pup rearing covered 38–50% of their winter ranges. In contrast, the spring-summer ranges of wolves in years when reproduction failed covered 70% of their cold-season ranges.

The same pattern of seasonal and sex/age-related variation was observed in core areas of wolves' ranges (MCP75 and MCP50, Table 1). Noteworthy is the fact that, in spring-summer, the core area (MCP50) of home ranges used by adult breeding females were very small (5 km^2, on average), and centred on the natal den with pups. In winter, the MCP50 core area was nearly 10 times larger (Table 1).

In spring-summer, MCP75 (equivalent to 75% of time spent by wolves) embraced 32–42% of the whole home range utilized by wolves in that season, and MCP50 covered only 2–13% of home ranges in that season. In autumn-winter, wolves utilized their home ranges more widely; MCP75 covered 42–52% of wolves' seasonal ranges, and MCP50 from 16 to 28% (Table 1).

In 6 cases (5 autumn-winter seasons and one spring-summer) we estimated home ranges used by 2 wolves that belonged to the same pack and were radio-tracked during the same season. Their MCP95 home ranges overlapped by 72 to 100% (average 91%, SE 3).

Table 1. Seasonal and age/sex-related variation in home range size of wolves in Białowieża Primeval Forest, eastern Poland. Spring-summer = 1 May–30 September, Autumn-winter = 1 October–30 April. Number of home ranges analyzed in each group: 8 and 8 of adult breeding females (spring-summer and autumn-winter home ranges, respectively), 3 and 4 of adult non-breeding females, 2 and 4 of subadult females, 1 and 2 of adult breeding males, and 1 of a subadult male (autumn-winter). Statistical differences between seasons and among sex/age groups of wolves tested by Kruskal-Wallis ANOVA for MCP95 (H = 20.6, DF = 8, p = 0.008), MCP75 (H = 22.7, DF = 8, p = 0.004), and MCP50 (H = 26.0, DF = 8, p = 0.001), and then within each MCP estimate pairwise tests between groups were done with Mann-Whitney U-test. Two groups marked with the same letters (e.g. $^{a-a}$) differ significantly from each other (p from 0.001 to 0.04).

Age and sex of wolves	Individual home range in km^2, mean ± SE (range)	
	Spring-summer	Autumn-winter
	Minimum convex polygons 95%	
Adult breeding females	73 ± 10 (38–129)[a,b]	191 ± 25 (102–283)[a]
Adult non-breeding females	146 ± 17 (119–178)[b]	205 ± 44 (112–302)
Subadult females	62 ± 12 (50–75)	125 ± 21 (68–158)
Adult breeding males	82	197 ± 9 (188–207)
Subadult male	–	207
	Minimum convex polygon 75%	
Adult breeding females	24 ± 7 (4–71)[c]	96 ± 13 (53–149)[c]
Adult non-breeding females	50 ± 9 (35–67)	107 ± 27 (71–181)
Subadult females	26 ± 3 (23–29)	53 ± 7 (32–63)
Adult breeding males	19	100 ± 5 (95–105)
Subadult male	–	82
	Minimum convex polygon 50%	
Adult breeding females	5 ± 1 (1–13)[d,e]	49 ± 9 (30–103)[d,f]
Adult non-breeding females	18 ± 3 (15–21)[e]	58 ± 26 (22–134)
Subadult females	8 ± 5 (3–14)	23 ± 4 (14–33)[f]
Adult breeding males	2	31 ± 2 (29–34)
Subadult male	–	23

