Decoupling residents and dispersers from detection data improve habitat selection modelling: the case study of the wolf in a natural corridor

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Resource selection analyses based on detection data are widely used to parametrize resistance surfaces used to identify ecological corridors. To successfully parametrize resistance, it is crucial to decouple resident and disperser behaviours yet to date connectivity studies using detection data have not addressed this issue. Here, we decoupled data of resident and dispersing wolves by analysing detection data collected within a natural corridor crossing a human dominated plain in Italy. To decouple residents and dispersers, we ran a Kernel Density analysis to investigate whether clusters of wolf detection points characterized by sharply higher points’ density exist and checked whether the areas outlined by these clusters (core areas) hold specific characteristics. Habitat selection analysis was then performed to compare the intensity of habitat selection carried out by putative residents and dispersers. We identified a high-density cluster of 30 detection points outlining a small core area stably located in the central part of the park. The dramatic differences of the R² and the AUC of the habitat selection models performed inside (R² = 0.506; AUC = 0.952) and outside (R² = 0.037; AUC = 0.643) the core area corroborated the hypothesis that the core area effectively encloses detection points belonging to residents. Our results show that through simple space use analyses it is possible to roughly discriminate between detection points belonging to resident-behaving and disperser-behaving individuals and that habitat selection models separately performed on these data have extremely different results with strong possible effects on resistance surfaces parametrized from these models.

KEY WORDS: Canis lupus italicus, dispersal, kernel density estimation, resource selection functions, space use analyses.

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INTRODUCTION

Ecological connectivity plays a key role for the long-term viability of animal populations in human-modified landscapes (e.g., Hanski 1998; Crooks & Sanjayan 2006; Cushman et al. 2013; Mateo-Sánchez et al. 2014; Saura et al. 2014; Abrahms et al. 2017). A critical tool to safeguard connectivity is identifying and conserving corridors, i.e., areas where dispersal between habitat patches is considered most likely to occur (Gilbert-Norton et al. 2010; Abrahms et al. 2017; Dondina et al. 2018a). The most widely used approach to identify corridors consists of estimating landscape resistance to movement (Zeller et al. 2012; Mateo-Sánchez et al. 2015; Carvalho et al. 2016; Abrahms et al. 2017; Scharf et al. 2018), which reflects the local cost of movement for an organism due to behavioural and physiological factors such as aversion, energy expenditure, or mortality risk associated with moving through a particular environment (Zeller et al. 2012; Mateo-Sánchez et al. 2015). Landscape resistance is generally represented as a raster resistance surface, in which data values correspond to the stepwise cost of moving through each cell (Adriaensen et al. 2003). Expert opinion is the mostly used information to parameterize resistance surfaces, followed by genetic, detection and movement data (Zeller et al. 2012). Expert opinion has been criticized for its use in the definition of resistance surfaces (Cushman et al. 2013; Peterman 2018) because it generally provides scarce parameterization of environmental variables when compared to empirical data (Pearce et al. 2001; Clevenger et al. 2002; Seoane et al. 2005). The use of genetic data allows inferring the influence of environmental variables on gene flow by measuring the correlation of observed genetic distance between individuals or populations with hypothesized values of resistance assigned to the environmental variables composing the landscape (Cushman et al. 2006; Epps et al. 2007; Bani et al. 2015, 2018). Resistance surfaces parametrized by using genetic data are useful in investigating the large-scale effect of landscape composition on gene flow, but they may not be as useful for predicting corridors at finer, management-relevant scales (Graves et al. 2013; Reding et al. 2013). Moreover, genetically derived resistance surfaces generally reflect past landscape permeability, due to the time-lag needed to detect barriers’ effect on genetic structures (15–100 generations, Langduth et al. 2010). In contrast to genetic data, detection and movement data allow for parametrization of landscape resistance at more immediate and fine scales when Resource Selection Functions (RSFs) are applied (Chetkiewicz & Boyce 2009). RSFs estimate the probability of use of given landscape variables by statistically comparing the characteristics of locations used by the study species with those of not used or random generated locations (Manly et al. 2002). The general assumption underlying the use of RSFs in connectivity studies is that habitat selection and dispersal are based on the same preferences, although it is known not to be necessarily true (Chetkiewicz et al. 2006; Beier et al. 2008; Shirk et al. 2010; Zeller et al. 2012; Mateo-Sánchez et al. 2015; Vasudev et al. 2015; Scharf et al. 2018). For example, in birds and mammals, habitat selection is often carried out by resident individuals (generally adults) and is driven by the use of habitats where they can establish home ranges and breed; conversely dispersal is often carried out by dispersers (generally juveniles) and is mainly driven by sub-optimal permeable habitats that are unlikely to be suitable habitats for breeding (Mateo-Sánchez et al. 2015; Dondina et al. 2018b). This implies that habitat selection of dispersers is generally much weaker than that of residents (Mateo-Sánchez et al. 2015; Imbert et al. 2016; Abrahms et al. 2017; Scharf et al. 2018; Río-Maior et al. 2019). Therefore, using distribution data of residents to develop resistance surfaces
can lead to an underestimation of the corridors used for dispersal (Ziółkowska et al. 2016). Errors can arise both using detection and movement data. Detectors usually represent within-home range habitat use patterns, while movement data used all together (as often happens) may confound different types of movement such as movements within habitat patches, movements between habitat patches within home ranges, and dispersal movements (Zeller et al. 2012; Cushman et al. 2013). Several recent studies dealing with movement data have separately parameterized resistance surfaces starting from data related to residents and dispersers showing very different results (e.g., Elliot et al. 2014; Zeller et al. 2014; Hinton et al. 2016; Ziolkowska et al. 2016; Abrahms et al. 2017; Rio-Maior et al. 2019). To successfully parametrize resistance surfaces it is thus crucial to decouple residents’ and dispersers’ behaviour before running RSFs (Zeller et al. 2012). Although this issue clearly emerged using movement data, it is a key point in all connectivity studies, specifically in those dealing with detection data, which are prevalent in wildlife studies (Zeller et al. 2012) and which will probably continue to figure prominently in resistance modelling in the future. However, to date no resistance modelling study using detection data only clearly addressed the issue of decoupling residents and dispersers, making it a priority (Zeller et al. 2012; Abrahms et al. 2017).

