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ORIGINAL RESEARCH

Multi-scalar habitat selection unveils ecological domains in wolves when selecting rendezvous sites

S. Droghei, M. Falco & P. Ciucci

Department of Biology and Biotechnologies "Charles Darwin", University of Rome La Sapienza, Rome, Italy

Keywords

Canis lupus; grain; homesite; resource selection function; site-attribute analysis; howling; habitat selection; human-dominated landscapes.

Correspondence

Paolo Ciucci, Department of Biology and Biotechnologies "Charles Darwin", Università di Roma La Sapienza, Viale dell'Università 32 – 00185 Roma, Italy.

Email: paolo.ciucci@uniroma1.it

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Abstract

Wolves are known to be habitat generalists, but they may have critical requirements during key life-cycle stages, such as reproduction and pup rearing. Especially in human-dominated landscapes, wolves may become particularly choosy concerning the location of their homesites to reduce human-related risk and disturbance, thus enhancing pup survival. From 2005 to 2010, we investigated habitat selection by wolves when establishing the territory at the landscape scale (i.e., 2nd order selection) and when locating rendezvous sites within the territory (i.e., 3rd order selection), the latter based on 31 acoustically and field-verified rendezvous sites (RVs) in 8 packs in the Abruzzo Lazio and Molise National Park, a historical stronghold of the species in central Italy where wolves always coexisted with humans. Using a hierarchical, multi-scale habitat selection approach through multi-grain resource selection functions (MRSFs), we investigated environmental, topographic, and anthropogenic factors affecting territory and RVs selection by wolves. At the landscape scale, wolves avoided human settlements and primary roads and selected forested areas, shrubland, and rough terrain, likely to improve concealment and decrease human-associated risks; however, they also positively selected pastures and trails to possibly improve efficiency in hunting and traveling. When locating RVs within the territory, wolves still selected forested areas, shrubland, and pastures but differently than the 2nd order, they avoided anthropogenic linear features (secondary roads and trails) and rough terrain. Our findings confirm that habitat selection by wolves is better understood through a multi-scalar approach, which may reveal trade-offs in selection decisions across different spatial scales.

Introduction

Although wolves are known to be habitat generalists, there are critical stages in their life cycle that require specific resources and conditions (Ciucci et al., 2024). One such stage is when wolves attend pups at homesites (i.e., den and rendezvous sites; Ausband et al., 2010; Ciucci et al., 2018; Houle et al., 2010; McLoughlin et al., 2004). During this period, pups are vulnerable, so wolves are expected to locate homesites strategically within their territory to ensure adequate protection from predators, including intraspecific territorial killing (Ausband et al., 2010; Benson et al., 2015; Smith et al., 2015). Once having vacated the natal den, pups are moved to rendezvous sites (RVs) where both breeding and nonbreeding wolves attend the pups, patrolling the site and systematically returning to provision them (Ausband, Mitchell, Bassing, Nordhagen, et al., 2016; Demma & Mech, 2009; Ruprecht et al., 2012). Generally, wolves can use several successive RVs from June to September–October, even though the number of homesites may be drastically reduced where encroachment by humans is substantial (Ciucci et al., 1997).

In human-dominated landscapes, wolves are selective when locating homesites in response to their need to meet ecological requirements while avoiding excessive human disturbance (Ahmadi et al., 2014; Iliopoulos et al., 2014; Kaartinen et al., 2010; Theuerkauf et al., 2003). In these conditions, RVs are known to be chosen in areas whose characteristics enhance concealment and segregation from humans, a behavior that appears to be more pronounced in European compared to North American wolves (Sazatornil et al., 2016). Indeed, the response to a particular disturbance seems to depend on the disturbance history, a critical concept in understanding the behavior of long-lived animals that learn through social transmission (Curatolo & Murphy, 1986). Accordingly, wolves living in human-modified landscapes appear relatively more tolerant of anthropogenic features at lower selection orders (i.e., 1st and 2nd orders of selection; Johnson, 1980) but exhibit stronger selection against them at higher orders of selection (i.e., 3rd and 4th orders of selection) (Sazatornil et al., 2016). Yet even though wolves in more pristine environments seem to be less tolerant of humans (Chapman, 1979), studies in North America also suggested that they can adapt to human activity even in proximity to homesites (Thiel et al., 1998).

Similar to other habitat selection processes, assessment of homesite choice by wolves is scale-dependent and is best achieved through multiple observational scales (i.e., grain and extent; *sensu* Wheatley & Johnson, 2009), an issue all too often neglected in previous homesite selection studies (Ciucci et al., 2024). First, wolves being territorial, a hierarchical habitat selection framework (Johnson's, 1980) would most properly account for the scalar extent of homesite selection (i.e., wolves select a homesite within their territory once the territory has been selected at the landscape scale; Ciucci et al., 2018). In use vs availability study designs (Thomas & Taylor, 2006), this markedly affects where resources available to wolves should be sampled. For instance, measuring availability at the landscape scale (i.e., study area) to contrast homesite selection by wolves would not only inflate Type I error rates, but also mask potentially relevant changes in ecological domains (Ciucci et al., 2018). Second, compared to fixed or arbitrarily defined distances within which to measure state variables in site-attribute studies, multigrain modeling techniques (e.g., Laforge et al., 2015) offer the opportunity to more objectively define the optimal grain that best describes habitat selection.

