



Opportunity and peril: how wolves use a dense network of forest roads

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Abstract

We investigated by snow tracking and GPS telemetry how wolves *Canis lupus* used a dense (4 km/km²) network of forest roads for travel and scent marking. Forty-six percent of wolf trails but only 4.6% of telemetry locations were on forest roads. Wolves used forest roads to travel fast and far across their home ranges but spent relatively little time on roads, especially on those with high traffic levels and during the time of highest human activity. The probability of scent marking was higher on roads than off-road and increased with traffic intensity on roads and close to junctions. Our findings suggest that wolves take advantage of the forest road infrastructure, while minimising human encounters by spatio-temporal avoidance of all roads, even those with negligible traffic. The ongoing expansion and improvements of the forest road network might lead to elevated costs for wolves associated with avoidance of humans and roads.

Keywords *Canis lupus* · Daily use · Forestry infrastructure · Movement · Scent marking

Introduction

Roads are an omnipresent and ever-expanding feature of all human-modified landscapes (Trombulak and Frissell 2000). High-traffic roads profoundly affect ecosystems by increasing wildlife mortality, changing animal abundance and behaviour, and modifying natural habitats (reviewed in Forman and Alexander 1998; Trombulak and Frissell 2000; Coffin 2007; Fahrig and Rytwinski 2009). Roads have been considered an important factor limiting distribution, dispersal and habitat quality for large carnivores, including wolves *Canis lupus* (Jędrzejewski et al. 2004; Potvin et al. 2005; Cullingham et al. 2016). Frequently used roads constitute hotspots of human-caused wolf mortality due to

traffic collisions, hunting, and poaching (Recio et al. 2018). Therefore, wolves tend to avoid high-traffic roads, especially during times of highest human activity (Theuerkauf et al. 2003, 2007; Lesmerises et al. 2013; Benson et al. 2015).

Roads less intensively used by humans can disturb ecosystems as well, but their ecological effects are subtler and more localised (Suárez-Esteban et al. 2013). Minor roads built for the purpose of forest management (hereafter: forest roads) contribute to forest fragmentation and degradation of forest ecosystems (Reed et al. 1996; Reimoser and Gossow 1996; Heilman et al. 2002; Saunders et al. 2002; Hall et al. 2003; Laurance et al. 2009). Although forest roads usually have too little traffic to pose a risk of wildlife–vehicle collisions, they may increase human disturbance and wildlife mortality by easing access for tourists, local inhabitants, hunters, and poachers (Wabakken et al. 2001; Person and Russell 2008). On the other hand, minor roads rarely used by humans may act as corridors for terrestrial animals and plants and enhance some ecosystem services (Haddad et al. 2003; Suárez-Esteban et al. 2013).

Studies on wolf response to forest roads showed contrasting results, from selection for movement and scent marking (Zub et al. 2003; Zimmermann et al. 2014; Dickie et al. 2017) to spatial and spatio-temporal avoidance depending on levels of human activity (Theuerkauf et al. 2003; Whittington et al. 2005). When travelling on roads, wolves move

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faster, cover larger daily distances, and encounter prey more often (James and Stuart-Smith 2000; Hebblewhite et al. 2005; Whittington et al. 2011; Dickie et al. 2017). Wolf response to roads with low traffic may vary according to wolf behavioural and social status, time of day and season (Zimmermann et al. 2014; Mancinelli et al. 2019). Moreover, minor roads can play an important role in scent communication, which serves as a main information medium for establishment and maintenance of wolf territories (Peters and Mech 1975; Rothman and Mech 1979; Zub et al. 2003). Forest roads and their junctions serve as conspicuous sites for scent marks, providing exposition and, therefore, enhancing the strength of scent signals (Rothman and Mech 1979; Asa et al. 1985). Several authors suggested that the response of wolves to roads depends also on road density, but the results varied among study areas (Whittington et al. 2005; Houle et al. 2010; Zimmermann et al. 2014).

In this study, we investigated the use of an exceptionally dense forest road network (4 km/km^2), the highest ever reported in wolf home ranges (Theuerkauf et al. 2007; Houle et al. 2010; Gurarie et al. 2011; Zimmermann et al. 2014; Dickie et al. 2017). Specifically, we used GPS telemetry and snow tracking to quantify (1) the daily distances travelled and the speed of wolves when on roads and when off-road, (2) the spatial and daily patterns of forest road selection for wolf travel and (3) scent marking in relation to traffic intensity.

