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Dispersal and settlement dynamics of wolves in a lowland ecological corridor in northern Italy: Effects of resource availability and human disturbance

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ABSTRACT

A dispersal strategy punctuated by breeding events along corridors is the most effective for sustaining recolonization and viable metapopulations of large mammals. Consequently, functional ecological corridors not only have to offer dispersal routes, but they must also provide suitable breeding conditions. This study investigated wolf spatio-temporal behavior within the Ticino Natural Park, an ecological corridor crossing a highly human-modified area in northern Italy. Wolves were systematically monitored from 2017 to 2023. Kernel and resource selection analyses showed that core areas characterized by high naturalness attracted transient individuals due to their suitability for potential settlement. Wolves selected core areas with low anthropogenic disturbance, high shrub cover, and prey abundance, aligning with behaviors observed in resident wolves. Despite the availability of favorable habitat conditions and the nocturnal behavior adopted by wolves, anthropogenic disturbance, including culling activities, human-induced mortality, and traffic roads, have been the primary limitation to pack establishment in the park so far. However, the observations of a stable wolf pair in the most recent core area in 2023–2024 and the consequent implementation of conservation management actions by park managers have permitted the very recent settlement of the first wolf pack within the protected area. This event will reinforce the ecological connectivity between Apennines and Alps wolf sub-populations and between the Italian and European populations. This study underscores the importance of actively protecting natural corridors able to support both dispersal and settlement to ensure recolonization of formerly occupied areas and the long-term large carnivore conservation in a landscape of coexistence.

1. Introduction

Dispersal from natal ranges is a key ecological process for the long-term viability of animal populations and metapopulations (Bennett, 2003). Dispersal prevents intraspecific competition and inbreeding risk and is the major mechanism of recolonization after local extinction events (Barry et al., 2020; Morales-González et al., 2022). In human-modified landscapes, dispersal occurs along ecological corridors (Bennett, 2003), i.e., pathways that offer lower resistance to animal movements compared to the surrounding inhospitable matrix (Dondina et al., 2018a). Many studies emphasize that the ecological requirements of individuals during dispersal are generally much weaker than those of resident individuals (e.g., Abrahms et al., 2017; Rio-Maior et al., 2019). It is therefore widely assumed that corridors merely need to provide sub-optimal environmental conditions for individuals that use them to move between suitable habitats (Palomares, 2001; Dondina et al., 2019). Nevertheless, individuals do not always disperse by direct movements that take them from one suitable site to another. Dispersal movements may be punctuated by one or more pauses for foraging or resting, lasting from hours to several months. In some species, if suitable environmental conditions and potential partners are found within the corridor, individuals can interrupt the dispersal process to reproduce. The offspring will then continue the dispersal process in subsequent generations, ensuring the dispersal flow among distant areas (Bennett, 2003).

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Individuals of the same species may adopt different dispersal strategies depending on individual behavioral inclinations and/or characteristics of the crossed landscape (Green et al., 2018; Morales-González et al., 2022; Torretta et al., 2023).

During prolonged rests along ecological corridors (with or without reproduction), individuals are more demanding in their ecological requirements, making the distinction between the resources to be provided by a corridor and those to be provided by a habitat very feeble (Green et al., 2018). Some authors have pointed out that functional corridors not only have to offer low resistance to individual movement but must also provide shelter, breeding sites, and food resources (Hilty and Merenlender, 2004; Dondina et al., 2016). Various studies have emphasized this finding for birds and small mammals (Dondina et al., 2016; Bani et al., 2018), while little is known about large mammal (Green et al., 2018). To achieve a satisfactory conservation status for these species, this knowledge gap should be addressed, because a dispersal strategy punctuated by prolonged rests is likely to be the most effective for recolonizing formerly occupied areas and maintaining long-term viable metapopulations of large mammals at regional/national scale (Bennett, 2003).

In this study, we focused on the wolf (*Canis lupus*), a large carnivore whose recolonization processes and long-term metapopulations' viability rely on large-scale dispersal events (Mech, 2020). Several studies reported evidence of radio-collared wolves dispersing over large distances, often occupying temporary stable territories for several weeks or months (e.g., Wabakken et al., 2007; Ciucci et al., 2009; Mancinelli and Ciucci, 2018; Barry et al., 2020; Musto et al., 2020; Torretta et al., 2023). While wolves undertaking direct dispersal or dispersal punctuated by short resting periods (hours/days) may exploit small patches of sub-optimal habitat that solely provide shelter (Torretta et al., 2023), we hypothesize that wolves that adopt a dispersal strategy through prolonged resting periods (weeks or months) should find their ecological requirements met in at least some portion of the dispersal pathway. In other words, a dispersal strategy punctuated by breeding events can occur only if the ecological requirements typical of stable wolf packs are met in some areas of ecological corridors. Wolf requirements in areas occupied by stable packs have been extensively studied, both in natural and in human-modified landscapes, and involve (i) good prey availability, and (ii) shelter areas that can minimize the risk of encounters with humans (Llaneza et al., 2012; Imbert et al., 2016).

