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Determinants of home range size and space use patterns in a protected wolf (*Canis lupus*) population in the central Apennines, Italy

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Abstract

Large carnivores are amongst the most susceptible species to human activities, and human-modified environments pose a threat to carnivore conservation. Wolves (*Canis lupus* Linnaeus, 1758) in the central Apennines, Italy, have coexisted with humans since historic times, and represent a good case study to assess their spatio-temporal response to anthropogenic factors. From 2008–2010, we investigated the spatial behavior of wolves (7 wolves in 5 packs, and 6 floaters) in the Abruzzo Lazio and Molise National Park. Orographically corrected annual home ranges of resident wolf packs, estimated through the Brownian bridge movement model, averaged 104 (± 24 SD) km², whereas floaters used 2- to 4-fold larger areas (293.8–408.7 km²). We did not detect any seasonal effect on home range size, but home ranges were larger during the night and in areas of greater road density, especially during summer. By estimating core areas through an individual-based approach, we also revealed a habitat-mediated response to human presence and activity as resident wolves preferentially established core areas at greater elevation and in the more forested and inaccessible portions of the home range.

Key words

(anthropogenic effects, Brownian Bridge Movement Model, *Canis lupus*, core areas, home range, GPS-telemetry, wolf)

Introduction

Large carnivores play a critical role in shaping the evolution, ecology, and behavior of prey species and other carnivores (Miller et al. 2001), as well as the trophic structure of ecosystems (Ripple and Beschta 2012). Although human-carnivore conflicts facilitate controversies surrounding large carnivore conservation, large carnivores are central to many conservation efforts because their populations are sensitive to anthropogenic activities (Linnell et al. 2000; Treves and Karanth 2003). In particular, increased public support and promotion of human-carnivore coexistence is essential for the persistence of carnivore populations in anthropogenic landscapes (Chapron et al. 2014). In this perspective, a better understanding of how carnivores behaviourally respond to human activity is essential for effective conservation planning.

Behavioural responses towards human activities have been reported for a variety of large carnivore species. For example, in North America, mountain lions [*Puma concolor* (Linnaeus, 1771)] increase nocturnal activity in areas with high human presence (Van Dyke et al. 1986), and coyotes (*Canis latrans* Say, 1823) living in urban landscapes avoid land-use types associated with human activity (Gehrt et al. 2009). Moreover, coyotes respond to disturbance related to military activity with habitat-mediated responses including dynamic expansion, reduction or temporary abandonment of home ranges (Gese et al. 1988), and increase diurnal activity after human exploitation cease (Kitchen et al. 2000). In Europe, brown bears (*Ursus arctos* Linnaeus, 1758) show spatio-temporal avoidance of humans during daytime (Ordiz et al. 2014), and the Eurasian lynx [*Lynx lynx* (Linnaeus, 1758)] also avoids areas with the highest human and road densities (Bouyer et al. 2015; but see Basille et al. 2009). Amongst large carnivores in Europe, the gray wolf (*Canis lupus* Linnaeus, 1758) proved to be the most successful in persisting in human-modified environments (Chapron et al. 2014). Coexistence tactics by wolves may involve increased nocturnal activity (Vila et al. 1993; Ciucci et al. 1997; Kusak et al. 2005; but see Theuerkauf et al. 2007), as well as increased avoidance of areas associated with humans (e.g., Theuerkauf et al. 2003a; Kaartinen et al. 2005; Kusak et al. 2005). Wolves in Scandinavia establish their home ranges in

high quality habitats characterized by low human activity (Karlsson et al. 2007), and also tend to avoid anthropogenic structures when moving within them (Kaartinen et al. 2005; Kojola et al. 2016). This pattern is even more apparent when referring to the selection of critical sites such as dens, rendezvous sites, and diurnal retreat areas (Theuerkauf et al. 2003b; Capitani et al. 2006; Iliopoulos et al. 2014).

In human-modified landscapes, the spatial behaviour of wolves may involve a complex integration between home range configuration and activity, revealing quite predictable spatio-temporal patterns complementary to human interference (Ciucci et al. 1997). Indeed, the effects of anthropogenic factors on the size and configuration of wolf home ranges have been extensively studied in Europe (e.g., Theuerkauf et al. 2003a; Kaartinen et al. 2005; Mattisson et al. 2013). However, such studies are still particularly rare in Southern Europe where, due to a relatively greater human density and impact on the landscape, conditions are ideal to investigate spatial and habitat correlates of behavioural responses by wolves. In Spain, wolves strongly selected forest cover during daytime to avoid humans (Vila et al. 1993), and similar patterns have been observed in Croatia (Kusak et al. 2005). Also wolves living in the open and agricultural landscapes of northern Greece have been recently reported to locate core areas in the more forested portions of their home ranges (Karamanlidis et al. 2016). Although critical, however, our knowledge in this respect is still limited to a paucity of studies, all of which are based on particularly low sample sizes (i.e., 1–2 collared packs per study; Vila et al. 1993; Ciucci et al. 1997; Kusak et al. 2005; Karamanlidis et al. 2016).