Methods

Study area

We conducted our study in the western part (ca. 250 km^2) of the Lower Silesia Forest, western Poland (N $51^\circ 14.2' - 51^\circ 27.1'$, E $14^\circ 57.5' - 15^\circ 10.9'$, Fig. 1). Average annual temperature during the study was 10°C (daily mean temperature varying between -16 and 29°C), and snow cover (up to 10 cm deep) persisted for 7–71 days each winter (data provided by the Institute of Meteorology and Water Management). The area is flat (altitude $120 - 160 \text{ m a.s.l.}$) and is predominantly covered by forests managed by the Polish State Forests, a governmental organisation specialised in timber production. Forests are primarily composed of even-aged Scots pine *Pinus sylvestris* plantations, which are managed throughout the year by regular clearcutting, planting, and fencing of young stands (Bena 2012). To improve the efficiency of forest management and to enable access to logging sites, the forest is divided into rectangular compartments of $750 \times 375 \text{ m}$, most of which are surrounded by straight forest roads of 3–5 m width. Many such compartments are intersected by an additional road, which further divides tree plantations into squares of $375 \times 375 \text{ m}$. As a result,

the landscape consists of rectangular patches divided by a network of straight forest roads (Fig. 1). The density of forest roads is almost uniformly 4 km/km^2 throughout the study area. Forest roads are used throughout the year, primarily by motor vehicles of foresters and heavy-duty machinery for wood extraction and transportation. Additionally, traffic on forest roads increases seasonally due to hunting, antler collecting, as well as berry and mushroom picking. The public is not allowed to use motor vehicles on forest roads. Due to shallow snow cover, these roads are rarely ploughed. Only few public paved roads run through the study area, their density is 0.2 km/km^2 .

Wolves began recolonising the study area in the 1980s and the process accelerated in the 2000s (Wolsan et al. 1992; Nowak and Mysłajek 2016). During the first two winters of our study (2012/13 and 2013/14), the area was occupied by one wolf pack, which later split its territory into two. The numbers of wolves in the original and the two resulting packs were dynamic throughout the study, counting from four to eight individuals per pack in winter. Wolves prey predominantly on three species of ungulates: red deer *Cervus elaphus*, roe deer *Capreolus capreolus* and wild boar *Sus scrofa* (Nowak et al. 2011). Wolves are legally protected in Poland; therefore, there has been no legal wolf hunting in the area since 1995. However, wolf poaching is regularly reported in the whole country (Gula 2008; Gula et al. 2009; Nowak and Mysłajek 2016).

Classification of forest roads

We classified roads by visual inspection at crossroads. Based on this inspection and through 100 photo-trapping (Bushnell Trophy Cam HD Aggressor) sessions (50 in winter and 50 in summer) lasting 6–10 days, we functionally classified forest roads into three categories: (1) high-traffic road (density 0.4 km/km^2): maintained hard-surfaced gravel road used frequently for wood transportation, forestry activities and hunting (traffic 5–20 motor vehicles per day), (2) medium-traffic road (0.8 km/km^2): road with visible signs of frequent use and little vegetation covering the middle of road surface, used regularly (up to five vehicles per day, mean four vehicles per week), (3) low-traffic road (2.8 km/km^2): mostly passable by four-wheel drive cars but with most of the surface overgrown by low vegetation, used only sporadically when logging or hunting activities occurred in its proximity. Overall traffic on forest roads peaked during the working hours of forestry personnel (0700–1600 h) and people rarely drove on forest roads during the night. In the study area, sunrise was between 0444 and 0803 h and sunset between 1553 and 2118 h of local time. We did not include logging trails in the analysis, as they appear only temporarily during wood harvesting.

