Forest Ecology and Management 497 (2021) 119511

Contents lists available at ScienceDirect

Forest Ecology and Management

journal homepage: www.elsevier.com/locate/foreco

Wolves under cover: The importance of human-related factors in resting site selection in a commercial forest

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ARTICLE INFO

Keywords:
Canis lupus
Resting behaviour
Avoidance of humans
Forest roads

ABSTRACT

We investigated winter selection of resting sites by wolves in a commercial pine forest to test if roads, settlements, and type of forest influenced the resting behaviour of wolves during the day and at night. At the landscape scale, wolves selected resting sites that were farther from settlements, public roads and high-traffic forest roads than random points. At the fine scale, wolves chose sites that were more concealed and farther from the closest forest road than random points. During the day, wolves tended to rest in thickets and forest with understorey, whereas at night they rested in more open habitats. The concealment of resting sites was higher when wolves rested closer to high-traffic forest roads and during the day. Our results indicate that certain forestry practices enhance concealment opportunities and might therefore be beneficial for wolves

1. Introduction

In recent years, large carnivores have been recolonising human-dominated landscapes of Europe, and the wolf *Canis lupus* has so far been the most successful species in densely populated areas (Chapron et al. 2014; Gula et al. 2020). Sharing the landscape with humans necessitates large carnivores to adjust behaviourally to minimise predation risk (Karlsson et al. 2007; Ordiz et al. 2011; Smith et al. 2017). One mechanism of this avoidance is habitat selection, which occurs at different spatial and temporal scales (Cristescu et al. 2013; Karlsson et al. 2007; Ordiz et al. 2011). For instance, carnivores locate cores of their home ranges far from areas of high levels of human activity (Bouyer et al. 2015a; Nellemann et al. 2007), and within their home ranges, they spatio-temporally segregate from humans (Bojarska et al. 2020; Martin et al. 2010; Theuerkauf 2009; Theuerkauf et al. 2003a, 2007). Avoidance of people may be essential during certain life phases and activities, especially when the animals are most vulnerable. Thus, avoiding humans seems particularly important when raising young, denning or resting (Elfström et al. 2008; Sazatornil et al. 2016; Theuerkauf et al. 2003b; White et al. 2015).

Resting is vital for the functioning of the neural system and maintaining the individual's performance (Cirelli and Tononi 2008). While resting, however, animals are vulnerable to predation, which makes the choice of a safe resting site crucial for survival (Hamilton et al. 1982). Thus, resting animals tend to hide in dense vegetation, which offers concealment from predators (Moreno et al. 1996; Mysterud and Østbye 1999) including humans, especially at times and places of high human activity (Ordiz et al. 2011; Podgórski et al. 2008). Another common strategy to minimise risk while resting is to choose a location far away from places where the risk of encountering humans is high (Bouyer et al. 2015b). As wolves spend up to fifty percent of their time resting (Theuerkauf et al. 2003c), the selection of resting sites appears to be particularly important. When resting during the day, wolves select sites located far away from main roads and settlements and avoid open habitats (Llaneza et al. 2016; Theuerkauf et al. 2003b; Zimmermann et al. 2014). Selection of nocturnal resting sites seems less affected by the proximity of roads than that of diurnal resting sites (Zimmermann et al. 2014), though the preference for night resting sites in wolves has been poorly studied, generally on the grounds that wolves are presumed to rest mostly during the day (Llaneza et al. 2016). When wolves relocate after being approached by humans, they select more concealed sites for resting but when not disturbed, they may prefer to rest at sites with a

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https://doi.org/10.1016/j.foreco.2021.119511
Received 29 March 2021; Received in revised form 30 June 2021; Accepted 4 July 2021
Available online 23 July 2021

good overview to more easily detect potential intruders (Wam et al. 2012). There have been no studies considering potential diel differences in fine-scale habitat selection, including visibility, by resting wolves.

In this study, we investigated the selection of resting sites by wolves in a heavily modified commercial forest at two spatial scales. First, we investigated which landscape characteristics affect resting site selection in wolves. Second, we examined the role of concealment, habitat type, and distances to forest roads in resting site selection during the day and at night. Based on research conducted in other areas (Llaneza et al. 2016; Theuerkauf et al. 2003b; Zimmermann et al. 2014), we hypothesised that at the landscape scale wolves prefer to rest far away from settlements, public roads and busy forest roads. At the fine scale, wolves should choose sites that are more concealed and farther from roads, and concealment should be more important during the day and in sites closer to sources of potential human disturbance.

