The Journal of Wildlife Management; DOI: 10.1002/jwmg.21440

Research Article

Hierarchical, Multi-Grain Rendezvous Site Selection by Wolves in Southern Italy

PAOLO CIUCCI,[1] *Department of Biology and Biotechnologies "Charles Darwin", University of Rome La Sapienza, Viale dell'Università 32, Roma 00185, Italy*

LUIGI BOITANI, *Department of Biology and Biotechnologies "Charles Darwin", University of Rome La Sapienza, Viale dell'Università 32, Roma 00185, Italy*

MATTEO FALCO, *Department of Biology and Biotechnologies "Charles Darwin", University of Rome La Sapienza, Viale dell'Università 32, Roma 00185, Italy*

LUIGI MAIORANO, *Department of Biology and Biotechnologies "Charles Darwin", University of Rome La Sapienza, Viale dell'Università 32, Roma 00185, Italy*

ABSTRACT Fine-scale knowledge of how anthropogenic effects may alter habitat selection by wolves (*Canis lupus*) is important to inform conservation management, especially where wolf populations are expanding into more populated areas or where human activity and development are increasingly encroaching on formerly pristine environments. From 1999 to 2003, we documented rendezvous sites ($n = 31$) used by wolves ($n = 6$ packs) in a previously unstudied wolf population in the southern Apennines, Italy (Pollino National Park [PNP]), where conditions are ideal to unveil behavioral adaptations of wolves living in human-dominated landscapes. We adopted a hierarchical, multi-scale habitat selection approach by using a set of environmental, topographic, and anthropogenic factors within multi-grain resource selection functions (MRSFs) at the landscape and the territory extent. Habitat selection by wolves was scale-dependent and different habitat components affected wolves at different grains. When establishing a territory at the landscape scale, wolves avoided areas featuring high densities of humans, paved roads, and trails, and they preferentially located territories where higher forest cover and rough terrain enhanced concealment and ensured reduced accessibility by humans. Concurrently, wolves also selected open areas and, at coarse grain, areas of high density of dirt roads and trails to enhance hunting and traveling efficiency. When selecting rendezvous sites within territories, wolves still selected for forest cover and lessened avoidance of anthropogenic features apparent at the lower order of selection. When choosing rendezvous sites, wolves also avoided low-use anthropogenic linear features and rough terrain, unveiling trade-offs in selection decisions across different spatial and temporal scales. Our results reinforce the notion that occurrence of wolves in human-modified landscapes is shaped by avoidance of anthropogenic pressure, but they also indicate that rendezvous site selection by wolves conform to a hierarchical decision-making process that is extent- and grain-dependent. Spatially explicit models of rendezvous site selection such as the one we developed for PNP enhance management effectiveness for strategies such as regulating human access and activity during the pup rearing seasons, preventing human persecution, mitigating livestock depredations, and designing cost-effective monitoring programs. © 2018 The Wildlife Society.

KEY WORDS *Canis lupus*, multi-scale habitat modeling, rendezvous sites, resource selection functions, scale-dependent habitat selection, scale optimization, wolf.

Wolves are generally regarded as habitat generalists because they occupy an array of environments (Mech and Boitani 2003). At finer scales, however, use of specific habitats is typically associated with certain wolf behaviors (e.g., killing prey, traveling, resting; James and Stuart-Smith 2000; Kunkel and Pletscher 2000; Ciucci et al. 2003; Whittington et al. 2005, 2011) and critical life-history stages (e.g., raising pups at homesites; McLoughlin et al. 2004, Ausband et al. 2010, Houle et al. 2010, Sazatornil et al. 2016). Wolf homesites include pre-weaning (i.e., dens) and post-weaning (i.e., rendezvous) sites (Joslin 1967), the latter being aboveground locations intensively used by the whole pack where breeding and non-breeding wolves systematically return to provision and protect pups (Demma and Mech 2009, Ruprecht et al. 2012, Ausband et al. 2016*b*). Rendezvous sites are generally used up to September–October (Packard 2003, Mills et al. 2008, Ruprecht et al. 2012, Ausband et al. 2016*a*) and, compared to dens, expose pups to greater risks of interference or predation because they are visible aboveground, the pups

Received: 3 September 2017; Accepted: 19 January 2018

[1] *E-mail: paolo.ciucci@uniroma1.it*

are more mobile, and attendance rates of the other pack members decline throughout the season (Ruprecht et al. 2012, Ausband et al. 2016*b*). More than 4 rendezvous sites may be used in each season (Ausband et al. 2016*a*), but Ciucci et al. (1997) recorded a pack using a single homesite in a landscape encroached by human activity. Given their relevance for reproductive success, wolves are expected to strategically locate homesites to ensure adequate parental care, food provisioning, and protection from predators, including intraspecific territorial killing (Harrington and Mech 1982*a*, Mech et al. 1998, Ausband et al. 2010, Benson et al. 2015). Placement of rendezvous sites is expected to affect fitness by influencing concealment and flight responses but also proximity to food sources, energetic balance, and insulation from wind and extreme temperatures (Ballard and Dau 1983, Norris et al. 2002, Person and Russel 2009, Ausband et al. 2016*a*).

During the pup rearing season, centripetal space use patterns by wolves about rendezvous sites (Demma and Mech 2009, Ruprecht et al. 2012) may expose the pack to increased risk due to human activity (Jędrzejewska et al. 1996, Kaartinen et al. 2010, Ahmadi et al. 2013, Iliopoulos et al. 2014). Although wolves at rendezvous sites have been reported to be tolerant and resilient to various levels of non-lethal human disturbance (Thiel et al. 1998, Frame et al. 2007, Argue et al. 2008), this may not be so where human activity and disturbance had long been associated with increased risk of persecution (Theuerkauf et al. 2003, Kaartinen et al. 2010, Ahmadi et al. 2013, Iliopoulos et al. 2014). In these conditions, factors enhancing concealment and segregation from humans should influence where wolves locate rendezvous sites. Accordingly, a recent meta-analysis at the global scale revealed that segregation and security from humans at homesites is more pronounced in Eurasian than in North American wolf populations, and is reflected by higher avoidance of settlements, anthropogenic linear features, and agricultural lands, and stronger selection for forest cover, higher elevation, and rough terrain (Sazatornil et al. 2016). Locally, however, homesite selection by wolves is markedly context-specific and varies based on prevailing ecological conditions and human disturbance. In the more pristine boreal and temperate ecosystems in North America, wolves preferentially locate rendezvous sites in proximity of meadows, wetlands or other water sources, and forests, with some variability concerning forest types, canopy closure, soil type, and topography (Trapp et al. 2008, Unger et al. 2009, Ausband et al. 2010, Benson et al. 2015, Klaczek et al. 2015). With increasing levels of disturbance and habitat modifications (e.g., forest roads, logging, other human activities), anthropogenic factors prevail over other landscape and habitat characteristics, and rendezvous sites are increasingly located apart from roads, developments, and disturbed areas (Theuerkauf et al. 2003, Person and Russel 2009, Houle et al. 2010, Kaartinen et al. 2010, Lesmerises et al. 2012). In human-modified landscapes, wolves maximizing concealment and security from humans preferentially locate rendezvous sites in densely forested areas at higher elevations, with steeper slopes and rougher terrain, while avoiding main roads and settlements (Capitani et al. 2006, Ahmadi et al. 2013, Iliopoulos et al. 2014).

Despite growing recognition of the importance of multi-scale approaches to elucidate species-habitat relationships, a small proportion of habitat selection studies have been designed to address multiple spatial and temporal scales (McGarigal et al. 2016). Nonetheless, multi-scale approaches to habitat modeling are being increasingly recognized to produce stronger and more reliable inferences than single-scale alternatives (Mayor et al. 2009, Wheatley and Johnson 2009, McGarigal et al. 2016). In addition, changes in habitat selection across ecological domains (Wiens 1989) may be revealed by accounting for multiple observational scales (including extent and grain; Wheatley and Johnson 2009), therefore enhancing our understanding of the behavioral processes underlying habitat decisions made by animals (Rettie and Messier 2000, Schaefer and Mayor 2007, Laforge et al. 2016). Whereas Johnson's (1980) hierarchical framework has been conveniently adopted to define given spatial (temporal, behavioral) extents (Mayor et al. 2009, Gaillard et al. 2010), determining the grain that best describes habitat selection is a major focus of current multi-scale habitat selection modeling (Mayor et al. 2009, McGarigal et al. 2016). For instance, Laforge et al. (2015) combined variables measured at different scales into a single multi-variable model (multi-grain resource selection functions [MRSFs]) and showed that it yielded more predictive power than traditional single-grain resource selection functions.

Unfortunately, most rendezvous site selection studies on wolves did not properly address scalar issues, even though scalar and hierarchical considerations of habitat selection especially apply to wolves (McLoughlin et al. 2004, Houle et al. 2010, Lesmerises et al. 2012). Being territorial, wolves that disperse through the landscape in search of reproductive opportunities are first expected to choose an area where to establish their territory, and then to select resources within the territory to fulfill their life-cycle requirements. Accordingly, accounting for scalar and hierarchical processes in homesite selection by wolves has important analytical implications, affecting extent and grain when measuring resources used and deemed available to wolves at each order of selection. Moreover, a multi-scale approach to homesite selection may unveil changes in habitat decisions across ecological domains, thus elucidating the association between habitat selection and the main fitness-related factors (Rettie and Messier 2000, Dussault et al. 2005).