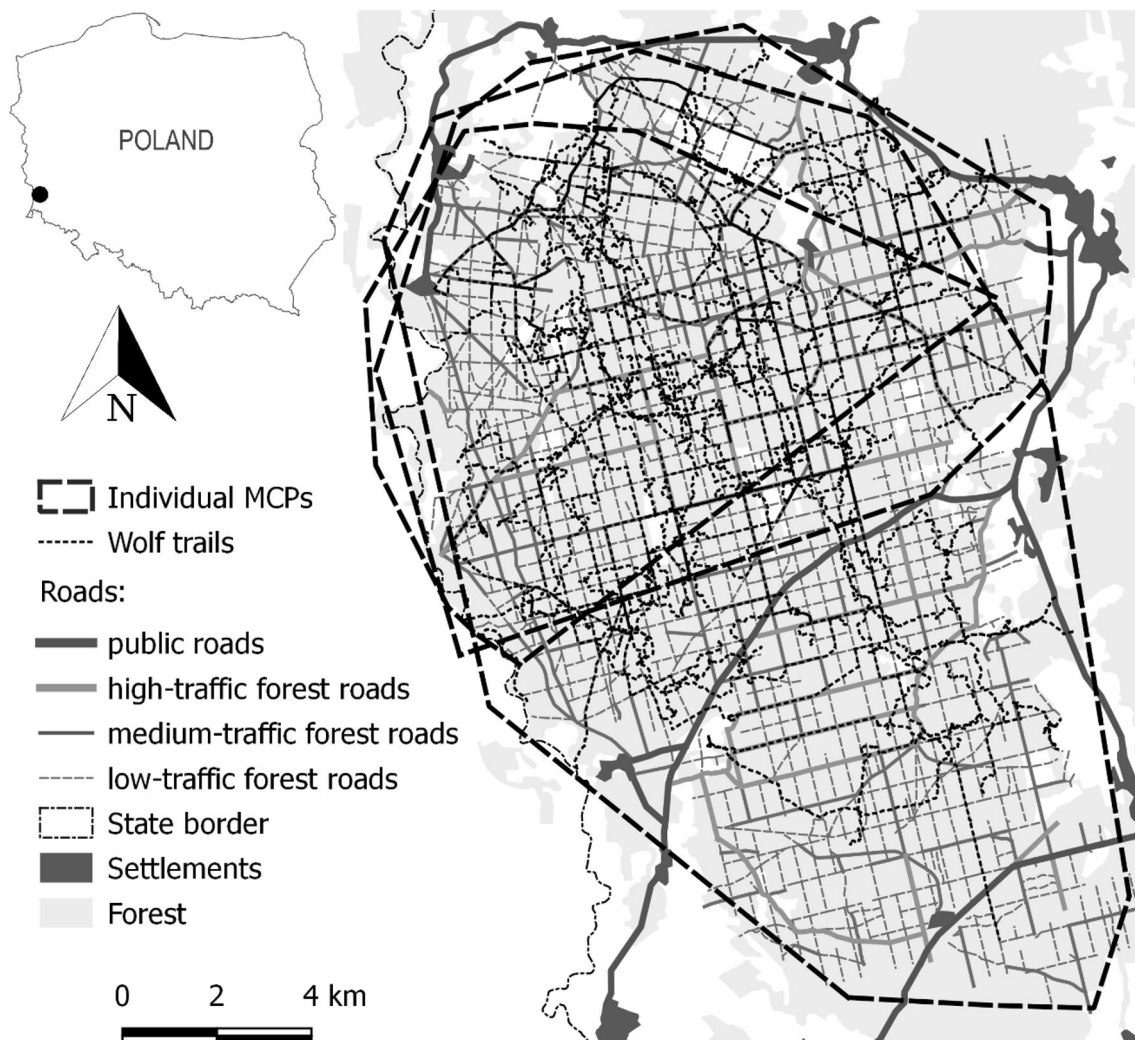


Fig. 1 Study area in the Lower Silesia Forest, Poland, with snow tracking trails (of three wolf packs) and 100% minimum convex polygons of three individuals followed by GPS telemetry (2963 locations)

Data collection

To investigate road selection using telemetry data, we captured three wolves using Belisle foot snares (Belisle Enterprises, Canada) and fitted them with GPS collars that also included VHF transmitters (LOTEK Wireless Inc., Canada). The three collared individuals belonged to two packs: a young female (monitored December 2012–January 2013) belonged to the original pack that later split its territory (see above), whereas a breeding female (January 2015–September 2016) and a young male (January–August 2016) belonged to the northern of the two packs created from the original pack (Fig. 1). There was no collared individual in the southern pack created by the split. The GPS collars obtained locations at various intervals: every 2 h for the young female, and at 11-h intervals for the other two

individuals with additional 1-h intervals for 1-week periods every month from December to April. The Polish authorities (General Directorate for Environmental Protection: DOP-OZGIZ.6401.08.12.2011.ls, and Regional Directorate for Environmental Protection in Gorzów Wielkopolski: WPN-I.6401.347.2015.JK) approved capture and handling protocols.

