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ORIGINAL PAPER

Resting in risky environments: the importance of cover for wolves to cope with exposure risk in human-dominated landscapes

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Abstract Centuries of persecution have influenced the behaviour of large carnivores. For those populations persisting in human-dominated landscapes, complete spatial segregation from humans is not always possible, as they are in close contact with people even when they are resting. The selection of resting sites is expected to be critical for large carnivore persistence in human-dominated landscapes, where resting sites must offer protection to counteract exposure risk. Using wolves (*Canis lupus*) as a model species, we hypothesised that selection of resting sites by large carnivores in human-dominated landscapes will be not only influenced by human activities, but also strongly determined by cover providing concealment. We studied the fine-scale attributes of 546 wolf resting sites and confronted them to 571 random points in NW Iberia. Half of resting sites (50.8 %) were found in forests (mainly forest plantations, 73.1 %), 43.4 % in scrublands, and only 5.8 % in croplands. Compared to random points, wolves located their resting sites far away from paved and large unpaved roads and from settlements, whereas they significantly selected areas with high availability of horizontal (refuge) and canopy cover. The importance of

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refuge was remarkably high, with its independent contribution alone being more important than the contribution of all the variables related to human pressure (distances) pooled (51.1 vs 42.8 %, respectively). The strength of refuge selection allowed wolves even to rest relatively close to manmade structures, such as roads and settlements (sometimes less than 200 m). Maintaining high-quality refuge areas becomes an important element to favour the persistence of large carnivores in human-dominated landscapes as well as human-carnivore coexistence, which can easily be integrated in landscape planning.

Keywords Resting behaviour · Carnivore persistence · *Canis lupus* · Refuge · Landscape planning · Human-wildlife interactions

Introduction

Historically, human societies have invested huge efforts to persecute and exterminate large carnivores (Boitani 1995; Frank and Woodroffe 2001). In Europe, as a result of such long-term persecution phenomena, by the first half of the last century, wolves (*Canis lupus*), brown bears (*Ursus arctos*) or Eurasian lynx (*Lynx lynx*) were absent from most of the continent (Chapron et al. 2014). For example, in the nineteenth-century in Spain, Iberian wolves were intensively persecuted using poison, firearms, wolf traps and removing litters, and only between 1855 and 1859, ca. 15,000 wolves were officially killed (i.e., between ca. 2500 and 3000 wolves per year; Rico and Torrente 2000). Although positive trends have been observed for large carnivore populations in recent times in developed countries (Chapron et al. 2014), humans are still behind the main causes of mortality for these species, and sometimes such mortality sources can even curb, slow down or prevent population recovery processes (Woodroffe and Ginsberg 1998; Creel and Rotella 2010; Goodrich et al. 2008; Liberg et al. 2012; López-Bao et al. 2015a, b).

Centuries of persecution have influenced large carnivore life-history patterns and behaviour, with these species actively avoiding contact with humans (Linnell et al. 2002; Swenson 1999; Zedrosser et al. 2011). As a consequence, many large carnivore populations have persisted in human-dominated landscapes by adapting their behaviour to share the landscape with humans (Athreya et al. 2013; Ahmadi et al. 2014; Bouyer et al. 2015; Chapron et al. 2014; Habib and Kumar 2007; Llaneza et al. 2012; Ordiz et al. 2011). Such persistence is driven to a large extent by the ability of large carnivores to minimise the probability of a risky encounter with humans. Thus, chances of survival (and persistence) will depend on the adoption of different behavioural mechanisms involving both temporal and spatial segregation, such as becoming more nocturnal (Ciucci et al. 1997; Vilà et al. 1995), avoiding areas with high human activities (Ahmadi et al. 2014; Iliopoulos et al. 2014; Llaneza et al. 2012; Theuerkauf et al. 2003) or maximising the selection of refuges facilitating that animals go unnoticed by humans (Cristescu et al. 2013; Llaneza et al. 2012; Ordiz et al. 2011).