We hereby report multi-scale habitat selection by wolves when locating their RVs in the Abruzzo Lazio and Molise National Park (PNALM, central Italy) that, established in 1923, has represented since a historical stronghold for wolves in Italy. Locally, wolves have always coexisted with humans (Zimen & Boitani, 1975) and they currently thrive at high density (i.e., >5 wolves/100 km^2), even though human-caused mortality is not trivial despite their legal protection (Mancinelli et al., 2018). In addition, we know that wolves' ecology and behavior are locally affected by interactions with humans (Ciucci et al., 2020; Mancinelli et al., 2019). Little is known, however, about the habitat requirements of wolves during the pup rearing season in this area, where multiple uses by humans (e.g., tourism, forestry, livestock grazing) are allowed year through. Using a multi-scalar modeling approach and based on 31 RVs detected in 8 wolf packs from 2005 to 2010, we therefore investigated whether environmental, topographic, and anthropogenic features affected habitat choice by wolves when selecting their RVs. We predicted that: (i) habitat and RVs selection by wolves would reveal avoidance of human disturbance both at the landscape and at the territory scales, and (ii) habitat selection at the two scales of analysis could reveal changes in ecological domains, suggesting a trade-off by wolves between security from humans and energetic requirements.

Study area

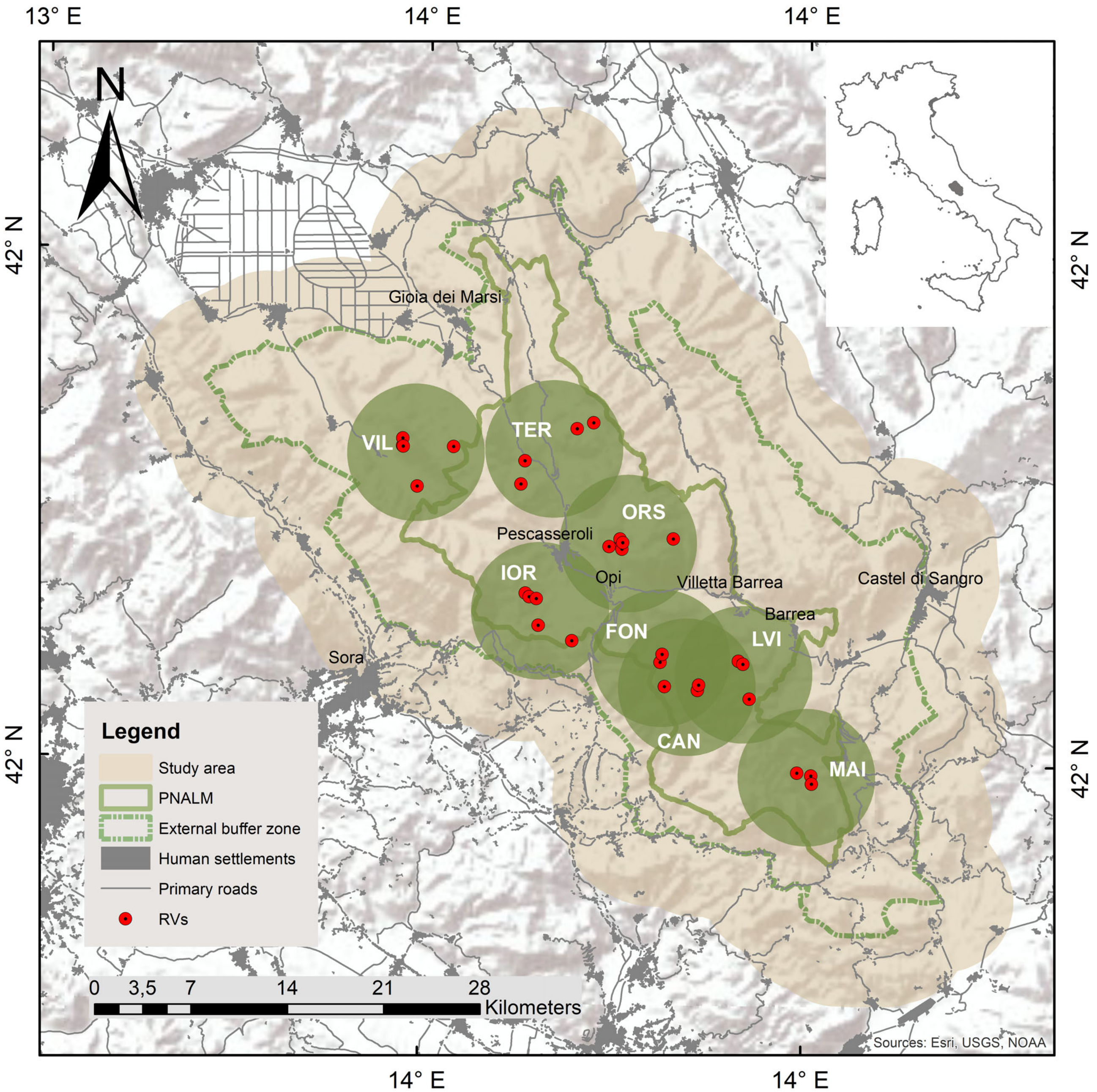
The study area (Fig. 1), located in the central Apennines (Italy), is the Abruzzo Lazio and Molise National Park (PNALM) and its external buffer zone (1294 km^2). The area is mountainous with elevations ranging between 400 and 2284 m, and temperatures ranging from 2°C in January to 20°C in July (Piovesan et al., 2003). Rainfall is most frequent in spring and fall, and snow cover generally extends from mid-December to March. The vegetation is characterized by beech (*Fagus sylvatica*) at higher altitudes and mixed forests mainly represented by oak (*Quercus spp*) and maple (*Acer spp*) at lower altitudes. The valley bottoms consist of abandoned or seasonally cultivated fields, while above 1800 m, alpine grasslands predominate. Human density is relatively high (Mancinelli et al., 2019), with an average of 14.6 inhabitants/km^2, clustered in a few small villages, while road density averages 31.5 km/100 km^2 and 67.4 km/100 km^2 for main and secondary roads, respectively.