Although the basic unit of wolf social ecology is represented by the territorial pack (Mech and Boitani 2003), wolf populations are also constituted by non-territorial wolves, generally referred to as floaters, that have to fit more or less temporarily the areas they use into the dynamic mosaic of adjacent packs (Mech and Boitani 2003). Floating wolves may comprise old animals forced to leave their former packs through social expulsion, as well as young individuals that eventually disperse and try to establish their own territories (Mech and Boitani 2003). Differently

than pack members, floaters are generally nomadic and do not maintain stable territories (Fuller et al. 2003). Moreover, floaters represent an important demographic and reproductive buffer, as they can readily replace losses of resident pack breeders (Fuller et al. 2003). Investigating space use in wolf populations including turn-over of territorial ownership and floaters movements is therefore important as it contributes to elucidate patterns that allow populations to persist and eventually expand in human-modified landscapes.

From 2008–2010, we studied home ranges, core areas, and spatial arrangement in one of the few historical strongholds of the Italian wolf population (Zimen and Boitani 1975), living in the Abruzzo Lazio and Molise National Park (PNALM; central Apennines, Italy). Locally, a relatively high wolf density (>5 wolves/100 km²) and a tight territorial mosaic are consistent with a wolf population about saturation levels (Ciucci and Boitani 2009; Boggiano et al. 2013; Molnar et al. 2015). Over the past few decades, wolves in the region have shifted from relying on anthropogenic food resources (e.g., garbage dumps; MacDonald et al. 1980; Boitani 1982) to wild prey [e.g., wild boar (*Sus scrofa* Linnaeus, 1758), roe deer (*Capreolus capreolus* Linnaeus, 1758)]. Nevertheless, despite improved positive attitudes by local residents (Glikman et al. 2012), wolves continue to suffer significant mortality by humans. In particular, during our study, 20 of 33 known wolf deaths in the PNALM were attributed to human activities, such as illegal take and vehicle collisions (L. Gentile, pers. comm.).

By investigating space-use patterns by wolves in the central Apennines we expect to reveal spatio-temporal adaptations by wolves to human presence and activity in an area of long-established coexistence with humans (Zimen and Boitani 1975). Overall, the aims of our work were: (i) to describe annual and seasonal space use patterns by wolves in the PNALM, discriminating between resident pack members and floaters; (ii) to assess seasonal and circadian effects on home range size, as well as the effect of the density of anthropogenic features (i.e., roads and settlements) within the home range; and (iii) to contrast landscape composition between core areas used by resident pack members and their entire home ranges, as this might reveal habitat-mediated adaptations to human-

altered landscapes. Specifically, we predicted that, to avoid human interference, wolves would tend to use smaller home ranges during periods of greater human activity (i.e., summer and daylight hours) whereas they would use larger home ranges, to compensate for reduced habitat quality where occurrence of anthropogenic features was greater. Additionally, we predicted that when establishing core areas within the home range, wolf packs selected for landscape and habitat features enabling them to minimize disturbance and interference by humans.

Materials and methods

Study area

Our 1,505 km² study area is centered in the Abruzzo, Lazio and Molise National Park (PNALM) and its external buffer zone in the central Apennines, Italy (Fig. 1). The area is typically mountainous, with elevations ranging from 400 to 2285 m, and is characterized by a Mediterranean montane climate, with dry summers and cold, snowy winters (Piovesan et al. 2003). Agricultural grasslands, pastures, and mixed forests, mainly comprised by oak (*Quercus* spp. L.) and maple (*Acer* spp. L.), predominate along valley bottoms. Higher elevations are mostly covered by deciduous forests, composed primarily of beech (*Fagus sylvatica* L.), whereas sub-alpine grasslands prevail above 1800 m. Human population density averages 14.6 inhabitants/km², even though residents live aggregated in a few mountain villages and many areas are virtually void of people (Ciucci et al. 2015). Both tourism and livestock grazing are important local economic activities. About 22.6% of the PNALM is covered by pastures, most of which are used by free-ranging cattle and horses during extended period throughout the year. Conversely, agriculture is scarce and mostly takes place along the valley bottoms near human settlements. Prey populations include wild boar (*Sus scrofa*), red deer (*Cervus elaphus* Linnaeus, 1758), roe deer (*Capreolus capreolus*) and Apennine chamois (*Rupicapra pirenaica ornata* Neumann, 1899), and their densities, albeit formally unknown, are relatively high based on sightings and pellet group counts (R. Latini, PNALM Scientific Service, pers. comm.).

