Speed and actual distances travelled by radiocollared wolves in Białowieża Primeval Forest (Poland)

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The relationship between the straight line distances (SLD), obtained from telemetry locations, and actual distances travelled by wolves *Canis lupus* (ADT), measured by snowtracking, was investigated in Białowieża Primeval Forest, E Poland, in winter 1995/96. Radiolocations determined at 15-min time intervals approximated the ADT by wolves reasonably well. If wolves were relocated at 0.5- to 2-h intervals, SLD can be multiplied by a correction factor of 1.3 to obtain ADT. Within the range of SLD from 1 to 10 km, they could also be converted into ADT using a regression equation: ADT = 0.34 + 1.19(SLD), with standard errors of prediction ± 0.13 to ± 0.3 km. The average travelling speed of wolves was 3.78 km/h (SD 1.23, range 1.6–6.1 km). Wolves walking the forest trails, roads and frozen rivers moved significantly faster than in the forest. Also, individuals travelling with other pack members moved faster than those walking singly.

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Introduction

Straight-line distances (SLD) between consecutive locations of radiocollared wolves *Canis lupus* often have been used to describe their movements (Mech 1970, 1994, Mech *et al.* 1971, Fritts and Mech 1981, Messier 1985, Fuller 1989, 1991). However, the SLD reflect the actual distances travelled (ADT) only in some situations, such as when an animal moves along a straight road. Thus, SLD data approximate the minimum rather than real distances covered by an animal. So

far, the only data on speed of wolves during their regular travel are available for individuals moving in open areas, namely on a frozen lake or barren ground (Mech 1970, 1994).

The aims of this study, conducted in the winter of 1995/96, were to: (1) investigate the relation between straight-line distances (SLD) covered by moving wolves as measured by radiotelemetry and actual distances travelled (ADT) measured during subsequent snowtracking, and (2) estimate the speed of moving wolves. We attempted to quantify the factors affecting variation in wolf speed and obtain the correction factors that could be applied to telemetry data to calculate ADT by radiotracked wolves. The study was part of a long-term project on wolf-ungulate relationships in the pristine temperate forests of Białowieża, E Poland (Jędrzejewski *et al.* 1992, in press, Jędrzejewska *et al.* 1996, 1997, Okarma *et al.* 1998).

Study area

Due to centuries-long protection as a hunting ground of Polish kings, Lithuanian dukes, and Russian czars, Białowieża Primeval Forest (= BPF, 1451 km^2, 52°30'–53°N, 23°30'–24°15'E) is one of the best preserved forest ecosystems in the lowlands of temperate Europe (details in Jędrzejewska *et al.* 1996). It is located on the Polish-Belarussian borderland and is composed of mixed and deciduous stands with spruce *Picea abies*, pine *Pinus silvestris*, oak *Quercus robur*, hornbeam *Carpinus betulus*, black alder *Alnus glutinosa*, ash *Fraxinus excelsior*, lime *Tilia cordata*, and maple *Acer platanoides*. Most of the Polish part of BPF (530 km^2) is a commercial forest exploited for timber and undergoing game management. The remaining portion of the Polish part (47 km^2) has been strictly protected since 1921 as Białowieża National Park, where neither timber exploitation nor hunting is allowed. In July 1996, the Park was enlarged to cover 100 km^2.

BPF harbours a rich community of ungulates: European bison *Bison bonasus*, moose *Alces alces*, red deer *Cervus elaphus*, roe deer *Capreolus capreolus*, and wild boar *Sus scrofa* coexist there with two species of large predators, the wolf and the lynx *Lynx lynx*. Since 1989, wolves have been protected in the Polish part of BPF, whereas they are hunted in the Belarussian part (Jędrzejewska *et al.* 1996).

The climate of BPF is transitional, but continental features prevail. The mean January temperature in 1996 was –8.5°C.

