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Research Article

Reclaiming the man-made plain: ecological factors influencing the colonization of the wolf *Canis lupus* in the western Po Plain (NW Italy)

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Abstract

The wolf *Canis lupus* is recolonizing the Po plain with variable intensity and patterns depending on the areas; in the province of Lodi, colonization by wolves seems to occur very quickly due to the proximity of the Trebbia and Nure valleys, whose wolf packs fuel the species dispersal. Between 2019 to 2024, we collected 109 observations for a total of 183 wolves, which settled in the central-southern part of the province, selecting the hilly areas and the banks of the Po, Adda and Lambro rivers. Intensive monitoring has provided useful data to estimate some population parameters; the average litter size was 4.8 pups and the pack size was 8–9 wolves, data in agreement with literature, while the average density, 0.9 ind /km^2 (range = 0.73–1.09), was lower than that of several European protected populations and close to the densities of culled ones. Roads, urban areas and meadows have a negative influence on the predator presence, which is favoured by green areas close to urban settlements and, though not significantly, by wetlands. On the other hand, a stable presence is favoured both by tree cover surrounded by extensive crops and by the presence of wetlands and water basins, which can provide prey such as the *Myocastor coypus* and perhaps make access to dens more difficult, thus reducing disturbance during reproduction. The road network has a negative effect on the presence of the wolf, but not on the stability of its settlement, despite the high mortality rate from vehicle collisions which can remove up to 75 % of the annual litter produced by some pairs. The low density observed so far makes a population increase likely in the next few years, but the speed of recolonisation throughout the territory may slowed down by the high mortality rate that hinders post-reproductive dispersal.

Introduction

The expansion of the wolf in a large part of its historical range in the western Palearctic has been described in detail (Chapron et al., 2014; Boitani et al., 2022). During its territorial expansion, the wolf has confirmed a strong environmental and behavioral adaptability (Zlatanova et al., 2014), moving into highly anthropized and urbanised habitats where it had been absent for several centuries (Herzog, 2018; Boitani et al., 2022; Zanni et al., 2023; Meggiorini et al., 2024; De Feudis et al., 2025).

In the western Po Valley, the expansion and dispersal of the wolf from high density mountain areas towards lower density ones such as the underlying plain (Meriggi et al., 2020) is a consequence of the demographic increase of the neighbouring Apennine populations (Torretta et al., 2024). In moving from the Apennines to the plains, the species experienced a radical change in habitat, diet and social relationships; it also entered a habitat heavily populated by humans, pets, livestock with a dense network of roads, motorways, channels and urban areas (Meriggi et al., 2020; Torretta et al., 2024). Researchers now have solid evidence that, despite the huge differences between native and colonised ecosystems, wolves can adapt quickly to new habitats (Mech, 2017), in particular by changing their diet, adapting to the few semi-natural vegetation remnants and reconstituting social groups after the dispersal phase. (Jędrzejewski et al., 2004, 2008; Kojola et al., 2006; Nakamura et al., 2021).

The Province of Lodi is a small area in the Lombardy region, extending from the Po River to the outskirts of the Milan metropolitan area (Roy, 2002); the rivers Po to the south, Lambro to the west and Adda to the east mark its natural boundaries, while the territory gradually meets the urbanised metropolitan matrix to the north. Although the territory is densely populated and developed, it is an important dispersal corridor for the wolf, as it is in front of the Apennine valleys (Trebbia and Nure valleys), which host numerous reproductive packs of this predator (Meriggi et al., 2015; Torretta et al., 2024).

In the Province of Lodi, the wolf became locally extinct in 1765, as evidenced by the last recorded report of a rabid female that was killed in Orio Litta, after attacking about 16 people (Archives Ospedale Maggiore of Milan). This report, however, already exhibited the characteristics of an exceptional event and concerned an isolated and ill individual (Comincini, 1991). It is highly probable that the wolf, as a native species capable of stable reproduction, had become extinct at least a century earlier.