In this study, we paired space use analyses and RSFs to decouple residents and dispersers from Italian wolf (Canis lupus italicus Altobello 1921) detection data collected within a recently (since 2017) recolonized lowland corridor in Northern Italy. We chose the wolf as study species because large carnivores are often one of the first species to be affected by loss of connectivity making them as appropriate focal species for connectivity studies (Mateo-Sánchez et al. 2014) serving as an umbrella for other affected species (Beier et al. 2008). Moreover, the wolf social structure, characterized by stable packs and lone wolves, makes the distinction between residents and dispersers particularly important for this species (Imbert et al. 2016). We focused on data collected within a lowland corridor in Northern Italy because of the strategic importance of such corridor in connecting Apennines to Central Alps (Dondina et al. 2020), surging the probability of a future stable dispersal flow between the otherwise isolated Italian and Dinaric-Balkan populations (Hindrikson et al. 2017). The study area was also selected because of previous evidence of a simultaneous use of the corridor by wolves behaving as residents or dispersers (O. Dondina personal observation). We stress that we use the terms resident and disperser to indicate different behaviours that do not necessarily depend on a breeding event but can also arise when different dispersal strategies are adopted. In fact, for other canids’ species, it has been observed that some of the individuals disperse through direct displacements (dispersers’ behaviour), while others temporarily use small areas with home range-like characteristics (defined as biding areas) to increment dispersers’ survivorship (residents’ behaviour) (Hinton et al. 2016). The authors also reported that, when opportunities arise, these temporary small areas could even be converted in stable territories.

To reach the aim of the study, we first investigated whether clusters of wolf detection points characterized by sharply higher points’ density compared to the rest of the study area exist. If one or more high-density clusters of detection points were detected, we checked whether the areas outlined by these clusters hold specific characteristics (small area, stability during seasons and a sufficiently high distance from the other detection points) that could suggest the presence of resident-behaving individuals within the corridor (Hinton et al. 2016; Mancinelli et al. 2018; Mancinelli & Ciucci 2018). We compared the environmental characteristics of these areas with
those of the areas frequented by putative dispersal-behaving individuals. Moreover, we investigated the intensity of selection of a set of environmental variables by separately considering the data classified as belonging to residents or dispersers in the first step of the analysis, depending on whether these fall into the areas outlined by high point-density clusters. We expected that residents, if present, should show a significantly stronger selection than dispersers (Mateo-Sánchez et al. 2015; Scharf et al. 2018). Finally, we discussed the practical and management implications that the simultaneous occurrence of resident and dispersing wolves could have in a corridor.