We investigated the drivers of the spatio-temporal patterns of wolves in the Ticino Natural Park, a wide riverine corridor that can significantly boost the wolf gene flow between the Italian and Dinaric-Balkan populations, supporting dispersal from the Northern Apennines to the Central Alps (Dondina et al., 2020). The Ticino Natural Park has recently been recolonized by the wolf: the first detection of the species, after 150 years of absence from the lowlands of northern Italy, dates to 2017 (Meriggi et al., 2020). This lowland Park has been mainly used by dispersing individuals, offering a unique alternative route to the historic dispersal path between the Apennine and Alpine sub-populations, i.e. the western Alps, which has become over-saturated with packs (La Morgia et al., 2022). Both direct dispersal and dispersal punctuated by rests in temporary stable territories have been documented as dispersal strategies adopted by the wolf within the Ticino Natural Park corridor between 2017 and 2023. This was ascertained based on the findings from a detailed study on presence signs collected in 2017–2018 (Dondina et al., 2022) and a study on a radio-collared wolf released in the protected area in 2019 (Torretta et al., 2023). Moreover, the presence of at least two wolf pairs was detected in 2021/2022 and 2023/2024 (Dondina unpublished data).

With this study, we analyzed wolf presence signs detected in the protected area over six-years of monitoring (spring 2017-spring 2023), to investigate how the predator space use has varied over time and if and how this was affected by environmental characteristics, prey availability, and anthropogenic disturbance. Moreover, we analyzed data collected by opportunistic camera trapping over the same period to investigate the possible evidence of temporal segregation between predator and human activities, a typical behavior enacted by wolves whose stable territories are located in areas characterized by high anthropogenic disturbance (Theuerkauf et al., 2003).

We hypothesize that if resource selection and activity patterns of wolves in some areas of the corridor are similar to those observed in areas occupied by stable packs, the Ticino Natural Park can support not only dispersal strategies punctuated by temporary rests but also by reproductive events. This would play a key role in the future wolf functional connectivity between the Apennines and Alps sub-populations and between the Italian and Dinaric populations affecting the future dynamics of wolf recolonization of southern Europe. Among large carnivores, the wolf is the most successful species at recolonizing its former ranges and expanding its populations (Kuijper et al., 2024). However, there are areas in southern and central Europe where wolves still struggle to achieve stable recolonization due to dispersal issues caused by ecological barriers (e.g., fenced highways or railways) or excessive conflict with humans (Nakamura et al., 2021). We expect that the findings of this study will provide insights into the dispersal dynamics adopted by wolves in human-modified landscapes providing additional knowledge to manage the complex wolf recolonization process across human-dominated areas (Chapron et al., 2014).

2. Material and methods

2.1. Study area

The Ticino Natural Park stretches across two administrative regions of northern Italy (Lombardy and Piedmont) and is managed by two different territorial authorities (Parco Lombardo della Valle del Ticino and Ente di Gestione delle Aree Protette del Ticino e del Lago Maggiore, respectively). The protected area is a lowland river park that longitudinally crosses the highly anthropized Po Valley, representing a natural ecological corridor between the hilly and mountain areas of the Apennines, to the south, and those of the Alps, to the north. The Park is covered for almost half of its extension by agricultural areas (croplands, meadows, traditional poplar cultivations and reforestations) and to a slightly lesser extent by lowland deciduous woodlands; the remaining surface is covered by water courses and urbanized areas, mainly isolated farmsteads. The Park offers an important refuge for several species in the highly modified Po Valley. Three wild ungulate species (the widespread wild boar *Sus scrofa* and roe deer *Capreolus capreolus*, and the sporadic fallow deer *Dama dama*) inhabit the protected area, while the wolf is the only large carnivore detected in the Park.

This study was carried out in an area of about 200 km^2 in the Lombardy portion of the Ticino Natural Park (Fig. 1).

2.2. Data collection

2.2.1. Wolf occurrence data

Wolf presence signs have been collected through a standardized monitoring protocol. Systematic data were collected along 30 routes along roads and trails (mean length: 8 km) covering the entire study area. Searching for signs of presence along roads and trails is a consistent method used to detect wolf presence and distribution in monitoring projects (e.g., Gervasi et al., 2024). Each route was designed to be as representative as possible of the habitat types composing the Ticino Natural Park (Fig. S1). During 2017 and 2018 each route was walked four times a year, once a season (spring: March–May; summer: June–August; autumn: September–November; winter: December–February). During 2019 and 2020, the systematic control of routes was suspended, while from 2021 to 2023 each route was walked systematically twice a year (autumn-winter: September–February; spring-summer: March–August). Wolf presence signs collected along routes included scats, predation remains, and sightings.