Wolf capture and GPS telemetry

Between December 2007 and October 2010, we live-trapped and equipped with GPS collars (Televilt-Tellus, Followit AB, Lindesberg, Sweden; and Vectronic Pro Light-1, Vectronic Aerospace GmbH, Berlin, Germany) 11 wolves (Table S1). To trap wolves we used modified Aldrich foot-snares with drags (M. Collinge, Animal Damage Control, Idaho, U.S.A., pers. comm.), baited with fresh wolf scats and/or urine, and set along trails and dirt roads. Using VHF trap-transmitters (Mod. 6, ATS, Isanti, Minnesota, U.S.A.), we remotely monitored activated traps 24-hr a day and were able to reach captured wolves within an average of 37 ± 21 min (range: 14–90 min) since caught. Using a blowpipe (Telinject, Agua Dulce, California, U.S.A.), we administered to captured wolves 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). Captured wolves were sexed, weighed, and classified as pups, yearlings, or adults based on tooth eruption and wear patterns (Gipson et al. 2000). Permit for wolf capture was obtained by the Italian Ministry of the Environment, and capture and handling procedures reflected international guidelines (Sikes et al. 2011). We equipped with GPS collars only wolves $\geq$ 8 months old, as they could wear radio-collars safely. We configured GPS collars according to 30-day cycles, during which fix attempts were programmed every 0.5–1 hours for 10 days, and every 3 hours for the successive 20 days. We downloaded GPS locations remotely through the Global System for Mobile Communications. However, we excluded from the analysis GPS data obtained from 3 collared wolves due to an acquisition rate $\leq 80\%$ or insufficient tracking period (< 4 months; see Table S1). Each year, we used intensive snow-tracking during winter to assess social association of GPS-collared wolves, with floaters consistently tracked alone and resident pack members frequently detected in groups of ≥ 2 wolves. We determined the minimum number of wolves in each GPS-tracked pack as the maximum number of wolves travelling together tracked throughout the winter. We also confirmed *a posteriori* the status of collared wolves using information derived from their GPS locations, with resident pack members sharing with other wolves the same exclusive area for ≥ 1 season, and floaters using larger areas across multiple wolf territories (Gese et al. 1988;

Kamler and Gipson 2000; Gehrt et al. 2009; Hinton et al. 2016). We revealed reproduction in each GPS-tacked pack by means of wolf howling surveys (Harrington and Mech 1982), and successively verified pup presence using remote cameras and field investigations of dens and rendezvous sites once these were vacated. To approximate the location of other, non-GPS-tracked packs in the study area, we used a 5-km radius (i.e., the mean radius of annual wolf territories in the PNALM, estimated using 95% BBMMs; see below), centered in the centermost point of all indirect signs of presence (e.g., scats, tracks in the snow, wolf-howling replies) of a given pack (Fig. 1), as determined through intensive and replicated annual surveys conducted throughout the study area.

Home range and core area analysis

We used the Brownian bridge movement model (BBMM; Horne et al. 2007) to estimate home range size. The BBMM estimator is particularly suited for large sets of autocorrelated GPS location data, as it avoids the assumption of independence among relocations by explicitly incorporating the time lag between them (Horne et al. 2007; Kittle et al. 2015). Two smoothing parameters are set into the BBMM: the Brownian motion variance (σ_1), that is related to the animal's mobility, and the location imprecision (σ_2). We estimated σ_1 following the maximum likelihood approach (Horne et al. 2007) using the R function *liker* (*adehabitatHR* R package, Calenge 2006), whereas we set $\sigma_2=20$ m, as 93.4% of our GPS locations were 3-dimensional, which generally have an error < 20 m (Di Orio et al. 2003). We preferred static over dynamics BBMMs (Kranstauber et al. 2012), as the latter require additional unknown parameters that may introduce some subjectivity in the analyses. To avoid overrepresentation of areas used during periods of greater fix rate (Fieberg 2007), we systematically subsampled GPS locations to obtain a comparable acquisition rate (i.e., 1 location/3 hrs) throughout the sampling period. As only 6.6% of the GPS locations that we obtained were 2-dimensional, and because estimates of animal home ranges are robust to expected levels of GPS measurement error (Frair et al. 2010), we did not use a data quality filter thus avoiding to further subsample our dataset. We estimated home ranges as that area encompassed by the 95% isopleth of the BBMM utilization distribution (UD; Laver and Kelly

2008) using a 20x20m grid size. As we distributed trapping effort across packs, we rarely had >1 collared wolf per pack and therefore assumed that GPS locations from 1 pack member adequately represented the entire pack's home range (Ciucci et al. 1997; Benson and Patterson 2014). In just one pack we had 2 collared pack members, and we retained in the analyses the one with the greater acquisition rate and longer tracking period. We also used 95% Brownian bridges to depict space use by floaters but, as these wolves did not necessarily remain stationary in a defined area, we used net squared displacement curves (NSD; Turchin 1998) to aid interpretation of their movements. Using the 3D Analyst Tools for ArcGIS (version 10.2.2), and a digital elevation model provided by the Italian Military Geographic Institute (20 m resolution), we performed a surface area correction to provide an orographically corrected (i.e., 3D) measure of the home range size in mountainous environments (Jenness 2004).