Since 2019, the wolf has been observed with an unusual frequency in the Lodi plain, where it has settled and reproduced since the first year of its presence, quickly establishing several packs and expanding rapidly northwards. Understanding the habitat and trophic characteristics that allowed the wolf to rapidly establish stable packs capable of feeding the species' expansion northwards is important in order to i) provide useful information to improve management of a large predator in densely populated areas, ii) understand how and whether lowland areas can support viable wolf populations, iii) understand if the ecological corridors in the Po Valley are able to guarantee the connectivity

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between the Apennine and Alpine wolf populations, in addition to those along the Ligurian Appennines

The aim of this study was to describe the dynamics of wolf expansion in the province of Lodi and to identify the environmental characteristics that allow the recolonization process. In particular, we analyzed the dynamics of the presence of the wolf in the municipalities of the province of Lodi (Lombardy) from 2019 to 2023 and we related the stable presence to the environmental characteristics. Our main hypothesis is that the wolf is favoured by the extension of the woods along the rivers and disadvantaged by the anthropization of the region.

Study area and methods

Study area and environmental variables

The study area (782 km^2) coincides with the province of Lodi located in southern Lombardy (Figure 1); it is the penultimate province in terms of surface area, but sixth out of 11 in terms of population density (293 inhabitants/km^2), which has been increasing rapidly over the last thirty years. The area is highly urbanized in the northern part bordering the metropolis of Milan while population density is lower in the southern part along the Po River. However, these areas are undergoing a rapid urban transformation due to the expansion of local industries and freight depots. The Po, Adda and Lambro rivers mark the southern, eastern and western borders. From a geological point of view, the area belongs to the Padana sedimentary basin and took its shape after the Wurm, when the fluvioglacial sedimentary phenomena stopped. At the end of the glacial period, the so-called fundamental level of the plain was created, which was gradually eroded by the rivers, creating fluvial valleys and terraces that can still be seen in the plain. The study area is characterized by a slight slope towards the south and a general morphological uniformity, except for the secondary water network, which extends for about 2300 km across the province. The environment of the Province of Lodi is characterised by large agricultural areas, mainly cereal crops, dominated by short rotation intensive crops (maize and related annual crops), which cover 74.3 % of the surface. Anthropised areas account for 13.1 %, including urban areas (6.2 %), industrial areas (4.7 %) and infrastructures (2.1 %); woodlands are a third important habitat variable (3.8 %). Other habitat variables, such as cultivated woodland and scrubland, together with roads and infrastructures, are each around 2 % of the total area, while water basins, oxbows and associated natural vegetation are less important and fall below 1 % (Table 1).

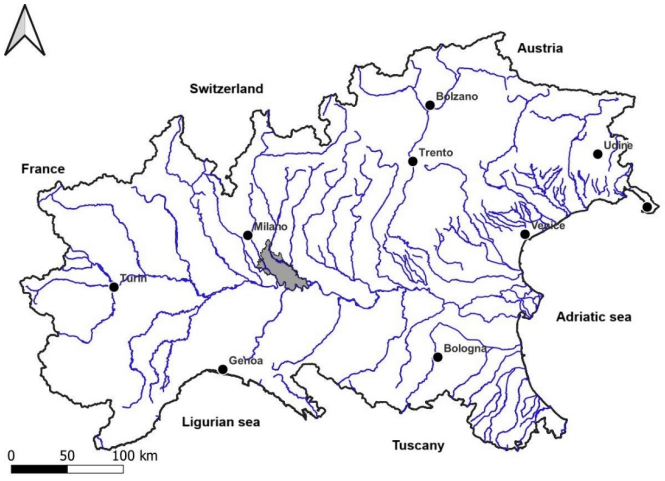

Figure 1 – Location of the province of Lodi in Northern Italy (in grey). The main towns and rivers are evidenced.

The climate is continental with hot, muggy summers (T max = 29.7 °C) and cold winters (mean T = –0.8 °C). Average precipitation amounts to 843 mm/year and is concentrated in spring and autumn.

The province of Lodi is an agricultural and husbandry area: in 2023 the livestock sector will consist of about 200,000 cattle, about 400,000 pigs and about 600,000 poultry (Coldiretti archives). This considerable supply of potential prey is essentially worthless to the wolf, since it is farmed under controlled conditions and in enclosed spaces. In recent years there has been a slight increase in the number of cattle reared outdoors, and a certain amount of prey is available during the temporary passage of sheep that settle in the lowlands during the winter. Wild ungulates such as roe deer *Capreoleus capreoleus*, fallow deer *Dama dama* and wild boar *Sus scropha* are found only in a few protected areas.