In Pollino National Park (PNP), southern Apennines, Italy, wolves have always coexisted with humans (Zimen and Boitani 1975) and conditions are ideal to unveil key behavioral adaptations of wolves living in human-modified landscapes (i.e., rendezvous site selection). Although wolves have been legally protected in Italy since 1971, human-caused mortality in PNP reflects tendencies nationwide (Lovari et al. 2007) and within other protected areas (Apollonio et al. 2004, Mancinelli et al. 2018), suggesting that persecution by humans acts as a permanent selection factor that may affect fitness and shape behavioral responses by wolves. Minimum known mortality during our study was 12 wolves, 3 of which died from unknown causes, 1 hit by a vehicle, and 8 poisoned, likely accounting for a permanent state of conflict with the livestock grazing sector (Ciucci et al. 2018).

Our objectives were to describe use and characteristics of rendezvous sites used by wolves, and to identify environmental, topographic, and anthropogenic features that most affected choice of rendezvous sites, according to a multi-scalar, multi-order habitat selection modeling approach. Given the levels of human-caused mortality of wolves in PNP, compounded by intense touristic and livestock grazing activities during the pup rearing season, we predicted that wolves would respond by making habitat decisions that favor concealment and security from humans, even if this would imply higher energetic costs due to increased movements and farther distances from areas of high prey availability. In addition, whereas prospects at the global scale predict that avoidance of anthropogenic features by wolves would intensify at higher selection levels (Sazatornil et al. 2016), we expected that a multi-scalar approach would better elucidate risk-mediated behavioral adaptations by wolves. Accordingly, we also predicted that, if fine-scale selection by wolves was restricted by habitat selection at lower orders of selection (i.e., landscape level), wolves would relax avoidance of anthropogenic features when locating rendezvous sites within the territory.

STUDY AREA

Our 2,351-km^2 study area (Fig. 1) was in the southern Apennines, Italy, and we operationally defined it as the landscape comprised within a 1-km buffer around the 1,926-km^2 PNP. The study area features a particularly varied but typically montane environment, with elevations ranging from 300 m to 2,267 m. Beech (*Fagus sylvatica*) and other mixed deciduous forests covered 53.7% of the area, including some of the particularly rare old-growth beech forests in the Mediterranean region (Lombardi et al. 2013), and 20.7% of the territory was used for agriculture. The area had a humid Mediterranean climate, with hot summers and cold and precipitous winters (mean annual precipitation >1,500 mm; Federico et al. 2010), and snow cover generally extended from November through April, with great variability due to elevation and aspect. Human density averaged 28 ± 283 (SD) inhabitants/km^2 at the township level (2001 census; Italian Institute of Statistics, www.istat.it, accessed 15 Sep 2017), with most people concentrated in few villages (most of which were in the peripheral portions of the park), whereas many portions of the park were void of people and settlements (Fig. 1). Densities of paved (main and secondary) and gravel roads were 0.6 km/km^2 and 0.5 km/km^2, respectively, the latter comprising low-use unimproved roads many of which were unpassable by 2-wheel vehicles. Additional anthropogenic linear features included trails (2.7 km/km^2), which were generally used for hiking and to a lesser extent biking and horse riding. Livestock grazing, agriculture, and tourism were important local activities. About 2,593 livestock farms (1.4 farms/km^2) were active in the study area during the years of the study, 60% of which raised sheep and 38% raised cattle (Gatto et al. 2005).

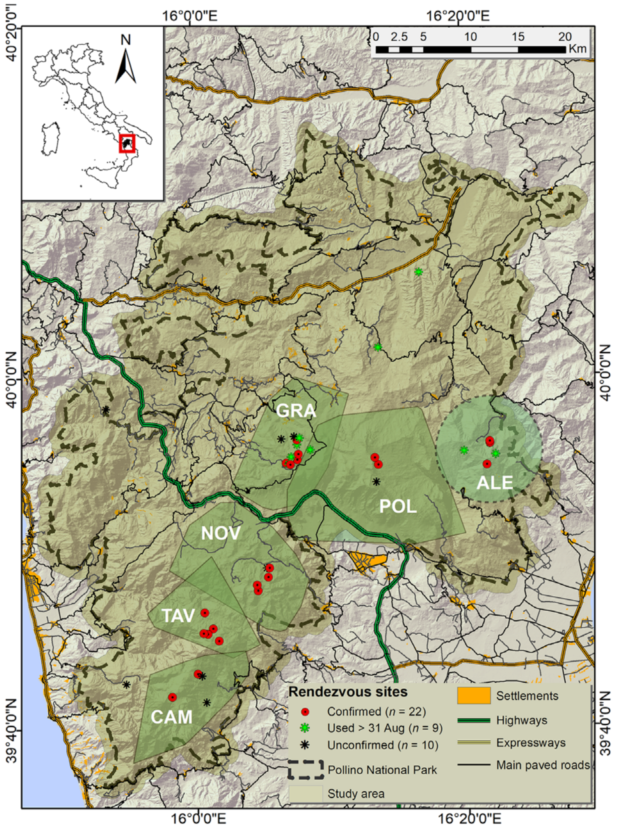

Figure 1. Pollino National Park in Italy (inlet), and rendezvous sites sampled within wolf pack territories from 1999–2003; from south to north packs include Campo (CAM), Tavolara (TAV), Novacco (NOV), Pollino (POL), Grattaculo (GRA), and Alessandria (ALE). We detected non-radioed wolf packs (dashed circles) using howling surveys in summer and snowtracking in winter, but only 1 (ALE) was included in the resource selection analysis.

Well before it was formally established (1993), PNP represented one of the most important historical strongholds for wolves in Italy, when the species was on the verge of extinction (Zimen and Boitani 1975). Because of its size and strategic location across the southern Apennines, PNP is of critical importance for the viability and connectivity of the southernmost Italian wolf subpopulations. During the years of the study we estimated 8–10 wolf packs in PNP (1.9 wolves/100 km^2; Ciucci and Boitani 2004). Although reproduction occurred successfully in each of 6 intensively monitored packs (66.7–100% per pack, $n = 28$ pack-years), pack size in winter was relatively small ($\bar{x} = 3$; range = 1–5 wolves per pack), likely reflecting nontrivial levels of illegal mortality. Wild boar (*Sus scrofa*) were largely distributed across PNP and constituted the bulk of the wolf diet, even though it was largely supplemented by cattle (Ciucci et al. 2018). Water was largely available to wolves during summer in the form of perennial streams and creeks, or off-stream, ephemeral water pools and artificially developed livestock watering points.

METHODS

Live Captures and Telemetry

From 1999 to 2003, we determined the location of wolf packs' territories using repeated snow-tracking during winter and howling surveys during summer, supported by very high frequency (VHF) telemetry in instrumented packs. From 2000 to 2003, we livetrapped 5 wolves in 6 packs using dragged, modified Aldrich foot-snares (M. D. Collinge, Idaho Wildlife Service, personal communication) set along trails and dirt roads and lured with fresh wolf scats and urine. Using VHF trap-transmitters (model 6; ATS, Isanti, MN, USA), we remotely monitored traps 24 hours a day and tranquilized captured wolves in an average of 72 ± 32 minutes (range = 47–120 min) since they were caught. Upon capture, we administered the Hellabrunner mixture of ketamine hydrochloride (3.5 mg/kg) and xylazine hydrochloride (2.7 mg/kg), the latter being antagonized upon release with 0.25 mg/kg of atipamezole (Antisedan). We sexed and weighed captured wolves, and classified them as pups, yearlings, and adults based on tooth eruption and wear patterns (Gipson et al. 2000). Capture and handling procedures were approved by the Italian Wildlife Management Authority (ISPRA), and permits for wolf capture were issued by the Ministry of the Environment (SCN/99/2D/15352).

We fitted captured wolves ≥8 months old with VHF-collars (Telonics, Inc., Mesa, AZ, USA), and attempted to locate them every 1–2 days, from 0000–2300, using sequential triangulation from track-mounted and hand-held Yagi antennas. Using program LOCATE III (Nams 2006), we estimated location error through triangulation based on 55 stationary collars posted at 40 cm and randomly located within 3 wolf pack territories. We assessed the social status of collared wolves (i.e., pack members vs. transients) using repeated snow tracking during winter and howling surveys during summer, and estimated territories limited to resident pack members. In doing so, we assumed VHF relocations from 1 pack member were representative of the territory of the whole pack (Ciucci et al. 1997). To reflect the maximum extent of annual wolf territories, we delineated 100% minimum convex polygons (MCP), excluding obvious outliers. Although the MCP has been criticized as a home range estimator (White and Garrott 1990), it is often adopted in use versus availability designs to represent the maximum area potentially used or available to animals (Dussault et al. 2005). For habitat modeling purposes, we considered multiannual MCPs for 3 wolves that we tracked for >1 year, because their annual territories were consistent from year to year. One dispersing wolf (M12) established a territory outside the study area and was not considered further in the analysis.