A diversity of wild ungulates occurs in the area, with wild boar (*Sus scrofa*) and red deer (*Cervus elaphus*), at relatively high but unknown densities, followed by Apennine chamois (*Rupicapra pirenaica ornata*) and roe deer (*Capreolus capreolus*). Brown bears (*Ursus arctos marsicanus*) are also present with a relict population at a relatively high density (i.e., 40 bears/1000 km^2; Ciucci et al., 2015). Free-ranging dogs are also locally present, especially around villages, either in the form of working or owned free-ranging dogs (Ciucci et al., 2020). Forestry, tourism, and livestock husbandry are the most important economic activities in the area (Ciucci et al., 2014). In particular, sheep (*Ovis aries*) represent the most abundant livestock species, followed by goats (*Capra hircus*), cattle (*Bos taurus*), and horses (*Equus caballus*) (Galluzzi, 2014).

Materials and methods

Field work

From 2005 to 2010, as part of a broader wolf ecology study, we detected the location and estimated the use of RVs by wolf packs in the PNALM. We investigated the local wolf population (i.e., number and size of packs, their location and reproduction success) by a combination of techniques, including snow-tracking in winter (December to March) and wolf-howling during the summer (June to September), aided by camera trapping, non-invasive genetics, and Global Positioning System (GPS) telemetry (Ciucci et al., 2020; Grottoli, 2011; Mancinelli et al., 2018, 2019). Specifically, to locate RVs, we conducted nighttime howling surveys from June through September each year throughout the study area, according to a saturation census design (*sensu* Harrington & Mech, 1982) broadcasting howls of a lone wolf recorded in captivity (Ciucci et al., 2018). Limited to elicited or spontaneous chorus howls comprising pups, distinguished by their high pitch (Harrington et al., 2003; Joslin, 1967), we then approximated RVs' locations by means of acoustic triangulation using 2–4 observers (Ciucci et al., 2018). However, because packs can split temporarily, or pups can be moved between different rendezvous sites during summer (Ausband, Mitchell, Bassing, Morehouse, et al., 2016; Frame et al., 2007; Ruprecht et al., 2012), we confirmed a RV location based on at least 2 replicated chorus howls at the same site on different, non



Color

Figure 1 General location of the Abruzzo Lazio and Molise National Park in Italy (inset), and the approximate location of the eight wolf packs investigated from 2005 to 2010 (CAN, Canneto pack; Fon, Fondillo pack; Ior, Iorio pack; LVI, Lago Vivo pack; MAI, Mainarde pack; Ors, Orsara pack; Ter, Terraegna pack; Vil, Villa pack).

successive days. Thereafter, howling surveys at known RVs were replicated every 4–7 days to determine the minimum number of days wolves used the RV. We assumed that an RV had been vacated after 2–3 successive sessions without replies. We accordingly defined the last day of RV use as the mid date between the last day we heard pups at the site and the first day we did not obtain a reply. If another RV was successively detected in the same wolf pack territory, we estimated its first day of use as the mid date between the last day we heard pups in the previous site and the first day we heard them in the new RV (Ciucci et al., 2018). During the period RVs were used by wolves we only remotely monitored their use (i.e., howling sessions), and never adopted camera traps or non-invasive genetic sampling at the site to avoid disturbance. However, once we obtained acoustic evidence that a RV had been vacated, a team of 2–5 operators conducted confirmatory field surveys on the site, searching for evidence such as network of trails, lowered grass, day beds, tufts of wolf hair, pup scats, and prey remains (Ballard & Dau, 1983; Ciucci et al., 2018; Unger et al., 2009). For modeling purposes, we recorded the coordinates of the RV's centroid using a hand-held GPS unit, coincident with the center-most point of all wolf activity (i.e., where most of the trails converged and most of the signs, especially bed sites, were found). For those RVs whose location had been previously estimated by acoustic triangulation, we used the on-site recorded RV's centroid to measure the linear error about the acoustic estimate; we also used the upper bound of the 95% confidence interval of these estimates across all detected RVs as a measure of the expected inaccuracy in estimating the RV location through acoustic triangulation. The same value was then used to represent the RV location in a Geographic Information System (GIS) environment for subsequent modeling (see below).

Resources variables

To account for habitat selection by wolves, we obtained GIS layers of environmental, topographic, and anthropogenic variables at a 20 m spatial resolution (Table 1). We obtained land cover data from the CORINE Land Cover database (III level; http://dataservice.eea.europa.eu/dataservice/). To reflect the main structural vegetation types, we aggregated the original land cover classes as reported in Table S1. We obtained elevation from the digital elevation model (DEM; Italian Military Geographic Institute), from which we calculated two indices of orographic complexity (i.e., mean slope and the terrain roughness index, TRI; Riley et al., 1999). Linear anthropogenic features were obtained integrating De Agostini GeoNext and Open Street Map (OSM; https://osmit.it/) data. Based on De Agostini GeoNext classification of intensity road use, we distinguished among primary roads, secondary roads, and trails (generally accessible by foot, bike, or horse).