2. Materials and methods

2.1. Study area

The study area (ca. 250 km^2) is located in the western part of the Lower Silesia Forest, southwestern Poland (N 51°14.2′ – 51°27.1′, E 14°57.5′ – 15°10.9′). The forest here consists primarily of Scots pine *Pinus sylvestris* plantations, which are managed by clearcutting (clear cuts up to 6 ha). Renewing of the forest is most often done by replantation of single-species stands (mostly pine) but sporadically by natural regeneration. The landscape is composed of rectangular patches of even-aged forest stands, divided by a network of forest roads with a density of 4 km/km^2, used mostly during the day for logging activities and not open for public motor vehicles (Bojarska et al. 2020). Some older forest stands have an understorey of naturally growing young trees, mostly pines. The density of public roads is 0.2 km/km^2. There are 13 villages and small towns situated mostly at the periphery of the study area, human population density is 25 inhabitants/km^2.

As in most of Poland, wolves were persecuted and nearly exterminated in the region until the 1970s but have been recovering since the 1980s, and breeding has been continuously observed since the 1990s (Gula et al. 2020). Currently, the entire complex of the Lower Silesia Forest is inhabited by 7–8 wolf packs, and wolf density is about 2.8 individuals/100 km^2 (European Commission 2018). At the beginning of the study, the study area was the home range of one wolf pack (7 individuals), which later split its territory into two of 2–8 and 4–7 individuals, depending on the year (Bojarska et al. 2020). Wolves in the study area prey on red deer *Cervus elaphus*, roe deer *Capreolus capreolus* and wild boar *Sus scrofa* (Bojarska et al. 2017).

2.2. Data collection

We exclusively analysed wolf resting sites that we verified in the field from December to April in 2012 –2016. We found resting sites either by snow tracking three wolf packs (of 4–5, 7 and 8 individuals) or during ground truthing of 1435 GPS locations of three radiocollared wolves belonging to the first two of these packs.

We located fresh wolf tracks with the help of recent GPS locations and VHF signals of collared individuals. During winters when no individual was collared or when tracking the non-tagged pack, we searched for wolf tracks while driving on forest roads. We then followed wolf trails on foot for 2 – 36.5 km (average tracking length: 8.3 km, 650 km in total). While following wolf trails in the snow, we searched for wolf beds (appropriately sized oval spots of compressed or melted snow). We classified a spot as a wolf resting site only when we found wolf hairs (N = 68). To identify wolf resting sites based on telemetry data, we inspected (not later than three days after the GPS fixes) 353 sites with at least two consecutive GPS locations (obtained every 1 or 2 h) at the same spot. We used trained dogs, especially when snow was absent, to find the beds and searched for wolf hairs to confirm they belonged to wolves. During the inspection of the sites with at least two consecutive wolf telemetry locations, we found 211 wolf resting sites, 79 belonging to the pack of 4–5 wolves and 132 to the pack of 7 wolves. We estimated the duration of resting bouts as the time between the first and the last of consecutive GPS fixes at a confirmed resting site plus the duration of one interval between GPS fixes (1 or 2 h).

2.3. Wolf resting site selection at the landscape level

To analyse which parameters affected wolf resting site selection at the landscape level, we used all resting sites identified during snow tracking or ground truthing (N = 279). We compared the resting sites to locations (n equal to the number of resting sites) generated randomly within the study area (defined as the 100% minimum convex polygon, MCP, encompassing all wolf GPS telemetry locations and wolf trails obtained via snow tracking). We used a generalized linear model (GLM) with binomial distribution and logit-link function in R 3.6.2 (R Core Team 2019) and a binary response variable (1: resting site, 0: random point). The explanatory variables included: distance to closest settlement, to public paved road and to high-traffic forest road (see Bojarska et al. 2020 for a detailed explanation of the road categorisation), measured with QGIS Desktop version 3.2 (Quantum GIS Development Team 2018).