Material and methods

Four wolves (2 adult females, 1 subadult female, and 1 young female) from two packs of 5–7 animals each were captured and fitted with radiocollars in 1994-1996 in the Polish part of BPF (see Okarma and Jędrzejewski 1997, Okarma *et al.* 1998 for details). The data presented here were collected in winter 1995/96 during several sessions of continuous (1 to 5-day) radiotracking. We obtained radiolocations from the ground by driving a car on forest roads. We tried to stay > 300 m from the monitored animal to avoid influencing its movement and < 1000 m away to obtain accurate locations. There was no indication that movements of wolves were affected by our presence. We estimate that the average error of radiolocations of moving wolves was about 300 m. For mapping the locations of wolves, we used forest maps with a grid of 533 × 533 m squares (forest compartments), into which BPF is divided for forestry practices. Depending on the estimated location of wolves, their
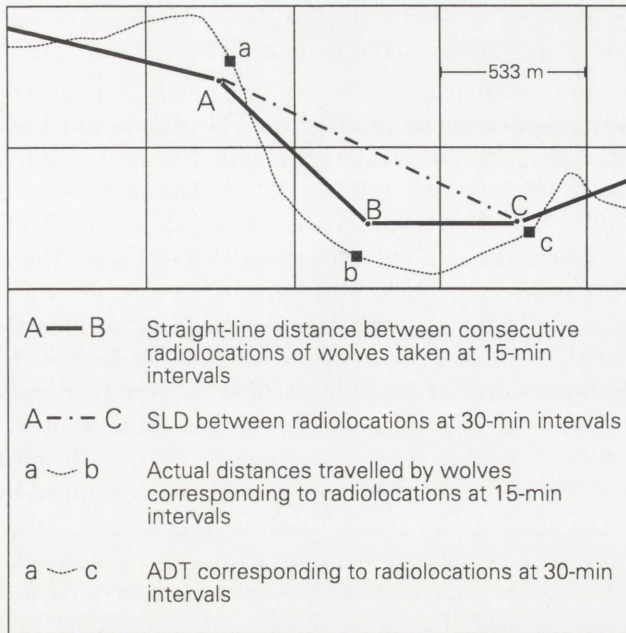
Fig. 1. Scheme of distances covered by wolves as sampled by radiotelemetry and snowtracking. The wolves tracks on snow (dotted line) were followed step by step between consecutive telemetry locations (A, B, and C). Starting and ending points of actual distances travelled by wolves (a, b, and c) were arbitrarily fixed on the wolves' route at half-way between two sides of the grid squares which were crossed by the radiotracked animals.

position was mapped as in the centre of a forest compartment, in the middle of a side of two adjacent squares, or in the corner between four adjacent squares. This method of mapping caused an additional error of wolf location averaging 67 m (maximally 133 m). Such locations were then converted into co-ordinates for further calculations. The shortest interval between two locations was 15 minutes. This was the minimum time needed to take the bearings, record time and location, and reach a new position.

Usually on the day following the night of radiotracking, the wolves' tracks on snow were followed step by step between every two telemetry locations. Starting and ending points of ADT were arbitrarily fixed on the wolves' route at half-way between two sides of a grid square, which was crossed by the tracked animal (Fig. 1). The length of each travel segment (ADT) was measured by pacing. Pace length depended on snow depth and averaged 0.68 m (SD 0.14). During the study, snow cover varied from 5 to 17 cm, ie it never exceeded 40 cm, the threshold beyond which the wolf's movements are impeded (Kelsall 1969, Mech 1970). Characteristics of the routes used by wolves were recorded during each session. Group size (1 or ≥ 2 wolves) was determined by counting any branching of their tracks. The routes travelled were arbitrarily classified as 'forest', 'trails and roads', and 'frozen rivers' when > 80% of the track length was confined to one of these substrates. A total of 13 travel segments were measured by both radiotracking and snowtracking. They represented 30 to 120-min long movements as recorded by radiotracking and corresponded to 1.5 to 11.9-km travels of wolves as measured during snowtracking (totally 70.07 km of snowtracking). Data on snow depth and temperature were provided by the Białowieża meteorological station.

Results

The SLD from our telemetry efforts were strongly correlated with the ADT measures obtained by snowtracking (Fig. 2). The regression line lies above the $x = y$ line. Radiotracking always underestimated the real lengths of wolf movements, on average by 21% (range 1–34%, SD 9). The regression equation makes it possible to convert the SLD into ADT with a rather small error; within the recorded range of distances covered by wolves (1.5–12 km), the standard errors of prediction varied from ± 0.13 to ± 0.30 km.