We estimated seasonal home ranges according to three periods: summer (May-September), corresponding to reproduction, pup attendance at dens and rendezvous sites, as well as to increased availability of livestock and human activity throughout the study area; fall (October-December), when packs are expected to travel together throughout their territory at their maximum size; winter (January-April), comprising the mating period, the peak of dispersal, and increased vulnerability of prey species due to food stress, clustered dispersion, and the presence of snow (e.g., Kunkel and Pletscher 2001; Smith et al. 2004). We assessed seasonal home range fidelity using an UD overlap index (UDOI; Fieberg and Kochanny 2005), as implemented in the *adehabitatHR* R package (Calenge 2006). For each season, we also estimated diurnal vs nocturnal home ranges by assigning GPS locations to daylight or night periods using the R function *solarpos* (*maptools* R package, Bivand and Lewin-Koh 2015). For resident wolves whose sampling period was long enough ($N=3$, based on the relation between the cumulative proportion of annual home range size and the number of months included in the sampling period; Mattisson et al. 2013), we also estimated home ranges on an annual basis.

We delineated seasonal core areas of resident wolf packs using a time-maximizing function based on exponential regression analysis (Vander Wal and Rodgers 2012). Using BBMM UD, we plotted UD area against volume, the latter indicating the likelihood of the animal spending time within different portions of its home range. As this relationship is approximated by an exponential regression, the point at which the slope (i.e., the tangent) of the exponential curve fitted to the data equals 1 represents the threshold beyond which the home range area begins to increase proportionally faster than the probability of use, thus delineating the core area boundary (Vander Wal and Rodgers 2012).

Statistical analysis

We used Generalized Linear Mixed Models (GLMMs; *nlme* R package, Pinheiro et al. 2016), with pack as a random factor, to assess seasonal and circadian effects on home range size, as well as the effect of the density of paved roads (km/km^2) and settlements (km^2/km^2) within wolf home ranges (Table S4). Random intercepts were included to accommodate the hierarchical structure of wolves within packs (Hebblewhite and Merrill 2008). The roads layer included all paved roads within the study area, and the settlements layer comprised all types of human constructions in the study area, including isolated houses. We included in these models only resident wolves whose sampling period was $\geq 50\%$ of the season length. Due to lack of annual replicates of seasonal home ranges, we pooled data across years and were not able to assess inter-annual variability in home range size. Using the orographically corrected home range size, log-transformed to account for normality, we investigated effects on home range size (response variable) due to season and circadian period as fixed factors, with fall and daylight as the reference levels, respectively. We used 22 circadian home ranges (5 summers, 3 falls, and 3 winters), estimated from 5 packs. Due to a relatively small sample size, we avoided fitting more complex models due to overfitting problems (Zuur et al. 2009). Given the correlation between the density of paved roads (km/km^2) and settlements (km^2/km^2) at the home range level (Pearson's $R = 0.7$), we used only road density as a proxy of anthropogenic disturbance. As the number of GPS locations

differed slightly among individual wolves due to variations in the acquisition rate and the effective sampling period, we accounted for the potential effect of sample size on home range estimates by including a fixed variance structure in LMMs (Zuur et al. 2009) proportional to the number of GPS locations. Starting with a saturated model, including all fixed factors and their interactions, we compared all possible models through dredging and finally performed model selection using the Akaike Information Criterion with small-sample size correction (AICc; Burnham and Anderson 2002). We then performed model averaging (*MuMIn* R package, Barton 2016), according to the natural average method and retaining models within $\Delta AIC \leq 10$ (Burnham and Anderson 2002), as we were interested in the descriptive power of the model. To assess goodness-of-fit of selected models, we computed their marginal and conditional coefficients of determination (R^2 ; Nakagawa and Schielzeth 2013) using the *r.squaredGLMM* function in the *MuMIn* R package (Barton 2016); in addition, we provided Pearson's correlation coefficient between observed home range sizes and those predicted by the averaged model as an additional measure of model validation.

We further investigated responses by resident wolves towards roads and settlements at the study area level (i.e., when establishing home ranges, or 2nd order selection; Johnson 1980) by contrasting (Wilcoxon test) road and settlement densities within annual home ranges with those within 20 virtual, randomly located wolf territories. These were built as circular buffers of 5-km radius, equal to the mean radius of observed wolf packs' home ranges (see results).

As composition of core areas may reflect habitat-mediated behavioral responses by wolves, we used a modified version of the Ecological Niche Factor Analysis (ENFA; Hirzel et al. 2002) to contrast the ecological conditions within the BBMM-defined core areas with those within the whole home range. The ENFA provides a measure of the realized niche within the available space, by computing two estimates for each variable considered in the analysis: 1) the marginality, that identifies the preference for a given variable by measuring the departure of the ecological niche from the average available condition, and 2) the specialization, that reflects the narrowness of the niche in terms of a given variable (Hirzel et al. 2002). Our aim was to identify the ecological

conditions that most differentiate the core areas (i.e., marginality), and the degree of environmental variation represented therein (i.e., sensitivity), with respect to the entire home range (e.g., Galparsoro et al. 2009; Xuezhai et al. 2012). To do this, we contrasted landscape variables of each pixel within the core area with those from the entire home range. We preferred this approach over more traditional Resource Selection Functions (Manly et al. 2002) as we were not interested in habitat selection per se as a behavioral response, but rather in assessing the overall landscape composition within CAs (i.e., though wolves may select against anthropogenic features, these features may still be comprised within CAs to some extent). We conducted the ENFA for each pack and season separately, and averaged ranks of marginality values to report the results at the population level. Spatial analysis was performed using ArcGIS (version 10.2.2), whereas the *adehabitatHR* R package (Calenge 2006) was used to run the ENFA.