2.4. Wolf resting site selection at the fine scale

To assess wolf habitat selection at the fine scale, we used resting sites from telemetry locations in order to be able to assign a time of day. When resting sites consisted of more than one bed, we randomly chose one bed for habitat analyses. We identified 137 wolf resting sites that could be classified either as diurnal (60 sites) or nocturnal (77 sites). We classified resting events as diurnal (when the whole resting period was between sunrise and sunset) or nocturnal (from sunset to sunrise) based on local sunrise and sunset times (https://www.sunearthtools.com/solar/sunrise-sunset-calendar.php#top). Eighty-two sites belonged to the pack of 7 wolves before the split and 55 sites to the pack of 4–7 wolves created after the split. We found more than one bed in most of the sites, indicating that they were used by more than one individual.

For each of the 137 resting sites, we generated a reference location at a 100-m distance (in a random direction) from the resting site. We assessed visibility in the field as maximal sighting distance (measured with a tape) in four cardinal directions from an observer to a vertical bicolour cylinder (46 cm high, 27 cm diameter) positioned onto the site, following the method of Ordiz et al. (2011) for brown bears, appropriately adjusted to fit the size of a wolf. Next, using a digital map of forest roads, we measured the distance of each resting site to the closest forest road of any traffic level in QGIS. We compared the characteristics of resting sites with their reference points using a generalised linear mixed model (GLMM) with binomial distribution and logit-link function in the lme4 package (Bates et al. 2015) in R 3.6.2. We used a binary response variable (1: resting site, 0: reference point). The explanatory variables included the visibility (averaged over four directions), the distance to the closest forest road, the wolf pack identity and the identity of the resting site with its reference point as a random factor.

For fine-scale selection, we additionally assessed the habitat type for resting sites and their reference sites in the field. We classified the habitat within a 50-m radius into five categories: (1) open habitats (meadows and very young forest plantations with trees up to 50 cm high), (2) thicket (young tree plantation, not thinned or after the first, limited thinning, trees still growing in visible rows), (3) young forest stands (trees up to 12 m high, after first intensive thinning operation), (4) medium or mature forest stand (>12 m high, after last thinning) with no understorey and (5) medium or mature forest stand with understorey. Typically, the understorey consisted of patches of young pines (up to 5 m tall) naturally growing under the canopy of older trees.

2.5. Mapping the probability for resting

We generated a map of probability of wolf resting within the study area using the predictions of the landscape-scale model and the distances to the closest forest road from the fine-scale model (see above). We generated separate raster layers based on modelled distances from settlements, public roads, high-traffic forest roads and closest forest road using the Euclidean Distance function in the Spatial Analyst extension of ArcGIS ver. 10.8 (ESRI 2019). Next, we reclassified each raster according to probability of wolf resting assigned by the relevant model. The final raster's cell value comprised the product of multiplied values of all probabilities.

2.6. Factors affecting concealment of resting sites

To test whether wolves chose more concealed places when resting during daytime, we only considered resting sites but not their reference sites. We used visibility as dependent variable in a linear model (LM) in R. We excluded the resting sites that lasted over both day and night from further analyses. Explanatory variables consisted of distance to forest roads of high traffic intensity, diel time (day or night) and the wolf pack identity.

For all the analyses, we ranked the models based on Akaike Information Criterion (AICc) in the MuMIn package (Barton and Barton 2015) and considered the models with ΔAICc values < 2 (Burnham and Anderson 2002).

3. Results

3.1. Wolf resting site selection at the landscape level

Resting sites were farther away from settlements (on average 2.83 ± 0.12 km; random points: 1.99 ± 0.15) and public roads (2.58 ± 0.14 km; random points: 2.30 ± 0.16), but not high-traffic forest roads (1.00 ± 0.11 km, random points: 0.95 ± 0.12), although the probability of resting sites increased with distance to all three human-made structures