MATERIAL AND METHODS

Study area

The study was carried out in an area of about 200 km² located along the stretch of the Ticino River in Northern Italy (Lombardy administrative Region). The Ticino River flows southwards from the Southern border of the Lake Maggiore to the median course of the Po River, forming a 110 km long and 7 km wide valley (Balestrieri et al. 2015). The study area corresponds to the Ticino Natural Park, a lowland river park longitudinally crossing the Northern Italian Po river plain offering a natural passage for wildlife from the Apennines to the Alps. Specifically, in a previous study (Dondina et al. 2020), the Ticino Natural Park resulted a functional corridor to sustain wolf dispersal flow from the Northern Apennines to the Central Alps. The Ticino Natural Park is covered for almost half of its extension by rotational crops (rice, winter wheat, maize and soybean, 26%), meadows (10%) and traditional poplar cultivations and reforestations (10%), which provide important secondary habitats for mammals in the study area (Chiatante et al. 2017). The remaining area is covered by lowland broadleaf woodlands (28% mesophilous with oaks Quercus sp. and common hornbeam Carpinus betulus dominant and 9% hygrophilous woods with alder Alnus glutinosa, poplars Populus sp. and willows Salix sp. dominant), and to a lesser extent by water bodies (11%) and urban areas (6%) (Fig. 1). The residual woodlands of the Ticino Natural Park offer an important refuge for several mammals (57 species), including three wild ungulates (the widespread wild boar Sus scrofa and roe deer Capreolus capreolus, and the occasional fallow deer Dama dama). The wolf is the only large carnivore inhabiting the Park.

Wolf detection data and environmental variables

To collect wolf detection data within the study area, we selected 30 transects (mean length 8 km) covering the entire surface of the Ticino Natural Park. Each transect was walked once per season (winter: December–February, spring: March–May, summer: June–August, autumn September–November) in the 2017–2018 years. Wolf presence signs, including scats, footprints, and predation remains were detected along the transects. Moreover, all the occasional observations of the species (i.e., camera trap detections and direct sightings) occurred during the study period were controlled and added to the data systematically collected along transects.

Based on the ecological requirements of the species, 10 environmental variables were selected to investigate the possible differences of habitat selection between resident and dispersing wolves. They included the abundance of the two most abundant wild ungulate species inhabiting the Park (i.e., the wild boar and the roe deer), the distance of each detection point from the banks of the Ticino River, and the fractional cover of seven land cover types (urban areas, arable lands, meadows, poplar cultivations, woodlands, riparian vegetation, and water bodies) calculated within a 100-m buffer around each detection point. We assessed wild ungulate abundance at transect level by computing an Index of Kilometric Abundance (IKA) (number of found signs divided by the transect length, Meriggi et al. 1991, 1996, 2015; Imbert et al. 2016) for
We used a fine spatial scale (100-m buffer) because it has been recently demonstrated that RSFs using detection data can be a useful tool to parameterize resistance surfaces provided that environmental variables are calculated at a fine spatial scale (Ziółkowska et al. 2016). The reference land use cartography was the DUSAF 4 (ERSAF 2014) with a spatial resolution of 10 m.

Based on the existing knowledge regarding the environmental characteristics typically selected by wolves in permanently occupied areas, we expected residents to strongly select areas with a high density of prey and a low human disturbance (Massolo & Meriggi 1998; Jędrzejewski et al. 2004; Eggermann et al. 2011; Imbert et al. 2016; Meriggi et al. 2020). Conversely, we expected a very weak selection, or even no evidence of selection, carried out by dispersers (Mateo-Sánchez et al. 2015; Imbert et al. 2016; Abrahms et al. 2017; Scharf et al. 2018; Rio-Maior et al. 2019).