Territories of wolf packs − variation in size and spatial structure

We analyzed 11 annual territories of 4 packs inhabiting BPF in 1995–1999 (Fig. 1, Table 2). The mean size of the Minimum convex polygons with all locations (100%) was 250 km^2 (range 162–350 km^2, Table 2) but, on average, 12% of that area comprised glades with farmlands and human settlements, which had never been used by wolves (Fig. 1). After excluding such areas, the adjusted MCP100 averaged 219 km^2 (range 137–323 km^2). The territories were utilized unevenly, with little use of the peripheral parts and rather intensive use

of small core areas; 90% of radio-locations were found within 74% of the whole territory (161 km^2, on average), and 75% of locations on 42% of the territory (92 km^2). In 50% of cases (i.e. MCP50), wolves were localized in a small core area of 35 km^2 (range 14–78 km^2), equivalent to 16% of the whole territory. Since the method of data collection reflects the time the wolves spent in each part of their territory, it can be said that wolves spent half of their daily time on rather restricted area of 35 km^2, and the other half on much larger outer part of the territory (on average 184 km^2; Table 2).

In 24 cases, we estimated the overlap of annual territories of the neighbouring packs. Two packs were
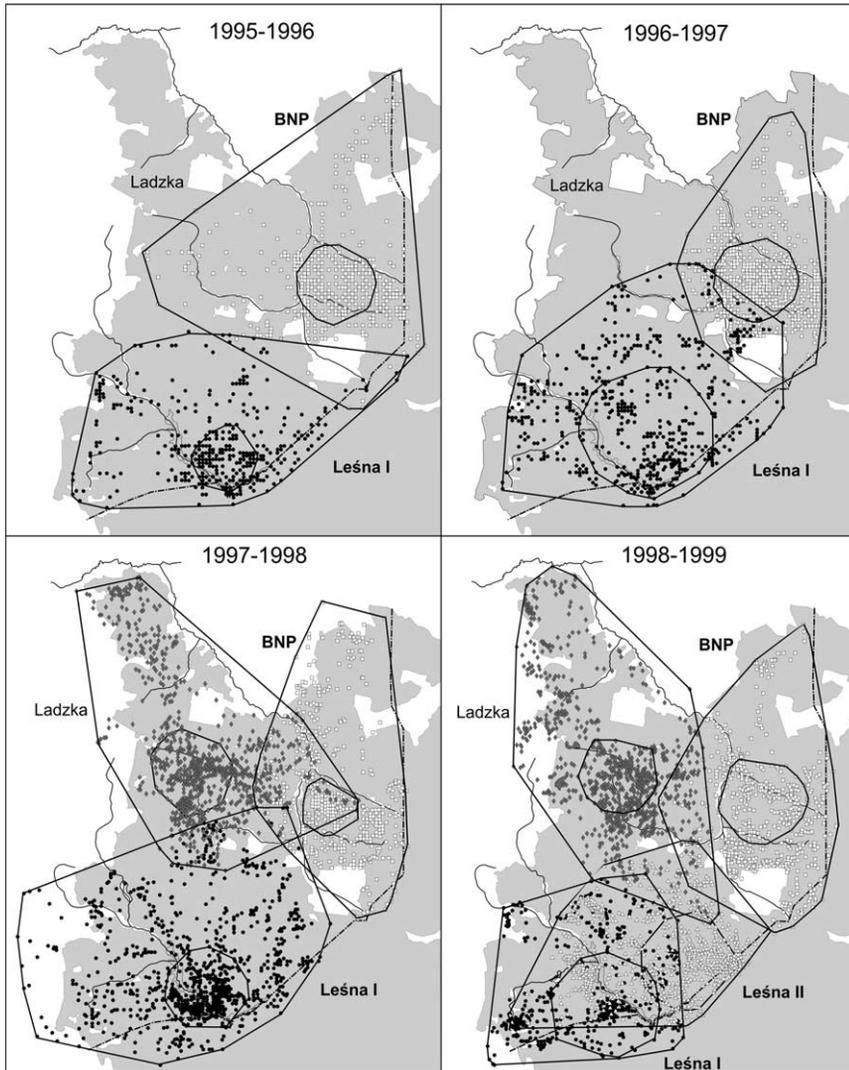
Fig. 1. Annual territories of 2 to 4 wolf packs inhabiting the Polish part of Białowieża Primeval Forest. Points are radio-tracking locations collected over the yearly periods (1 May–30 April). Polygons are Minimum convex polygons with 100 and 50% of locations. Ladzka pack was not radio-tracked before October 1997, but it was recorded by snow tracking. In the winter season 1997/98, the Leśna pack split into two packs (Leśna I and II). Shaded area denotes forests. Scale: lower right panel = 32 × 41 km.