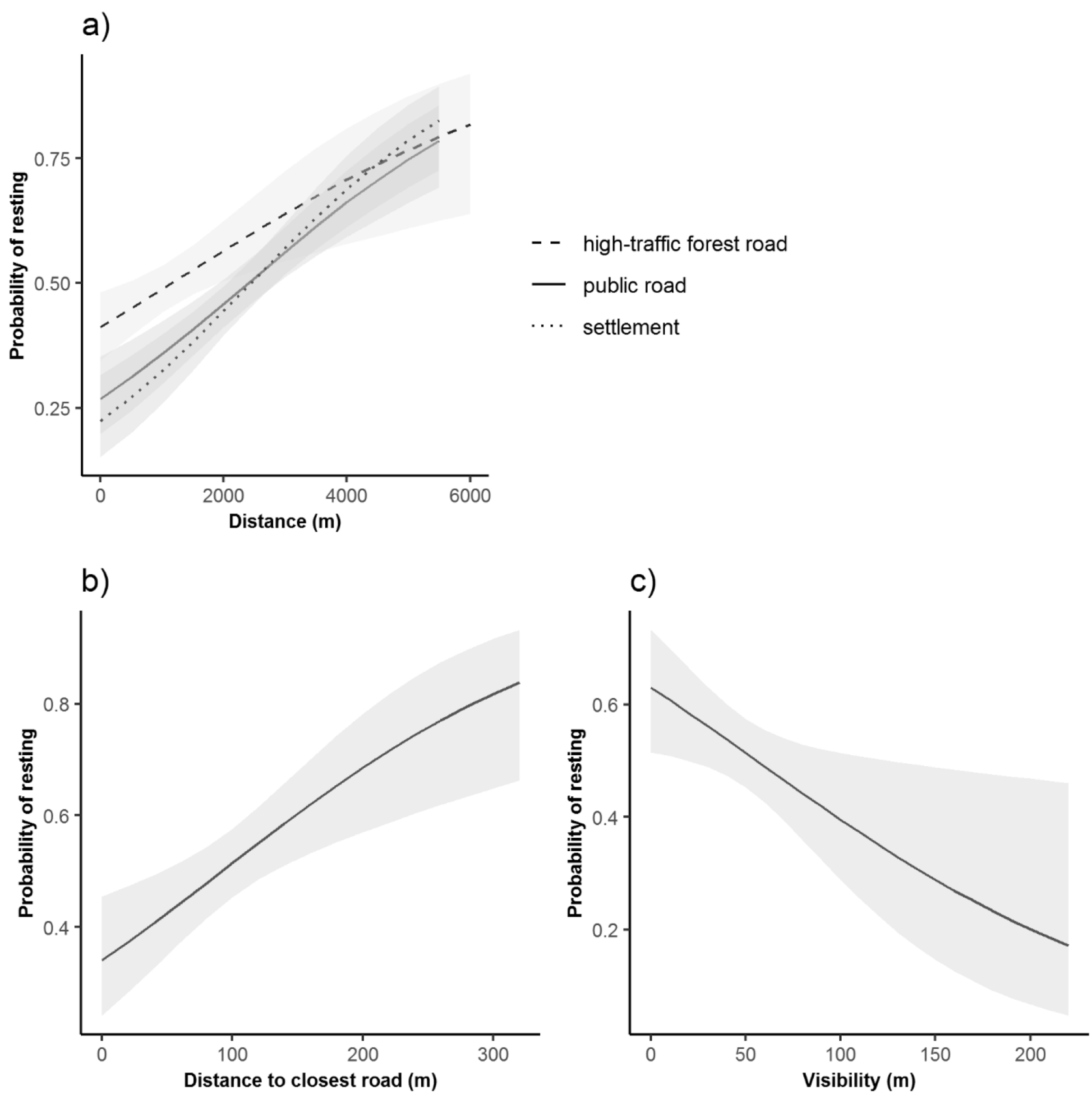

Fig. 1. Probability (GLM) of occurrence with 95% confidence bands of wolf resting sites (a) in relation to roads and settlements at the landscape scale (N = 279 resting sites and 279 random sites), and (b) in relation to the closest road and (c) in relation to visibility at the fine scale (N = 137 resting sites and 137 reference sites) in the Lower Silesia Forest, SW Poland.

(Fig. 1a, Fig. 2, Table 1). All three parameters (distance to settlements: sum of ω = 1.0; distance to public roads: sum of ω = 1.0, distance to forest roads of high traffic: sum of ω = 0.97) were included in the best model predicting the occurrence of wolf resting sites (Table 1).

3.2. Wolf resting site selection at the fine scale

The best predictors of wolf resting sites at the fine scale were the distance to the closest forest road (113 ± 10 m, reference sites 87 ± 10 m, sum of ω = 0.99) and visibility (45 ± 5 m, reference sites 55 ± 5 m, sum of ω = 0.75) (Table 2). The probability of resting increased with