Fig. 1. — Wolf distribution in Italy drawn by merging information from the report on species of community interest compiled by ISPRa for the National Biodiversity Strategy and more recent results by Marucco et al. (2018) (a); and study area in Northern Italy (b).
Space use analyses

To investigate whether residents, other than dispersers, inhabit the Ticino Natural Park, we first produced an interpolation map of the detected point-density across the whole study area. To this aim, we fit a smoothly curved surface over each point and the neighbour points within a circular buffer, according to a quartic kernel function (Silverman 1986; Soh et al. 2013). The surface values ranged from a maximum value at the focal point location to zero at the distance corresponding to the buffer radius and whose integral equals one. Buffer radius (i.e., bandwidth) was proportional to the minimum between the median of the distances of each point from the mean centre of all points and the standard distance (a measure of dispersion around the mean centre) and it was inversely proportional to the number of points. We produced a raster map (50-m resolution) of point density by a pixel-wise summation of the values of the pixel overlapping kernel surfaces. Point density estimation was performed using the Kernel Density Estimation tool (KDE) in Arcgis 10.5 (ESRI 2011).

Subsequently, we associated the KDE point density value to each detection point, and we analysed their frequency distribution to search for a cut-off that separates high KDE density values from low KDE density values. We considered the detection points associated to a point density higher than the cut-off as belonging to resident individuals, while detection points associated to a point density lower than the cut-off as belonging to dispersers. Moreover, we considered areas characterized by a point density higher than the cut-off as core areas. Then, we investigated if core areas showed specific characteristics generally associated to home ranges or biding areas, that is, a small area, a stability across seasons, and a sufficiently high distance of their centroids from detection points falling outside the core areas (Hinton et al. 2016; Mancinelli & Ciucci 2018). We calculated the area occupied by putative resident wolves by calculating the Minimum Convex Polygon (MCP) identified by the detection points falling inside the core areas and compared it with the area of the MPC identified by the detection points falling outside the core areas, which likely belong to dispersers (Imbert et al. 2016). We preferred MCP to straight measurement of core areas’ extension from KDE results, because MCP was proved more effective with a small sample size (Boyle et al. 2009) and linear point pattern shapes (Downs & Horner 2009) and because it gives comparable results with recently published wolf studies (Mancinelli et al. 2018). We investigated the seasonal stability of the identified core areas by visually comparing the maps created by separately running the KDE on the detection points collected in spring-summer and those collected in autumn-winter. Finally, we calculated the proportion of detection points falling outside the core areas located at a sufficiently high (> 10 km) distance from the centroids of the core areas. The threshold distance was set to 10 km, because it corresponds to the mean maximum net displacement from the centroids of packs’ home ranges walked by wolves during extraterritorial forays, i.e., displacements outside the home range with the aim of exploring the land (Mancinelli & Ciucci 2018).

To compare the environmental characteristics of the core areas with those of the areas frequented by putative dispersers we calculated the fractional cover of each land cover type within the MCP identified by the detection points falling inside and outside the core areas.

Habitat selection analyses

To investigate possible differences of habitat selection between resident and dispersing wolves in the Ticino Natural Park we used a presence vs availability approach. We used a ratio between presence and availability points of 1:5 and availability points were randomly generated along transects maintaining a number of points proportional to the length of each transect to avoid possible sampling bias (Jarnevich et al. 2015). We split the wolf detection points according to whether they fall inside or outside the core areas identified through KDE. In order to avoid computational issues related to small data samples, we adopted penalized generalized linear models (GLMs) with a binomial error distribution by using a ridge penalty to relate the wolf presence inside and outside the core areas to the 10 selected environmental variables.
Specifically, we ran the penalized GLMs by optimizing the cross-validated likelihood to find the optimal value of the tuning parameter λ using the Brent algorithm for minimization without derivatives (Brent 1973) (penalized R package; Goeman 2018). Subsequently, the two models were evaluated for their accuracy using the R² and for their performance in predicting wolf occurrence using the area under the curve (AUC) of the Receiver Operating Characteristic plot (ROC curve) (Pearce & Ferrier 2000; Fawcett 2006). We classified the accuracy of the diagnostic test by the traditional academic point system (Swets 1988): 0.90–1.00 = excellent; 0.80–0.90 = good; 0.70–0.80 = sufficient; 0.60–0.70 = poor; 0.50–0.60 = fail. Before running the models, we standardized the covariates by centring and scaling each independent variable and we checked pairwise Pearson’s correlation coefficient between covariates and verified that no variable pair had a coefficient higher than 0.60 (Khosravi et al. 2018). We checked the absence of spatial autocorrelation of the residuals using Moran’s I test with 999 permutations (Cliff & Ord 1981).