All the occasional wolf presence signs detected during the study

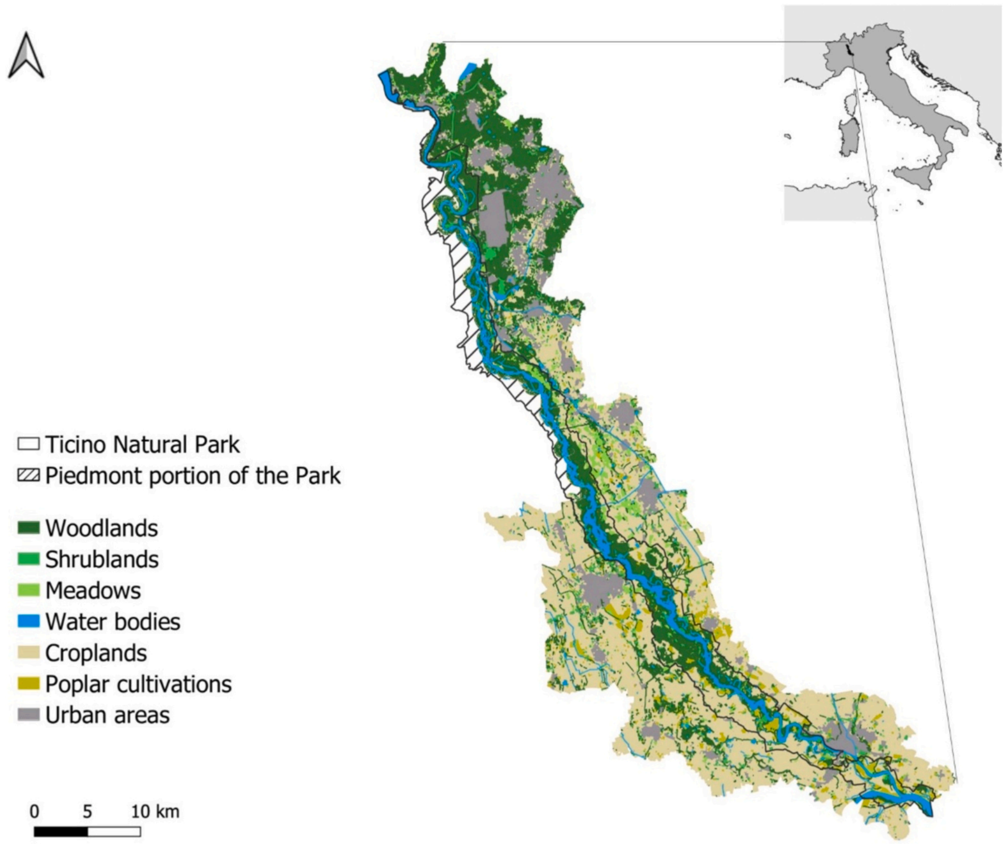

Fig. 1. Study area. Lombardy portion of the Ticino Natural Park in northern Italy.

period were checked by an expert researcher, by visual inspection of wolf photos and videos or by examination of collected scats or predation remains, and added to the data systematically collected along routes. The combined use of occasional and systematically collected data is a commonly used method when studying elusive species (Gervasi et al., 2024) in areas mainly used for dispersal (Dondina et al., 2022).

Occasional data also included photos and videos obtained through the opportunistic placement of 24 camera traps by the Ticino Natural Park and University staff, both in the Lombardy and Piedmont portions of the Park. Camera-traps were placed throughout the 7 years of monitoring at >50 different sites, located in opportunistically chosen areas. These included areas of evident passages of animals in woodland and riparian zones, areas close to locations where sightings or suspected predation events occurred, and areas close to inhabited farmsteads. Although we did not adopt a standardized sampling design for camera trap placement, as it was considered too costly for an elusive species in a territory mainly used for dispersal, we believe that the surveyed sites were representative of the environmental heterogeneity and the areas the species frequented within its boundaries (Fig. S2). Photos and videos collected in the Piedmont portion of the Park were used only for the activity rhythms analysis (see subsection 2.3.3).

All collected data were classified according to their degree of verifiability using the SCALP (from the Status and Conservation of the Alpine Lynx Population project) criteria (Molinari-Jobin et al., 2012; La Morgia et al., 2022): C1 = hard facts (dead animal, genetic records, location by telemetry, high-quality pictures/videos), C2 = confirmed observation (tracks, scats, etc. confirmed by an expert) and C3 = unconfirmed data (e.g. sightings not confirmed by an expert). Among C3 records, there are often many false absences. For this reason, the creators of the SCALP method recommend treating this category with particular caution, especially for studies on large carnivores.

2.2.2. *Prey abundance*

Wild boar and roe deer occurrence data were collected during the systematic monitoring along routes in 2017 and 2018. Relative abundance was estimated at the route level, by calculating the Index of Kilometric Abundance (IKA) (number of detected signs divided by the route length, Meriggi et al., 2015; Imbert et al., 2016) for each species. IKA values used in this study were obtained by averaging the values of the IKA associated with winter and spring monitoring periods (for details see Dondina et al., 2022). Summer and autumn were excluded from the calculation of the index to prevent underestimating ungulate presence in open areas compared to woodlands, and vice versa. During summer, detecting signs is challenging in open areas due to extremely dry ground conditions. Conversely, in autumn, litter accumulation on roads and trails hinders accurate estimation of ungulate presence signs in woodland areas.

2.2.3. *Environmental predictors*

Environmental predictors were the fractional cover of seven land cover types, namely urban areas, croplands, meadows, poplar cultivations, shrublands, woodlands, and water courses. The reference cartography was the vectorial land use layer of Lombardy, DUSAF 6 (ERSAF, 2018). In addition, as roads are an important source of risk for wolves and they strongly affect their movements and behavior (Zimmermann et al., 2014), the spatial distribution of paved roads within the study area was also considered (map data copyrighted by OpenStreetMap contributors and available from https://www.openstreetmap.org; accessed on 6 June 2023).

2.2.4. *Human disturbance induced by recreational activities*

To investigate the possible human disturbance induced by recreational activities, 30 detection points were surveyed in autumn-winter (November and December 2022) and in spring (April 2023). Detection points were identified along the 30 routes in the Lombardy portion of the Ticino Natural Park and were located in areas where tourists' passage is likely concentrated (e.g., at the beginning of paths starting from car parks, at intersections between paths, etc.) (for detection point locations see Fig. S1). Surveys were carried out during central daytime hours (10:30 a.m.-2:30 p.m.) on public holidays, when tourists' frequentation of the Park was at its highest, to estimate the maximum level of disturbance that wolves might experience during resting periods. Each survey lasted 30 min during which the number of people passing through, distinguishing between walkers and cyclists, was recorded.