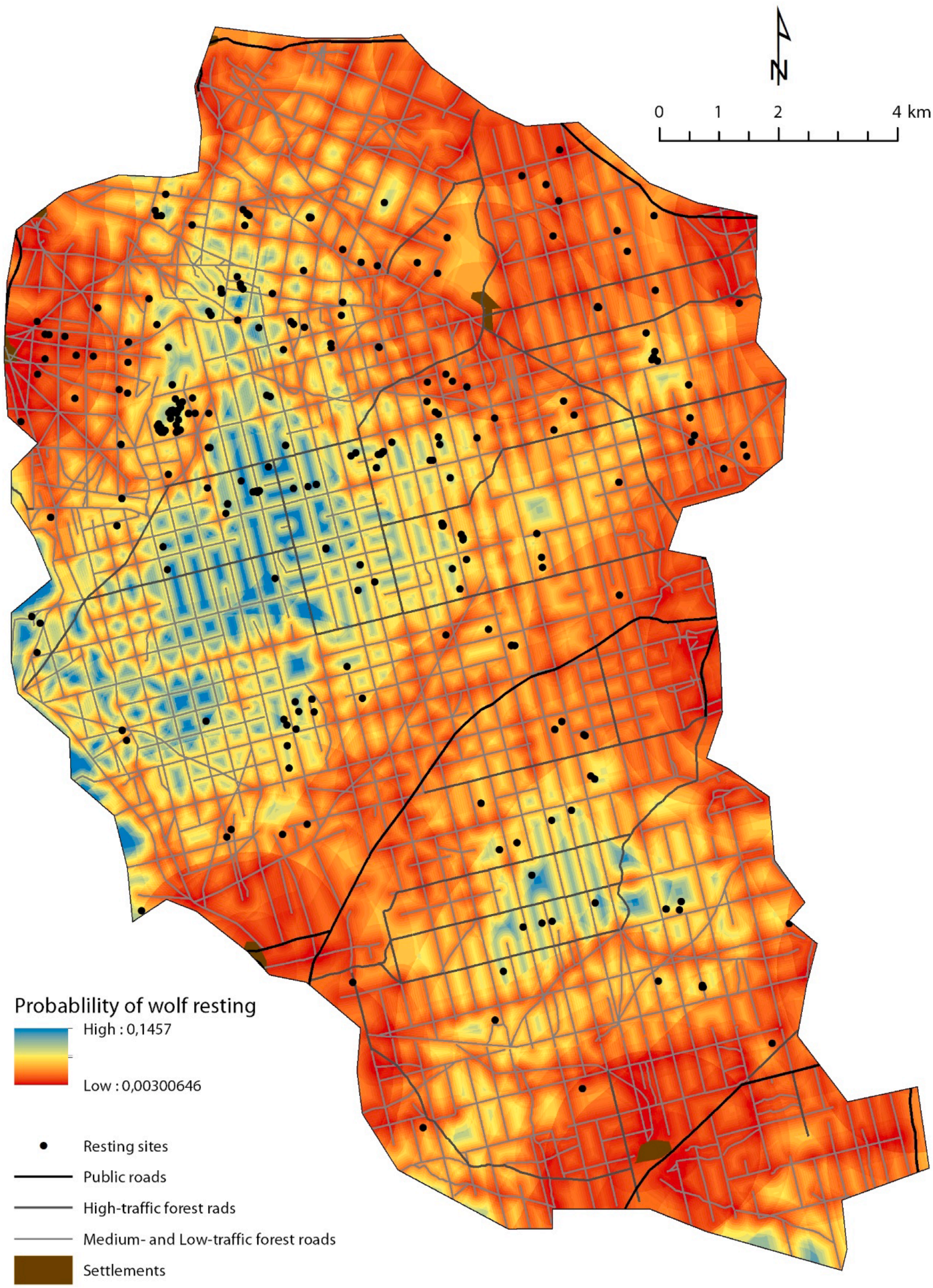

Fig. 2. Spatial distribution of wolf resting sites (N = 279) during snow tracking and inspection of GPS-telemetry locations and probability of wolf resting (generated by GLMs) based on the distances from settlements, public roads, and forest roads in the Lower Silesia Forest, SW Poland.

Table 1
Models (GLM) explaining the probability of a wolf resting at the landscape scale in the Lower Silesia Forest, SW Poland, ranked by AICc (N = 279 wolf resting sites and 279 random sites). The variables included in models were distance to the closest settlement (parameter estimate: 0.0005, SE = 0.00009), public paved road (parameter estimate: 0.0004, SE = 0.0007) or high-traffic forest road (parameters estimate: 0.0003, SE = 0.0001). We present only models with ωAICc > 0.01.