To investigate road selection using snow-tracking data, between December and March of 2012–2017, we located fresh wolf tracks when snow cover permitted. We used recent (obtained during the last 24 h) GPS locations and VHF signals of collared individuals to locate tracks. During winters when no individual was collared (2011/12, 2013/14 and 2016/17) or when tracking the non-collared pack, we searched for wolf tracks on forest roads, driving the road network of 1.5×1.5 km mesh size intersecting the whole

study area. In the latter case, snow tracking always started at places where wolves crossed roads. When we found fresh wolf trails, we followed them on foot while recording the tracks on a hand-held GPS (Garmin GPSmap 62 s) set to record locations at 20-m intervals. We followed the wolf trails in both directions as long as the tracks were visible, or only backwards in case of very fresh tracks.

Finally, to investigate road use for scent marking, during snow-tracking sessions, we recorded all wolf scent marks on the trail (urination, scratching, defaecation). We attributed wolf trails and scent marks to a road if they were located on the road surface or within 3 m from the road edge. To avoid overestimation of road use by wolves, we excluded from the analyses trails that were shorter than 1 km or entirely on roads.

Data analysis

To analyse road selection using GPS-telemetry data, we applied a generalised linear model (GLM) with binomial distribution and logit-link function in R 3.6.1 (R Core Team 2019) using a binary response variable (1: wolf telemetry location, 0: random point). We generated random points within the seasonal (winter: December–March, spring–autumn: April–November) home ranges (100% minimum convex polygons) of each GPS-collared individual. For each wolf and each season, we used the same number of random points as there were telemetry locations (2,963 random points in total). We included as fixed variables the habitat type as a categorical factor with four levels (0—off-road, 1—low-traffic road, 2—medium-traffic road, 3—high-traffic road) and period of day as a nominal factor (working hours of forestry personnel: 0700–1600 h, off-work: the remaining time). We considered a telemetry location or a random location as on a road (road types 1–3) if it was within a 15-m buffer of the midline of the road, which corresponds to the location accuracy of the GPS collars model that we used (Di Orio et al. 2003).

To analyse road selection using snow-tracking data, we applied a GLM the same way as described above, but without the variable “period of day”. We generated wolf trail points every 218 m (to achieve the same number as of telemetry locations) along the wolf trails recorded during snow tracking (2963 wolf trail points) and the same number of random points inside the minimum convex polygon encompassing all the wolf trails.

To assess the daily distances travelled by wolves, on roads and off-road, we used telemetry data obtained during 128 days of intensive sampling of GPS locations (1-h or 2-h intervals) in winter. We corrected distance travelled by dividing the cumulative straight-line distances between consecutive wolf locations by correction coefficients provided by Mills et al. (2006): 0.68 and 0.60 for 1-h and 2-h GPS fix

intervals, respectively. To assess wolf travel speed on roads and off-road, we combined telemetry data (proportion of time spent on roads) with snow-tracking data (proportion of distance on roads).

To analyse wolf use of roads for scent marking, we used GLM with binomial distribution and logit-link function in R 3.6.1 to test whether the probability of scent marking was related to its location (on roads or off-road, road category) and distance to junctions. We included a binary response variable (scent mark location/random point along wolf trail) and three fixed variables: habitat type (0—off-road, 1—low-traffic road, 2—medium-traffic road, 3—high-traffic road), distance to the closest junction (m) and their interaction. We performed the analyses separately for each type of scent marking (scats, urination, scratching). We generated the random points along wolf trails in numbers equal to numbers of scent marks of each type.

All spatial analyses were performed in QGIS version 3.2.3 (Quantum GIS Development Team 2018). We used model selection based on the Akaike Information Criterion (AICc) to rank models in the MuMIn package (Bartoń 2019) in R 3.6.1.