Rendezvous Site Location and Use

In addition to telemetry, we used howling surveys and field investigations to locate and subsequently verify rendezvous site location (Ruprecht et al. 2012, Iliopoulos et al. 2014). We conducted nighttime (2000–0500) howling surveys each year during June–September (Harrington and Mech 1982*b*) using broadcasted howls recorded from solitary wolves in captivity (P. Rivoira, University of Turin, unpublished data). In the first 2 years of the study, we conducted howling surveys to systematically locate all breeding (non-instrumented) packs throughout the study area (i.e., saturation census: Harrington and Mech 1982*b*). In the following years, we restricted systematic surveys to areas used by non-instrumented wolves, whereas we conducted howling surveys opportunistically in areas of concentrated use as revealed by VHF-telemetry (instrumented packs). For the scope of this study, we considered only elicited or spontaneous chorus howls comprising pups that we acoustically distinguished by their high pitch (Joslin 1967, Harrington and Asa 2003). However, because packs can split temporarily, or pups can be moved between different rendezvous sites during summer (Frame et al. 2007, Ruprecht et al. 2012, Ausband et al. 2016*a*), to attain evidence of protracted activity at a site we aimed to obtain replicates in the days following our first detection of pups at a site. This also allowed us to estimate with greater accuracy the location of the suspected rendezvous site, with 2–4 observers dispersed at 500–1,000 m and recording bearings towards the approximate direction of the elicited replies. Similar to estimating radio-telemetry error (White and Garrot 1990), we then used acoustic bearings and the Lenth estimator (program LOCATE III, Nams 2006) to delineate a 95% confidence ellipse area that most likely included the pup's location. We used the same procedure to define 95% confidence ellipses for suspected rendezvous sites revealed by telemetry but for which we did not obtain an acoustic confirmation. In packs where we lacked VHF-equipped wolves, we replicated howling surveys at the site every 4–7 days to determine the minimum number of days a rendezvous site was used by wolves. We assumed the site had been vacated after 2–3 successive sessions without replies, and accordingly defined the last day of rendezvous-site use as the mid date between the last day we heard pups at the site and first day we did not obtain a reply. Then, if we detected another sequentially used rendezvous site within the same wolf 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 rendezvous site.

Once vacated, 2–5 operators field investigated all alleged rendezvous sites using handheld global positioning system (GPS) units and scanning the area comprised within the 95% error ellipse, searching for evidence such as a diffuse network of trials, lowered grass, day beds, tufts of wolf hair, pup scats, and prey bone remains (Kolenosky and Johnston 1967, Ballard and Dau 1983, Unger et al. 2009). We then recorded the coordinates of the center of activity of the site, defined as the center-most point of all wolf activity signs, generally coinciding with the point where most of the trails converged and most of the signs, especially bed sites, were found. Limited to rendezvous sites whose location had been previously estimated by acoustic triangulation, we used the on-site recorded center of activity to measure the linear error about the acoustic estimate; we accordingly used the 95% confidence interval upper bound of the linear error as a measure of the expected inaccuracy in estimating the location of a rendezvous site through acoustic triangulation. We then adopted this value as a radius to represent rendezvous sites in a geographic information system (GIS) environment for subsequent modeling (see below). We attempted to ground-truth all detected rendezvous sites, including those located only through a single, unreplicated pup's reply, or inferred exclusively from telemetry locations (Table S1, available online in Supporting Information).

Resource Variables

To account for habitat selection by wolves, we considered a set of 10 environmental, topographic, and anthropogenic variables in a GIS environment (Table 1). We re-sampled all layers to a common origin and 20-m^2 cell size, corresponding to the spatial resolution of the available variables, with the only exception of land cover (100 m^2). We obtained land-cover data from the CORINE Land Cover database (IV level; http://dataservice.eea.europa.eu/dataservice/, accessed 30 Oct 2016).

We obtained human population density information from the Italian Institute of Statistics (updated 2001). The road network was provided by a combination of the De Agostini, GeoNext, and TeleAtlas databases (updated to 2003), integrated with our own field surveys and hand digitized topographic maps especially for dirt roads and trails (scale 1:25,000). We made a distinction between paved and dirt roads, both modeled in terms of density (km/km^2; Table 1). Paved roads connected main villages across the study area and were regularly plowed during winter, whereas dirt roads mostly comprise unimproved dirt and forest roads, many of which were accessible to 4-wheel vehicles only and unplowed during winter. We also considered mapped trails accessible to horse riding, biking, hiking, or all-terrain vehicles.

To account for topographic variables, we used a digital elevation model (original resolution 20 × 20 m) obtained by Italian Military Geographic Institute. Although prey availability influences wolf homesite location in pristine ecosystems (Heard and Williams 1992, Benson et al. 2015, Klaczek et al. 2015), this information was not available for wild boar (i.e., the main prey of wolves) in PNP. However, wild boars were present at a relatively high density and wide distribution in our study area, likely adding little to the explanatory power of the other modeled covariates possibly associated with prey distribution (e.g., forest and shrub cover, open areas).

Using the focal statistics tool in ARCMAP (ARCGIS 10.1, Environmental Systems Research Institute, Redlands, CA, USA), for each variable we ran a map-algebra focal function over the entire study area using a circular moving window and changed the radius to account for different grain sizes in the multi-grain analysis (see Multi-Grain Resource Selection Functions). This function allowed for a better approximation of the composition of the environment surrounding an observation compared to modeling approaches based on single pixel values (Falcucci et al. 2009).

Multi-Grain Resource Selection Functions

For each order of habitat selection, we used MRSFs (Laforge et al. 2015) to account for different grain sizes for different variables. We first evaluated the effect of changing the grain size of 1 focal variable at the time to determine its most parsimonious scale (i.e., single variable grain analysis; Laforge et al. 2015). We set the minimum (200 m) and maximum (5,630 m) grain size to reflect the expected error in the acoustic location of rendezvous sites and the mean radius of wolf pack territories in PNP, respectively. We chose intermediate grain sizes (i.e., from 500 m to 5,000 m) to reflect a continuous scale of increments of 500 m. To examine collinearity among the 12 variables at each of the grain size, we used pairwise Pearson's rank correlation ($r \geq |0.6|$) and the variance inflation factors (VIF > 3; AED R package; Zuur et al. 2007, 2009). For one variable at the time, we then compared all models with (i.e., global model) and without (i.e., quasi-global model) the focal variable measured at each grain size, using the sample-size corrected Akaike's Information Criterion (AIC_c; Burnham and Anderson 2002); that is (Laforge et al. 2015):

$$\Delta AIC_c \text{ variable } (x) = AIC_{c \text{ global model}} - AIC_{c \text{ global model}-\text{variable } (x)}$$

By plotting grain size versus ΔAIC_c, we then identified the most parsimonious scale (i.e., minimum ΔAIC_c values) for

Table 1. Covariates originally considered to construct multi-grain resource selection functions to investigate territory and rendezvous site habitat selection by wolves in the Pollino National Park, southern Italy, 1999–2003. Because of collinearity, we did not retain all covariates in the final models. We averaged mean and standard deviation values across moving windows with a radius of 200 m centered at each 20 × 20-m pixel within a given spatial extent.

Variable			Wolf pack territories		Rendezvous sites[b]	
Type	Description	Study area[a]	$\bar{x}$	SD	$\bar{x}$	SD
Environmental	Forest cover (%)[c]	63.3	76.4	14.9	99.1	3.6
	Open areas (%)[d]	13.2	14.6	11.4	0.7	3.2
	Agricultural areas (%)	20.7	8.8	8.7	0	0
Topographic	Elevation (m)	1,146	1,304	543	1,480	224
	Mean slope (°)	19.0 (±8.6)	21.3	9.2	23.2	4.5
	Terrain roughness (slope SD)	7.1 (±2.8)	7.4	2.9	8.2	1.7
Anthropogenic	Human density (inhabitants/km^2)	28.3 (±283)	8.0	98.1	1.2	1.2
	Paved road density (km/km^2)	0.6	0.3	0.2	0	0
	Dirt road density (km/km^2)	0.5	0.4	0.1	0.2	0.9
	Trail density (km/km^2)	2.7	2.0	0.4	1.4	2.2

[a] Actual values, or $\bar{x}$ (±SD) where feasible.
[b] Within a 200-m buffer radius ($n = 22$ rendezvous sites).
[c] Including shrublands.
[d] Including meadows, pastures, alpine prairies, and clearings.

that variable, and subsequently used this grain size to enter the variable into our final multi-grain models. In addition to the ΔAIC_c values, we also supported choice of the most parsimonious scale for each variable comparing the model-averaged β-coefficients and their 95% confidence intervals, both estimated using the MuMin R package (Bartoń 2016). If the effect of a variable had a different sign at different grain sizes (i.e., reflecting different selection processes), we retained both grain sizes for the final, multi-grain model, provided the 2 were not correlated. We repeated the procedure above for second- and third-order selection, identifying for each the most parsimonious grain size(s) for each of the candidate covariates (Figs. S1 and S2, available online in Supporting Information).

We used the package lme4 (Bates et al. 2016) in R (version 3.3.2, www.r-project.org, accessed 31 Oct 2017) to develop mixed effects logistic regression models (GLMM). The response variable was a binary term of 1 for used and 0 for available observations, and we used a pack identification number as a random intercept to account for repeated observations within the same wolf pack and variation in the number of observations for each pack (Gillies et al. 2006). At each order of analysis, we standardized each variable by subtracting the mean value from each observation and dividing by its standard deviation to allow comparison of covariates' effects and to improve model convergence (Zuur et al. 2009).