All the analyses were performed using R v. 4.0.3 (R Core Team 2020).

RESULTS

Space use analyses

We collected 59 wolf detection points within the Ticino Natural Park (Table S1 and Fig. S1 in Supplemental Data) during the study period, corresponding to scats (79%), camera trap detections (8%), predation remains (7%), sightings and footprints (3% each). The analysis of frequencies of KDE point density identified a bimodal distribution with two clear cut-offs that separated detection points (N = 29) falling in areas characterized by a low-density of points (< 0.4 points/km²) from detection points (N = 30) falling in areas characterized by a high-density of points (> 0.9 points/km², Fig. 2). Spatially, the upper cut-off outlined a single clearly defined core area located in the central part of the corridor (Fig. 3a). The MCP identified by the detection points falling inside (N = 30) and outside (N = 29) the core areas measured 2.9 km² and 417.1 km², respectively. Among all the points, 20 were collected in spring-summer while 39 in autumn-winter. The presence and spatial location of the core area remained stable in the seasons, while its size clearly increased from spring-summer to autumn-winter (Fig. 3b-c). The 86% of detection points falling outside the core area were located more than 10 km apart from the centroids of the core area.

The fractional cover of land cover types calculated within the MCP identified by the detection points falling inside and outside the core areas highlighted evident differences. Specifically, the core area was characterized by a fractional cover of woodlands considerably higher respect to the fractional cover observed outside the core area and a fractional cover of urban areas and arable lands considerably lower respect to that observed outside the core area (Fig. 4).

Habitat selection analyses

We randomly generated 150 availability points, but we excluded four points, which fell on the outer edge of the study area for a final number of 146 availability points. The penalized GLM developed on the wolf detection points falling inside the core area had a R² of 0.506 and an excellent performance in predicting species occurrence (AUC = 0.952). The environmental variables mostly affecting the probability of wolf occurrence within the Ticino Natural Park were the IKA of the roe deer with
a positive effect and the Euclidean distance from the banks of the Ticino River, the fractional cover of urban areas and water bodies and the IKA of the wild boar with a negative effect (Table 1 and Fig. 5). Conversely, the penalized GLM developed on the wolf detection points falling outside the core area had a $R^2$ of 0.037 and a poor performance in predicting species occurrence (AUC = 0.643). This model did not show a relevant effect for any of the analysed variables (all coefficients have values lower than 0.25) (Table 1).

**DISCUSSION**

To successfully estimate landscape connectivity, it is fundamental decoupling resident-like and disperser-like behaviour of individuals from original data (Zeller et al. 2012; Mateo-Sánchez et al. 2015; Scharf et al. 2018). This issue is particularly urgent when dealing with detection data due to their prevalence in wildlife studies because of their easiness to be collected and economic convenience. However, until today no connectivity study using detection data addressed this issue (Zeller et al. 2012; Abrahms et al. 2017). In order to take a step in this direction, we tried to decouple data related to resident and dispersing wolves by analysing detection data collected within the Ticino Natural Park, an ecological corridor connecting the Northern Apennines and the Central Alps.

KDE performed on the wolf detection points collected within the study area during the 2017–2018 years identified a clearly defined core area (i.e., an area characterized by a significantly high wolf point density) located in the central part of the corridor. The space use analyses showed that this core area had specific characteristics suggesting the presence of resident wolves within the corridor. First, the area identified by the detection points falling inside the core area was dramatically smaller than the area identified by the detection points falling outside the core area. The use of a smaller and more localized area by residents compared to that used by dispersers was also emphasized in other studies (e.g., Hinton et al. 2016; Mancinelli et al. 2018). Second, the core area detected by KDE showed stability during seasons, being present in the same place both in spring-summer and in autumn-winter. A single centre of activity throughout the year, without seasonal changes, has been identified as a typical characteristic of the central area of wolf packs’ home ranges, both in the grey wolf and in other wolf species (Ciucci et al. 1997; Hinton et al. 2016; Mancinelli et al. 2018). The only difference observed between the 2 seasons was an increase in the size of the core area from spring-summer to autumn-winter, another expected behaviour of resident wolves (Jedrzejewski et al. 2001; Packard 2003; Theuerkauf et al. 2003; Iliopoulos et al. 2014). Finally, the space use analyses showed that almost all the detection points collected outside the core areas were located at a distance from the centroid of the core area greater than the maximum distance generally travelled by individuals during extraterritorial forays (Mancinelli & Ciucci 2018). Therefore, the presence signs collected outside the core area were unlikely left by resident individuals inhabiting the core area during exploratory movements. Furthermore, we excluded that these signs have been left by individuals during pre-dispersal movements, on average characterized by greater net displacements (Mancinelli & Ciucci 2018), because during and after the study period there were no dispersal events, which, in our study area, would probably have resulted in the disappearance of the core area.
The area identified by the detection points falling inside the core area differs from the area identified by the detection points falling outside the core area not only in physical characteristics but also in environmental composition. The composition of the core area is more natural than the composition of the area used by putative dispersal-behaving individuals, with considerably higher fractional cover of woodlands and a shortage of arable lands and urban areas.