Results

From December 2007 to October 2010, we live-trapped and equipped with GPS collars 11 wolves, 6 females and 5 males (Table S1). Eight of these wolves were permanently or temporarily members of 5 packs (Table S1), including M22 who became a floater after losing his alpha status in the Villa pack, and F24 who dispersed from the Villa pack and eventually pair-bonded and established a new pack (Bisegna pack) in spring 2010. Three other collared wolves, all females, were floaters when first captured (Table S1). While two of them maintained this status for the remainder of the study, the other (F23) pair-bonded with M26 establishing a new pack (Canneto pack) in fall 2009. Excluding 3 wolves whose GPS data and tracking period were considered inadequate (Table S1), we GPS-tracked the remaining collared wolves for 3.5–19.3 months, with an average acquisition rate of 87.2 (± 5.1)% (range: 80.7–93.8%; Table S1). We estimated that a minimum of 7 months was necessary to approximate annual home ranges of resident pack members (Fig. S1). The average annual home range size of resident packs ($N=3$) was 104 (± 24 SD) km² (95% BBMM, with 3D correction; Fig. 1 and Table 1). Road and settlement densities within annual home ranges averaged 29.4 (± 11.3 SD) km/100 km² and 1.4 (± 1.0 SD) km²/100 km², respectively,

and neither of them were different from those within the study area ($W=230$, $P=0.20$, and $W=180$, $P=0.70$, respectively). Mean seasonal (3D) home range size ranged from $63.9 (\pm 18.4 \text{ SD}) \text{ km}^2$ in summer ($N=5$ packs) to $113.4 (\pm 39.9 \text{ SD}) \text{ km}^2$ in fall ($N=3$ packs), with intermediate values reported for winter ($80.6 \pm 29.9 \text{ SD km}^2$; Supplementary Table S3, Supplementary Fig. S2). Wolf packs showed a marked fidelity to their seasonal home ranges, with mean UDOI values ranging from $1.1 (\pm 0.3 \text{ SD})$ between winter and summer to $1.2 (\pm 0.3 \text{ SD})$ between the other seasons.

According to the best supported models (Table 2 and Suppl. Mat., Table S4), wolves used larger home ranges both during the night ($\beta_{\text{night}}=0.52$, $\text{SE} = 0.24$, $P\text{-value} = 0.04$; Fig. 2), and at greater road densities ($\beta_{\text{road}}=0.02$, $\text{SE} = 0.01$, $P\text{-value} < 0.01$). Season per se did not affect home range size, although the difference between daily and nocturnal home range was highest in summer compared to the other seasons ($\beta_{\text{summer_night}}=0.43$, $\text{SE} = 0.17$, $P\text{-value} = 0.03$). Marginal and conditional R^2 of the top model, including the circadian and road density effects only, were 0.79 and 0.99, respectively, whereas R^2 of the following models ranged 0.66-0.89 and 0.98-0.99 for marginal and conditional value, respectively (Supplementary Table S4). Averaged models' predicted values also indicated a good model fit (Pearson's $R = 0.93$).

Core areas were delineated by isopleth values whose seasonal averages ranged from $70.7 (\pm 1.1 \text{ SD})\%$ in summer to $72.9 (\pm 2.8 \text{ SD})\%$ in fall (Supplementary Table S3). Based on the ENFA marginality values (Supplementary Table S5), core areas during summer were established in the more forested and inaccessible (i.e., higher elevation, steeper, and orographically complex terrain) portions of home ranges, with a tendency towards prevailing north-easterly slopes compared to the rest of the home range (Fig. 3). On the other hand, roads, settlements, agricultural areas and shrublands were markedly avoided when establishing core areas (Fig. 3). Conversely, during fall and winter we did not reveal marked differences in environmental variables between home ranges and core area (Supplementary Table S5).

We tracked floaters ($N=4$) for 5.5–15 months each (Table S1), and the area (3D-corrected) they used ranged $293.8\text{--}408.7 \text{ km}^2$ (Table 1), from 2- to 4-fold larger than the annual home range

size of wolf pack members (Supplementary Fig. S3). Using NSD curves, we revealed that individual floaters employed markedly different space use patterns (Supplementary Fig. S4).