Results

Daily patterns of road use

We obtained 2963 GPS locations of wolves, 2009 in winter (488 of young female, 989 of breeding female, 532 of young male) and 954 during the rest of the year (breeding female: 732, young male: 222). The breeding female and her son spent most of the time separately; only 28% of telemetry locations obtained simultaneously for the two individuals ($n=396$) were within a 300-m distance from each other. Only 4.6% of all wolf telemetry locations were on roads (Table 1). The probability of a wolf location was best explained by the type of habitat and its interaction with the time of day (Table 2). Thus, based on telemetry data, wolves strongly avoided roads, especially medium- and high-traffic roads (Fig. 2a). The avoidance of medium- and high-traffic roads was stronger during the working hours of forestry personnel; whereas, period of day had no effect on the use of low-traffic roads (Fig. 2a).

Road use and selection based on snow tracking

We collected snow tracking data from 646 km of wolf trails in 74 continuous tracking sessions (1.9–36.5 km) over the course of six winters (2011/12–2016/17). Most of the trails (48 tracking sessions, 424 km, winter seasons 2011/12–2013/14) belonged to the original pack, which later split its territory (see above). Twenty-two tracking sessions

Table 1 Wolf road use for travel and scent marking based on 646 km of snow tracking of three wolf packs and GPS telemetry of three collared wolves in the Lower Silesia Forest, Poland, in 2012–2017

	Forest roads			Off-road
	Low-traffic	Medium-traffic	High-traffic	
Proportion of wolf trail	0.260	0.124	0.077	0.539
Proportion of telemetry locations				
Winter ($n=2009$)	0.040	0.011	0.003	0.946
Spring–autumn ($n=954$)	0.026	0.001	0.001	0.972
Scent marking intensity (km^{-2})				
Urinations ($n=769$)	1.439	2.619	1.912	1.191
Scratching ($n=278$)	0.482	1.235	0.926	0.431
Scats ($n=231$)	0.315	0.547	0.745	0.358

Table 2 Models explaining the probability of a wolf location in the Lower Silesia Forest, SW Poland, ranked by AICc

Model structure	AICc	ΔAICc	ωAICc
Habitat + Daytime \times Habitat	7890.1	0.00	0.988
Habitat	7898.9	8.78	0.012

The variables included in models were: habitat (off-road as a reference, and forest road of low, medium, and high traffic intensity) and interaction between habitat and daytime (working hours of forestry personnel: 7 am–4 pm, off-work as a reference)

(147 km, winter seasons 2014/15–2017/18) belonged to the after-division northern pack with the GPS-collared breeding female and young male. Four tracking sessions (75 km, winter seasons 2014/15–2017/18) were located in the after-division southern pack's territory (without GPS-collared individuals). Out of 74 tracking sessions, 44 originated from locations obtained via telemetry (22 tracking sessions of the original pack and 22 of the northern pack with two collared individuals). Almost half of the wolf trails were located on forest roads (Table 1). Based on snow-tracking data, wolves strongly selected roads (Table 3). Wolves preferred to travel on forest roads of medium and high traffic levels (Fig. 2b).

Daily travel distances and speed in winter

Wolves travelled on average 20.1 ± 1.8 km/day (mean \pm 95% CI), which, considering an average of 46% of length travelled on roads in winter, corresponds to 9.3 ± 0.8 km on roads daily. As wolves spent only 5.4% of time on roads in winter (Table 1), this corresponds to an average of 1.3 h per day. Wolf locations appeared on high-traffic roads on only 0.8% of the days when telemetry locations were obtained (on average 4 min per day), on medium-traffic roads in 3.1% of the days (16 min per day), and on low-traffic roads on 12.3% of the days (58 min per day). Their mean speed on roads was 7.1 km/h and was highest on high-traffic roads (21.5 km/h),