2.2.5. Wild boar culling activities

The wild boar population in the Ticino Natural Park is managed through control activities year-round. Control activities are coordinated by the Park Authority through the Surveillance Office and the Wildlife Management Office. Culling activities are carried out by the Park rangers and licensed hunters who have been specifically trained by the Prak staff. The techniques used for wild boar population control include: shooting from high hides, stalking, and driven hunt with hounds. Other hunting activities are forbidden within the protected area boundaries.

Data on culled wild boar have been systematically collected by the Park Authority since 2018: for each animal, the killing date and location/coordinates, along with the culling method, were recorded. To investigate a possible effect of wild boar culling activities on wolves within the protected area, we processed data provided by the Park Authority as follows: each culled animal (from 2018 to 2022) was assigned to the route nearest to the killing location (or to two or three routes if equally near). For each route, we calculated the following variables: the number of culling events concluded with at least one animal culled, the total number of animals culled, and the number of animals culled categorized according to the culling technique.

2.3. Data analyses

2.3.1. Space use analyses

To investigate the species distribution pattern in the Ticino Natural Park, wolf utilisation distribution and core areas were identified as the 95 % and 50 % isopleths, respectively, estimated through Kernel Density Analyses (KDAs) using a fixed kernel estimator with the reference smoothing parameter (h_{ref}) (Worton, 1989). KDAs were at first performed on all the C1 and C2 data collected during the entire study period (from March 2017 to February 2023). To investigate the changes that may have occurred from the beginning of the recolonization of the Ticino Natural Park, we performed a KDA on the C1 and C2 data for the first (2017–2018) and the sixth (2022−2023) monitoring year. A monitoring year corresponds to a wolf biological year (sensu Karppinen et al., 2022), i.e., from March of one year to February of the following year. The other monitoring years were not analyzed individually due to insufficient data.

The KDAs were run using the kernelUD function in the *adehabitatHR* package (Calenge, 2006) of the R software (R Core team, 2023).

2.3.2. Resources selection analyses

To investigate the effect of environmental characteristics, prey abundance, and human disturbance on wolf distribution within the Park, we used a presence vs. availability approach. Wolf presence points were the C1 and C2 presence signs collected from March 2017 to February 2023 within the study area. Availability points were randomly generated within the study area, with a ratio between presence and availability points of 1:5 (Jarnevich et al., 2015).

The fractional cover of land cover types was calculated within a 100 m buffer around each presence/availability point. A fine spatial scale was selected to calculate land cover variables because wolves in the Ticino Natural Park were most likely dispersers or temporarily resident individuals (Ziółkowska et al., 2016). The effect of roads was considered by calculating the distance of each presence/availability point from the nearest paved road. The value of roe deer and wild boar IKA and the anthropogenic disturbance related to recreational activities and wild boar culling were assigned to each presence/availability point based on the variable's value associated with the nearest route. These elaborations were carried out with ArcMap (v. 10.5; ESRI, 2011).

Univariate generalized linear models (GLMs) with a binomial error distribution were first developed for each independent variable. Subsequently, a multiple GLM with binomial error distribution was developed entering as independent variables only those variables that had a significant ($p < 0.05$) or nearly significant ($0.05 < p < 0.1$) effect in the univariate GLMs. Before running the multiple regression model, we scaled all the continuous predictors and we checked pairwise Spearman's correlation coefficient between covariates and verified that no variable pair had a coefficient $> |0.7|$ (Dormann et al., 2013). To select the most important variables in influencing the wolf presence probability we used an Information-Theoretic Approach by means of the Akaike Information Criterion adjusted for small samples (AICc) through a "stepwise both" (both backward and forward) procedure (Burnham and Anderson, 2002).

The goodness of fit of the best model was estimated by the percentage of deviance explained and its accuracy was evaluated using the area under the curve (AUC) of the Receiver Operating Characteristic plot (ROC curve) (Pearce and Ferrier, 2000; Fawcett, 2006).

We verified that all GLM requirements were met by checking diagnostic plots. We checked the absence of spatial autocorrelation in models' residuals using Moran's I test with 999 permutations (Cliff and Ord, 1981).

The analyses were performed using R packages *spdep*, *stats*, and *verification* (Bivand et al., 2017).

2.3.3. Activity rhythms analyses

Wolf activity rhythms analyses were performed on photos and videos collected by camera trapping in both the Lombardy and Piedmont portions of the Park during the period May 2017–February 2023.

To evaluate a possible non-homogeneous distribution of activity events during the day, a Watson test was run (Pewsey et al., 2013). The probability of a wolf activity event occurring during the 24-h period was estimated and graphically represented.

The analyses were developed using *lubridate* (Grolemund and Wickham, 2022) and *circular* (Agostinelli and Lund, 2022) R packages.

3. Results

3.1. Collected data

From March 2017 to February 2023, 127 wolf presence signs were collected within the study area. Of these, 102 were classified as C1 and C2, namely scats ($N = 76$, 75 %), camera trap detections ($N = 18$, 18 %), predation remains ($N = 4$, 4 %), and sightings (N = 4, 4 %).

From May 2017 to February 2023, 29 photos and videos were collected by camera trapping in the Lombardy and Piedmont portions of the Park.