To model resource selection at the landscape extent (i.e., second-order selection; Johnson 1980), we followed a type II design (Thomas and Taylor 2006) and quantified use within each wolf pack territory and availability at the study area level. We recognize that this procedure may overestimate resources truly accessible to wolves because wolves trying to establish their own territory would not have access to the resources comprised within already occupied territories, especially in saturated wolf populations. However, this source of bias should be limited because dispersers can float through established wolf territories and try to be integrated into an existing pack or pair-bond with a pack member (Mech and Boitani 2003). For each of 6 packs, resource use within the territory was represented by random points within the MCP sampled at a density of 100 locations/100 km^2 to account for differences in territory size among packs, whereas available observations were randomly selected within the study area ($n = 10{,}000$ for each pack). Using these thresholds, model coefficients stabilized and did not change using more or different random locations. In addition to the 5 wolf packs territories estimated by means of VHF-telemetry (Table S2, available online in Supporting Information), we also considered the approximate territory of a pack of non-instrumented wolves (Alessandria Pack; Fig. 1), tracked by means of repeated snow tracking and howling surveys from 1999 to 2002, and whose territory was approximated by a buffer of 5,630 km (i.e., the mean radius of the 5 telemetry-based annual MCPs) around the focal point of the packs' signs of presence (Mattisson et al. 2013). We developed MRSFs by allowing covariates to enter the model at different grain sizes, as previously indicated by the single variable grain analysis (Laforge et al. 2015). To examine collinearity (Dormann et al. 2013), we used pairwise Pearson's rank correlation ($r \geq |0.6|$) and variance inflation factors (VIF > 3; AED R package; Zuur et al. 2007, 2009). We discarded 3 variables that were inter-correlated with forest cover (Table S3, available online in Supporting Information) retaining in subsequent models 7 uncorrelated covariates (Table S4, available online in Supporting Information). Because our analysis was based on a relatively small sample size, we accounted for overfitting problems (Anderson 2008) by considering models with low complexity and a limited number of covariates, and by reducing the number of models to be compared. In addition, the aim of our models was not to make predictions of habitat use by wolves outside the study area, further reducing the negative effects of potential overfitting (Zellner et al. 2001, Anderson 2008). We performed model selection using the sample-size corrected Akaike's Information Criterion (AIC_c) and adopted multi-model inference averaging estimates based on model weights (R package MuMIn; Bartoń 2016) limited to models whose AIC_c value was ≤ 2 from the best supported model (Burnham and Anderson 2002). As few candidate models received Akaike weights > 0, we did not incur 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 and Anderson 2002). To assess the calibration power of the final model (i.e., how much model predictions differ from a random expectation; Vaughan and Ormerod 2005), we used a jackknife-based k-fold cross-validation (Boyce et al. 2002). By removing observations of 1 pack at time (validation dataset), we used the remaining training set to predict the MRSF coefficients of the fixed effects for the validation dataset, repeating the procedure for all 6 packs. Using deciles, we then split the MRSF values into 10 bins, computing for each the ratio between the relative frequencies of used (predicted) and available (expected) observations. The Boyce et al. (2002) index (i.e., 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.

To model rendezvous site selection within the territory (i.e., third-order selection; Johnson 1980), we followed a type III design (Thomas and Taylor 2006), quantifying use and availability at the individual pack level. For each rendezvous site used in the analysis, we represented availability by sampling 100 random points within the corresponding pack territory. Nine rendezvous sites were asynchronous (1–2 yr) with respect to the year when we estimated the pack's MCP; however, we assumed that slight variations in the conformation of the territory from year to year did not markedly affect availability as measured in MRSFs (Benson et al. 2015). This assumption was supported by the relative stability of wolf territories in the study area as assessed by repeated snow-tracking and howling surveys during our study (Ciucci and Boitani 2004). In addition, because of a limited sample size, we pooled data across years for each pack, assuming that year had a negligible effect on rendezvous site selection. To apply the MRSF at the third-order of selection, we checked for collinearity among covariates (see above), and discarded 2 variables that were inter-correlated with forest cover ($r \geq |0.6|$; Table S3) plus elevation and mean slope (VIF > 3), therefore retaining 6 uncorrelated covariates in subsequent models (Table S4). We followed the same procedures used at the second order of analysis for model building and validation. For the latter, we removed 1 rendezvous site at a time in the jackknife procedure, repeating the process 22 times. In addition, to further support model validation, we also used the 9 verified rendezvous sites excluded from the analysis as an independent validation dataset.

RESULTS

During 2000–2003, mean annual home-range size for the 5 radio-monitored packs was $99.6 \pm 43.8\,\mathrm{km}^2$ (Table S2). Mean VHF-location error was 153 ±133 m (95% CIs = 117 −188 m). In addition to the 5 radio-monitored packs, we also located the territories of the other 4–5 wolf packs in the study area, but we only obtained enough data for the Alessandria Pack to reliably approximate its territory location (Fig. 1). Wolf pack territories featured on average a lower degree of anthropogenic footprint with respect to the entire study area, as indicated by lower human and road density, a lower proportion of agricultural lands, and higher forest cover (Table 1).

Overall, from 1999 to 2003, we identified 41 potential rendezvous sites in all packs within PNP (Fig. 1). However, 10 rendezvous sites were indicated by a single, unreplicated acoustic detection and were excluded from the analysis. Of the remaining 31 accurately located (i.e., by means of replicated, triangulated acoustic detection, or VHF-telemetry) rendezvous sites, 2 belonged to 2 packs lacking sufficient data to reliably approximate their territory, and 7 were used by wolves later than the end of August, when the improved mobility of pups may increasingly confound habitat selection decisions (Gray 1993, Benson et al. 2015). We thus included in our MRSF 22 rendezvous sites from 6 packs (1–3 rendezvous sites/pack/year; $n = 16$ pack-years; Table S1). Based on field surveys conducted on 14 of 23 rendezvous sites originally located by means of acoustic triangulation, the mean linear error of their acoustically estimated location was 149 ± 95 m (95% CI = 98–201 m; range = 29–300 m).

Limited to accurately located rendezvous sites ($n = 31$), the earliest date we acoustically detected pups at a rendezvous site was 30 June and the latest 24 October (Table S1). Based on 17 rendezvous sites in 6 packs for which we acoustically estimated the first and last date of pup presence at the site, the minimum period of rendezvous site use averaged 28 ± 17 days, ranging from 4 to 61 days. In 5 packs, we detected a minimum of 2–3 rendezvous sites sequentially used within the same year, which were located 1.4 ± 0.3 km apart (range = 0.7–1.9 km; 95% CI = 1.1–1.7 km; $n = 12$ intra-pack pairwise distances; $1 \leq n \leq 6$ pairwise distances/pack; Table S5, available online in Supporting Information). Only 1 pack exhibited fidelity at 1 rendezvous site in 2 successive years (Tavolara Pack, 2001–2002). For all other packs, mean distances between rendezvous sites used in different years were 2.1 ± 0.9 km (range = 1.1–3.3 km; 95% CI = 1.3–2.9 km; $n = 61$ pairwise distances within 5 packs; $1 \leq n \leq 39$ pairwise distances per pack; Table S5). The distance between rendezvous sites concurrently used by adjacent packs in the same year averaged 9.6 ± 3.1 km (range = 6.1–13.5 km; 95% CI = 6.8–12.3 km; $n = 5$ pairwise distances in 4 adjacent packs), and we observed similar distances when we compared all neighboring packs regardless of simultaneous rendezvous site use ($\bar{x} = 9.7 \pm 3.0\,\mathrm{km}$; range = 6.1–13.5 km; 95% CI = 7.0–12.3 km; $n = 11$ pairwise distances in 6 adjacent packs).

For second-order selection, the most parsimonious grain varied across covariates (Fig. S1, available online in Supporting Information). The global multi-grain model was the best supported ($w_i = 1.0$; Table 2), corresponding to a Boyce index of $r_s = 0.94$. Wolves selected for areas of higher forest and shurbland cover, interspersed with open meadows and prairies, and higher terrain roughness (Table 3). They also strongly avoided anthropogenic features, including human density, main roads, and trails at closer distances, but selected dirt roads and trails at the home range scale (Table 3). The most parsimonious grain also varied across covariates at the third order of selection (Fig. S2, available online in Supporting Information); the most-parsimonious grain for forest cover was markedly smaller compared to the second order of selection (Table 3). Two subsets of the multi-grain global model were the best supported models ($w_i = 0.69$; Table 2), indicating that at the third order of selection human and main road density were not so important to describe rendezvous site selection. The Boyce index for the averaged model was $r_s = 0.88$ according to the jackknife procedure, and $r_s = 0.83$ using the validation set of late rendezvous sites ($n = 9$). Wolves located rendezvous sites with forested areas in close proximity (i.e., 500 m) and even terrain at coarser grain but avoided low-use, linear anthropogenic features, comprising trails at close distances (Table 3). Contrasting the 2 levels of selection, when placing rendezvous sites within the territory wolves relaxed avoidance of areas with higher human and main road density but intensified selection for forest cover and avoidance of trail density at fine grains (Fig. 2A and B), and switched selection of areas with high terrain roughness and dirt road density (Fig. 2C and D).

DISCUSSION

Wolves in Europe have a pronounced habitat specificity when selecting rendezvous sites. Especially where wolves have been exposed to human persecution, avoidance of anthropogenic pressure plays a critical role in affecting habitat decisions by wolves. Our findings also show that contrasting habitat selection at multiple scales may more thoroughly elucidate trade-offs in behavioral responses of wolves to anthropogenic features (Lesmerises et al. 2012).

Table 2. Multi-grain, mixed effects logistic regression model selection to assess the effects of environmental, topographic, and anthropogenic variables on habitat selection when establishing a territory (second-order selection) and when choosing a rendezvous site within the territory (third-order selection), in the Pollino National Park, southern Italy, 1999–2003. K = number of parameters; AIC$_c$ = Akaike's Information Criterion adjusted for small sample size; w_i = Akaike weights.