For large carnivores persisting in multi-use landscapes, complete spatial segregation from humans is not always possible, being in close contact with people even when they are resting. In these landscapes, large carnivores are mainly active at night or at twilight (Ciucci et al. 1997; Heurich et al. 2014; Moe et al. 2007; Theuerkauf 2009), resting or sleeping mainly during daylight. At that moments risk perception decreases; therefore, the vulnerability of animals increases (Lima et al. 2005). As a consequence, the selection of resting sites in human-dominated landscapes is expected to be critical for large carnivores, where resting sites must offer protection to counteract exposure risk (Cristescu et al. 2013; Ordiz et al. 2011; Podgórski et al. 2008).

Wolves are more resilient to persist in humanised landscapes compared to other large carnivore species (Chapron et al. 2014). It has been suggested that wolves perceive mortality risks associated with humans, adjusting, for instance, the use of the space at different scales accordingly (Agarwala and Khumar 2009; Ahmadi et al. 2014; Habib and Kumar 2007). However, the risk for wolves of being detected while resting is high because of the costs associated with fleeing in daylight (Ordiz et al. 2011). Therefore, it is expected that wolves will strongly minimise the chance of detection when selecting resting sites. In human-dominated landscapes, this would translate into the avoidance of manmade infrastructures where the probability of interaction with humans is high, as well as a strong selection for dense and inaccessible vegetation covers (i.e., refuge).

Here, we have evaluated the characteristics of resting sites for Iberian wolves equipped with GPS collars in human-dominated landscapes of Galicia, NW Iberia. Although Iberian wolves have been traditionally pursued using a great variety of methods (Álvares et al. 2011; Fernández and De Azúa 2010; Rico and Torrente 2000), they have persisted in areas with high levels of human activities such as Galicia (mean human population density: 93 inhabitants/km^2, 1 human settlement/km^2; mean paved road density: 2.7 km/km^2; INE 2014), and where the human–wolf conflict has been evident for a long time, considering the feeding ecology of the species (feeding considerably on livestock; Cuesta et al. 1991; López-Bao et al. 2013; Llaneza and López-Bao 2015). Indeed, wolf abundance in Galicia is remarkable, with an estimate of 2.2 and 2.8 wolf packs per 1000 km^2 between 1999 and 2003, and between 2013 and 2014, respectively (Llaneza et al. 2005, 2014).

We aimed to increase our understanding of the mechanisms allowing the persistence of large carnivores in human-dominated landscapes. In particular, if wolves select resting sites according to perceived exposure risk, we hypothesised that selection of resting sites will be not only influenced by human activities, but also strongly determined by environmental attributes such as dense vegetation cover providing concealment. By comparing resting sites of wolves with random points, we predicted that (i) resting sites would be located in more concealed places than random points, and furthermore that the strength of the effect of dense vegetation cover (refuge) should be stronger compared to other fine scale attributes; (ii) wolves would actively avoid locating their resting sites close to those manmade structures where human activity will be more predictable; (iii) wolves would avoid locating their resting sites close to patch edges and in small patches of refuge, which are expected to increase exposure risk. We additionally explored whether individual attributes (sex and age) and seasons influenced the selection patterns of resting sites.

Materials and methods

Study area

This study was carried out in Galicia, NW Spain (ca. 30,000 km^2) (specifically in A Coruña, Lugo and Pontevedra provinces; 22,500 km^2). The study area was characterised by a patchy landscape highly transformed by agriculture and livestock activities. During the twentieth century the landscape experienced an important transformation because of a generalised increment of forest plantations (*Eucalyptus* spp. and *Pinus* spp.). As a result, the cover percentage in Galicia of forest plantations rose to 23 % in recent times, whereas less than 10 % of the area is covered by woodland deciduous forests and most of them have been managed for a long time (i.e., timber harvest). The remainder of the land in the area mainly is used as pastures and crops (40 %) and scrublands (27 %). The outcome of the interaction between a human-dominated patchy landscape and the fact that wolves here can feed remarkably on anthropogenic sources of food (Cuesta et al. 1991; López-Bao et al. 2013: Llaneza and López-Bao 2015), translates into a scenario where it is expected that wolves will maximise the concealment of resting sites in relation to human-derived risk.