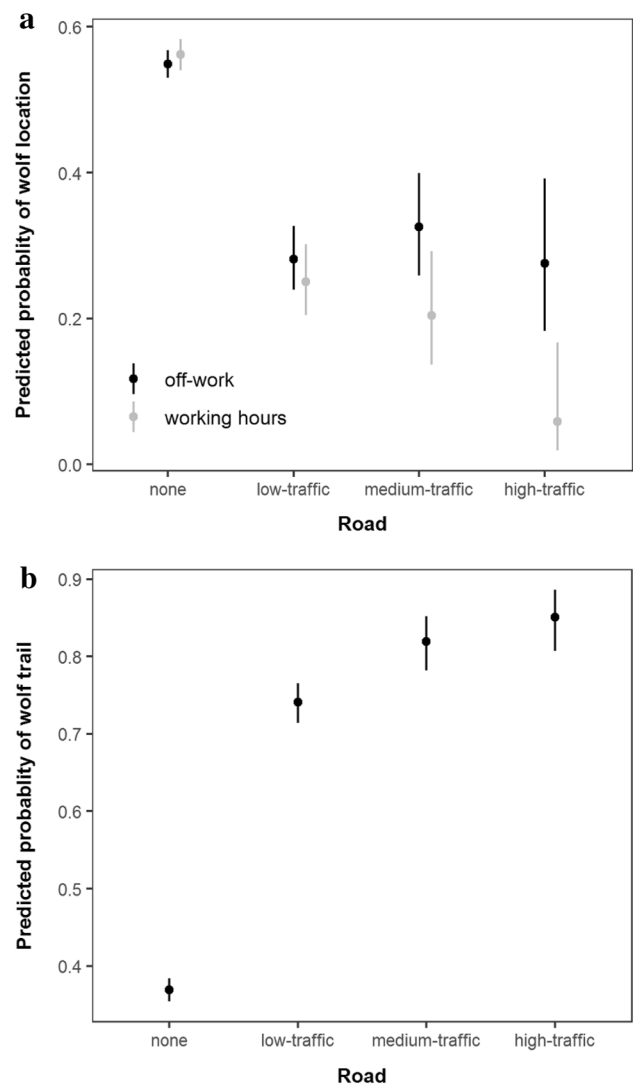


Fig. 2 Relative probability predicted by GLM (with 95% CI) of **a** a wolf telemetry location (during the working hours of forestry personnel and during the rest of the day) and **b** a wolf snow trail point location to be off-road or on a forest road (low, medium and high traffic intensity) in the Lower Silesia Forest, western Poland in 2012–2017 ($n=2963$ telemetry locations of three individuals and 646 km of snow tracking)

Table 3 Results of GLM describing the probability of a wolf trail point location in relation to habitat (off-road as a reference or forest road of low, medium and high traffic intensity) on 646 km of snow tracking of three wolf packs in Lower Silesia Forest, western Poland

Habitat	Estimate	95% CI	<i>p</i>
Low-traffic road	1.59	0.16	<0.001
Medium-traffic road	2.05	0.26	<0.001
High-traffic road	2.28	0.31	<0.001

intermedium on medium-traffic roads (9.4 km/h) and lowest on low-traffic roads (5.4 km/h).

Scent marking

During snow tracking, we found 1,278 wolf scent marks, of which 71% were located on roads. Average scent-marking intensity was 2.0 scent marks per km of wolf trail, and 1.1 and 3.1 scent marks/km off-road and on roads, respectively (Table 1). Probability of marking with scats was best explained by the type of habitat; whereas, the probability of urination or scratching was also affected by the distance to the closest crossroad and the interaction of these variables (Table 4). Thus, wolves selected roads for scent marking and the probability of marking with scats increased with traffic intensity on roads (Fig. 3). Wolves were more likely to scent mark with urine and by scratching close to junctions when marking on roads (Fig. 4).

Discussion

Wolves in our study area used forest roads to travel fast and far across their home ranges but spent relatively little time on roads. Almost half of the trail length (revealed by snow

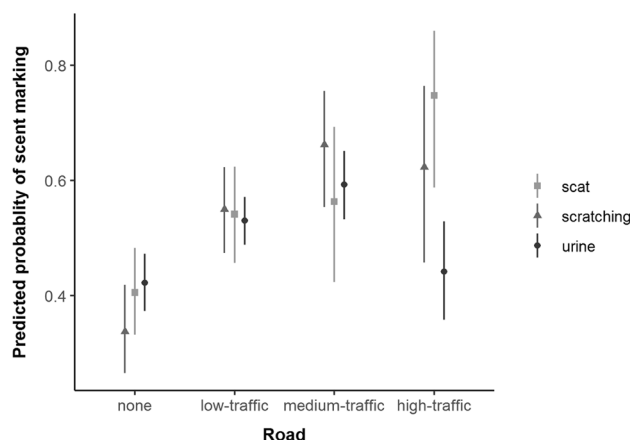


Fig. 3 Relative probability predicted by GLM (with 95% CI) of a wolf scent marking (scats, urine and scratching) in relation to habitat (off-road or forest road of low, medium and high traffic intensity) in the Lower Silesia Forest, western Poland in 2012–2017 (*n* = 1278 scent marks)