We checked how the ADT compares to our SLD at various time intervals of radiolocations. For that purpose, each of the 13 snowtracked routes was taken as a whole and additionally broken into all possible shorter segments corresponding to 15-min interval and its multiplicities, making a total of 60 samples (Fig. 3). The mean ratio of ADT to SLD values was lowest (1.01) at 15-min time intervals between successive radiolocations. Therefore, wolf routes mapped by radiolocations at 15-min intervals yielded the most accurate estimates of the real distances covered. However, such frequent radiolocations were subject to the largest variation in SLD to ADT ratio, CV (coefficient of variation) = 37%. With increasing time intervals between radiolocations, mean ratios of ADT to SLD grew and reached a plateau at 30–120 min (Fig. 3). Mean ADT/SLD ratios for radiolocations taken at 30 to 120-min intervals were from 1.28 to 1.43 (1.3 on average). Also,
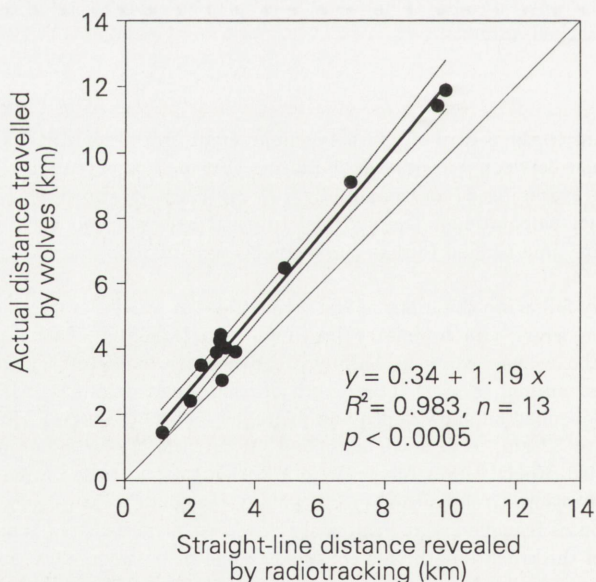

Fig. 2. Relationship between straight-line distances covered by wolves (estimated by radiotelemetry) and actual distances travelled (measured during successive snowtracking) for 13 routes of wolves in Białowieża Primeval Forest, winter 1995/96.
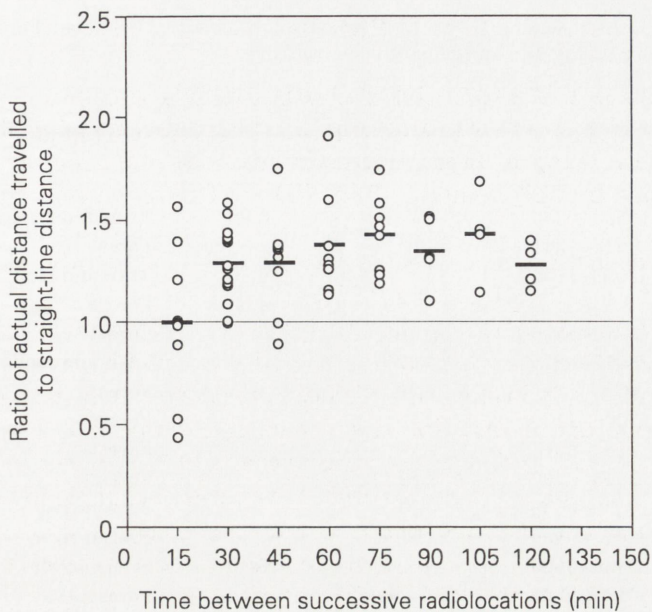
Fig. 3. Ratios of snowtracked ADT to telemetry SLD in wolf movements in relation to time intervals (15-min and its multiplicities) between successive radiolocations. For this presentation, data for 13 routes covered by both radio- and snowtracking were broken into all possible shorter time intervals. Bars are mean values.

variation around mean values was much lower, CV from 9 to 20%. Hence, a correction factor of 1.3 can be applied to SLD obtained by our telemetry method to estimate ADT of wolves.