Discussion

We investigated home range use and spatial arrangement of wolves in a protected area of the central Apennines where wolves had been long coexisting with humans (Zimen and Boitani 1975). Average size of annual home ranges (MCP 100%: $\bar{X} = 152 \pm 60 \text{ km}^2$, planar size) falls within the range for established wolf populations in Southern and Central Europe (MCP 100%: 82–243 km^2 ; Okarma et al. 1998), as well as in North America (e.g., MCP 100%: $116.3 \pm 30.6 \text{ km}^2$; Fuller 1989; $219.6 \pm 160.6 \text{ km}^2$; Fritts and Mech 1981). Much larger home ranges have been reported at greater latitudes both in North America (e.g., MCP 100%: $1,868 \pm 249 \text{ km}^2$, Ballard et al 1997; $3,375 \pm 1,973 \text{ km}^2$, Ballard et al. 1998; $42,847 \pm 6,542 \text{ km}^2$, Walton et al. 2001) and in northern Europe (e.g., MCP 100%: $1,372.4 \pm 514.4 \text{ km}^2$, Kaartinen et al. 2005; $1,017 \pm 73 \text{ km}^2$, Mattisson et al. 2013). Home range size in wolves has been shown to relate negatively to prey abundance (Wydeven et al. 1995; Fuller et al. 2003; Jedrzejewski et al. 2007) and wolf density (Peterson et al. 1984; Ballard et al. 1987), but positively to latitude, a proxy of dietary productivity (Okarma et al. 1998; Mattisson et al. 2013), and human density (Rich et al. 2012). Unfortunately, due to lack of accurate data on prey density and distribution in the PNALM, we could not assess the effect of prey abundance on wolf packs' home range size. However, following wild prey reintroductions in the PNALM since the mid '70s (Apollonio and Lovari 2001), local prey availability and diversity are amongst the highest in the central Apennines, corresponding to a relatively high density of wolves in the area. Whereas this should correspond to relatively smaller home ranges (Fuller et al. 2003), the PNALM wolves had home ranges on average larger compared to wolves thriving exclusively on wild boar in the southern Apennines (MCP 100%: $\bar{X} = 99.6 \pm 43.8 \text{ km}^2$, $N = 5$ packs; P. Ciucci unpubl. data), and this difference may be related to pack size, on average larger in the PNALM.

In addition to wild prey and wolf density, other factors may act as determinants of home range size in wolves, especially in human-modified landscapes (e.g., Rich et al. 2012; Mattisson et

al. 2013). As expected, anthropogenic and circadian effects appear to be relevant in our study area. Larger nocturnal compared to diurnal home ranges tend to be a common feature of wolves (e.g., Poland: Theuerkauf et al. 2003a) as well as of other canids [e.g., coyotes: Holzman et al. 1992; Grindler and Krausman 2001; red wolves (*Canis rufus* Audubon and Bachman, 1851): Hinton and Chamberlain 2010] living in human-dominated areas. Where human presence and activity during daylight hours exceeds a minimum threshold, wolves may display spatial avoidance by restricting their movements and activity during daytime (Ciucci et al. 1997; Hebblewhite and Merrill 2008; Kojola et al. 2016). However, the impact due to increased human activity during daylight could also act indirectly, for example mediated by the spatial behaviour and activity of prey species that also try to avoid contacts with humans (Bonnot et al. 2013; Theuerkauf and Rouys 2008) and may be affected by seasonal variation (see below). We observed a positive correlation between home ranges of wolf packs and road density, which roads were highly correlated with human settlements in our study area. This likely allows wolves to compensate for adequate levels of prey availability while ensuring effective spatial segregation from humans (e.g., Murray et al. 2010; Rich et al. 2012). Habitat fragmentation caused by roads may also force wolves to increase home range size to encompass retreat areas large enough and secluded enough from human activity to meet their ecological needs, such as resting, denning and attending pups. The positive relationship we detected between wolf home range size and the density of anthropogenic features is consistent with this argument, and has been similarly reported for other carnivore species living in human-dominated landscapes (e.g., coyotes; Kitchen et al. 2000; Gehrt et al. 2009).

We did not observe a seasonal effect on home range size, whereas we expected to detect smaller home ranges during summer to reflect avoidance of areas with greater human activity during the touristic and grazing season (Theuerkauf et al. 2003b; Iliopoulos et al. 2014), or due to centripetal movements of wolves attending pups at dens and rendezvous sites (Jedrzejewski et al. 2001; Packard 2003). Concurrently, we did not detect a noticeable shift among seasonal home ranges of resident wolf packs, possibly due to the combined effect of a high density of non-

migratory prey and a tight arrangement of wolf pack territories (Fritts and Mech 1981; Sillero-Zubiri et al. 1995). In wolves, seasonal variation in home range size has been associated to annual differences in prey density and distribution (e.g., Ballard et al. 1997). Such differences, however, have not been reported in areas where wolves thrive on non-migratory ungulates (e.g., Minnesota: Fuller 1989; Yukon: Hayes et al. 1991). Similar evidences from other canids (e.g., coyotes: Hinton et al. 2015; red wolves: Hinton et al. 2016) suggest that lack of seasonal changes in home range size and configuration may be an indication that these species use home ranges large enough to accommodate for seasonal variation in the availability of resources. Nevertheless, we found that season interacted with circadian period in affecting home range size, revealing that the reduction of daily vs nocturnal home ranges was proportionally greater during summer compared to the other seasons. Accordingly, summer likely represents a period during which wolves restrict their diurnal movements the most to avoid increased levels of human disturbance, although studies from different areas, and possibly based on a larger number of packs, are needed to strengthen this conclusion.