The high differences in $R^2$ and AUC between the model performed on the detection points falling inside and that on detection points falling outside the core area suggest that the former set of points most likely belong to resident individuals, which typically show a strong habitat selection, while the latter could belong to usually less selective dispersers (Zeller et al. 2012; Mateo-Sánchez et al. 2015; Abrahms et al. 2017; Scharf et al. 2018; Rio-Maior et al. 2019). Several studies pointed out that the distribution of wolves is generally affected by the abundance of prey and by the risk associated with the presence of humans (Massolo & Meriggi 1998; Jędrzejewski et al. 2004; Eggermann et al. 2011; Imbert et al. 2016; Meriggi et al. 2020) and the results we obtained for the data collected inside the core area basically followed these preferences. The local abundance of roe deer was by far the most important factor in determining the probability of wolf occurrence in our study area. Wolf occurrence was proved to increase where the roe deer is present with high densities so as the encounter rate with the carnivore is high (Huggard 1993; Meriggi et al. 1996; Meriggi & Lovari 1996; Jędrzejewski et al. 2002). The Ticino Natural Park is the most suitable area for the roe deer in the highly modified western lowland area in Northern Italy (Dondina et al. 2019) and the location of the identified core area is characterized by a very high roe deer density ($30.7 \pm 4.1$ individuals/km$^2$; De Pasquale et al. 2019).

![Fig. 2. — Frequency distribution of KDE point density for 59 wolf detection points collected within the Ticino Natural Park in 2017–2018.](image-url)
Fig. 3. — Spatial Kernel Density Estimation of wolf detection points (N = 59) collected within the Ticino Natural Park in the 2017-2018 years. (a) Whole period, (b) spring-summer, (c) autumn-winter.
Conversely, even if with a lower effect on wolf presence probability, the model highlighted an avoidance of areas characterized by high abundances of wild boars. The core area is characterized by a wild boar abundance (average IKA within the core area = 2.8 number of signs/km) lower than the abundance detected in other areas of the Park (e.g., IKA = 8.2 number of signs/km about 10 km south of the core area centroid); nevertheless, the core area is the only site characterized by a balanced abundance of both wild boar and roe deer proving that an abundant and diversified community of wild ungulates is one of the most important drivers in determining the stable presence wolves (Meriggi et al. 2020). Moreover, resident wolves avoided urban areas, while selected areas close to the Ticino River that are the most internal and least disturbed areas of the park (Balestrieri et al. 2015; Rio-Maior et al. 2019). Resident wolves seem then to select the areas near the river, thickly covered by woodlands, without however going into the riparian areas, as confirmed by the negative effect of the fractional cover of water bodies on the species occurrence probability. The riparian areas were probably avoided by wolves because they were less frequented by ungulates.

On the contrary, the habitat preferences analysis performed on the detection points collected outside the core area generated a model characterized by an extremely low explanatory and discriminatory power that did not highlight a relevant effect of any variable. The lack of habitat selection is a typical behaviour of dispersers. Several studies based on movement data found that dispersers not only do not use areas with higher suitability than the surrounding areas for their movements (e.g., Scharf et al. 2018), but they also use low-suitability areas (e.g., Mateo-Sánchez et al. 2015; Gastón et al. 2016; Abrahms et al. 2017). The general lack of habitat and prey selection by dispersers mainly depends on the fact that dispersing wolves (usually young individuals) cover great distances in a short time and therefore do not have the time to learn...
the distribution of resources in the landscape (Linnell et al. 1999; Imbert et al. 2016). Moreover, dispersing wolves tend to avoid suitable areas where adult residents are generally settled, such as inner woodlands (Bowler & Benton 2005; Elliot et al. 2014).