Model	Description[a]	K	AIC$_c$	ΔAIC$_c$	w_i
Second order					
1	$\text{For}_{5630}+\text{Open}_{4500}+\text{HDen}_{2000}+\text{MRDen}_{1000}+\text{DRDen}_{5630}+\text{TDen}_{500}+\text{TDen}_{5630}+\text{SDSlo}_{5630}$	10	6,504	0.00	1.0
2	$\text{For}_{5630}+\text{Open}_{4500}+\text{DRDen}_{5630}+\text{TDen}_{500}+\text{TDen}_{5630}+\text{SDSlo}_{5630}$	8	6,530	25.98	0.0
3	$\text{For}_{5630}+\text{HDen}_{2000}+\text{MRDen}_{1000}+\text{DRDen}_{5630}+\text{TDen}_{500}+\text{TDen}_{5630}+\text{SDSlo}_{5630}$	9	6,624	119.63	0.0
4	$\text{For}_{5630}+\text{HDen}_{2000}+\text{DRDen}_{5630}+\text{TDen}_{500}+\text{TDen}_{5630}+\text{SDSlo}_{5630}$	8	6,652	147.81	0.0
5	$\text{For}_{5630}+\text{DRDen}_{5630}+\text{TDen}_{500}+\text{TDen}_{5630}+\text{SDSlo}_{5630}$	7	6,685	180.32	0.0
6	$\text{For}_{5630}+\text{TDen}_{500}+\text{TDen}_{5630}+\text{SDSlo}_{5630}$	4	6,890	385.38	0.0
7	$\text{For}_{5630}+\text{SDSlo}_{5630}$	2	6,938	433.99	0.0
Third order					
1	$\text{For}_{500}+\text{DRDen}_{5000}+\text{TDen}_{500}+\text{SDSlo}_{4500}$	6	233.20	0.00	0.38
2	$\text{For}_{500}+\text{HDen}_{3500}+\text{DRDen}_{5000}+\text{TDen}_{500}+\text{SDSlo}_{4500}$	7	223.65	0.45	0.31
3	$\text{For}_{500}+\text{HDen}_{3500}+\text{MRDen}_{1500}+\text{DRDen}_{5000}+\text{TDen}_{500}+\text{SDSlo}_{4500}$	8	234.76	1.57	0.18
4	$\text{For}_{500}+\text{TDen}_{500}+\text{SDSlo}_{4500}$	5	235.67	2.48	0.11
5	$\text{For}_{500}+\text{SDSlo}_{4500}$	4	239.05	5.85	0.02

[a] For = forest and shrubland cover; Open = open areas; HDen = human population density; MRDen = main paved road density; DRDen = dirt road density; TDen = trail density; SDSlo = slope standard deviation. Subscripts denote most parsimonious grain size (m) based on single variable grain analysis.

Although telemetry was essential in our study to delineate wolf pack territories and detect some rendezvous sites, capturing wolves in multiple packs is costly, and radio-collaring non-breeding pack members might not always be indicative of homesite locations (Demma and Mech 2009, Ruprecht et al. 2012). Global positioning system telemetry has boosted studies of wolf ecology at homesites, whose detection is greatly facilitated by tracking GPS-collared female breeders (Demma and Mech 2009; Ruprecht et al. 2012; Ausband et al. 2016*a*,*b*). However, the adoption of complementary field techniques to locate rendezvous sites is advantageous, especially if it entails on-site field confirmation (Ruprecht et al. 2012). Howling surveys are a cost-effective, complementary survey method to acoustically locate rendezvous sites (Capitani et al. 2006, Ausband et al. 2010, Iliopoulos et al. 2014). However, we advocate the adoption of conservative criteria (e.g., accurate triangulation, replicated replies), followed by field verification, to reliably and accurately estimate rendezvous site locations. In addition, we caution that using howling surveys to locate wolf rendezvous sites in densely populated countries might unwillingly reveal the pups' presence and jeopardize the security of the entire pack. Indeed, this is the reason why we did not conduct repeated howling surveys in wolf packs inhabiting the peripheral and more populated northern and western portions of PNP (Fig. 1).

We revealed that wolves in PNP used at least 2–3 rendezvous sites each year, shifting their location as the pup rearing season progressed, as is commonly observed in many other wolf populations (Peterson et al. 1984, Demma and Mech 2009, Ruprecht et al. 2012, Benson et al. 2015). This contrasts the conditions described in the central Apennines of Italy in the late 1980s, where wolves used a single homesite year round, comprising den and rendezvous sites during the summer, and the most frequently used retreat site during the rest of the year (Ciucci et al. 1997). This difference most

Table 3. Coefficients of multi-grain resource selection functions to investigate habitat selection by wolves when establishing territories (second-order selection) and rendezvous site (third-order selection) in the Pollino National Park, southern Italy, 1999–2003.

	Second order						Third order					
					95% CI						95% CI	
Variable[a]	Grain (m)[b]	Relative importance	β	SE	Lower	Upper	Grain (m)[b]	Relative importance	β	SE	Lower	Upper
(Intercept)			−5.472	0.168	−5.801	−5.143			−5.731	0.546	−6.801	−4.660
For	5,630	1.0	0.965	0.065	0.838	1.092	500	1.0	1.906	0.733	0.469	3.343
Open	4,500	1.0	0.516	0.047	0.423	0.609						
HDen	2,000	1.0	−0.309	0.107	−0.518	−0.099	3,500	0.56	0.168	0.221	−0.265	0.601
MRDen	1,000	1.0	−0.254	0.065	−0.381	0.127	1,500	0.20	−0.065	0.206	−0.469	0.338
DRDen	5,630	1.0	0.656	0.048	0.563	0.750	5,000	1.0	−0.484	0.236	−0.946	−0.026
TDen	500	1.0	−0.104	0.043	−0.188	−0.020	500	1.0	−0.615	0.276	−1.156	−0.073
TDen	5,630	1.0	0.185	0.050	0.088	0.283						
SDSlo	5,630	1.0	0.468	0.052	0.365	0.571	4,500	1.0	−0.714	0.261	−1.225	−0.202

[a] For = forest and shrubland cover; Open = open areas; HDen = human population density; MRDen = main paved road density; DRDen = dirt road density; TDen = trail density; SDSlo = slope standard deviation.

[b] Most parsimonious grain size based on single variable grain analysis.

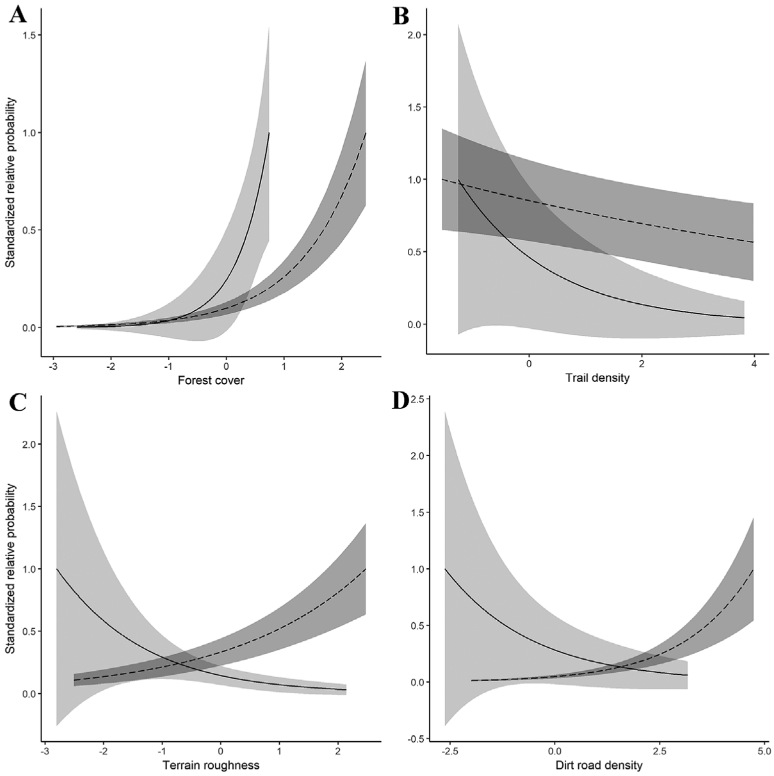

Figure 2. Relative probability of wolves establishing a territory (dashed line) and locating a rendezvous site (solid line) as a function of some of the factors affecting habitat selection based on multi-grain resource selection functions at the second and third selection order, respectively. To facilitate comparability between orders of selection, relative probability (*y*-axis) has been standardized by dividing predicted values by their maximum. Gray areas represent predicted 95% confidence intervals. Predictors comprise forest cover (A), trail density at fine grains (B), terrain roughness (C), and dirt road density (D), all standardized at each order of selection by subtracting their mean value and dividing by the standard deviation. In all panels, the other predictors included in the models were set at their mean values at each order of selection. Data refer to 22 rendezvous sites in 6 pack territories in Pollino National Park, southern Italy (1999–2003).

likely reflects the enhanced availability of wild prey (i.e., wild boar) to wolves in PNP, compared to lack of prey but abundant and predictable anthropogenic food sources at garbage dumps in the 1980s (Macdonald et al. 1980, Ciucci et al. 1997). Unfortunately, we could not ascertain why some rendezvous sites were used longer than others, and further research is needed to understand the ecological and demographic correlates of differential rendezvous site use (Ausband et al. 2016*a*).