Studying wolf resting behaviour

We investigated the selection of resting sites by wolves by studying the spatial behaviour of 16 animals equipped with GPS-GSM collars (Followit, Sweden). Between 2006 and 2011, wolves were captured with Belisle® leg-hold snares (Edouard Belisle, Saint Veronique, PQ, Canada) and chemically immobilised by intramuscular injection of medetomidine (Dormitor®, Merial, Lyon, France). Immobilisation was reversed by the intramuscular injection of atipamezole (Revertor®, Merial, Lyon, France). Sex and age were determined in situ. Age was estimated by dental pattern and tooth wear (Gipson et al. 2000) and wolves were classified into two categories: juvenile/sub-adults ($<$2 years) and adults ($\geq$2 years). All wolves, excepting two individuals, were wolves belonging to different packs, or to the same pack but in different sampling years.

All captured wolves were evaluated as clinically healthy at the moment of capture, and they only presented minor lesions associated with trapping (such as edema or skin abrasions). Snares were monitored twice every day, in the early morning and late afternoon. Wolves included in this study were captured under permits 19/2006, 71/2009 and 86/2011 from the Regional Government of Galicia. All fieldwork procedures were adhered to the animal welfare regulations. GPS collars were scheduled to take a position every hour during the diurnal period (from 8:00 to 20:00 GTM), and every 2 h during night-time. We used a total dataset of 57,837 locations (mean number of locations per wolf = 3615, range 755–10,181).

We identified wolf resting sites by studying clusters of locations. Although wolves can rest during short time periods even a night-time, in this study, we focused on long-term resting sites, assuming that when wolves rest for long periods, they will maximise concealment. Therefore, we focused our study on diurnal resting sites. Wolf locations were plotted in ArcGIS (ESRI, California, USA). Then, we studied the spatial distribution of consecutive locations from 8:00 to 20:00 GTM to identify potential resting sites. The criteria used to define a resting site were successive locations during at least a 6 h period with a maximum distance between hourly locations of less than 30 m, to account for GPS location errors (see Online Resources, Fig. S1; Dussault et al. 2001). As resting sites were defined by multiple locations, we calculated the centroid to characterise each site. Next, we randomly selected around 30 non-overlapping resting sites per wolf (mean = 34). A minimum distance of 250 m was set to select non-overlapping resting sites. Selected resting sites were spatially spread at the landscape level. The mean distance among resting sites per wolf was 6.3 km (range 1–17.5 km). Moreover, within each wolf territory (calculated as the minimum convex polygon considering 100 % of locations) we generated a similar number of non-overlapping random points (mean = 36) (a minimum distance of 250 m was also set to select random points) to contrast with resting sites. A total of 1117 spatial points were considered in this study, 546 resting sites and 571 random points.

Characterising resting sites and random points

Once we selected resting sites and random points, we characterised each point in relation to different topographic, vegetation (cover) and human attributes (Table 1). First, we compiled two variables associated with low human densities and activities, altitude and slope (Glenz et al. 2001; Llaneza et al. 2012). For each point, we calculated the altitude (m) and the slope of the 25 × 25 m cell of each point location from the Spanish Digital Elevation Model (Ministerio de Fomento 1999) using ArcGIS. Second, by using high-resolution orthoimages from the same study period, we measured the distance from each resting site and random point to four manmade structures: (i) the nearest settlement with more than 5 buildings, (ii) the nearest paved road, (iii) the nearest unpaved road wider than 4 m (large unpaved roads) and (iv) the nearest small unpaved road. We considered that the predictability of human activity was correlated with ease of driving with a car, being different across linear infrastructures as follows: paved roads > large unpaved roads > small unpaved roads.