Table 1 – General habitat characteristics of the study area. Data are the total surface for the whole municipality of the Province of Lodi ($n = 61$).

Variable	total area (ha)	%	min	max
Cultivated land	61166.5	74.3	170.2	2567.4
Urban areas	5119.1	6.2	6.1	590.1
Woodland	3121.7	3.8	1.9	206.7
Reforestation, poplar groves	2939.0	3.6	0	437.8
Factories	2509.4	3.0	0.8	207.8
Farmhouse	1925.4	2.3	4.7	92.8
River and riparial habitat	1870.9	2.3	0	242.4
Shrubland	1642.4	2.0	1.2	136.5
Roads and highways	1268.3	1.5	0	156.0
Urban parks	338.3	0.4	0	63.2
Water basin	252.3	0.3	0	48.1
Natural habitat	133.3	0.2	0	25.4
Landfills and degraded areas	66.7	0.1	0	11.7

Data collection

We collected the informations about wolf presence either opportunistically or as a result of ad hoc research carried out in the province of Lodi, along the territorial borders or in municipalities that historically belonged to the province (e.g. hilly area of San Colombano al Lambro (MI).

We classified the observations according to the SCALP criteria (Molinari-Jobin et al., 2012; La Morgia et al., 2022). Category 1(C1) = certain evidence from observations of live or dead individuals, georeferenced photographs and videos, genetic records; Category 2 (C2) = observation confirmed by experts as scats, predation upon wild or domestic animal, spontaneous or induced howls, direct observations without supporting documentation; Category 3 (C3) = any other type of report or testimony or unconfirmed data (e.g. sightings not confirmed by an expert).

Since C3 observations must be considered with caution as they can include both false absence and wrong identification, all C3 reports were validated only if they refer to at least 3 data collected by at least 2 observers in the same area; moreover, all observations of tracks and footprints were excluded from analysis. This selection eliminated 29 observations not fully reliable and a total of 109 observations were confirmed between 2019 and 2024.

Then we classified the municipalities by the presence or absence of the wolf in each year and calculated the frequency of wolf sightings and the number of wolves for each observation. We also classified the municipalities as municipalities with wolf presence (at least one year of presence) and absence (absence in all years); furthermore, we classified the municipalities as having stable wolf presence ($\geq$ 3 years of occupancy) or sporadic presence (< 3 years of presence).

Habitat variables

We analysed a total of 28 environmental variables for the 63 municipality in the study area. We used the software QGIS v. 3.22.2 and the regional land use map (DUSAF https://www.geoportale.regione.lombardia.it/news/-asset_publisher/80SRILUddraK/content/dusaf-7.0-uso-e-copertura-del-suolo-2023) to calculate the environmental variables for each municipality.

Main variables were: urban areas including hamlets, farmhouse, urban surface, factories; infrastructures including highways and rail-

ways; agricultural environment including horticulture, garden, orchards, rice fields, meadows, and cereal crops; woodland areas including poplar groves, mixed natural woodland, riparian vegetation, and shrubland; natural habitat including the course of rivers, their beds along with the riverbeds, oxbows, water basins and channels; Protected Areas i.e. Nature Reserve and SCI. Environmental metrics of the study area are in Table 1 and Appendix A SD.

Data analysis

We tested for statistical differences of the 28 variables between municipalities with and without the species by the Student t-test; we carried out the analysis by pooling occupancy data from 2019 to 2024 and then considering the stable and sporadic presence of the wolf over the whole study period. To identify which variables influenced the wolf presence in the municipalities of the study area, we formulated two GLM models (family Binomial, function Logit) with the environmental variables as predictors, the first to forecast the simple presence of wolves with as dependent variable the presence in at least one year of the study period (1) and the absence throughout the period (0) and the second to predict the probability of stable wolf occurrence, with as dependent variable the stable presence (1) and absence or sporadic presence (0) in the municipalities. Variable selection was made by the stepwise forward procedure and the Akaike Information Criterion corrected for small samples (AICc, Akaike 1973; Anderson et al. 2000, 2001; Burnham and Anderson 2002) and the significance of coefficients was tested by the Wald statistic. We evaluated the model performance by the explained deviance (D^2; Yee and Mitchell 1991; Boyce et al. 2002; Zuur et al. 2007, 2009, 2010) and by the area under the Receiver Operating Characteristics (ROC) curve (AUC), which can assume values ranging from 0.50 (random prediction of the model) to 1.00 (perfect prediction of the model). Model discrimination ability was categorized as excellent for AUC > 0.90, good for 0.80 < AUC < 0.90, acceptable for 0.70 < AUC < 0.80, bad for 0.60 < AUC < 0.70 and null for 0.50 < AUC < 0.60 (Swets, 1988). Finally, we computed the Variance Inflation Factor (VIF) to test for variable collinearity, and the Q-Q plot to check for residual normality (Quinn and Keough, 2002; Zuur et al., 2010). We performed statistical analyses with the package R Commander (Fox et al., 2024).