Model development

We investigated habitat selection by wolves at RVs, accounting for the hierarchical nature of habitat selection (Johnson, 1980). This implied developing two multi-grain resource selection functions (MRSFs), one at the 2nd order of selection (i.e., selection of territories at the landscape scale) and one at the 3rd order of selection (i.e., selection of RVs within the territory) (Ciucci et al., 2018). To model habitat selection at the landscape scale, we followed a type 2 design (Thomas & Taylor, 2006). For each pack, we represented use (coded as 1) by randomly selecting points (1 point/km^2) within the pack's territory (see below), and availability (coded as 0) by randomly selecting points within the study area, defined as the extent encompassed within a 5-km buffer beyond the PNALM's external buffer zone (Fig. 1), a distance that corresponds to the mean territory radius of wolf packs in the PNALM (Mancinelli et al., 2018). To model RV selection within the territory, we followed a type 3 design (Thomas & Taylor, 2006) by contrasting in each pack confirmed RVs (i.e., use; coded as 1) with points randomly selected (i.e., availability; coded as 0) within the territory. Only RVs that were confirmed by replicated acoustic triangulation and successively verified by field surveys, and whose use was limited to September 30, were included in the study. Availability at the 2nd and 3rd orders of selection was sampled at a density of 1 point/10 km^2 and 1 point/km^2, respectively, as these values were the smallest to stabilize the variability of the covariates to be subsequently used in MRSFs (Fig. S1). Because for only 3 of the 8 wolf packs we accurately determined the annual territory by means of GPS-telemetry, we approximated each wolf pack's territory using a 5-km radius centered in the RVs geometric mean location to enhance comparability among packs (Mancinelli et al., 2018).

For both orders of selection, we used a MRSF approach to account for variable grain size. Starting with a single variable grain analysis, in which we changed the grain size of one variable at a time, and using the sample-size corrected Akaike's Information Criterion (AICc), we determined the optimal grain size at which resource selection decisions are made (Laforge et al., 2015). Specifically, using the same modeling approach described below (i.e., MRSF approach), we first estimated the differences of the AICc (i.e., ΔAICc) values between the global model and the same model with the variable excluded (i.e., quasi-global model), and then selected the grain size corresponding to the minimum ΔAICc, which represents the most parsimonious scale for that variable (see Laforge et al., 2015 for further details on MRSFs). To this aim, for each used and available point, we set the minimum grain size at 500 m, to account for the estimated error in the acoustic location of RVs, and the maximum at 5000 m reflecting the mean territory radius of wolves in the PNALM, using 500 m and 1000 m incremental units up to and beyond 2000 m, respectively. We modeled linear features effects as a function of log-transformed Euclidean distance. The other variables were modeled as proportions using the focal statistics tool in ARCMAP (ARCGIS 10.1, Environmental Systems Research Institute, Redlands, CA, USA) over incremental radii (from 500 to 5000 meters) to represent different spatial scales (i.e., grains) (Figs S2 and S3). We standardized the variables, subtracting the mean and dividing by the standard deviation, to allow comparison of covariates' effects and to improve model convergence (Zuur et al., 2009). To account for collinearity among the variables, we used the Pearson's rank correlation ($r > 0.7$) and the Variance Inflation Factor (VIF > 3; *AED* R package; Zuur et al., 2009). Due to their high correlation ($r \geq 0.70$) across all grains of analysis in both orders of selection, we merged human settlements and primary roads into a new anthropogenic variable representing the distance to both human settlements and main roads (Table 1).

For both orders of selection, we developed MRSFs estimating a generalized linear mixed model (GLMM) using the *lme4* R package (Bates et al., 2016). For both orders of selection, we used pack ID as a random effect to account for repeated observations within the same wolf pack and variation in the number of observations across packs (Gillies et al., 2006). We allowed covariates to enter the model at different grain sizes, as previously indicated by the single variable grain analysis

Table 1 Variables used to develop multi-grain resource selection functions to investigate territory and rendezvous site habitat selection by wolves in the Abruzzo Lazio and Molise National Park, 2005–2010

Variables			Wolf pack territories	Rendezvous sites[a]
Type	Description	Study area	Mean ± SD	Mean ± SD
Environmental[b]	Forest (For)	57.6%	68.4 (±9.4) %	75.3 (±8.8) %
	Shrubland (Shrub)	4.6%	3.9 (±4.6) %	2.8 (±6.7) %
	Pastures (Past)	18.9%	17.4 (±5.0) %	2.9 (±4.1) %
	Agricultural (Agri)[c]	14.3%	1.8 (±1.2) %	1.7 (±9.3) %
Topographic	Elevation (DEM)[c]	1115 (±451) m asl	1492 (±115) m asl	1547 (±204) m asl
	Mean slope[c]	18.3 (±11.8)°	22.0 (±3.4)°	21.0 (±5.0)°
	Terrain roughness (TRI)[d]	4192 (±2205)	5081 (±766)	4973 (±1362)
Anthropogenic	Human settlements[e]	1945 (±1542) m	3144 (±611) m	3617 (±1287) m
	Primary roads (Dist_Iroads)[e]	1602 (±1384) m	2622 (±829) m	3186 (±1238) m
	Secondary roads (Dist_IIroads)	572 (±566) m	583 (±190) m	685 (±474) m
	Dist_Iroads_human	1519 (±1300)	2642 (±812) m	3098 (±1240) m
	Trails (Dist_trails)	3669 (±3711) m	478 (±122) m	526 (±292) m

Due to collinearity, not all covariates were retained in the final models.
[a]Calculated within a 500 m buffer around the RVs' centroid.
[b]Except non-vegetated and anthropogenic areas.
[c]Excluded from the model due to collinearity.
[d]Terrain roughness index range in the study area is 2.24–18636.43.
[e]Due to high correlation between these two variables, they were merged into a unique composite anthropogenic variable (Dist_Iroads_human).

(Laforge et al., 2015). We standardized the variables and accounted for collinearity using the same approach of the single variable grain analysis (see above). To account for overfitting, we considered models of low complexity and reduced the number of models to compare (Anderson, 2007). We also did not account for annual variation, assuming it did not significantly affect RVs selection by wolves during our study.