As previously reported in a limited number of wolf rendezvous site selection studies (Norris et al. 2002, Person and Russel 2009, Kaartinen et al. 2010), we found that behavioral decisions by wolves are affected at different grain sizes for different resources and, more importantly, across orders of selection. In addition, although wolves made similar habitat decisions at the 2 orders of selection, selection relaxed, intensified, or changed for different habitat components when choosing rendezvous sites compared to when establishing a territory, indicating that habitat selection in wolves is scale-dependent. Overall, habitat decisions by wolves in PNP reflected several adaptations to optimize concealment and safety and minimize chances of disturbance by humans, while enhancing traveling and foraging efficiency.

As detected at the second order of selection, wolf aversion of human density and main roads reflects their tendency to reduce the risk associated with human disturbance. This response, however, appears to be integrated into a broader ecological and topographic context because wolves selected for forested areas and roughness but also open areas when establishing a territory, likely reflecting improved concealment and security from humans and increased availability of the main prey. Concurrently, selection for low-use anthropogenic linear features (i.e., dirt roads and trails, at coarse grain) likely accounted for improved hunting efficiency and movement rates, the latter enhancing prey encounter rates and efficiency of territory patrolling and scent-marking (Whittington et al. 2011, Lesmerises et al. 2012). This is in line with previous findings, according to which wolves generally avoid main roads at the landscape scale (Thiel 1985, Mladenoff et al. 1995), even though they may select low-use dirt roads and trails (Thurber et al. 1994, Musiani et al. 1998), especially in mountainous areas where these features are most expected to facilitate movement rates (Ciucci et al. 2003, Whittington et al. 2011). Our multi-scale analysis, however, revealed that selection for low-use linear features may be grain-size dependent, corresponding to different selection decisions made by wolves at different scales. For example, at the second order of selection, trails are selected at a coarse grain and are likely to enhance movement and traveling efficiency, whereas at a finer grain (e.g., when choosing daily resting locations), they may be perceived as a potential source of disturbance and are accordingly avoided. This tendency is further strengthened when wolves select rendezvous sites and, at this order of selection, wolves intensified their cautionary response to humans by reinforcing selection for close forest cover (i.e., 500 m). Likewise, although wolves selected dirt roads at the landscape scale, they avoided them when locating rendezvous sites, possibly because wolves associate dirt roads with increased pup vulnerability to humans. Like dirt roads, change in selection for rough terrain reveals that this feature is viewed differently by wolves at different scales. Although roughness is selected at the landscape scale because it may offer concealment and inaccessibility from humans, it is avoided when using rendezvous sites because it may entail higher energetic costs associated with centripetal, daily movements, especially in mountainous areas (Person and Russel 2009, Ausband et al. 2010).

Our findings illustrate that variation in habitat selection at different scales may unveil changes in the perceived costs and benefits underlying selection decisions by wolves (Lesmerises et al. 2012), thereby revealing trade-offs in habitat selection (Thompson and McGarigal 2002, Leblond et al. 2011). It has been speculated that wolves living in densely populated countries would be expected to be relatively more tolerant of anthropogenic features at lower selection orders, and to exhibit stronger selection against factors facilitating exposure to human-related risks at higher orders of selection (Sazatornil et al. 2016). However, our findings only partly support this hypothesis, suggesting that scale-dependent habitat selection in wolves could be more complex than previously thought. Indeed, when selecting rendezvous sites within the territory, wolves in PNP increased selection of forests and shifted from selection to avoidance of low-use anthropogenic linear features. However, we did not detect an overall higher degree of tolerance of human-made structures at the second order of selection and at this extent, selection for lower human and main road densities was stronger and compounded by selection of rougher terrain to further minimize exposure to human-related risk. Rather than focusing on patterns, a process-focused approach may add to the understanding of different selection decisions made by wolves at different scales. For instance, Rettie and Messier (2000) proposed that animals select for factors most limiting their fitness at the spatial scale at which these factors have highest heterogeneity. It follows that across-scale differences in spatial heterogeneity of the most relevant limiting factors could inform predictions of the scale at which selection for a given factor should be expected the most (Gaillard et al. 2010). For wolves living in densely populated countries, this might correspond to understanding the main sources of human-caused mortality or impaired fitness, and accordingly assess their spatial variation across scales. The same reasoning would account for the fact that, in more pristine ecosystems of North America where anthropogenic effects are less apparent, proximity to water and prey availability are among the features most selected by wolves when selecting rendezvous sites (Trapp et al. 2008, Unger et al. 2009, Ausband et al. 2010, Benson et al. 2015).

In conclusion, we recognize that although we lacked data on forest structure and density, and especially hiding cover at ground level, these factors could play an important role in shaping rendezvous site selection in PNP (Trapp et al. 2008, Kaartinen et al. 2010, Lesmerises et al. 2012). Indeed, several rendezvous sites in our study area were located inside relatively young, regenerating beech forest stands, which have stem densities that likely provide excellent hiding cover and ensure inaccessibility by humans (Fig. S3, available online in Supporting information). This aspect deserves further investigation in study conditions similar to ours, especially in the light of the important reflections it may hold for forestry practices inside protected areas. In addition, although wolf pack territories were on average located at higher elevation compared to the rest of the study area, and elevation has often been revealed to affect habitat selection by wolves at the landscape extent (Lesmerises et al. 2012, Llaneza et al. 2012), we discarded this variable at both orders of selection because it was redundant with other ecologically more informative covariates. We believe that elevation often reflects ecological gradients and, in human-modified landscapes, elevational dispersion of anthropogenic landscape attributes (Capitani et al. 2006, Boutros et al. 2007). This does not necessarily mean that elevation *per se* is not an important descriptor of habitat selection by wolves, but that, based on collinearity, other ecological or anthropogenic variables may convey more direct, explicit, and meaningful information on wolf-habitat relationships.

MANAGEMENT IMPLICATIONS

Improved knowledge of multi-scale, hierarchical rendezvous site selection by wolves can be of practical value to inform management in several respects. First, we can refine the understanding of factors responsible for the distribution and long-term establishment of reproductive wolf packs at the local scale to produce rendezvous site probability (Fig. S4, available online in Supporting Information). We emphasize that neglecting the hierarchical nature of rendezvous site selection may lead to inaccurate and overestimated predictions of their potential availability at the landscape extent. Second, we can assess to what extent current networks of protected areas capture habitat conditions that facilitate reproduction (i.e., availability of rendezvous sites) in local wolf packs. Third, we can provide spatially explicit indications to inform proactive management aimed to reduce depredation on livestock during summer. Specifically, maps like ours (Fig. S4) indicate where strict overlap between unattended free-ranging livestock and areas where wolves will likely locate their rendezvous sites should be prevented. Fourth, we can aid the design and interpretation of large-scale howling surveys. For example, in environmental settings like ours, detecting successively used rendezvous sites using howling surveys at distances $\leq$1.7 km (i.e., upper 95% CL of intra-pack linear distances) could be a reliable confirmation that they belong to the same pack, whereas distances $\geq$6.8 km (i.e., lower 95% CI of inter-pack linear distances) should be regarded as indicative of different packs. Similarly, because howling surveys based on a saturation census design (Harrington and Mech 1982*b*) can be prohibitively costly over large areas (Crête and Messier 1987), howling stations could be efficiently skipped if $\leq$6.8 km from known rendezvous sites because they will unlikely reveal the presence of another reproductive pack.

ACKNOWLEDGMENTS

We are indebted to M. Tripepi for his patronage and continuous encouragement of our research activities. We thank all technicians who helped conduct the study, especially L. Artoni, N. Boldrini, C. Braschi, M. Caporioni, S. D'Alessio, I. Gatto, and G. Gervasio. We also acknowledge the many students and volunteers who participated in the field work, especially A. Bertrand, C. Bueno De Campos, F. Crispino, S. Liccioli, I. Orlando, C. Solsbury, A. Testa, and E. Tosoni. P. Rivoira provided tracks of wolf howling. We gratefully acknowledge comments and insights from the editors and 2 anonymous referees that improved our manuscript. The Istituto of Ecologia Applicata, Rome, Italy, provided logistical support for our work. This study was funded by the PNP Authority and L. M. was supported by a postdoc fellowship provided by a donor through the International Wolf Center (Ely, MN, USA).

LITERATURE CITED

Ahmadi, M., M. Kaboli, E. Nourani, A. A. Shabani, and S. Ashrafi. 2013. A predictive spatial model for gray wolf (*Canis lupus*) denning sites in a human-dominated landscape in western Iran. Ecological research 28:513–521.

Anderson, D. R. 2008. Model based inference in the life sciences: a primer on evidence. Springer, New York, New York, USA

Apollonio, M., L. Mattioli, M. Scandura, L. Mauri, A. Gazzola, and E. Avanzinelli. 2004. Wolves in the Casentinesi Forests: insights for wolf conservation in Italy from a protected area with a rich wild prey community. Biological Conservation 120:249–260.

Argue, A. M., K. J. Mills, and B. R. Patterson. 2008. Behavioural response of eastern wolves (*Canis lycaon*) to disturbance at homesites and its effects on pup survival. Canadian Journal of Zoology 86:400–406.

Ausband, D. E., M. S. Mitchell, S. B. Bassing, A. Morehouse, D. W. Smith, D. R. Stahler, and J. Struthers. 2016*a*. Individual, group, and environmental influences on helping behavior in a social carnivore. Ethology 122:963–972.