Regarding human disturbance induced by recreational activities, 117 tourism events were recorded during the autumn-winter survey (total number of walkers = 205; total number of cyclists = 119) and 127 during the spring survey (total number of walkers = 123; total number of cyclists = 110) (Dondina et al., 2024).

According to the data collected by the Park Authority, 2712 wild boars were culled in the study area between 2018 and 2022 (Dondina et al., 2024).

3.2. Data analyses

3.2.1. Space use analyses

Space use analyses were performed on the 102 C1 and C2 wolf presence signs collected from March 2017 to February 2023 and, separately, on the data from the first (2017–2018, 41 wolf occurrence data) and the sixth (2022–2023, 29 wolf occurrence data) monitoring years (Fig. 2).

Total wolf utilisation distribution (2017–2023) covers an area of 964 km^2. Compared to the first monitoring year, in the sixth year wolf utilisation distribution slightly increased its surface (from 982 km^2 to 1187 km^2) and expanded southwards.

Within the total wolf utilisation distribution, two core areas occurred, a larger one in the central area of the Park and a smaller one just further south (total area of 170 km^2). From the first to the sixth monitoring years, the core areas increased their surface (178 km^2 and 223 km^2 in the first and sixth year, respectively) and the two core areas present in 2017–2018 merged into a single larger one in 2022–2023. The overall spatial location of the core areas remained relatively stable over the years, while a centroid southward shift was evident (Fig. 2).

3.2.2. *Resources selection analyses*

Results of univariate GLMs are showed in Supplementary materials (Table S1).

The multiple GLM was developed entering 13 independent variables with a significant or nearly significant effect in the univariate GLMs (Table S1). The best selected model (AICc = 370.31) had an explained deviance of 34 % and a good-excellent accuracy (AUC = 0.873). The predictors mostly affecting the probability of wolf occurrence within the Ticino Natural Park were the fractional cover of shrublands, the IKA of the roe deer, the distance from the nearest paved road, and the number of wild boar culling events (linked to the population control within the protected area), with a positive effect. Conversely, the percentage cover of water courses and croplands showed a significant negative effect. The distance from the Ticino River had a nearly significant negative effect (Table 1).

3.2.3. *Activity rhythms analyses*

The analyses carried out on the 29 photos and videos collected by camera trapping (May 2017–February 2023) showed that the distribution of wolf activity events was significantly non-homogeneous (Watson's Test = 0.535, $p < 0.01$), exclusively occurring at night or dusk or dawn (from 6 p.m. to 8 a.m). The probability of a wolf activity event during the 24-h period was the highest between 11 p.m. and 8 a.m. (Fig. 3).

Table 1
Results of the best selected multivariate GLM (AICc = 370.31) performed on wolf detection points (N = 102) collected from 2017 to 2023 in the Ticino Natural Park (northern Italy). SE: standard error of estimates. z: Wald statistic for testing the hypothesis that the corresponding estimate is equal to zero (null hypothesis). Pr(>|z|): probability that the null hypothesis is true.

Covariate	Estimate	SE	z	Pr(>|z|)
(Intercept)	−2.352	0.193	−12.175	<0.001
Urban area cover	−0.323	0.216	−1.494	0.135
Cropland cover	−0.576	0.211	−2.730	0.006
Meadow cover	0.194	0.129	1.503	0.133
Shrubland cover	0.274	0.103	2.667	0.008
Water course cover	−0.701	0.202	−3.473	<0.001
Distance from the Ticino River	−0.392	0.201	−1.949	0.051
IKA roe deer	0.574	0.158	3.641	<0.001
Distance from the nearest road	0.853	0.145	5.878	<0.001
N. culling events	0.470	0.139	3.377	<0.001

4. Discussion

This study aimed to investigate the dispersal dynamics of wolves in areas heavily modified by humans, to increase knowledge on how to facilitate the recolonization of wolves, and potentially other large carnivores, in areas formerly occupied by these species. Specifically, we investigated the dispersal dynamics of wolves in a key ecological corridor crossing a highly anthropized area in northern Italy. Our hypothesis was that if wolf spatial distribution pattern, resource selection, and activity rhythm in the Ticino Natural Park were similar to those observed in areas occupied by stable packs, this important ecological corridor could support a wolf dispersal strategy punctuated by reproductive events, which is likely to be the most effective for the species at a regional/national scale (Bennett, 2003).

Monitoring activities and occasional wolf presence signs detection revealed that the Ticino Natural Park has been frequented by wolves in