We performed model selection using the AICc and adopted multi-model inference averaging estimates based on model weights (MuMIn R package; Barton, 2016) limited to models whose AICc value was <2 from the best supported model (Burnham & Anderson, 2002). Because few candidate models received Akaike weights >0, this avoided the risk of spurious results from averaging parameter estimates of too many models with low weight (Grueber et al., 2011). We estimated unconditional standard errors and 95% confidence intervals for averaged parameters and determined the relative importance of each covariate by summing the AIC weights of all models in which the covariate was included (Burnham & Anderson, 2002).

At the 2nd order of selection, we used a k-fold cross-validation, removing 10% of the observations at a time (validation dataset) and using the remaining data (training dataset) to predict the MRSFs coefficients of the fixed effects for the validation dataset, repeating the procedure 100 times. We then split the MRSFs predicted values into 10 bins, computing for each the ratio between the relative frequencies of used (predicted) and available (expected) observations and used the Boyce index (Boyce et al., 2002) to assess the calibration power of the model. The Boyce index is based on the Spearman's rank correlation coefficient (r_s) between the mean value of each habitat suitability class (bin) and the predicted-to-expected ratios, with values close to 1 indicating a high predictive value. At the 3rd order of selection, we assessed the calibration power of the MRSF using the leave-one-out cross-validation (LOOCV), by removing one RV at a time and then following the same procedure used at the 2nd order of analysis.

Based on the models' coefficients, we developed a map of RVs suitability for wolves in the PNALM. We first produced a habitat suitability map at the 2nd order; then, based on the cut-off value that maximizes sensitivity and specificity ($P = 0.26$), we delineated the area within the PNALM where wolves have a higher probability to establish a territory and used this area to project suitability for RVs at the 3rd order. To enhance interpretation for practical management, we then discretized continuous values into 3 classes (low, medium, and high) based on quantiles.

Results

Out of 60 sites in 9 wolf packs from which we successfully elicited chorus howls with pups, 31 in 8 packs reflected our criteria to be subsequently used in MRSFs (3–7 RVs per year; Table S2). We detected use of RVs from 25 June to 30 September and, based on wolf howling replicates, each RV was used on average for 32 (±22 SD) days. In all cases, their location was estimated through acoustic triangulation, aided in three cases by GPS locations of a collared wolf in the pack, and in 18 cases supported by on-site confirmatory field surveys (Table S1). On average, the latter were conducted 29 (±16 SD) days after RVs had been vacated by wolves. Based on field verifications, the linear error of the acoustically estimated RVs' locations averaged 339 (±180 SD) m (95% CIs: 300–480 m).

At the 2nd order of selection, two subsets of the global model were most supported (Table 2), with adequate

Table 2 Multi-grain, mixed effects logistic regression model selection to assess the effects of environmental, topographic, and anthropogenic variables on habitat selection by wolves when establishing the territory within the landscape (2nd order selection), and RVs within the territory (3rd order selection) in the Abruzzo Lazio and Molise National Park, central Italy, 2005–2010

Order of selection	Variables	d.f.	AIC_c	ΔAIC_c	w_i
2nd order	$Forest_{5000m}$ + $Pasture_{5000m}$ + $Shrubland_{5000m}$ + TRI_{500m} + Dist_trails + Dist_Iroads_human	8	2279.14	0.00	0.71
	$Forest_{5000m}$ + $Pasture_{5000m}$ + $Shrubland_{5000m}$ + TRI_{500m} + Dist_ trails + Dist_Iroads_human + Dist_IIroads	9	2280.93	1.78	0.29
	$Forest_{5000m}$ + $Pasture_{5000m}$ + TRI_{500m} + Dist_ trails + Dist_Iroads_human	7	2282.40	3.25	0
3rd order	$Forest_{500m}$ + $Pasture_{3000m}$ + $Shrubland_{1500m}$ + TRI_{500m} + Dist_ trails + Dist_IIroads	8	208.17	0.00	0.61
	$Forest_{500m}$ + $Pasture_{3000m}$ + $Shrubland_{1500m}$ + TRI_{500m} + Dist_ trails + Dist_IIroads + Dist_Iroads_human	9	209.11	0.93	0.39
	$Forest_{500m}$ + $Shrubland_{1500m}$++TRI_{500m} + Dist_ trails + Dist_IIroads	8	211.59	3.41	0

Variables' subscripts indicate the optimal grain size as estimated through single variable grain analysis (see text). All models with ΔAIC ≤4 are shown.

AIC_c, Akaike's Information Criterion adjusted for small sample size; d.f., degrees of freedom; Dist_IIroads, distance to secondary roads; Dist_Iroads_human, distance to primary roads and human settlements; Dist_trails, distance to trails; TRI, terrain roughness; w_i, models' Akaike weights.

calibration power (Boyce index: r_s = 0.76). Accordingly, when establishing territories in the study area, wolves selected at a wide grain (i.e., 5000 m) forested areas and shrubland cover, with the presence of pastures; they also selected higher roughness and areas further from primary roads and settlements, and closer to trails (Table 3). At the 3rd order of selection, two subsets of the global model were most supported (Table 2), also with adequate calibration power (Boyce index: r_s = 0.78). Similar to the 2nd order selection, within their territories wolves responded at finer grains (i.e., 500–3000 m) selectively locating RVs in forested areas, shrubland cover with the occurrence of pasture (Fig. 2). Compared to the 2nd order, however, wolves relaxed avoidance of areas closer to primary roads and settlements, increased avoidance of areas closer to secondary roads (Fig. 2), and switched selection for (i.e., avoided) complex orography and proximity to trails (Table 4; Fig. 3).