Table 2. Mean ($\pm$SE) number of wolves in a pack, densities of wolves and ungulates, and size of wolf pack territories in BPF, 1995–1999. Densities of wolves were calculated as the total number of wolves in the area covered by all studied territories. Pack territories were calculated for one-year periods (1 May–30 April), pack size and wolf densities – data for late winter (January–March), summer data for September. Winter densities of ungulates – January–March.

Parameter	Mean $\pm$ SE	Range
Mean size of a wolf pack (n wolves)		
Summer	6.0$\pm$0.4	4–8
Winter	4.6$\pm$0.3	3–7
Mean density of wolves (n wolves 100 km^{-2})		
Winter	2.6$\pm$1.6	2.3–3.0
Abundance of ungulates		
Winter density of red deer (n km^{-2})	3.5$\pm$0.6	2.9–4.6
Winter density of roe deer (n km^{-2})	2.1$\pm$0.6	1.2–3.2
Winter density of wild boar (n km^{-2})	2.9$\pm$0.7	2.2–4.3
Combined density of 3 ungulate species (n km^{-2})	8.5$\pm$1.2	6.2–10.1
Encounter rate of ungulates in autumn-winter season (n ungulates seen h^{-1})	0.585$\pm$0.177	0.201–1.776
Size of annual territories of wolf packs (km^2)		
Minimum convex polygon with 100% locations	250$\pm$19	162–350
MCP100, unused areas of villages excluded	219$\pm$18	137–323
MCP95	201$\pm$19	116–310
MCP90	161$\pm$17	85–260
MCP75	92$\pm$9	56–147
MCP50	35$\pm$5	14–78

closely related genetically, while in all other cases the neighbouring territories belonged to unrelated packs (details in Jędrzejewski et al. 2005). In non-related packs, the percentage overlap averaged 11% in MCP100, declined to 3% in MCP90 and 0 in MCP75 (Table 3). The territories of closely related packs, in the first year after they had split, overlapped in 62% (MCP100). However, overlap of core areas of territories (MCP50) was only 3% (Table 3).

Table 3. Percentage overlaps of annual territories of the neighbouring wolf packs in BPF. Non-related packs: n$=$22 pack-years, related packs: n$=$2 pack-years (Leśna I and II, Fig. 1).

Territory estimate	Percentage overlap of the neighbouring territories, mean$\pm$SE (range)	
	Non-related packs	Related packs
MCP100	11$\pm$2 (0–26)	62 (61–63)
MCP95	7$\pm$2 (0–35)	49 (46–51)
MCP90	3$\pm$1 (0–28)	44 (42–47)
MCP75	0	37 (36–39)
MCP50	0	3 (3–4)

The average pack size was 4.6 wolves in winter (range 3–7) and 6 wolves in summer (range 4–8). The mean winter density of wolves during the study period was 2.6 individuals 100 km^{-2} (Table 2). Winter density of ungulates (data available for 3 yr during 1995–1999) varied from 6.2 to 10.1 individuals km^{-2} (mean 8.5); 41% of ungulate numbers were red deer, 34% wild boar, and 25% roe deer (Table 2). Moose and European bison occurred in very low densities and were not included here, as they fell as prey to wolves very rarely (Jędrzejewski et al. 1992, 2000). In winter, the average territory of wolves in BPF included 756 red deer, 626 wild boar, and 454 roe deer, for a total of 1836 ungulates. The predator-prey ratios were 165 red deer, 136 wild boar, and 99 roe deer per wolf (in total 400 ungulates/wolf) in late winter.