Model structure	AICc	ΔAICc	ωAICc
Settlement + Forest Road + Public Road	671.6	0.00	0.986
Settlement + Public Road	680.1	8.49	0.014

Table 2
Models (GLM) explaining the probability of a wolf resting in relation to visibility (parameter estimate: −0.008, SE = 0.004), distance to the closest forest road (parameter estimate: 0.007, SE = 0.002) and the wolf pack identity (parameter estimate: −0.07, SE = 0.26) at the fine scale in the Lower Silesia Forest, SW Poland, ranked by AICc (N = 137 wolf resting sites and 137 reference sites). We present only models with ωAICc > 0.001.

Model structure	AICc	ΔAICc	ωAICc
Forest Road + Visibility	359.7	0	0.536
Forest Road + Visibility + Pack	361.7	1.98	0.199
Forest road	361.9	2.15	0.183
Forest road + Pack	363.8	4.06	0.071
Visibility	368.3	8.53	0.008
Pack + Visibility	370.3	10.57	0.003

distance to the closest forest road and decreasing visibility (Fig. 1b,c, Fig. 2). During the day, wolves rested most often in thickets and mature forest with understorey, whereas they used more open habitat types more often at night than in the day (Fig. 3).

3.3. *Factors affecting concealment of resting sites*

Diel time (sum of ω = 0.97) and distance from high-traffic forest road (sum of ω = 1.0) were the most important predictors of concealment of wolf resting sites (Table 3). The visibility at resting sites increased with increasing distance from high-traffic forest roads (Fig. 4a). Wolves selected concealed sites in the day but not at night (Fig. 4b). There was no difference in duration between resting bouts during the day (4.3 ± 0.6 h) and at night (4.9 ± 0.7 h).

Table 3
Models (LM) explaining the visibility at wolf resting sites (N = 137) in relation to Daypart (day or night, parameter estimate: 14.4, SE = 4.9), distance to high-traffic forest road (parameter estimate: 0.016, SE = 0.003) and the wolf pack identity (parameter estimate: 6.9, SE = 5.0) in the Lower Silesia Forest, SW Poland, ranked by AICc. We present only models with ωAICc > 0.01.

Model structure	AICc	ΔAICc	ωAICc
Daypart + Forest Road	1311.9	0	0.500
Daypart + Forest Road + Pack	1312.1	0.15	0.464
Forest Road + Pack	1318.5	6.56	0.019
Forest Road	1318.7	6.78	0.017

4. Discussion

Wolves in our study area adjusted their choice of winter resting sites to the spatial and temporal distribution of human presence. At the landscape scale, wolves selected resting areas located far away from settlements and roads with high traffic levels, namely public roads and main forest roads. Forest roads intersect the whole study area, and the heavily used ones are a daily source of human activity even in the core of wolf home ranges. Wolves have been shown to avoid human settlements and public roads spatially (Carricondo-Sanchez et al. 2020; Kaartinen et al. 2005) and spatio-temporally (Theuerkauf et al. 2003a). They also tend to locate dens and rendezvous sites as far as possible from settlements and public roads (Theuerkauf et al. 2003b). Therefore, it is likely that human impact on resting site selection is even stronger during the summer, when wolves rest at the den and at rendezvous sites, as shown in the Białowieża Forest, north-eastern Poland (Theuerkauf et al. 2003b). Although resting sites in the Białowieża Forest (Theuerkauf et al. 2003b) were at similar distances to settlements (2.8 ± 0.5 km Białowieża Forest vs 2.8 ± 0.1 km this study) and public roads (3.3 ± 0.8 km Białowieża Forest vs 2.6 ± 0.2 km this study) to those in the Lower Silesia Forest, the effect was less visible, probably due to the smaller sample size. However, it is noteworthy to point at the similar distances in both areas despite the different conditions as random points in the Białowieża Forest were farther away from settlements and roads than in the Lower Silesia Forest. A possible explanation could be the range that sound travels. Resting too close to sources of noise such as settlements