We measured a set of predictors related to cover and refuge provided by vegetation, which have been shown to be determinant factors in locating resting sites by large carnivores (Cristescu et al. 2013; Ordiz et al. 2011; Podgórski et al. 2008). For descriptive purposes, we recorded, in situ, whether a resting site was located in forest, scrubland or cropland, and the dominant species in each case. On the other hand, we also measured, in situ, the concealment offered by each point by focusing on the cover of different

Table 1 Predictors used to study resting site selection by wolves in human-dominated landscapes of NW Iberia

Group	Predictor	Definition
Topographic features	Altitude	Altitude in the 25 × 25 m cell where the central point of the resting or random site was located (see Online Resources, Fig. S2)
	Slope	Slope in the 25 × 25 m cell where the central point of the resting or random site was located (see Online Resources, Fig. S2)
Vegetation features	Patch size	Size (ha) of the vegetation patch where the central point of the resting or random site was placed
	Distance to the edge patch	Euclidean distance (m) from the central point of the resting or random site to the edge patch
	Canopy cover (vertical cover)	Proportion of canopy cover in a radius of 5 m (averaged value from the 5 points, see Online Resources, Fig. S2)
	Refuge (horizontal cover)	Proportion of forest and dense shrub >50 cm in a radius of 5 m (averaged value from the 5 points, see Online Resources, Fig. S2)
Human pressure	Distance to small unpaved roads	Euclidean distance (m) from the border to the central point of the resting or random site
	Distance to large unpaved roads (>4 m wide)	Euclidean distance (m) from the border to the central point of the resting or random site
	Distance to paved roads	Euclidean distance (m) from the border to the central point of the resting or random site
	Distance to settlements	Euclidean distance (m) from the central point of the resting or random site to the nearest settlement with >5 buildings

functional vegetation structures minimising exposure risk for wolves. To do this, considering the location of each focal point (centroids for resting sites), we generated four extra points 20 m separated from the focal point, in the cardinal directions, and we generated a sampling area of 5 m radius for each point. Thus, we estimated the cover on a 50 × 50 m area with five points of measurement (see Online Resources, Fig. S2). Despite the fact that wolves are adaptable to a wide range of vegetation types (even areas without plant cover; Ahmadi et al. 2014; Boitani 1982; Jedrzejewski et al. 2008; Mech and Boitani 2010), we counted as refuge only those vegetation types that could effectively conceal wolves (vegetation types > 50 cm high): scrublands, woodlands and forest plantations. Functionally, we assumed that these vegetation types provided similar conditions of refuge for wolves (Llaneza et al. 2012), and therefore, we measured the proportion of these three vegetation types in situ being pooled together in a single variable denominated refuge (i.e., horizontal cover). Moreover, to account for the effect of vertical cover on resting site selection, we also measured the proportion of canopy cover in the five sampling points. We estimated refuge and canopy cover as the average values obtained in the five sampling points for each site (Table 1). Finally, using high-resolution orthoimages in ArcGIS, we delineated the habitat patch where each point was located, calculated its size, and measured the distance from the point to the nearest edge patch (Table 1).

Data analyses

We used general linear mixed models (GLMMs) with binomial error distribution and logit link using the '*lme4*' package (Bates et al. 2014) in R (R Core Team 2014) to test for the influence of the ten selected predictors (Table 1) on wolf resting site selection in human-dominated landscapes. We created a set of candidate models (including the null model) considering all possible combinations among these predictors and compared them using the Akaike Information Criterion and the AIC weights (w_i) calculated using the '*MuMIn*' package (Barton 2013) in R, to determine the relative strength of support for each candidate model. Models within ΔAIC < 2 from the highest-ranked model were combined to calculated model-averaged parameter estimates in order to reduce model selection bias effects on regression coefficient estimates (Burnham and Anderson 2010). In addition, we used AIC weights to generate Relative Variable Importance weights (RVI) for each predictor (Burnham and Anderson 2010). We standardised the predictors before running analyses. The magnitude of multicollinearity among predictors was assessed by considering the size of the variance inflation factor (VIF). In our case, VIFs were always below 2.2. We also estimated the marginal and the conditional R^2 of the top-ranking model following Nakagawa and Schielzeth (2013). Marginal R^2 represented the variance explained by fixed predictors, whereas Conditional R^2 is interpreted as the variance explained by both fixed predictors and the random factors.