We checked if the variation in territory size was affected by abundance of ungulates and number of wolves in a pack. The abundance of ungulates changed
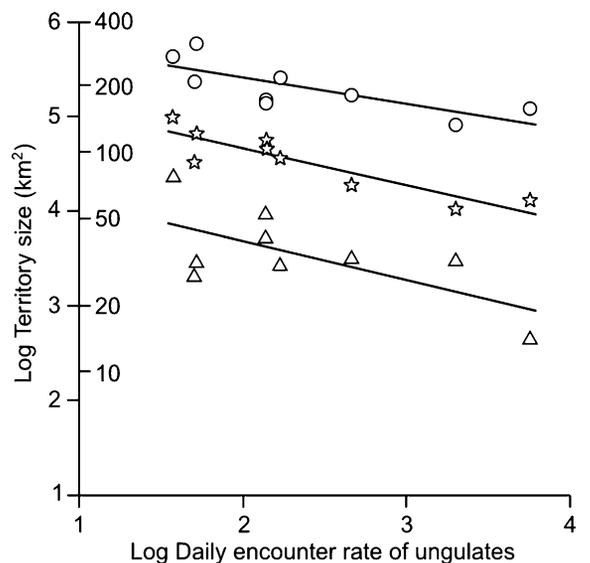
MCP 100%

○ —— Y = 5.964-0.276X, R^2= 0.58, p = 0.016

MCP 75%

☆ —— Y = 5.445-0.390X, R^2= 0.80, p = 0.001

MCP 50%

△ —— Y = 4.516-0.415X, R^2= 0.44, p = 0.05

Fig. 2. Size of annual territories of wolf packs (km^2) in BPF in relation to the encounter rates of ungulates in the territories (mean number of ungulates seen per day by a human observer); both variables log transformed. MCP-Minimum convex polygons, MCP100% – territories based on 100% of radio-locations minus areas of human settlements and agricultural glades, which were not used by wolves.

somewhat from year to year and varied among parts of BPF (Jędrzejewska et al. 1994). We applied the encounter rate of ungulates by human observers (number of animals seen per hour spent in the forest) as an index of ungulate abundance for each year and each territory. The encounter rates of ungulates, available for 9 annual territories, varied from 0.201 to 1.776 animals seen per hour (mean 0.585), which is equivalent to 4.8–42.6 (on average 14) ungulates encountered per day.

The size of wolf annual territories was negatively correlated with the encounter rate of ungulates and the relationship was linear when the variables were log-transformed (Fig. 2). Territory size (from MCP100 to MCP50) declined with increasing mean daily encounter rates of ungulates (summed index of red deer, wild boar, and roe deer; R^2 from 0.44 to 0.80, n = 9, p from 0.05 to 0.001). Though red deer was a dominant prey of wolves (Jędrzejewski et al. 1992, 2000), there was no significant correlation with red deer alone. At the scale of local population, pack size did not have a significant effect on territory size (p > 0.5).

Factors affecting territory size of wolf packs in the Holarctic region

Literature review yielded information on the size of wolf territories (MCP95) from 11 localities in North America and 3 localities in Europe. For most of the data, estimates of prey density (recalculated by us into prey biomass) and pack size were also available (Appendix 2). From 42 to 66°N, territories of sedentary packs of wolves ranged from 78 to 4312 km^2 (mean 701, SE 69). Standing crop of prey biomass (ungulates) varied between 63 and 634 kg km^{-2} (mean 231, SE 18). Pack size ranged from 2 to 19 individuals (mean 6.8, SE 0.4).