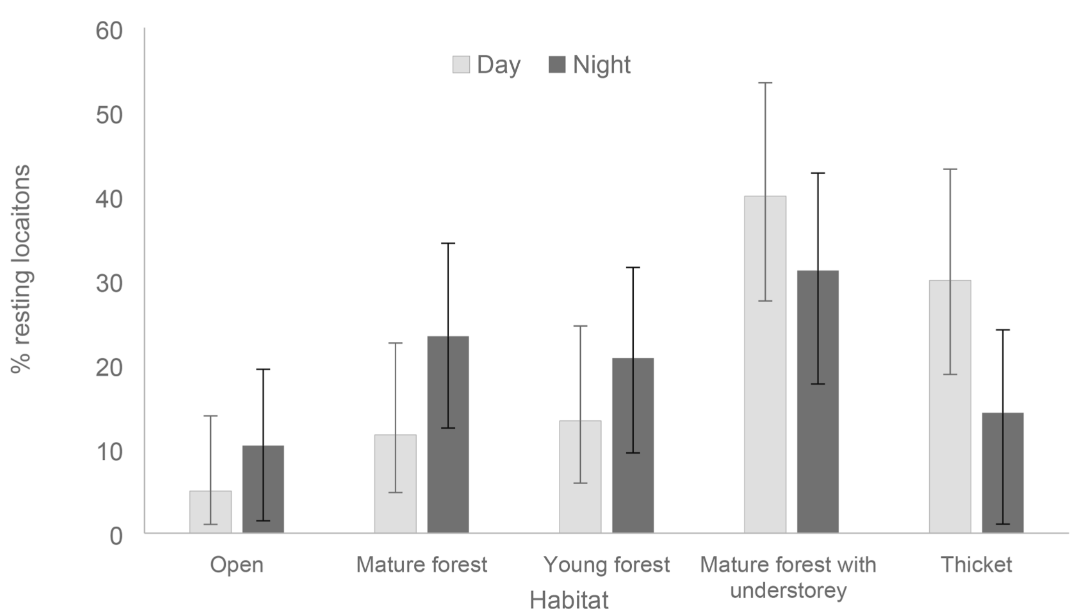

Fig. 3. Percentage (with 95% confidence intervals) of wolf resting sites in different habitats during the day (N = 60) and at night (N = 77) in the Lower Silesia Forest, SW Poland.

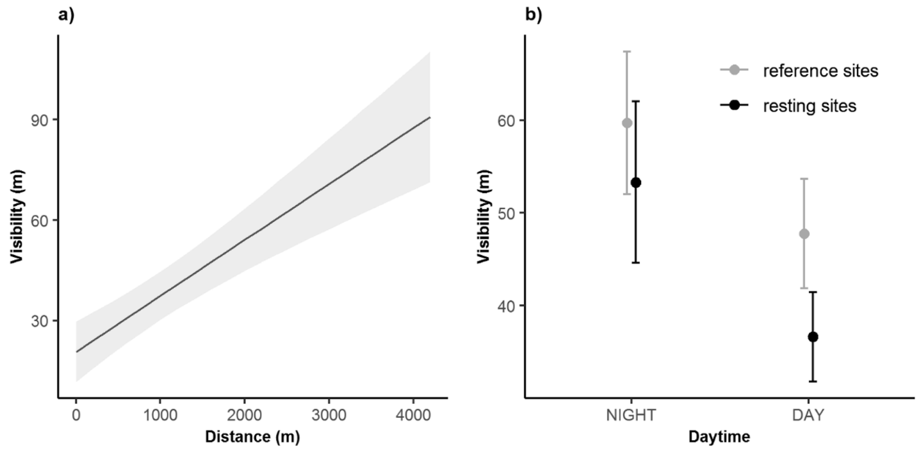

Fig. 4. (a) Predicted visbility with 95% confidence bands (LM) at wolf resting sites (N = 137) in relation to distance to the closest high-traffic forest road and (b) average (with 95% confidence intervals) visibility at resting sites during day and night compared to nearby (at a 100-m distance) reference sites in the Lower Silesian Forest, SW Poland.

and public roads could make it more difficult to hear potential intruders and hamper long distance howling, a form of communication that in natural conditions can be heard by other wolves at a maximum distance of 10 km (Harrington and Mech 1978). This might be another motivation for wolves to avoid noise-polluted areas.

When choosing a site for resting at the fine scale (within 100 m), wolves avoided not only public roads but also forest roads, even low-traffic roads that are rarely used by people. Concealment was an important predictor of wolf resting site location at the fine scale. As predicted, we found lower visibility at resting sites than at reference sites. Wolves in our study selected more concealed resting sites during the day than at night, similarly to herbivores that avoid visually-oriented predators (Moreno et al. 1996) and in line with findings of other large carnivores that select more concealed sites during periods of higher human activity (Ordiz et al. 2011; Wam et al. 2012). The fact that the concealment of resting sites increased closer to high-traffic forest roads corroborates findings on hiding in dense vegetation as an important strategy of large carnivores resting close to areas frequented by people (Llaneza et al. 2016; Ordiz et al. 2011). It also points at the high-traffic forest roads as the main source of human activity in our study area, especially during the day.