Ausband, D. E., M. S. Mitchell, S. B. Bassing, M. Nordhagen, D. W. Smith, and D. R. Stahler. 2016*b*. Dog days of summer: influences on decision of wolves to move pups. Journal of Mammalogy 97:1282–1287.

Ausband, D. E., M. S. Mitchell, K. Doherty, P. Zager, C. M. Mack, and J. Holyan. 2010. Surveying predicted rendezvous sites to monitor gray wolf populations. Journal of Wildlife Management 74:1043–1049.

Ballard, W. B., and J. R. Dau. 1983. Characteristics of gray wolf, *Canis lupus*, den and rendezvous sites in south-central Alaska. Canadian Field-Naturalist 97:299–302.

Bartoń, K. 2016. MuMIn: multi-model inference. R package version 1.15.6. http://CRAN.R-project.org/package=MuMIn. Accessed 28 Aug 2016.

Bates, D., M. Maechler, and B. Bolker. 2016. lme4: linear mixed-effects models using 'Eigen' and S4. R package version 1.1-12. https://CRAN.R-project.org/package=lme4. Accessed 28 Aug 2016.

Benson, J. F., K. J. Mills, and B. R. Patterson. 2015. Resource selection by wolves at dens and rendezvous sites in Algonquin park, Canada. Biological Conservation 182:223–232.

Boutros, D., C. Breitenmoser-Würsten, F. Zimmermann, A. Ryser, A. Molinari-Jobin, S. Capt, M. Güntert, and U. Breitenmoser. 2007. Characterisation of Eurasian lynx *Lynx lynx* den sites and kitten survival. Wildlife Biology 13:417–429.

Boyce, M. S., P. R. Vernier, S. E. Nielsen, and F. K. A. Schmiegelow. 2002. Evaluating resource selection functions. Ecological Modelling 157:281–300.

Burnham, K. P., and D. R. Anderson. 2002. Model selection and multi-model inference: a practical information-theoretic approach. Second edition. Springer-Verlag, New York, New York, USA.

Capitani, C., L. Mattioli, E. Avanzinelli, A. Gazzola, P. Lamberti, L. Mauri, M. Scandura, A. Viviani, and M. Apollonio. 2006. Selection of rendezvous sites and reuse of pup raising areas among wolves *Canis lupus* of north-eastern Apennines. Italy. Acta Theriologica 51:395–404.

Ciucci, P., L. Artoni, F. Crispino, E. Tosoni, and L. Boitani. 2018. Inter-pack, seasonal and annual variation in prey consumed by wolves in Pollino National Park, southern Italy. European Journal of Wildlife Research 64:5.

Ciucci, P., and L. Boitani. 2004. Research on wolf ecology and conservation in Pollino National Park. Technical Report. Ente Parco Nazionale del Pollino, Rotonda, Italy.

Ciucci, P., L. Boitani, F. Francisci, and G. Andreoli. 1997. Home range, activity and movements of a wolf pack in central Italy. Journal of Zoology 243:803–819.

Ciucci, P., M. Masi, and L. Boitani. 2003. Winter habitat and travel route selection by wolves in the northern Apennines, Italy. Ecography 26:223–235.

Crête, M., and F. Messier. 1987. Evaluation of indices of gray wolf, *Canis lupus*, density in forests of southwestern Quebec. Canadian Field Naturalist 101:147–152.

Demma, D. J., and L. D. Mech. 2009. Wolf use of summer territory in northeastern Minnesota. Journal of Wildlife Management 73:380–384.

Dormann, C. F., J. Elith, S. Bacher, C. Buchmann, G. Carl, G. Carré, J. R. G. Marquéz, B. Gruber, B. Lafourcade, P. J. Leitão, T. Münkemüller, C. McClean, P. E. Osborne, B. Reineking, B. Schröder, A. K. Skidmore, D. Zurell, and S. Lautenbach. 2013. Collinearity: a review of methods to deal with it and a simulation study evaluating their performance. Ecography 36:27–46.

Dussault, C., J.-P. Ouellet, R. Courtois, J. Huot, L. Breton, and H. Jolicoeur. 2005. Linking moose habitat selection to limiting factors. Ecography 28:619–628.

Falcucci, A., P. Ciucci, L. Maiorano, L. Gentile, and L. Boitani. 2009. Assessing habitat quality for conservation using an integrated occurrence-mortality model. Journal of Applied Ecology 46:600–609.

Federico, S., L. Pasqualoni, E. Avolio, and C. Bellecci. 2010. Calabria daily rainfall from 1970 to 2006. Natural Hazards Earth Systems Science 10:717–722.

Frame, P. F., H. D. Cluff, and D. S. Hik. 2007. Response of wolves to experimental disturbance at homesites. Journal of Wildlife Management 71:316–320.

Gaillard, J. M., M. Hebblewhite, A. Loison, M. Fuller, R. Powell, M. Basille, and B. Van Moorter. 2010. Habitat–performance relationships: finding the right metric at a given spatial scale. Philosophical Transactions of the Royal Society of London B: Biological Sciences 365:2255–2265.

Gatto, I., F. Rotondaro, and P. Serroni. 2005. Monitoraggio del conflitto tra lupo e zootecnia nel parco nazionale del Pollino: quantificazione del fenomeno ed indagine conoscitiva sulle tipologie di allevamento e sull'atteggiamento degli allevatori. Biologia e Conservazione della Fauna 115. [In Italian with English summary.]

Gillies, C. S., M. Hebblewhite, S. E. Nielsen, M. A. Krawchuk, C. L. Aldridge, J. L. Frair, J. Saher, C. E. Stevens, and C. L. Jerde. 2006. Application of random effects to the study of resource selection by animals. Journal of Animal Ecology 75:887–898.

Gipson, P., W. Ballard, R. Nowak, and L. D. Mech. 2000. Accuracy and precision of estimating age of gray wolves by tooth wear. Journal of Wildlife Management 64:752–758.

Gray, D. R. 1993. The use of muskox kill sites as temporary rendezvous sites by arctic wolves with pups in early winter. Arctic 46:324–330.

Grueber, C. E., S. Nakagawa, R. J. Laws, and I. G. Jamieson. 2011. Multimodel inference in ecology and evolution: challenges and solutions. Journal of Evolutionary Biology 24:699–711.

Harrington, F. H., and C. S. Asa. 2003. Wolf communication. Pages 66–103 *in* L. D. Mech, and L. Boitani, editors. Wolves: behaviour, ecology and conservation. The University of Chicago Press, Chicago, Illinois, USA.

Harrington, F. H., and L. D. Mech. 1982*a*. Patterns of homesite attendance in two Minnesota wolf packs. Pages 81–105 *in* F. H. Harrington, and P. C. Paquet, editors. Wolves of the world. Perspectives of behavior, ecology and conservation. Noyes Publishing, Park Ridge, New Jersey, USA.

Harrington, F. H., and L. D. Mech. 1982*b*. An analysis of howling response parameters useful for wolf pack censusing. Journal of Wildlife Management 46:686–693.

Heard, D. C., and T. M. Williams. 1992. Distribution of wolf dens on migratory caribou ranges in the Northwest Territories, Canada. Canadian Journal of Zoology 70:1504–1510.

Houle, M., D. Fortin, C. Dussault, R. Courtois, and J.-P. Ouellet. 2010. Cumulative effects of forestry on habitat use by gray wolf (*Canis lupus*) in the boreal forest. Landscape Ecology 25:419–433.

Iliopoulos, Y., D. Youlatos, and S. Sgardelis. 2014. Wolf pack rendezvous site selection in Greece is mainly affected by anthropogenic landscape features. European Journal of Wildlife Research 60:23–34.

James, A. R., and A. K. Stuart-Smith. 2000. Distribution of caribou and wolves in relation to linear corridors. Journal of Wildlife Management 64:154–159.

Jędrzejewska, B., W. Jedrzejewski, A. N. Bunevich, L. Miłkowski, and H. Okarma. 1996. Population dynamics of wolves *Canis lupus* in Białowieza Primeval Forest (Poland and Belarus) in relation to hunting by humans, 1847–1993. Mammal Review 26:103–126.

Johnson, D. H. 1980. The comparison of usage and availability measurements for evaluating resource preference. Ecology 61:65–71.

Joslin, P. W. B. 1967. Movements and home sites of timber wolves in Algonquin Park. American Zoologist 7:279–288.

Kaartinen, S., M. Luoto, and I. Kojola. 2010. Selection of den sites by wolves in boreal forests in Finland. Journal of Zoology 281:99–104.

Klaczek, M. R., C. J. Johnson, and H. D. Cluff. 2015. Den site selection of wolves (*Canis lupus*) in response to declining caribou (*Rangifer tarandus groenlandicus*) density in the central Canadian Arctic. Polar Biology 38:2007–2019.

Kolenosky, G. B., and D. H. Johnston. 1967. Radio-tracking timber wolves in Ontario. Integrative and Comparative Biology 7:289–303.

Kunkel, K. E., and D. H. Pletscher. 2000. Habitat factors affecting vulnerability of moose to predation by wolves in southeastern British Columbia. Canadian Journal of Zoology 78:150–157.

Laforge, M. P., A. Uzal, S. A. Medill, and P. D. Mcloughlin. 2016. Scale-dependent effects of density and habitat on foal survival. Journal of Wildlife Management 80:347–354.

Laforge, M. P., E. Vander Wal, R. K. Brook, E. M. Bayne, and P. D. McLoughlin. 2015. Process-focussed, multi-grain resource selection functions. Ecological Modelling 305:10–21.