tracking) was along roads, which is a higher proportion than in other studies, conducted in areas of lower road density in Canada and Poland (Whittington et al. 2005; Pirga 2011). However, our telemetry results indicated that the proportion of time that wolves spent on roads was similar or lower than reported in areas of lower road density (up to 1.5 km/km²) in Canada, Scandinavia and Finland (Gurarie et al. 2011; Zimmermann et al. 2014; Dickie et al. 2017). This seeming contradiction between wolf preference for roads based on telemetry and snow tracking illustrates how different methods may yield opposing results in wildlife studies. Snow tracking does not account for time; whereas, telemetry data require high-frequency acquisition rates to capture and depict behavioural details such as resting and use of roads. Therefore, while wolves used the roads for fast movement,

Table 4 Ranking of models explaining the probability of wolf scent marking by with scats, urination and scratching in the Lower Silesia Forest, SW Poland

Model structure	AICc	ΔAICc	ωAICc
Scats			
Habitat	576.2	0.00	0.63
Habitat + Dist. to crossroad	578.3	2.02	0.23
Habitat + Dist. to crossroad + Habitat × Dist. to crossroad	579.1	2.87	0.15
Urinations			
Habitat + Dist. to crossroad + Habitat × Dist. to crossroad	1845.2	0.00	1.00
Habitat + Dist. to crossroad	1907.8	62.59	0.00
Habitat	1911.5	66.27	0.00
Scratching			
Habitat + Dist. to crossroad + Habitat × Dist. to crossroad	623.7	0.00	0.99
Habitat + Dist. to crossroad	636.1	12.39	0.01
Habitat	651.8	28.12	0.00

The variables included in models were: habitat (off-road as a reference, low-traffic road, medium-traffic road), distance to crossroad and their interaction

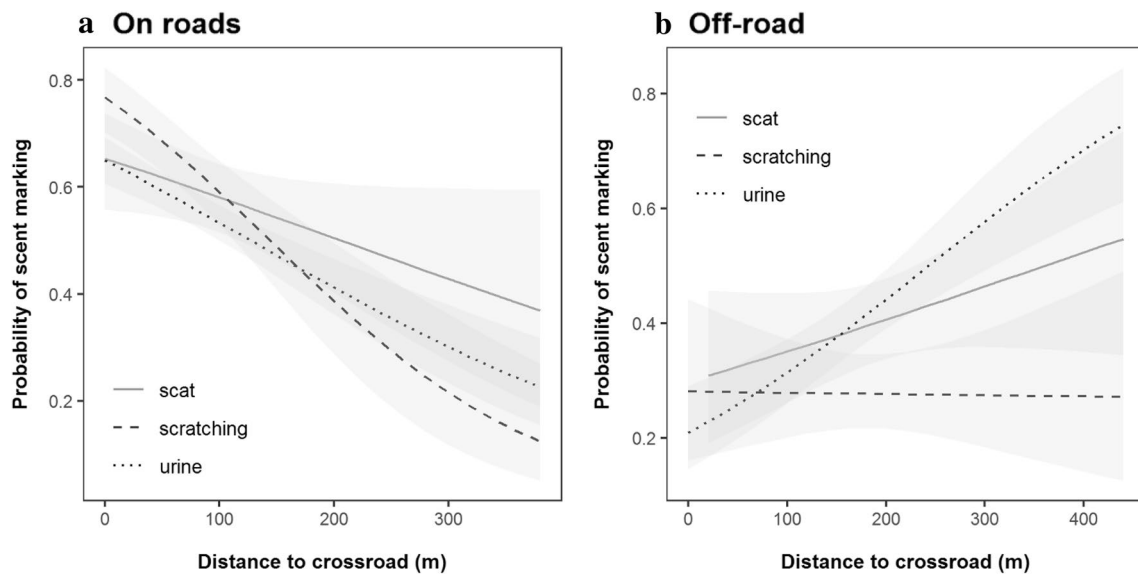


Fig. 4 Relative probability predicted by GLM (with 95% CI) of a wolf scent marking (scats, urine and scratching) in relation to distance to the closest crossroad: **a** scent marks on roads, **b** scent marks