The habitat choice for resting seemed also to be associated with cover. For resting, wolves selected patches of denser habitats that potentially provide shelter from human sight, especially during daylight hours. In our study area, which consists of commercial pine stands, refuges for wolves were either very young forest stands before thinning operations, or patches of understorey within older forest stands. Podgórski et al. (2008) found that also Eurasian lynx *Lynx lynx* selected thickets and understorey for resting in the much more diverse habitats of the Białowieża Forest. Theuerkauf et al. (2003b) found that wolves in the Białowieża Forest did not select more concealed sites nor any particular type of forest for resting. However, average sighting distances at both random (21 m) and resting sites (20 m) in the Białowieża Forest were, due to the denser forest structure, more than twice lower than resting (45 m) and reference sites (55 m) in our study area. Thus, it seems that wolves need to be more selective when resting in more open commercial pine forest stands compared to forest with a more natural structure.

Our results corroborate the importance of human activity in shaping habitat use in large carnivores (Bouyer et al. 2015b; Musiani et al. 2010; Sazatornil et al. 2016), and resting site selection in particular (Cristescu et al. 2013; Sunde et al. 1998; Theuerkauf et al. 2003b). Our study shows that even in areas with low human population density, no legal large carnivore hunting and generally low levels of human presence, large carnivores modify their behaviour to avoid encounters with humans. In such areas, forestry practices and forestry-related traffic on forest roads may be the major factor shaping habitat selection in large carnivores (Houle et al. 2010; Roever et al. 2008). Although some forest management practices may be occasionally beneficial for large carnivores (Bojarska et al. 2017; Scrafford et al. 2017), they may also become a major source of disturbance and a reason for habitat deterioration in intensively managed forest stands. Our study confirms that forest roads can profoundly affect wolf behaviour, but their effect depends on the traffic levels and day time (Bojarska et al. 2020; Zimmermann et al. 2014). Here, we showed how resting behaviour, during which animals are particularly vulnerable to human-related risk, may be influenced differently by settlements and roads of various traffic depending on the spatial scale. Moreover, contrary to what was suggested by previous studies (e.g. Llaneza et al. 2016), we found no evidence that wolves rest more often nor for longer periods during the day than at night. Thus, it is important to consider both day and night when analysing resting behaviour in wolves.

The relatively large distances from settlements and public roads to resting wolves point at the importance of forest cohesion for wolves. Even landscapes that are forested to a high degree but consist of a very fragmented mosaic of forest and areas used by humans might be still not suitable for wolves because of their resting and denning habitat demands. Our results also suggest that in commercial forest stands, certain forestry practices enhance concealment opportunities for wolves. For example, later or less intensive thinning of young forest stands, as well as maintaining natural understorey or introducing understorey in older stands, might improve wolf habitat suitability. A more passive way to improve concealment may be restraining from removal of fallen trees, although this measure is unlikely to be implemented in commercial coniferous stands. The above-mentioned practices may be beneficial particularly in the vicinity of forest roads of high traffic levels, which would partially compensate for the potential disturbance associated with these roads. Implementing these measurements could also improve the refuge quality for wild ungulates, as well as other large carnivores, especially for lynx (Podgórski et al. 2008). Finally, to avoid deterioration of wolf habitats, the density of large forest roads should be kept to a minimum and existing forest roads should be closed for unauthorised motor vehicles.

Author contribution

Conceptualization: KB, LM, RG. Data curation: KB, LM. Formal analysis: KB, LM, WK. Funding acquisition: KB, RK, HO, RG. Investigation: KB, LM. Methodology: KB, LM, JT, RG. Project administration KB, HO, RG, Writing - original draft KB, LM. Writing - review & editing KB,

LM, RK, WK, JT, HO, RG.

Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

Acknowledgements

This study was funded by the Polish National Science Centre (Research Grants NCN2011/01/B/NZ8/04233 and NCN2012/05/N/NZ8/00860) and SAVE Wildlife Conservation Fund Polska. We are grateful to volunteers and forestry personnel for their support during fieldwork.

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