Next, considering those predictors included in the best candidate model, we run a hierarchical partitioning analysis to identify the independent and joint contribution of each predictor with all other predictors (Chevan and Sutherland 1991; Mac Nally 2000). Hierarchical partitioning was conducted using logistic regression and log-likelihood as the goodness-of-fit measure. This statistical procedure allowed us to identify those predictors with an important independent correlation to the selection of resting sites by wolves (Mac Nally and Horrocks 2002). Statistical significances of the independent contributions of selected predictors were tested by a randomization procedure (100 randomizations), which yielded Z-scores for the generated distribution of randomised independent contributions, and an indication of statistical significance ($P < 0.05$) based on an upper 0.95 confidence limit ($Z \geq 1.65$; Mac Nally and Horrocks 2002). Hierarchical partitioning analyses were carried out using the *"hier.part"* package (Walsh and Mac Nally 2008).

Finally, to evaluate the influence of individual attributes on the selection of resting sites we tested the influence of sex and age (two levels), and their interaction, on those predictors showing the highest independent contribution obtained in the hierarchical partitioning analyses. In this case, we treated such predictors as the explanatory variables. The same procedure was used to test for potential seasonal differences in resting site selection (two levels according to weather conditions and temperatures; Season 1: October–March [autumn–winter]; Season 2: April-September [spring-summer]). We run GLMMs using the '*glmmADMB*' package (Skaug et al. 2014) in R with a Beta error distribution and logit link function to model proportions, and with a gamma error distribution and the inverse link function to model distances. Individual identity and year were included as random factors in all models to account for repeated measures.

Results

Half of the 546 studied resting sites (50.8 %) were found in forested areas (41.7 and 31.4 % were in forest plantations of *Pinus* spp. and *Eucalyptus* spp., respectively), 43.4 % were found in scrublands (48.2, 17.6 and 15.4 % were in gorses [*Ulex* spp.], ferns and heaths [*Erica* spp.], respectively), and only 5.8 % were found in croplands (64.5 and 32.3 % were in grasslands and corn fields, respectively). Wolves located their resting sites far away from paved and large unpaved roads, and settlements, compared to random points, as well as in areas with high availability of horizontal (refuge) and vertical (canopy) cover (Table 2; Fig. 1). All variables, excepting altitude and slope, significantly differed between resting sites and random points (univariate Mann–Whitney U tests; Table 2).

Table 2 Descriptive statistics (mean, standard deviation and 95 % confidence intervals) for the ten selected predictors used to study resting site selection by wolves in human-dominated landscapes of NW Iberia for both resting and random points

	Resting sites				Random points				P
	Mean	SD	95 % CI		Mean	SD	95 % CI		
Distance to small unpaved roads	126.3	117.9	116.4	136.2	92.7	96.7	84.7	100.6	*
Distance to large unpaved roads	273.2	250.5	252.2	294.3	173.3	176.6	158.8	187.9	*
Distance to roads	619.2	413.9	584.4	653.9	373.1	377.7	342.1	404.2	*
Distance to settlements	859.1	462.6	820.2	897.9	621.1	550.0	575.8	666.3	*
Distance to the edge patch	208.8	330.9	181.0	236.6	183.0	325.5	155.9	210.1	*
Patch size	177.6	237.8	157.6	197.5	191.2	489.8	150.4	232.1	*
Slope	10.1	43.9	6.5	13.8	6.7	9.3	5.9	7.5	n.s.
Altitude	467.8	188.3	451.9	483.6	461.5	195.6	445.4	477.6	n.s.
Canopy cover	16.8	19.4	15.2	18.5	12.4	18.4	10.9	13.9	*
Refuge	70.7	30.1	68.2	73.2	42.0	37.2	38.9	45.1	*