Akaike's information criterion showed that the best model (Akaike's weight $\omega_i = 0.971$) explained 77% of variation in wolf territory size and included 2 variables (Table 4); territories increased with latitude (from south

to north) and declined with growing abundance of prey biomass ($R^2 = 0.77$, n = 114, p < 0.0001). Squared semi-partial correlations (Tabachnick and Fidell 2001) indicated that the contribution of latitude ($sr^2 = 0.522$) was much stronger than that of prey abundance ($sr^2 = 0.074$). Prey biomass generally decreased towards the north, but the relationship was weak; latitude explained only 8% of the observed variation in prey biomass ($R^2 = 0.083$, n = 116, p = 0.002). This resulted from the fact that, at high latitudes (>60°N), prey biomass
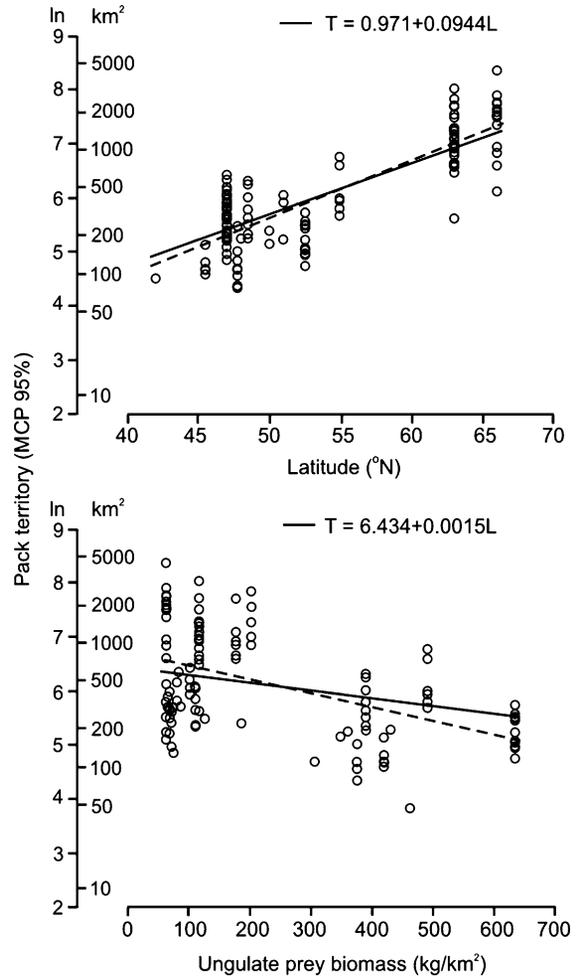
Fig. 3. Territory size (T) of wolf packs in North America and Europe in relation to latitude (L; upper graph) and standing crop of prey (ungulate) biomass (P; lower graph). Each point is an annual (or autumn-winter) territory of a wolf pack or mean value for several territories in one locality (Appendix 2). Multiple regression analysis with both independent variables: $T = 1.318 + 0.0944L - 0.0015P$, $R^2 = 0.77$, n = 114, p < 0.0001. Thick lines are regression lines (x on y) calculated from the multiple regression equation with the second independent variable (z) held constant at its mean value (mean L = 54.2°N, mean P = 231.4 kg km^{-2}). Broken lines are linear regression lines for single independent variables.

Table 4. Multi-model inference based on regression models on effect of latitude (L), prey biomass (P), and pack size (S) on territory size (T, log-transformed) in wolves in the Holarctic zone. n-sample size (n territories), ω_i-Akaike's weight (in model testing by Akaike's information criterion-AIC). The best model is on top of the list.

Model	n	AIC_i	ω_i
T = f (L+P)	114	−167.84	0.971
T = f (L+P+L ×P)	96	−159.73	0.017
T = f (L+P+L ×P+L ×S)	96	−158.22	0.008
T = f (L+P+S)	96	−155.96	0.002
T = f (L+P+S+L ×S)	96	−155.46	0.002
T = f (L)	120	−145.44	0.000

Table 5. Summer and winter home ranges of wolves in relation to latitude. Minutes in latitude are shown in a decimal system. F-females, M-males.