Table 3 Coefficients of multi-grain resource selection functions to investigate habitat selection by wolves when establishing territories at the landscape scale (2nd order selection), in the Abruzzo Lazio and Molise National Park, central Italy, 2005–2010

Variable	β	SE	95% Confidence intervals Lower	Upper
Intercept	−1.573	0.077	−1.724	−1.422
$Forest_{5000m}$	1.168	0.116	0.937	1.395
$Pasture_{5000m}$	0.373	0.096	0.181	0.556
$Shrubland_{5000m}$	0.128	0.054	0.019	0.231
TRI_{500m}	0.209	0.057	0.094	0.319
Dist_trails	−0.510	0.079	−0.667	−0.353
Dist_Iroads_humans	0.581	0.062	0.459	0.681
Dist_IIroads	−0.030	0.063	−0.154	0.093

Variables' subscripts indicate the optimal grain size as estimated through single variable grain analysis.

Dist_IIroads, distance to secondary roads; Dist_Iroad_humans, distance to primary roads and human settlements; Dist_trails, distance to trails; TRI, terrain roughness.

Discussion

Conducted in a historical stronghold of wolves in Italy, where the species always cohabited with humans, our findings concur in documenting that, although adaptable in terms of habitat requirements, wolves display specific selection patterns for certain behaviors and life cycle events (Ciucci et al., 2024). This is the case for the pup rearing period, during which wolves attend vulnerable pups at dens and rendezvous sites (homesites), whose locations reveal selection for habitat features that may enhance pup survival (Benson et al., 2015; Kaartinen et al., 2010; Sazatornil et al., 2016). In the human-modified landscape of our study area, we expected wolves to avoid human disturbance both at the landscape and at the territory scales, a tendency that would become more apparent when establishing RVs by selecting habitat features that ensure cover and enhanced safety from humans. The results we obtained confirm our hypotheses, revealing a habitat-mediated behavioral response by wolves when living in human-modified landscapes. This is in line with previous studies indicating that the avoidance of anthropogenic pressure plays a critical role in wolves' habitat decisions, a tendency particularly apparent when locating homesites (e.g., Iliopoulos et al., 2014; Kaartinen et al., 2010; Theuerkauf et al., 2003). We caution, however, that even though we sampled the great majority of wolf packs in the PNALM, our study has a relatively limited number of wolf packs and RVs, forcing us to develop relatively simple models.

At the landscape scale, wolves in the PNALM positively selected forest, shrubland, and rough terrain, all features related to cover and areas hardly accessible by humans; wolves also positively selected pastures, a likely proxy of prey availability and hunting grounds (Heard & Williams, 1992). Distance to human settlements and primary roads combined was also

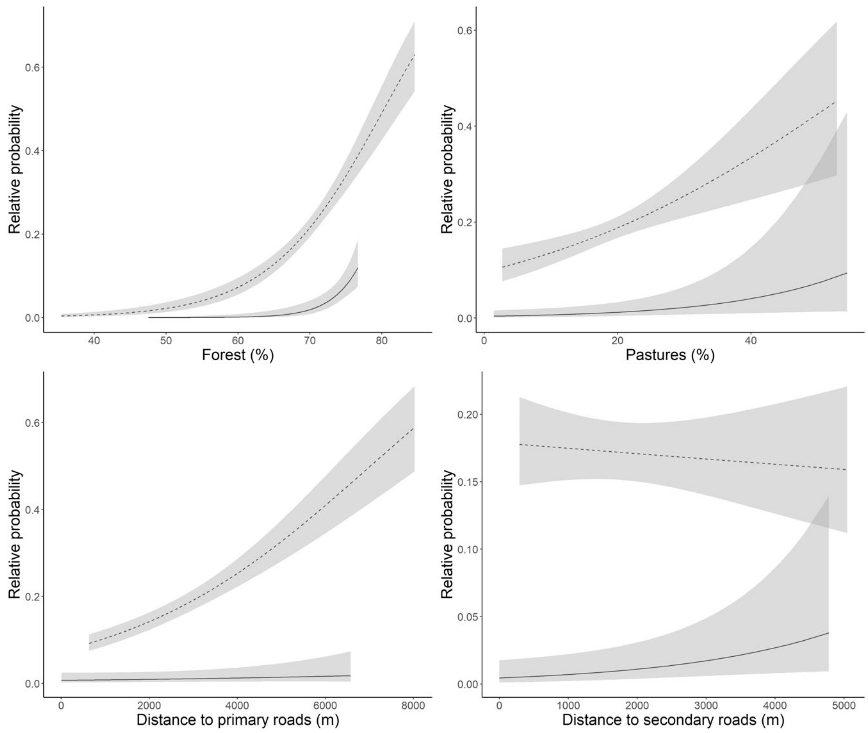


Figure 2 Relative probability of wolves establishing a territory within the landscape (2nd order selection; dashed line) and locating a rendezvous site within the territory (3rd order selection; solid line) as a function of land cover and anthropogenic variables based on multi-grain resource selection functions in the Abruzzo Lazio and Molise National Park, central Italy. To enhance comparability between orders of selection, relative probability (y-axis) has been standardized by dividing predicted values by their maximum.