Leblond, M., J. Frair, D. Fortin, C. Dussault, J.-P. Ouellet, and R. Courtois. 2011. Assessing the influence of resource covariates at multiple spatial scales: an application to forest-dwelling caribou faced with intensive human activity. Landscape Ecology 26:1433–1446.

Lesmerises, F., C. Dussault, and M. H. St.Laurent. 2012. Wolf habitat selection is shaped by human activities in a highly managed boreal forest. Forest Ecology and Management 276:125–131.

Llaneza, L., J. V. López-Bao, and V. Sazatornil. 2012. Insights into wolf presence in human-dominated landscapes: the relative role of food availability, humans and landscape attributes. Diversity and Distributions 18:459–469.

Lombardi, F., G. Chirici, M. Marchetti, R. Tognetti, B. Lasserre, P. Corona, A. Barbati, B. Ferrari, S. di Paolo, D. Giuliarelli, F. Mason, F. Iovino, A. Nicolaci, L. Bianchi, A. Maltoni, and D. Travaglini. 2013. Deadwood in forest stands close to old-growthness under Mediterranean conditions in the Italian Peninsula. Italian Journal of Forest and Mountain Environments 65:481–504.

Lovari, S., A. Sforzi, C. Scala, and R. Fico. 2007. Mortality parameters of the wolf in Italy: does the wolf keep himself from the door? Journal of Zoology, London 272:117–124.

Macdonald, D. W., L. Boitani, and P. Barrasso. 1980. Foxes, wolves and conservation in the Abruzzo mountains. Pages 223–235 *in* E. Zimen, editor. The red fox. Springer, Dordrecht, The Netherlands.

Mancinelli, S., L. Boitani, and P. Ciucci. 2018. Determinants of home range size and space use patterns in a protected wolf (*Canis lupus*) population in central Apennines, Italy. Canadian Journal of Zoology. In press.

Mattisson, J., H. Sand, P. Wabakken, V. Gervasi, O. Liberg, J. D. C. Linnell, G. R. Rauset, and H. C. Pedersen. 2013. Home range size variation in a recovering wolf population: evaluating the effect of environmental, demographic, and social factors. Oecologia 173:813–825.

Mayor, S. J., D. C. Schneider, J. A. Schaefer, and S. P. Mahoney. 2009. Habitat selection at multiple scales. Ecoscience 16:238–247.

McGarigal, K., H. Yi Wan, K. A. Zeller, B. C. Timm, and S. A. Cushman. 2016. Multi-scale habitat selection modeling: a review and outlook. Landscape Ecology 31:1161–1175.

McLoughlin, P. D., L. R. Walton, H. D. Cluff, P. C. Paquet, and M. A. Ramsay. 2004. Hierarchical habitat selection by Tundra wolves. Journal of Mammalogy 85:576–580.

Mech, L. D., L. G. Adams, T. J. Majer, J. W. Burch, and B. W. Dale. 1998. The wolves of Denali. University of Minnesota Press, Minneapolis, USA.

Mech, L. D., and L. Boitani, editors. 2003. Wolves: behaviour, ecology and conservation. University of Chicago Press, Chicago, Illinois, USA.

Mills, K. J., B. R. Patterson, and D. L. Murray. 2008. Direct estimation of early survival and movements in eastern wolf pups. Journal of Wildlife Management 72:949–954.

Mladenoff, D. J., T. A. Sickley, R. G. Haight, and A. P. Wydeven. 1995. A regional landscape analysis and prediction of favorable gray wolf habitat in the northern Great Lakes region. Conservation Biology 9:279–294.

Musiani, M., H. Okarma, and W. Jędrzejewski. 1998. Speed and actual distances travelled by radiocollared wolves in Białowieża Primeval Forest (Poland). Acta Theriologica 43:409–416.

Nams, V. O. 2006. Locate III user's guide. Pacer Computer Software, Tatamagouche, Nova Scotia, Canada. http://www.locateiii.com/Download.htm. Accessed 14 Aug 2016.

Norris, D. R., M. T. Theberge, and J. B. Theberge. 2002. Forest composition around wolf (*Canis lupus*) dens in eastern Algonquin Provincial Park. Ontario. Canadian Journal of Zoology 80:866–872.

Packard, J. M. 2003. Wolf behaviour: repdoductive, social, and intelligent. Pages 35–65 *in* L. D. Mech, and L. Boitani, editors. Wolves: behaviour, ecology and conservation. University of Chicago Press, Chicago, Illinois, USA.

Person, D. K., and A. L. Russel. 2009. Reproduction and den site selection by wolves in a disturbed landscape. Northwest Science 83:211–224.

Peterson, R. O., J. D. Woolington, and T. N. Bailey. 1984. Wolves of the Kenai peninsula, Alaska. Wildlife Monographs 88:1–52.

Rettie, W. J., and F. Messier. 2000. Hierarchical habitat selection by woodland caribou: its relationship to limiting factors. Ecography 23:466–478.

Ruprecht, J. S., D. E. Ausband, M. S. Mitchell, E. O. Garton, and P. Zager. 2012. Homesite attendance based on sex, breeding status, and number of helpers in gray wolf packs. Journal of Mammalogy 93:1001–1005.

Sazatornil, V., A. Rodríguez, M. Klaczek, M. Ahmadi, F. Álvares, S. Arthur, J. C. Blanco, B. L. Borg, D. Cluff, Y. Cortés, E. J. García, E. Geffen, B. Habib, Y. Iliopoulos, M. Kaboli, M. Krofel, L. Llaneza, F. Marucco, J. K. Oakleaf, D. K. Person, H. Potočnik, N. Ražen, H. Rio-Maior, H. Sand, D. Unger, P. Wabakken, and J. V. López-Bao. 2016. The role of human-related risk in breeding site selection by wolves. Biological Conservation 201:103–110.

Schaefer, J. A., and S. J. Mayor. 2007. Geostatistics reveal the scale of habitat selection. Ecological Modelling 209:401–406.

Theuerkauf, J., S. Rouys, and W. Jedrzejewski. 2003. Selection of den, rendezvous, and resting sites by wolves in the Bialowieza Forest, Poland. Canadian Journal of Zoology 81:163–167.

Thiel, R. 1985. Relationship between road densities and wolf habitat suitability in Wisconsin. The American Midland Naturalist 113:404–407.

Thiel, R. P., S. Merril, and L. D. Mech. 1998. Tolerance by denning wolves, *Canis lupus*, to human disturbance. Canadian Field-Naturalist 112:340–342.

Thomas, D. L., and E. J. Taylor. 2006. Study designs and tests for comparing resource use and availability II. Journal of Wildlife Management 70:324–336.

Thompson, C. M., and K. McGarigal. 2002. The influence of research scale on bald eagle habitat selection along the lower Hudson River, New York (USA). Landscape Ecology 17:569–586.

Thurber, J. M., R. O. Peterson, T. D. Drummer, and S. A. Thomasma. 1994. Gray wolf response to refuge boundaries and roads in Alaska. Wildlife Society Bulletin 22:61–68.

Trapp, J. R., P. Beier, C. Mack, D. R. Parsons, and P. C. Paquet. 2008. Wolf, *Canis lupus*, den site selection in the Rocky Mountains. Canadian Field-Naturalist 122:49–56.

Unger, D. E., P. W. Keenlance, B. E. Kohn, and E. M. Anderson. 2009. Factors influencing homesite selection by gray wolves in northwestern Wisconsin and east-central Minnesota. Pages 175–189 *in* E. Heske, T. R. Deelen, and A. P. Wydeven, editors. Recovery of gray wolves in the great lakes region of the United States. An endangered species success story. Springer-Verlag, New York, New York, USA.

Vaughan, I. P., and S. J. Ormerod. 2005. The continuing challenges of testing species distribution models. Journal of Applied Ecology 42:720–730.

Wheatley, M., and C. Johnson. 2009. Factor limiting our understanding of ecological scale. Ecological Complexity 6:50−159.

White, G. C., and R. A. Garrott. 1990. Analysis of wildlife radio-telemetry data. Academic Press, San Diego, California, USA.

Whittington, J., M. Hebblewhite, N. J. DeCesare, L. Neufeld, M. Bradley, J. Wilmshurst, and M. Musiani. 2011. Caribou encounters with wolves increase near roads and trails: a time-to-event approach. Journal of Applied Ecology 48:1535−1542.

Whittington, J., C. C. St Clair, and G. Mercer. 2005. Spatial responses of wolves to roads and trails in mountain valleys. Ecological Applications 15:543−553.

Wiens, J. A. 1989. Spatial scaling in ecology. Functional Ecology 3:385–397.

Zellner, A., H. A. Keuzenkamp, M. McAleer. 2001. Simplicity, inference, and modeling. Cambridge University Press, Cambridge, United Kingdom.

Zimen, E., and L. Boitani. 1975. Number and distribution of wolves in Italy. Säugetierkunde 40:102−112.

Zuur, A. F., E. N. Ieno, and G. M. Smith. 2007. Analysing ecological data. Springer, New York, New York, USA.

Zuur, A., E. N. Ieno, N. Walker, A. A. Saveliev, and G. M. Smith. 2009. Mixed effects models and extensions in ecology with R. Springer-Verlag, New York, New York, USA.

Associate Editor: Ryan Long.

SUPPORTING INFORMATION

Additional supporting information may be found in the online version of this article at the publisher's website.