Latitude	Region	Mean home range size ($\pm$SE), km^2		Source
		Summer	Winter	
47.75°N	Minnesota, USA	110	116	Fuller (1989)
52.75°N	E Poland	95$\pm$13	196$\pm$21	This study
54.92°N	NW Alberta, Canada	263$\pm$52	502$\pm$97	Bjorge & Gunson (1983)
63°N	NW Alaska, USA	622$\pm$149[a]	1372$\pm$181[a]	Ballard et al. (1997)
	''	1406$\pm$418[b]	3056$\pm$630[b]	Ballard et al. (1998)
64.45°N	Northwest Territories, Canada	1130$\pm$251 F 2022$\pm$659 M	37360$\pm$7290 F 45543$\pm$17968 M	Walton et al. (2001)

[a]Data from traditional radio-tracking.
[b]Data from satellite telemetry in the same population.

was always low (63–203 kg km^{-2}), whereas at southern latitudes (<55°N) it was variable, from as low as that in the north to very high (63–634 kg km^{-2}). Thus, the effect of latitude on wolf territory size did not result from a mutual correlation of latitude and prey biomass, but these 2 variables had strong effects at least in part independently of each other. Thus, we separately presented the effects of each of them on territory size (i.e. relationship of x on y), while holding the second independent variable (z) constant at its mean value (Fig. 3). Interestingly, although European data generally were characterized by higher abundance of prey and smaller packs of wolves, they fitted very well to the same biogeographic relationship as data from North America.

Wolf pack size was larger towards the north and was positively correlated with territory size (r = 0.598, n = 102, p < 0.0005). However, testing of multiple regression models with AIC showed that pack size was not important for explaining the large-scale variation in territory size (Table 4). The northward increase in pack size did not keep pace with enlargement of territories, such that within-territory density of wolves declined from 2.5–3 wolves 100 km^{-2} at 40–45°N to 0.7 wolves 100 km^{-2} at 60°N.

Studies in North America and Europe documented that summer ranges of wolves usually are about half the size of their winter areas, although in the far North, where wolves follow migratory caribou, summer ranges may cover only 3–4% of the winter areas (Table 5). In contrast, in southern populations of wolves, where territories are rather small (ca 100 km^2), their seasonal variation is smaller. Finally, it is worth noting that these data demonstrate great variation in wolf territory size at local scales. In one locality and in conditions of similar prey abundance wolf territory size may vary from 2 to 10-fold (see the range of y-points for the same or nearby x-points in Fig. 3).

Discussion

Territorial behaviour is an expression of competition for space and for resources, such as prey population, that are linked to space (Gordon 1997). In our study, we examined territory size of wolves at 2 nested spatial scales: local (BPF) and biogeographic (Holarctic). We found that both intrinsic (social) and extrinsic (prey abundance and latitude) factors played roles in determining wolf territory size. Seasonal variation (smaller ranges in summer than in winter) has been caused by the fact that, in spring, wolf packs are bound to a den with pups, and later mobility of the pack is limited by the pups' incapacity for long-distance travel.

Two recent studies analyzed the relationship between wolf territory size and latitude (Mech and Boitani 2003) and prey biomass (Fuller et al. 2003) for North American wolves. Fuller et al. (2003) documented that wolf territories declined with increasing index of prey biomass. Mech and Boitani (2003) found a strong latitudinal gradient of increasing wolf territories towards north. Although the 2 factors were analyzed separately, Mech and Boitani (2003) proposed that the latitudinal gradient reflected a decline in prey abundance.