Significance levels from Mann–Whitney U-tests comparing resting sites versus random points are shown (* $P < 0.001$)

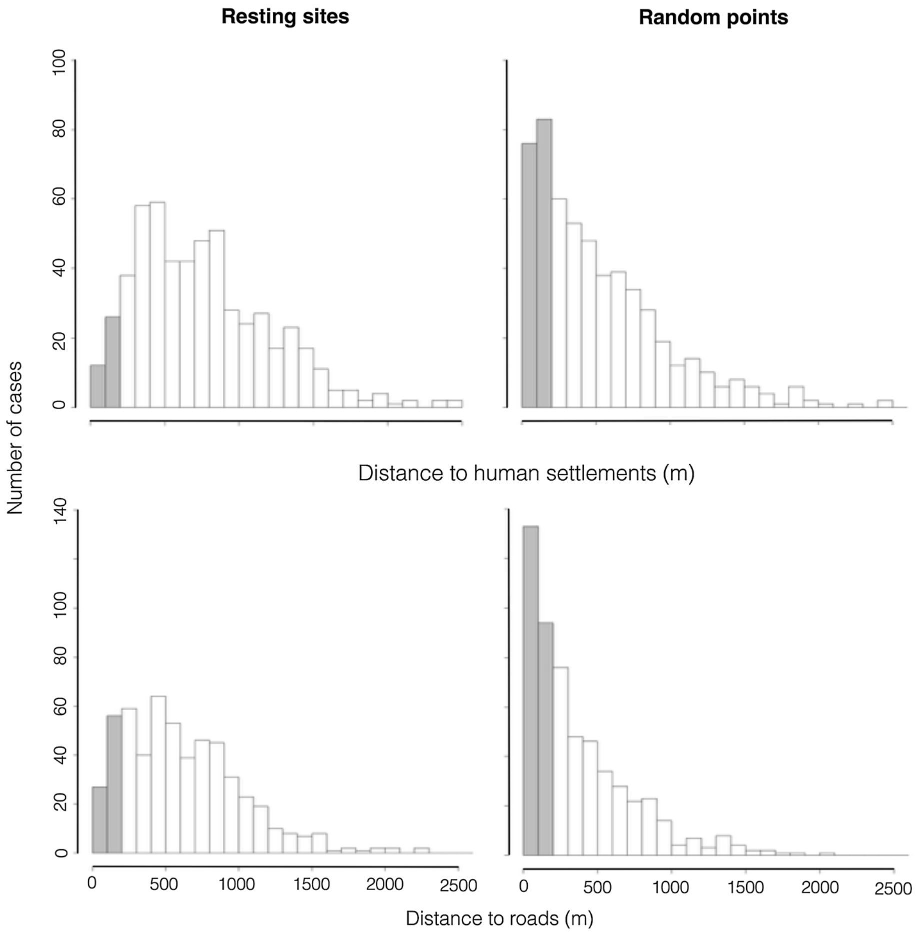

Fig. 1 Distribution frequencies of the distances (intervals of 100 m) between wolf resting sites and manmade structures: human settlements and roads. *Bars* showing distances less than 200 m are highlighted in *grey*

Five candidate models showed ΔAIC < 2 (Table 3), and the best model included the distances to roads, large unpaved roads and settlements, as well as refuge, canopy cover, slope and altitude (Table 3). All predictors excepting slope and altitude were the most important fine-scale predictors determining resting site selection by wolves based on their relative variable importance weight (RVI; Table 4). Averaging the coefficient estimates of the five selected candidate models showed that wolves significantly avoided choosing resting sites close to human settlements and paved or large unpaved roads, whereas they significantly selected areas with high availability of refuge and canopy cover (Table 4). Compared to the AIC value obtained for the best candidate model (AIC = 1140.61; Table 3), the AIC value of the random model was 1439.6. Considering the best candidate model, marginal R2 was 0.33 and conditional R2 was 0.48.