The 13 snowtracked routes included 3 cases of wolves travelling in forest trails and roads, 3 on frozen rivers, 5 in the forest, and 2 routes located partly on roads and partly in the forest. Five snowtracking samples were of wolves travelling with other members of the pack and 8 of wolves moving alone. The speed of wolves varied from 1.61 to 6.10 km/h, mean 3.78 km/h, SD 1.23 (Table 1). Wolves travelling on trails, roads and frozen rivers moved significantly faster (mean 4.7 km/h, SD 0.97) than in the forest (mean 3.0 km/h, SD 0.86; $t = 3.545$, df = 13, $p = 0.004$). Also, when travelling in a pack, wolves moved notably faster (mean 4.8 km/h, SD 1.06) than in cases of moving singly (mean 3.1 km/h, SD 0.82; $t = 3.493$, df = 13, $p = 0.004$). Moreover, the same pattern (slower pace when moving in the forest) was apparent in both packs and single wolves (Table 1). Indeed, these two factors (substrate and pack/single) explained 74% of the observed variation in the speed of wolves moving in BPF (ANOVA, $F = 10.1$, $p = 0.009$ for substrate and $F = 9.9$, $p = 0.009$ for pack factor). Within the observed range of snow depth (5–17 cm), snow did not affect the wolves' speed ($R^2 = 0.02$, df = 13, $p > 0.6$).

Table 1. Speed of wolves moving in winter 1995/96 in Białowieża Primeval Forest (E Poland) as determined by radiotracking and subsequent snowtracking.

Date	Hours	Speed (km/h)		Substrate	Snow depth (cm)
		Single wolves	Groups ≥ 2 inds		
Nov 22, 1995	0530–0730		5.96	Trail and road	5
Dec 19, 1995	0915–1045	1.61		Forest	9
Jan 4, 1996	1030–1230		4.70	Trail and road	12
			4.53	Forest	12
Jan 7, 1996	1715–1830	3.56		Forest	12
Jan 15, 1996	0615–0815	4.02		Trail and road	11
		2.49		Forest	11
Jan 18, 1996	1000–1130	2.70		Forest	12
Jan 20, 1996	2145–2215	2.90		Forest	12
Jan 29, 1996	0645–0800	2.81		Forest	13
Jan 30, 1996	0530–0630	3.91		Frozen river	13
Jan 31, 1996	0030–0130	3.96		Frozen river	13
Feb 1, 1996	0430–0500		6.10	Frozen river	13
Feb 12, 1996	2230–2345		3.42	Forest	17
Feb 14, 1996	1915–2115		4.05	Trail and road	17
Mean values (SD)					
Forest		2.7 (0.64)	4.0 (0.78)		
Trail, road, and frozen river		4.0 (0.06)	5.2 (0.99)		
Total		3.78 (1.23)			12.2 (3.1)

Discussion

According to Breitenmoser *et al.* (1992), the best way to evaluate the real distances covered by a radiocollared animal would be to track it parallel to a continuous radiolocation series, and compare the accumulated SLD with the real distance travelled in order to obtain a correction factor. We did that for wolves living in the dense temperate forests of Białowieża. We concluded that: (1) if wolves are radiolocated at 15-min intervals, the summed straight-line distances between radiolocations are good enough approximation of the actual distance travelled, given that the sample of radiolocations is large; (2) if wolves are radiolocated at 0.5 to 2-h intervals, the correction factor of 1.3 should be applied to SLD; and (3) within the range of 1–10 km, SLD can also be converted to ADT based on regression between those two estimates. Although this project was done in winter, the conditions were fairly mild and snow did not affect wolves activity. Thus, we think that the results are applicable to other seasons of the year, as well.

The proposed method for estimating ADT of wolves has its limitations. First, as a measure of the total movement activity of wolves, it is still an underestimate,

because we snowtracked directional movements of wolves and not the cases of their spatially concentrated bustling, eg around resting site or prey killed. Secondly, the conversion proposed here cannot be applied to data obtained by radiolocating wolves at intervals longer than a few hours.

The speed of wolves recorded by us (1.6–6.1 km/h) is lower than those reported for wolves travelling on the tundra (8.7 km/h) and the iced surface of a lake (8 km/h) (Mech 1970, 1994). Mech observed the wolves directly, whereas we radio-tracked and subsequently snowtracked them, so our results included situations when they might have paused or stopped for a short time. Furthermore, the wolves observed by Mech were travelling in the open terrain. In BPF, wolves also moved significantly faster on frozen rivers and forest roads than in the forest proper. The slower pace of wolves moving singly, as documented in this study, may be a result of greater vigilance and caution of wolves which temporarily broke away from their packs or different activites (eg searching).

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