positively selected, indicating a tendency to minimize the risk associated with a higher level of human presence and activity. Overall, these findings concur in revealing that wolves in human-modified landscapes, given the opportunity, select their territories in a way to minimize encounters with humans, therefore necessitating particular combinations of land cover types and orography (Ciucci et al., 2018; Iliopoulos et al., 2014). Yet, when establishing their territories, wolves selected for proximity to trails, suggesting that the different nature and lower intensity of human disturbance along trails allow wolves to take advantage of them to enhance traveling efficiency (e.g., hunting, territory patrolling). It has also been reported elsewhere that wolves tend to select linear features to facilitate travel (Ciucci et al., 2003; Dickie et al., 2017; James & Stuart-Smith, 2000; Whittington et al., 2005), enhancing efficiency compared to traveling in the forest (Dickie et al., 2017; Zimmermann et al., 2014) and increasing prey encounter rates (Dickie et al., 2017; Frid & Dill, 2002). Based on resource and step selection functions at the 3rd order of selection, however, we showed that the response by wolves to roads is quite complex, varying seasonally and depending on road type (i.e. main vs secondary roads), the time of the day, social context (i.e. pack members vs solitary floaters), and behavior (i.e., traveling vs resting) (Mancinelli et al., 2019). During summer, coincident with our study, pack members avoided main roads throughout the day, both when traveling and resting, and showed a similar response to secondary roads, although relaxing avoidance when traveling during the night (Mancinelli et al., 2019). Unfortunately, in that study we did not investigate the response by wolves to trails.

Table 4 Coefficients of multi-grain resource selection functions to investigate habitat selection by wolves when locating a RV within the territory (3rd order selection) in the Abruzzo Lazio and Molise National Park, central Italy, 2005–2010

Variable	β	SE	95% Confidence intervals Lower	Upper
Intercept	−4.610	0.566	−5.684	−3.536
Forest$_{500m}$	2.580	0.670	1.440	4.075
Pasture$_{3000m}$	0.588	0.248	0.100	1.076
Shrubland$_{1500m}$	0.528	0.173	0.187	0.869
TRI$_{500m}$	−0.720	0.271	−1.253	−0.188
Dist_trails	0.546	0.181	0.189	0.903
Dist_Iroads_humans	0.092	0.183	−0.205	0.686
Dist_IIroads	0.546	0.215	0.124	0.968

Variables' subscripts indicate the optimal grain size as estimated through single variable grain analysis.
Dist_IIroads, distance to II roads; Dist_Iroad_humans, distance to primary roads and human settlements; Dist_trails, distance to trails; TRI, terrain roughness.

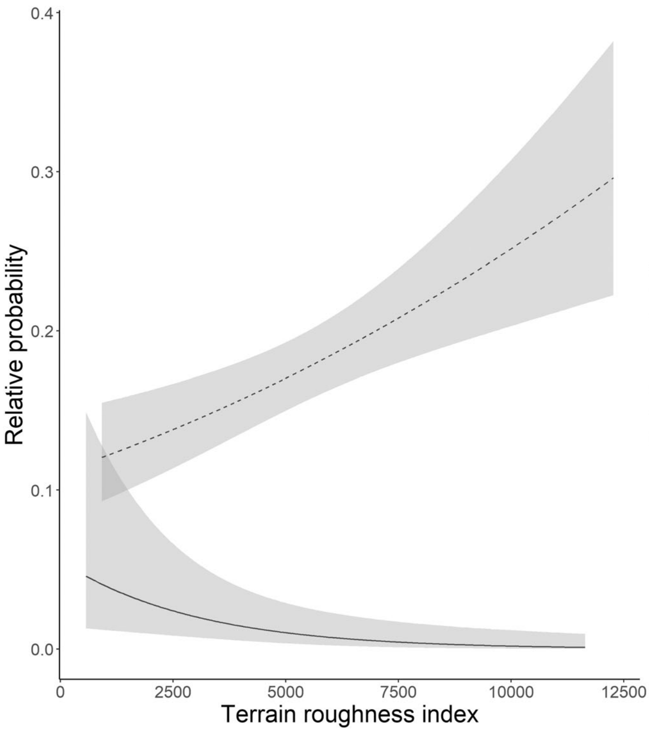


Figure 3 Relative probability of wolves establishing a territory within the landscape (2nd order of selection; dashed line) and locating a rendezvous site within the territory (3rd order of selection; solid line) as a function of (a) Terrain Roughness Index (TRI), and (b) Distance to trails based on multi-grain resource selection functions in the Abruzzo Lazio and Molise National Park. To enhance comparability between orders of selection, relative probability (y-axis) has been standardized by dividing predicted values by their maximum.

When choosing RV location within the territory, wolves in the PNALM still positively selected forest and shrubland cover, possibly to ensure concealment and safety for the litter, and again positively selected for pastures as a likely proxy of prey occurrence. In contrast to the 2nd order of selection, however, when selecting RV locations, they avoided terrain roughness at fine grains, similar to wolves when traveling across their territory (Mancinelli et al., 2019). Especially in mountainous areas, more gentle terrain in proximity to RVs would be functional to save energy for the daily, centripetal travels from and to the RVs (Ausband et al., 2010; Ciucci et al., 2018; Person & Russell, 2009). In addition, also different from the 2nd order of selection, when locating RVs, wolves avoided proximity to secondary roads and trails, as this implies increased risks of impact by humans (Capitani et al., 2006; Ciucci et al., 1997, 2018; Person & Russell, 2009; Theuerkauf et al., 2003).