Hierarchical partitioning analysis run on the best candidate model (Table 3) revealed that the predictor showing the highest proportion of independent contribution to explaining

Table 3 Selected candidate generalized linear mixed models explaining wolf resting site selection in NW Iberia

Competing models	AIC	ΔAIC	w_i
Altitude + Canopy cover + Distance to large unpaved roads + Distance to paved roads + Distance to settlements + Refuge + Slope	1140.61	0	0.30
Canopy cover + Distance to large unpaved roads + Distance to paved roads + Distance to settlements + Refuge + Slope	1141.16	0.55	0.23
Altitude + Canopy cover + Distance to the edge patch + Distance to large unpaved roads + Distance to paved roads + Distance to settlements + Refuge + Slope	1141.70	1.09	0.17
Canopy cover + Distance to the edge patch + Distance to large unpaved roads + Distance to paved roads + Distance to settlements + Refuge + Slope	1141.76	1.15	0.17
Altitude + Canopy cover + Distance to large unpaved roads + Distance to paved roads + Distance to settlements + Refuge	1142.26	1.65	0.13

Models are ranked based on AIC, difference in AIC relative to the highest-ranked model (ΔAIC) and AIC-weights (w_i). By simplicity, we show only those models with ΔAIC < 2

Table 4 Model averaged coefficient estimates (Estimate), adjusted standard errors, (Adjusted SE), level of significance (P) and relative variable importance weight (RIV) for the predictors included in the selected candidate models explaining resting site selection by wolves in human-dominated landscapes of NW Iberia (models with ΔAIC < 2)

Predictor	Estimate	Adjusted SE	P	RIV
Intercept	0.08	0.45	n.s.	
Altitude	−0.17	0.19	n.s.	0.6
Canopy cover	0.43	0.15	0.005	1
Distance to large unpaved roads	0.85	0.18	<0.0001	1
Distance to roads	1.15	0.22	<0.0001	1
Distance to settlements	0.59	0.23	0.010	1
Refuge	1.82	0.17	<0.0001	1
Slope	0.37	0.33	n.s.	0.87
Distance to the edge patch	−0.07	0.14	n.s.	0.34

the selection of resting sites by wolves was refuge (horizontal cover) (51.1 %), followed by distance to roads (19.5 %), distance to large unpaved roads (12.5 %) and distance to settlements (10.8 %). The remaining predictors showed independent contributions <5 % (canopy cover = 4.7 %; slope = 1.4 %). The importance of refuge was remarkably high in this human-dominated landscape. The independent contribution of this predictor alone was more important than the contribution of all the predictors related to human pressure (distances) pooled (42.8 %). Indeed, the joint contribution of refuge was small (4 %) compared to human-related predictors (between 9 and 19 % of joint contribution). The independent effects of all included predictors were statistically significant (see Online Resources, Table S1).

Considering those predictors with important independent contribution (refuge, distance to roads, distance to large unpaved roads and distance to settlements), we did not detect significant differences in resting site selection patterns associated with individual attributes or seasons (see Online Resources, Tables S2 and S3).

Discussion

The persistence of wolves in human-dominated landscapes is probably favoured by multiple behavioural adaptations to cope with risk and positively affecting the chances of survival (Ahmadi et al. 2014; Chavez and Gese 2005; Capitani et al. 2006; Llaneza et al. 2012; Kusak et al. 2005; Theuerkauf et al. 2003). Among these adaptations, as we predicted, our results support the idea that wolves adaptively select resting sites to minimise exposure risk. The fact that resting site selection patterns did not vary between seasons suggest that wolves continuously minimise exposure risk when selecting the location of resting sites.