Both the space use and habitat selection analyses suggested that the core area identified by KDE is defined by detection points belonging to resident-behaving wolves. However, we do not have enough information to speculate on the presence of one or more breeding residents, perhaps a pair, within the park (during the study period a male and a female were camera-trapped within the core area but never together). We cannot even know if the individuals who occupied the core area during the study period were stable residents or dispersers temporarily settled in what Hinton et al. (2016) have defined a biding area, that is, a temporary resting area smaller than a typical pack’s home range [104 (± 24 SD) km² for the Italian wolf, Mancinelli et al. (2018)] where dispersers carry out a habitat selection similar to that carried out by residents in their home range and where they could settle down as residents in the future in the case they met a mate.

We acknowledge that sample size could have affected the core area identification, although both whole and within-season sample size are greater than the threshold suggested by Silverman (1986) to obtain a relative mean square error lower than 0.1. The low sample size could be a common condition when dealing with corridors and recently colonized areas as opposed to reproductive areas where stable territories are settled-up. To enlarge the sample size, we considered both data collected along transects and occasional observations. Although it may partially affect the analyses, merging data collected through standardized sampling design and occasional records (often obtained from citizen science) is a common practice in studies dealing with
Fig. 5. — Plots showing the effect sizes of environmental variables on the wolf presence probability. The line represents the effect of a covariate obtained from penalized GLMs when all the other independent variables equal their average value. Unit of measure: IKA (number of signs/km), distance from the Ticino River (m), land cover types (m²).
elusive mammals. Despite these issues, the consistency of our results among the checked criteria suggests that the method could be robust to low sample bias and inclusion of data obtained from different sources.

Our findings regarding the simultaneous occurrence of resident and dispersing wolves within the studied corridor have important practical and management implications. First, our results show that, even without applying particularly complex spatial analyses, it is possible to have a rough distinction of detection points belonging to residents (or temporary settled dispersers) and dispersers. Furthermore, the developed models clearly show that the habitat preferences evaluated starting from detection points belonging to dispersers or residents are extremely different. If this distinction is not made, the results of connectivity studies can be extremely misleading. In particular, connectivity analyses using resistance surfaces obtained from RSFs developed from detection points belonging to both dispersers and residents would lead to important underestimations of the possible corridors exploited by the study species in a landscape (Ziółkowska et al. 2016).

From a management point of view, the simultaneous occurrence of resident and dispersing wolves within a corridor leads to the urgent need of a revision of management actions aimed to the species conservation. In particular, the degree of protection of areas inhabited by residents should be considerably higher than that generally required for the protection of areas used for dispersal (Rio-Maior et al. 2019). On the other hand, given the typical social structure of the wolf, the presence of resident individuals within a narrow corridor could create a deterrent to dispersers to cross the corridor, interrupting the dispersal flow and invalidating the ecological functionality of the entire corridor (Imbert et al. 2016; Rio-Maior et al. 2019). Finally, knowledge about the occurrence of both resident and dispersing wolves is crucial for the management of possible conflicts between the carnivore and human activities that can arise in newly colonized areas (Dondina et al. 2015).

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DISCLOSURE STATEMENT

No potential conflict of interest was reported by the authors.

AUTHOR CONTRIBUTION

Conceptualization: O. Dondina, A. Meriggi, L. Bani and V. Orioli; Data collection: O. Dondina and A. Meriggi; Data analysis: O. Dondina and V. Orioli; Writing – original draft
preparation: O. Dondina; Writing – review and editing: A. Meriggi, L. Bani and V. Orioli; Supervision: A. Meriggi and L. Bani. All authors read and approved the final manuscript.

SUPPLEMENTAL DATA

Supplemental data for this article can be accessed at https://doi.org/10.1080/03949370.2021.1988724

DATA ACCESSIBILITY

All data analysed during this study are included in this published article [and its Supplemental Data].

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