Home range size and configuration of wolves in the PNALM are likely expression of a more complex behavioral response by wolves that also entails habitat-mediated adaptations (Glenz et al. 2001). According to our prediction, we revealed that wolves configured core areas where environmental, topographic, and anthropogenic features ensured proper retreat and concealment from humans and where human accessibility was particularly limited, especially during summer. Concurrently, we observed a less pronounced avoidance of anthropogenic features within core areas during fall and winter, likely reflecting lower susceptibility by wolves to anthropogenic disturbance in these seasons, reduced human activity, or both. In addition to anthropogenic impact, other factors may as well drive selection of core areas by wolves within their home ranges. Specifically, the selection of north-easterly facing slopes within core areas in summer may account for microclimate selection of home sites (i.e., to facilitate thermoregulation of pups), or increased forage availability and quality for prey species (Albon and Langvatn 1992).

In addition to ecological factors which may act as drivers of home range size, methodological caveats are of paramount importance when estimating and comparing home ranges across studies (Laver and Kelly 2008). In our study, we attempted to address some weaknesses commonly found in home range estimation, such as the use of planar measures in mountainous environments. Estimating home ranges of species living in areas with rough topography using planar measures can be quite misleading, whereas correcting planar measures to account for orographic relief can be easily done using any GIS platform and high-resolution Digital Elevation Terrain models (Jenness 2004). Not only neglecting orography-corrected measures of home range size may obscure meaningful comparison across studies, but it may also limit interpretation of the home range as an informative parameter of space-use patterns. Orography affects the spatial behaviour of a species, and it is correlated with both energetic constraints (Stamps 1995) and resources acquisition (Powell and Mitchell 1998). In territorial predators such as wolves, the energetic costs of patrolling and defending territories are directly related to territory size (Rich et al. 2012) and are expected to be highest in mountainous environments. For this reason, we used 3D-corrected home range estimates as a more meaningful response variable in our models.

Core areas are an important descriptor of home range configuration, and both their size relative to the home range and habitat composition may reveal important aspects of a species' adaptation to human-modified landscapes. Also in this case, however, methodological artifacts such as an arbitrary threshold to delineate them (e.g., 50% of UD volume) may obscure biologically meaningful patterns. To this aim, we used a data-driven and individual-based procedure that reflects the intensity of space use within the home range based on a time-maximizing function (Vander Wal and Rodgers 2012). This procedure has the advantage to account for the expected individual variability in home range behavior, in turn reflecting the local heterogeneity in the distribution of critical resources (Vander Wal and Rodgers 2012). Notably, none of the core areas we estimated within wolf pack home ranges was in fact outlined by the 50% isopleth traditionally reported in the

literature. By using the traditional 50% threshold we would have underestimated core areas and undervalued the habitat features therein.

Wolves in the PNALM live at high density and are believed to have reached saturation levels, and these conditions are possibly affecting home range size and location through marked intra-specific constraints (Fritts and Mech 1981; Zubiri et al. 1995). Six of the 8 GPS-collared wolves that we tracked were permanently or temporarily members of 5 resident packs during the study, with the proportion of floaters annually ranging 16.7–75% ($\bar{X}$ = 58.3 ± 52.0% SD) of collared wolves. Although our sample size is clearly too small to draw any conclusion, most wolf and coyote studies in North America report that about 25–40% of radiocollared animals are non-residents (e.g., Fuller et al. 2003; Hinton et al. 2016), similarly to what estimated in a human-dominated region in Spain (33.5%; Blanco and Cortéz 2007). Floaters serve as a surplus of individuals that may be periodically recruited into the resident, reproductive segment of wolf populations (Fuller et al. 2003). In the PNALM, the high reproductive success from local wolf packs, coupled with a relatively high prey density, may in part explain the high proportion of floaters, a mechanism ensuring a consistently high wolf density and reproductive output despite the relatively high levels of anthropogenic mortality (Molnar et al. 2015). For example, wolf F23, a floater when first captured, readily pair-bonded and settled in a territory formerly occupied by another pack that abruptly vanished possibly due to a poisoning event (unpublished data; Fig. S3).

Although the ecological context of the PNALM differs from more pristine environments elsewhere, habitat conditions of our study area can be considered as relatively ideal for wolves compared to other, more densely populated areas, both in Italy and elsewhere in southern Europe (e.g., Llaneza et al. 2012). Wolves in the PNALM live at high density and display a tight territorial mosaic, and both their reproductive performance and the proportion of floaters seem capable of ensuring both the replacement of pack breeders lost due to natural or human-induced mortality. Accordingly, with respect to the whole Apennine range, we would expect that areas of comparable size or larger, featuring similar habitat conditions with similar or lower extent of anthropogenic

impact, are critical for the stable occupancy of wolves. Although space-use patterns and habitat-mediated behavioral adaptations of wolves in the PNALM are apparently not sufficient to prevent a non-trivial share of human-caused mortality, they nevertheless account for the stable occupancy and reproductive success of wolves in the area. As wolves are expanding their range through natural recolonization also in agricultural and densely populated settings both in Italy (e.g., Marino et al. 2016) and elsewhere in Europe (e.g., Llaneza et al. 2012), further research is needed in such conditions to assess functional responses in space-use patterns.