Humans influenced the selection of resting sites by wolves (see also Theuerkauf et al. 2003). We found that resting sites were placed in dense cover areas (both in terms of horizontal and vertical cover) as well as further from manmade structures compared to random points. Interestingly, because human activities were spread over the entire study area, as we expected, the strength of the selection for refuge was stronger compared to single or pooled manmade structures. The lack of significant effects of patch size on resting site selection suggest that the selection of resting sites is a fine-scale process (Ordiz et al. 2011), with their selection being determined more by the quality of the refuge than by its quantity (i.e., extension). Indeed, wolves located their resting sites in places with abundant refuge at fine spatial scale, and we found resting sites in pine and eucalyptus forest plantations, semi-natural woodlands or scrublands (dense and prickly gorses, for instance, provide good concealment to wolves in this area; see Online Resources, Fig. S3). The strength of refuge selection in human-dominated landscapes may be adaptive to compensate for uselessness defences during resting (Cristescu et al. 2013).

The observed strong selection for refuge allowed wolves to rest relatively close to manmade structures (e.g., in 15 and 7 % of cases, wolves rested less than 200 m from roads and human settlements, respectively; n = 546; Fig. 1), and occasionally even at less than 50 m from these structures (in 2 and 0.5 % of cases, wolves rested less than 50 m from roads and human settlements, respectively; Fig. 1). However, whereas wolves were sensitive to roads with predictable human activity (roads and large unpaved roads), they did not avoid small unpaved roads. On the one hand, this result supports the idea that wolves are capable of perceiving different spatiotemporal exposure risks associated with different manmade structures (Ahmadi et al. 2014; Benson et al. 2015). On the other hand, as small unpaved roads are expected to have less human activity, this linear element may also facilitate wolf movement and escape in a risky situation (Latham et al. 2011; Zimmermann et al. 2014).

Contrary to the patterns observed in bears (black—*Ursus americanus*—and brown bears), where these species locate their beds close to habitat patch edges (Lyons et al. 2003; Moe et al. 2007; Ordiz et al. 2011), we did not find evidence of the influence of this factor on wolf resting site selection patterns. Moreover, slope and altitude had poor predictive power for explaining resting site selection. This could be explained by the fact that the most important factor governing resting site selection, dense vegetation cover areas (horizontal and vertical cover), are not necessarily distributed at high altitudes or steep slopes in our study area (Spearman rank correlation analyses between refuge and altitude or slope, both $P > 0.622$).

Quantitative information on the mechanisms for wildlife to coexist with humans at fine spatial scales is scarce (Carter et al. 2012). Our results show that when wolves and humans share the landscape and overlap their activities at fine spatial scales, refuge selection for concealment during the day may be an important mechanism favouring the persistence of wolves in human-dominated landscapes (similar to the microhabitat use by subordinate carnivores when coexisting with apex predators; e.g., Viota et al. 2012). How wolves adapt this behaviour at different periods of human activity (e.g., hunting vs. non-hunting season) (e.g., Ordiz et al. 2011) or the influence of thermal cover or wind shelter deserves further investigation.

Effective conservation of large carnivores in human-dominated landscapes depends on their conservation outside reserves (Chapron et al. 2014; López-Bao et al. 2015b). In this regard, understanding the selection patterns of resting sites by wolves in such landscapes may add valuable information to delineate effective conservation measures (Cristescu et al. 2013). In this regard, our results provide basic information on the minimum requirements of wolf resting sites, which can easily be implemented in landscape planning. The selection for dense cover areas by wolves to rest may also favour human-wolf coexistence because this behavioural adaptation decreases the probability that people will have a direct experience with wolves (e.g., to spot a wolf at daylight resting). Because such types of experiences can contribute to changing attitudes of people toward wolves (Karlsson and Sjöström 2007; Williams et al. 2002), maintaining high-quality refuge areas becomes an important element for both favouring the persistence of the species in human-dominated landscapes and human-wolf coexistence.

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