Our study showed that prey abundance was an important factor determining the size of wolf territories, both locally and at a large geographic scale. A similar relationship between wolf territory size and their corresponding deer densities in a local population was documented by Wydeven et al. (1995) in Wisconsin, USA. At the biogeographic scale, wolf territories increased exponentially with declining prey biomass. Indeed, in conditions of critically scarce and highly dispersed ungulates (such as migratory caribou in NW Canada), wolves became migratory as well, and except for a pup rearing period in summer, they roamed over an area up to 100 000 km^2 (Walton et al. 2001). On the other hand, in conditions of high abundance of

ungulates, wolves did not reduce their territories below a certain asymptotic value (ca $80-100$ km^2), even if prey numbers continued to grow. Such a minimal exclusive territory is probably a prerequisite for successful breeding and may be determined by intrinsic, social factors. The necessity to hold an exclusive territory during pup rearing was exemplified by the 2 genetically related packs in BPF, which were fully separated from each other only in the core areas around breeding dens (Jędrzejewski et al. 2004, 2005). Therefore, we propose that minimal sizes of wolf territories at high abundance of prey are determined by social factors, whereas with declining abundance of prey, extrinsic factors become more important.

Interestingly, latitude – besides expressing an obvious aspect of varying productivity of ecosystem in the south-north gradient – exerted some additional impact on wolf space use, more influential than prey abundance. Based on the multiple regression analysis (Fig. 3), we can predict that at similar standing crop of ungulate biomass (e.g. 100 kg km^{-2}), wolf territories would cover, on average, 140 km^2 at 40°N, 370 km^2 at 50°N, and 950 km^2 at 60°N. Indeed, latitude, and not prey biomass, was the single best predictor of wolf territory size. In our analyses, we used the standing crop of ungulate biomass. Yet for wolves, productivity of the prey population (i.e. the annual production of vulnerable young) may be essential, and this parameter may also vary with latitude. Carbone and Gittleman (2002) postulated that in Carnivora, predator populations are sustained by productivity rates of prey populations rather than by prey biomass. Fuller et al. (2003) suggested that vulnerable prey biomass (rather than standing crop of all potential prey species) can be the primary factor, to which wolves respond. Mech et al. (1998) and Jędrzejewski et al. (2002) evidenced that prey vulnerability increased with snow cover, thus linking prey availability with abiotic environmental factors. The effect of latitude may also include the fact that the same biomass of ungulates would include much fewer individuals in more northern regions (with moose as the dominating species) than in southern regions (deer, wild boar), so in the north wolves might have to travel more extensively to find vulnerable individuals.

Latitudinal increase in pack size may partly result from lower human disturbance of wolves in the northern parts of Canada and Alaska than in the southern, more populated regions. An inverse relationship between wolf pack size and level of human persecution was reported from Europe (Okarma et al. 1998). This cannot, however, be a sufficient explanation of the observed geographic variation. Jędrzejewski et al. (2002) proposed that the maximum pack size of wolves is determined by the size of dominant prey species such that all pack members can satisfy their daily food requirements at a single kill, if consumed immediately.

Medium-sized and small prey species (deer in the genera *Odocoileus* in North America, and *Cervus* and *Capreolus* in Europe) that occur in southern latitudes support smaller packs than do moose, a large-sized, dominant prey of wolves in northern latitudes. Indeed, data reviewed by Fuller et al. (2003) indicated that the maximum pack size in wolves hunting predominantly on *Odocoileus* sp. was, on average, 11 individuals (n = 9 populations), those living on elk (*C. elaphus*), 16 wolves (n = 3 populations), and the maximum pack size in wolves hunting on moose averaged 17 individuals (n = 14 populations).

In conclusion, our analyses revealed similarities regarding the role of prey resources in shaping wolf territoriality at the different spatial scales. We have shown that local-scale analyses help identify variables that affect animal population at the biogeographic scale as well. Moreover, a macroecological approach revealed additional factors affecting wolf territory size that were not predictable from knowledge of local population. As the spatial structure of wolf population changes along the temperature-determined productivity gradient, the role of wolf predation in limiting ungulate populations may also vary with latitude. Large-scale observational data on wolf abundance should further be used to generate hypotheses about macroecological patterns in wolf predation on ungulates. Furthermore, our results point out that the multi-scale understanding of ecological processes is much needed for other Carnivora, a group which includes many rare and endangered species.

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