Through our multiscale modeling approach, we confirmed that both extent and scale affect our ability to assess selection patterns by wolves (Ciucci et al., 2018). First, we revealed that different grains explained habitat selection both among variables at the same order of selection (e.g., forest cover and roughness at the 2nd order of selection; Figs S2 and S3) and for the same variable between orders of selection (e.g., forest cover at the 2nd and 3rd order of selection; Figs S2 and S3). Taken together, these findings reveal that habitat variables are perceived differently by wolves and that their response to a given variable may vary depending on the prevailing behavior (e.g., establishing a territory vs ensuring offspring safety). For instance, the smaller grain (i.e., 500 m) at which forest cover was selected when choosing RVs within the territory reveals the immediacy of response by wolves compared to the broader selection for cover across the entire territory (i.e., 5000 m grain; Table 2). Second, we revealed that selection for specific habitat variables changed (i.e., relaxed, intensified, or switched) across orders of selection, indicating possible ecological domains and the corresponding behavioral mechanisms. Compared to the 2nd order of selection, wolves relaxed the avoidance of human settlements and primary roads when locating RVs within the territory (Tables 3 and 4), likely because such avoidance already took place when establishing the territory at the landscape scale, ensuring an adequate level of security. Similarly, they changed response towards secondary roads and trails, switching selection from positive to avoidance at the 2nd and 3rd order, respectively. Similar insights into ecological domains might enhance our understanding of the inherent complexity and the adaptive value of habitat choices. For example, changing responses towards secondary roads, trails, and rough topography from the 2nd to the 3rd order of selection may be an indication that, during the energetically demanding period of pup rearing, wolves in the PNALM strategically choose RVs locations to enhance traveling and hunting efficiency, thus maximizing food intake and minimizing the time pups are left unattended. In addition, whereas selection for rough topography at the landscape scale may indicate that wolves preferentially use areas hardly accessible to humans, selection of relatively more gentle terrain in the proximity of RVs suggests that wolves inhabiting mountainous areas have an ergonomic response when traveling centripetally about the RV during the pup rearing period. An ergonomic interpretation of the landscape by wolves is also consistent with previous findings in the PNALM, showing that wolves tend to prefer more gentle topography when traveling across the territory as opposed to higher roughness when resting (Mancinelli et al., 2019).

Rendezvous sites selection by wolves in the PNALM is highly consistent with a similar multiscale study conducted in the Pollino National Park, another historical stronghold of wolves in Italy (Zimen & Boitani, 1975), located in the southern Apennines at about 320 km south-east from the PNALM and featuring quite different ecological and anthropogenic conditions (i.e., lower prey abundance, lower wolf density, and higher human and road density; Ciucci et al., 2018). Although this similarity reflects comparable modeling approaches and habitat variables, it is remarkable that selection patterns were very similar and that in both studies we revealed the same shifts in habitat selection between the 2nd and the 3rd orders of selection, indicating that scale-dependency in habitat choice by wolves may be consistent across different study areas. In turn, while adding to the generalizability of our results, this indicates how replication of local studies can contribute to our understanding of broader ecological phenomena.

Management implications

The spatially explicit version of the RVs habitat model for wolves in the PNALM (Fig. S4; also available in raster format) is meant to inform and support conservation management. First, by visualizing the areas within the park most likely to host a RV, it allows assessing the extent to which the location of wolves' homesites during summer is compatible with the park's internal zoning system (i.e., regulations involving human activities such as tourism, livestock grazing, and forestry). Second, understanding where wolves would most likely locate their homesites may be useful to prevent close proximity and avoid spatio-temporal overlap between RVs and grazing allotments during the pups rearing season (Fig. S4). Third, the efficacy and efficiency of wolf monitoring programs during summer (e.g., by means of wolf howling, camera trapping, and non-invasive genetic sampling) could be dramatically improved if conducted in areas of higher probability of RVs occurrence.

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Conflict of interest

The authors declare they have no conflict of interest.

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Supporting Information

Additional Supporting Information may be found in the online version of this article:

Table S1. Land cover variables used to develop habitat selection models for wolves in the Abruzzo Lazio and Molise National Park, central Italy, and corresponding original CORINE land cover classes and their description (III level).

Table S2. Rendezvous sites (n = 31) detected in eight wolf packs the Abruzzo Lazio and Molise National Park from 2005 to 2010, and subsequently used to develop a Multigrain Resource Selection Function to assess habitat choice by wolves when locating RVs sites. Location of all RVs were estimated through acoustic triangulation by 2–4 observers listening from the distance to elicited chorus howls comprising pups. A subsample of the RVs was verified through ground-truthing surveys after the sites had been vacated by wolves.

Figure S1. Variability of the covariates used to represent availability within the study area (a, 2nd order of selection) and within each wolf pack's territory (b, 3rd order of selection) at increasing densities of randomly sampled points. In the boxplots, the thick horizontal line depicts the median value, the box the 25th–75th percentile range, the whiskers the most extreme values (i.e., within 1.5 times the interquartile range), and the points outliers beyond this range.

Figure S2. Grain selection for environmental variables, except distance-based variables, through multigrain resource selection function at the 2nd order of selection. For each variable, the plots depict, across incremental grain sizes (x-axis), the effect of adding a given variable to the quasi-global resource selection model (sensu Laforge et al., 2015) both as the variation in the AIC score (ΔAICc, top row) and as the model coefficients (β ± 95% confidence intervals, bottom row).

Figure S3. Grain selection for environmental variables, except distance-based variables, through multigrain resource selection function at the 3rd order of selection. For each variable, the plots depict across incremental grain sizes (x-axis) the effect of adding a given variable to the quasi-global resource selection model (*sensu* Laforge et al., 2015) both as the variation in the AIC score (ΔAICc, top row) and as the model coefficients (β ± 95% confidence intervals, bottom row).

Figure S4. Map of predicted habitat suitability for rendezvous sites of wolves in the Abruzzo, Lazio, and Molise National Park. Suitability values, based on a multi-grain resource selection function at the 3rd order (i.e., RV site selection within the territory), are plotted, limited to areas of high suitability at the landscape scale (i.e. 2nd order selection). The map is depicted in two versions: (a) continuous suitability values; (b) suitability classes based on quantiles. The latter is also available in raster format upon request.