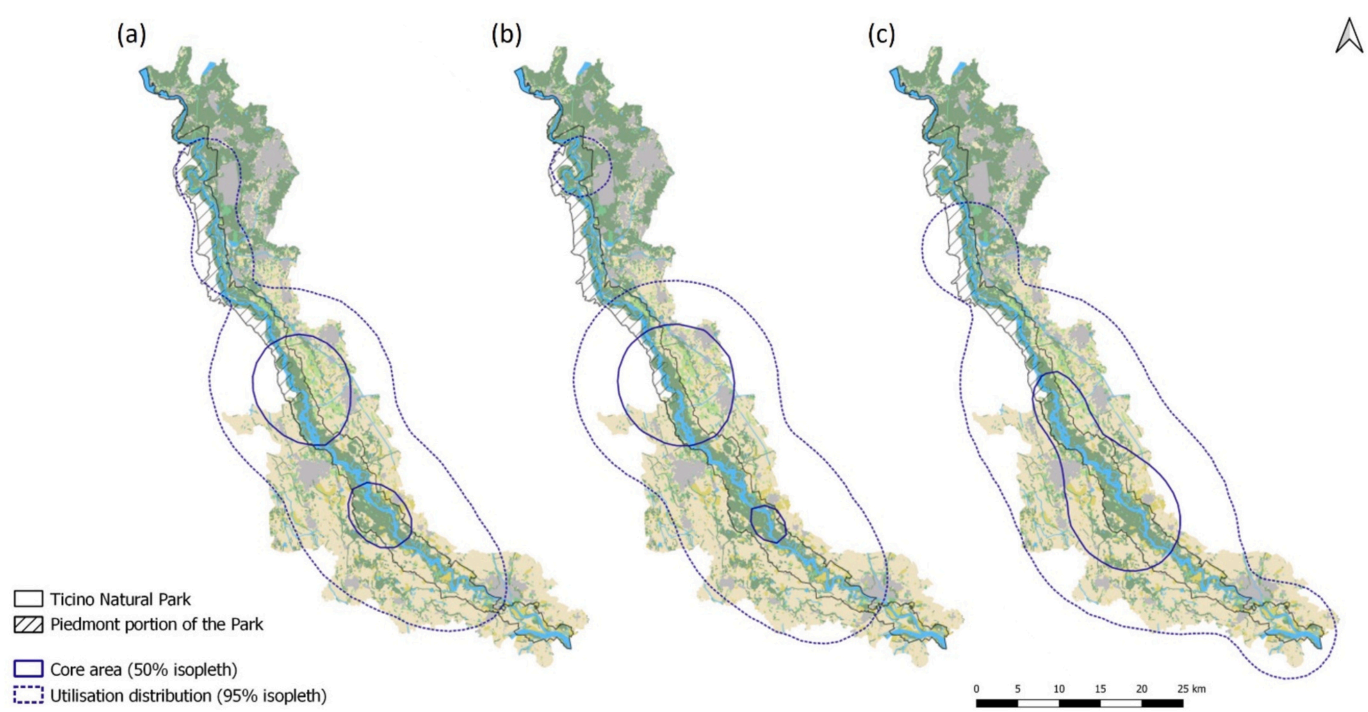

Fig. 2. Kernel Density Estimation of wolf occurrences collected within the Ticino Natural Park: a) in the whole 2017–2023 period (N = 102); b) in the first monitoring year (2017–2018, N = 41); c) in the sixth monitoring year (2022–2023, N = 29).

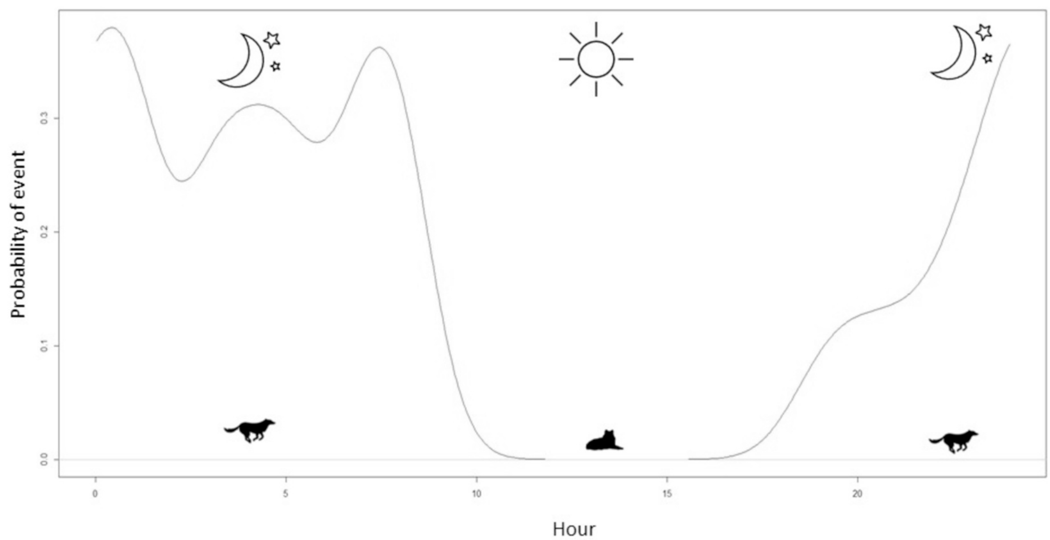

Fig. 3. Probability of a wolf activity event occurring during the 24-h in the Ticino Natural Park (northern Italy).

every season from March 2017 to February 2023 and the occurrence of core areas in the central zone of the park is evident. Since a pack has never been detected in the Park until 2024 (see below) our hypothesis is that between 2017 and 2023 different temporary stable individuals selected the same core areas at different times due to their high naturalness and food resource availability. This hypothesis is supported by several pieces of evidence, including (i) the stable settlement in the central part of the northern core area of at least one individual in 2017–2018 (Dondina et al., 2022); (ii) the months-long settlement in the same core area by a radio-collared wolf in 2019 (Torretta et al., 2023); (iii) the detection through camera traps in late 2021 and early 2022 of at least one wolf pair in the northernmost part of the core area identified for the 2022–2023 (Dondina unpublished data).