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FIGURES CAPTIONS

Figure 1. Location of the study area in Italy (inset) and spatial distribution of home ranges of resident wolf (*Canis lupus*) packs (95% BBMMs) in the central Apennines, Italy, 2008–2010. Approximate territories of packs in which we did not collared wolves are reported with circular, dashed buffers of 5-km radius (equal to the average annual home range calculated using 95% BBMMs).

Figure 2. Diurnal (dashed line) and nocturnal (solid line) BBMM-home ranges of 4 wolf (*Canis lupus*) packs (A=Orsara, B=Villa, C=Collelongo, D=Bisegna) in the central Apennines, Italy, 2008–2010.

Figure 3. Boxplot of ranks of Ecological Niche Factor Analysis (ENFA) marginality values of environmental and anthropogenic covariates when comparing summer home ranges and corresponding core areas in 5 wolf (*Canis lupus*) packs in the central Apennines, Italy, 2008–2010 (see Supplementary Table S2 for variables description).

Location of the study area in Italy (inset) and spatial distribution of home ranges of resident wolf (*Canis lupus*) packs (95% BBMMs) in the central Apennines, Italy, 2008-2010. Approximate territories of packs in which we did not collared wolves are reported with circular, dashed buffers of 5-km radius (equal to the average annual home range calculated using 95% BBMMs).

209x225mm (300 x 300 DPI)

Diurnal (dashed line) and nocturnal (solid line) BBMM-home ranges of 4 wolf (*Canis lupus*) packs (A=Orsara, B=Villa, C=Collelongo, D=Bisegna) in the central Apennines, Italy, 2008-2010.

406x462mm (300 x 300 DPI)

Boxplot of ranks of Ecological Niche Factor Analysis (ENFA) marginality values of environmental and anthropogenic covariates when comparing summer home ranges and corresponding core areas in 5 wolf (*Canis lupus*) packs in the central Apennines, Italy, 2008-2010 (see Supplementary Table S2 for variables description).

209x114mm (300 x 300 DPI)

Table 1. Annual home range size (BBMM: 95% Brownian Bridge Movement Model; MCP: 100% Minimum Convex Polygon) and anthropogenic descriptors as estimated in a protected wolf (*Canis lupus*) population in the Abruzzo Lazio and Molise National Park (central Apennines, Italy, 2008–2010). GPS-tracked wolves are distinguished based on their social status (i.e., resident pack members vs floaters). For floaters, home ranges are intended as areas used during the whole tracking period.

Wolf status ^a	Wolf ID	GPS locations	Home range (km ²)				Elevation ^b	Anthropogenic features	
			BBMM		MCP			Settlements	Roads ^c
		(no.)	3D	2D	3D	2D		(km ² /100 km ²)	(km/100 km ²)
Canneto	M26 ^d	2,135	130.1	113.2	254.1	221.1	1,440 (717–2,228)	0.40	32.3
Orsara	F25	1,467	83.1	74.8	129.7	115.4	1,397 (974–2,256)	1.39	38.9
Villa	F24	1,093	98.7	90.8	126.5	116.4	1,287 (659–1,963)	2.46	16.9
Floater	F21	2,402	297.3	267.6	724.7	645.0	1,354 (659–2,096)	1.1	24.1
Floater	F23	1,389	293.8	258.5	643.2	572.5	1,433 (417–2,256)	0.7	36.6
Floater	F29	3,170	408.7	355.6	772.9	636.2	1,365 (390–2,256)	0.4	37.3
Floater	M22	486	406.3	377.9	434.7	378.2	1,148 (630–1,988)	1.6	33.7

^a Name of pack if pack member, or Floater otherwise.

^b Mean (min-max) within the home range (BBMM).

^c Primary and secondary paved roads.

^d Although M26 pair-bonded with F23, we selected the former due to its longer tracking period and greater acquisition rate.

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Table 2. Results of the Generalized Linear Mixed Model used to investigate seasonal, circadian and road density (km/km²) effects on wolf (*Canis lupus*) home range size (3D-corrected) in the central Apennines, Italy (2008–2010). In all models, fall and daylight hours were used as reference levels at the seasonal and circadian scale, respectively. Pack ID was added as random effect. We also added a fixed variance structure proportional to the number of GPS locations used to estimate home ranges.

Variable	Regression coefficient	SD	P-value ^a
Night	0.517	0.236	0.037
Road density	0.021	0.005	< 0.01
Night*road density	-0.011	0.007	0.134
Summer	-0.318	0.203	0.147
Winter	-0.062	0.151	0.713
Night*summer	0.433	0.176	0.030
Night*winter	0.058	0.227	0.822

^a Computed using the *model.avg* function of the *MuMIn* R package (Barton 2016).