off-road in the Lower Silesia Forest, western Poland in 2012–2017 ($n = 1278$ scent marks)

they preferred to rest or feed away from roads, hence the relatively higher numbers of locations off-road, which was also observed by Zimmermann et al. (2014).

Wolf use of forest roads in our study was related to traffic level and period of day. The strong preference of high-traffic roads detected by snow tracking and higher speed on that roads can be explained by the ease of travel on roads (Dickie et al. 2017). The very strong and time-dependent avoidance of high-traffic roads revealed by telemetry was likely an effect of higher risk of encountering humans on roads, especially during working hours of forestry personnel. Wolves preferred low-traffic roads during working time of forestry personnel and selected high-traffic roads at times of low human activity.

The dense road network in our study area had a strong impact on wolf scent-marking behaviour. Wolves increased rates of all three types of scent marking on roads, contrary to previous studies, in which wolves increased only scratching rates (Zub et al. 2003) or scratching and urination rates (Peters and Mech 1975) on roads. Road junctions seemed to play an important role for urine marking and scratching in our study area; however, contrary to other studies, wolves did not select junctions for scat deposition (Peters and Mech 1975; Zub et al. 2003; Barja et al. 2004). Moreover, scent marking intensity also varied in relation to road category, as wolves preferred to scratch and deposit scats on high-traffic roads. Our study is the first to document differences in response to roads relatively rarely used by humans based on variation in traffic (<20 vehicles/day).

Wolves in our study area took advantage of dense road network for travel and scent marking while avoiding spending time on them to minimise the probability of encountering humans. Similar ambivalent responses towards infrastructure have been suggested as one of the key factors for the recent wolf recovery in human-dominated landscapes (Zimmermann et al. 2014). The adjustment of the daily pattern of road use to human activity is another example of the behavioural plasticity of wolves in avoiding human encounters. It seems that although wolves in our study area have not been legally hunted for over 20 years, they still might perceive forest roads as sites of elevated risk. Since there is no wildlife mortality caused by collisions with vehicles on forest roads in our study area, we believe that illegal wolf shooting, which is regularly reported in Poland (Gula 2008; Gula et al. 2009; Nowak and Mystajek 2016), contributes to maintaining this behaviour.

The avoidance of roads of negligible traffic suggests that the effect of roads on wolf behaviour is not solely a function of the level of human activity (Hebblewhite and Merrill 2008). Our results suggest that in areas of very high road density, even roads sporadically used by humans, may influence wolf behaviour. Development and improvement of forestry infrastructure, especially of forest roads, in Poland and several other European countries, have accelerated since the transition to the market economy, and have been fostered further by European funds since the admission to the European Union. The ongoing expansion and improvement of the forest road network might lead to increased human-caused mortality and elevated costs of the avoidance of humans and

roads. Therefore, in densely populated countries with fragmented forests, like Poland, forest roads should be considered in wolf habitat assessments, and formally existing bans for non-authorized vehicles on forest roads should be reinforced. Finally, our results show that the high-traffic forest roads offer the highest probability to find wolf scats, which may be helpful in the collection of non-invasive material for molecular analyses (Waits and Paetkau 2005).

Limitations of the study

This study has several limitations related to the small sample size (only three individuals and three packs). First, we were not able to address the inter-individual differences in road use, especially the influence of social status on wolf behaviour, which can be an important determinant of wolf response to roads (Zimmermann et al. 2014). Second, the small number of locations during the spring–autumn period likely contributed to the lack of seasonal patterns in road use and selection in our study. Third, the small study area (and uniform road density within) prevented us from addressing the relationship between road density and road use within wolf home ranges and among wolf packs.

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Compliance with ethical standards

Conflict of interest All authors have participated in (a) conception and design, or analysis and interpretation of the data; (b) drafting the article or revising it critically for important intellectual content; and (c) approval of the final version.

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