An active wolf selection behavior of areas with good environmental conditions within the corridor was confirmed by the results of the resource selection analyses. In the Ticino Natural Park, wolves have actively selected areas with low anthropogenic disturbance (i.e., away from roads and with low arable land cover), shelter accessibility (areas with high shrub cover), and high prey availability (positive relationship with roe deer IKA). These preferences match the resource selection behavior of resident wolves, which typically settle in areas with low anthropic disturbance and high prey abundance (Dondina et al., 2015; Imbert et al., 2016; Rio-Maior et al., 2019; Meriggi et al., 2020). In particular, these findings align with the expansion pattern of the species observed in the northern Apennines (Lombardy), where the colonization, which occurred from the mountains to the hills bordering the Po Plain, has been driven by roe deer abundance (Torretta et al., 2024). Moreover, the area of the northern Apennines likely represented the source area for the dispersing individuals who have utilized the ecological corridor along the Ticino River over the years (Dondina et al., 2020). Consistently, van den Bosch et al. (2023) found that dispersing wolves or floating individuals enact resource selection based on the same preferences of residents when movements occur in sufficiently natural areas.

The Ticino Natural Park is the most natural area in the highly anthropized western lowland area of Northern Italy and our results suggest that its naturalness is sufficiently high to allow dispersing wolves to enact a habitat selection behavior analogous to that of resident wolves. Indeed, our results reinforce the hypothesis proposed by Torretta et al. (2024), suggesting that wolf expansion will follow that of the roe deer across the Po Plain with the settlement of wolf packs in roe deer high-density areas (see below). The Ticino Natural Park is the most suitable area for the roe deer within the Po Plain (Dondina et al., 2019), and, in particular, the core areas selected by wolves during the study period host a very high roe deer density (30.7 $\pm$ 4.1 individuals/km^2) (De Pasquale et al., 2019), potentially offering sufficient food resources for the permanent settlement of the predator.

In other large carnivore species, the selection of small areas able to meet the environmental requirements of resident individuals has been observed for dispersers when they try to acquire a territory after an exploratory phase (Palomares, 2001). Overall, the results of the spatial pattern and resource selection analyses suggest that the identified core areas are characterized by conditions that meet the ecological requirements of the wolf and can support its eventual settlement, provided a suitable mate is found. We hypothesize that the several settlement attempts made by different wolves in the identified core areas were unsuccessful because individuals failed to find or maintain a partner before the breeding season, leading them to start dispersal again, as observed in other studies (Wabakken et al., 2007; Ciucci et al., 2009; Mancinelli and Ciucci, 2018; Barry et al., 2020; Musto et al., 2020; Torretta et al., 2023). During 2021–2022, a wolf pair was observed in the northern region of the 2022–2023 core area, proving that this particular area could offer adequate conditions for a pair to settle. Nevertheless, no packs have been observed in the following months. In the spring of 2023 a dead wolf, a feasible poaching victim, was found within the core area (Dondina unpublished data).

Further validating our hypothesis that the identified core areas were suitable for a wolf pack settlement, a new stable pair has been detected since November 2023 (i.e., beyond the timeframe of our analysis) in the south-western part of the 2022–2023 core area (Regione Lombardia, 2023). The pair successfully reproduced, and in August 2024, the first wolf litter of the Ticino Natural Park was documented.

The greatest hindrance to the wolf's chances of using this crucial corridor by adopting a dispersal strategy punctuated by breeding events is therefore not the lack of resources, but the anthropogenic disturbance. Direct or indirect human-induced mortality can hinder long-range dispersal events with intense consequences on landscape-scale populations' dynamics (Quevedo et al., 2019).

While disturbance due to tourist-recreational activities appears to be minimal because the carnivore enacts spatio-temporal segregation at a fine scale (Thorsen et al., 2022), the selection of areas characterized by a high number of wild boar control events raises some concern. Surprisingly, several studies have shown that the effect of wild boar culling on wolf presence is absent or even positive (Ruth et al., 2003; Torretta et al., 2017; Coppola et al., 2022; Petridou et al., 2023). These authors hypothesized that wild boar carcasses abandoned on site, or injured animals that hunters fail to retrieve and die not far away, provide an easily accessible and predictable food source for wolves, which prefer to feed on carcasses when accessible, even if abundant wild prey are available (Ciucci et al., 2020). This does not necessarily mean that wolves do not avoid the risk associated with wild boar culling activities violating the "ecology of fear" hypothesis (Brown et al., 1999). Viola et al. (2021), for instance, observed that in an area of Central Italy, wolves recurrently avoided approaching culling areas on the same day culling activities occurred, instead frequenting them on subsequent days in search of carrions. This is a result that will need to be carefully considered because habituation by wolves to easily accessible anthropogenic food sources is extremely problematic, as this can alter their behavior (not only from a dietary point of view but also affecting their spatial distribution, density, social relationships, etc.), with significant ecological and conservation consequences (Carricondo-Sanchez et al., 2020). Based on this evidence, in April 2024 the Park managers designated a buffer area surrounding the territory of the breeding pair detected in 2023–2024, forbidding wild boar control activities to reduce behavioral alterations and possible disturbance induced by culling activities. The effectiveness of this management action seems to be confirmed by the successful breeding of the wolf pair and the survival of the pups within the no-culling zone.

Another conservation concern that emerged from this study is the negative effect of traffic roads. The results of this study showed that wolves select areas furthest away from roads wherever possible, confirming the detrimental impact of such infrastructure not only on dispersal, as previously highlighted (Dondina et al., 2020), but also as a disturbance in the choice of resting areas. In our study area, the negative effect of traffic roads could have significant future implications for both the potential stability of the newly formed pack and the chance of successful dispersal by the new pups. In general, ensuring areas sufficiently far from traffic roads within ecological corridors while avoiding intensification of existing road networks is a necessary management action (Rio-Maior et al., 2019).

Finally, the analyses of activity rhythms showed that wolves in the Park have distinctly nocturnal behavior. Temporal segregation with human activities is a typical behavioral adaptation of wolves that allows them to permanently inhabit areas highly frequented by humans while minimizing the encounter rate and risk exposure (Gaynor et al., 2018; Torretta et al., 2023).

The results of this study provided key insights into wolf behavior and dispersal dynamics within large ecological corridors crossing heavily anthropized areas. These findings offer important perspectives from a conservation and management standpoint. However, it is important to acknowledge some limitations of this study, as it allows for the identification of areas where further research can enhance the robustness of the current evidence and extend the findings presented. The main limitation concerns the small sample size of the analyzed wolf presence signs (C1 and C2 presence signs: $N = 102$). While this number is adequate to run robust and reliable resource selection models, it is less adequate for developing KDAs to design utilisation distributions and core areas, particularly when data have been split between the two analyzed periods (2017–2018: $N = 41$; 2022–2023: $N = 29$). In this case, the main issue is the comparison of utilisation distributions and core areas designed based on a few occurrences that also differs in number between the two periods. To be sure that the difference in sample size in the two periods was not the cause of the observed differences in utilisation distributions and core areas in 2017–2018 and 2022–2023, we randomly subsampled the occurrences collected in 2017–2018 to obtain the same number of observations collected in 2022–2023 (N = 29). This procedure was repeated 10 times and showed that the differences in utilisation distributions and core areas highlighted between 2017 and 2018 and 2022–2023 are truthful and consistent, as the 2017–2018 utilisation distributions and core areas remain virtually unchanged even when subsampling the original data pool to match that of 2022–2023 (Fig. S3). Moreover, the activity rhythms analysis was developed on a sample of data (N = 29) just under the sample size threshold identified to obtain reliable results ($N = 30$; Lashley et al., 2018). The rather small sampling size added to the lack of a standardized sampling design for camera trap placement implies treating the results regarding the species activity rhythms within the park with particular caution.

The reason why the number of collected presence signs was fairly low is that, during the study period, there were no stable wolf nuclei in Ticino Natural Park, to which most of the presence signs found in a territory generally belong (Dondina et al., 2018b). Nonetheless, the extensive monitoring effort made allowed us to obtain an appropriate number of data to provide useful information.

5. Conclusions

Conservation and management of wolves, and large carnivores in general, must necessarily come through effective land-use planning based on the "landscape of coexistence" principle (Oriol-Cotterill et al., 2015). Designing a "landscape of coexistence" for wolves should involve the protection of areas suitable as stable packs' home-ranges, as well as corridors that effectively sustain dispersal movements across more human-modified sectors of the landscape, though this idea has rarely been evaluated empirically (Rio-Maior et al., 2019). In this study, we analyzed in detail the spatial use, resource selection, human-associated risk response, and activity rhythms of wolves that have frequented a critical ecological corridor whose use-patterns would have important consequences on the dynamics of future dispersal and recolonization by wolves both in northern Italy and in neighboring European countries. Our results showed the importance of this corridor in ensuring food resources and facilitating spatial and temporal segregation with human presence and activities. Over time, from transitory or temporarily resident individuals, two pairs tried to settle in the core areas identified in the corridor: the first one failed likely due to human illegal killing, while the second one successfully reproduced, resulting in the establishment of the first pack in Ticino Natural Park after the local extinction of the species occurred in the late 1800s (Dondina unpublished data). The management measures implemented by the Park managers to protect the areas frequented by this second pair proved successful, serving as a virtuous example of policy actions targeted at wolf conservation in heavily anthropized areas.

Over the original concept of "landscape of coexistence," our results reveal a very interesting insight, i.e. the conditions of corridors connecting widely distant areas should have suitable characteristics that, at least in some of their portions, can guarantee the implementation of a dispersal strategy punctuated by reproduction events. Moreover, where necessary, the relevant local authorities can intervene with targeted management actions to create/ameliorate such conditions. This would have a dual benefit for the conservation of the wolf and, potentially, other large carnivores. On the one hand, a dispersal strategy punctuated by breeding events is the most effective for maintaining long-term viable metapopulations of large carnivores (Bennett, 2003). On the other hand, suitable corridors that can guarantee the spatio-temporal segregation with anthropic activities would reduce the encounter rate between wolves and humans promoting their long-term coexistence (Llaneza et al., 2016) during the natural process of carnivore recolonization of currently human-dominated landscapes (Kuijper et al., 2024).

CRediT authorship contribution statement

Camilla De Feudis: Writing – original draft, Investigation, Formal analysis. **Elisa Torretta:** Writing – review & editing, Investigation. **Valerio Orioli:** Writing – review & editing, Methodology, Data curation. **Pietro Tirozzi:** Writing – review & editing, Investigation. **Luciano Bani:** Writing – review & editing. **Alberto Meriggi:** Writing – review & editing, Conceptualization. **Olivia Dondina:** Writing – original draft, Supervision, Methodology, Formal analysis, Conceptualization.

Declaration of generative AI and AI-assisted technologies in the writing process

During the preparation of this work the authors used ChatGPT in order to improve the readability and language of the manuscript. After using this tool, the authors reviewed and edited the content as needed and take full responsibility for the content of the published article.

Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.biocon.2024.110936.

Data availability

I have cited the link to my data within the manuscript.

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