Results

Temporal dynamics of recolonisation.

The colonization of Lodi province by wolves started in 2019 when we recorded the species presence in four municipalities covering in total 74.12 km^2. In the following years, the presence of the wolf spread, arriving in 2023 to progressively occupy 253.76 km^2 and 18 municipalities. In 2024, we recorded a slight contraction of the wolf range with 14 municipalities occupied for a total of 223.0 km^2 (Figure 2); at the end of the study period in 2024, wolves were recorded on 27.1 % of the total area of the study area.

From 2019 to the end of 2024, we collected in the province 109 reports of wolves, representing 183 observations (Appendix B SD). The data include direct observations of individuals (84.7 %) and predations (7.7 %), while vehicle collisions and signs of presence accounted for 6.0 % and 1.6 % respectively. Over the observation period, the average number of individuals per observation (± SE) was 1.7 ± 1.25 (1-9), ranging from a maximum of 2.3 ± 2.5 in 2019 to a minimum of 1.3 ± 0.6 in 2020, while the total number of individuals recorded reached a maximum of 57 and 62 in 2021 and 2023, respectively.

Reproductions of the species have been repeated over the years and breeding pairs and small packs have become permanently established in some of the first areas of settlement, all of which are located near protected areas and nature reserves along the river Adda. A first breeding was reported in 2019 along one of the natural channels near the river Adda, but it did not recur. No breeding was confirmed in 2020, but in 2021 a pair bred along the major course of Adda river. From 2022 onwards, at least 4 reproductions were yearly reported in four the municipalities (Figure 2); a possible reproduction was also reported

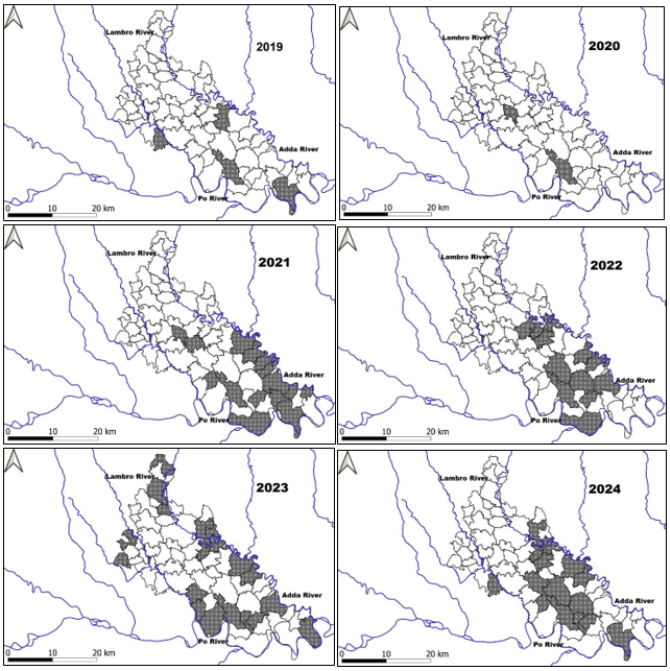

Figure 2 – Time scan of grey wolf *Canis lupus* colonization in the study area (2019-2024).

along the course of the river Adda north of Lodi, but it was not possible to verify it. Litters averaged 4.8 ± 2.1 pups and annual averages varied from a minimum of 3.7 ± 0.5 in 2022 to a maximum of 6.3 ± 2.5 the following year. The repetition of reproductive events favoured the constitution of at least three wolf packs in the territories of three municipalities, one of which was formed by as many as 9 individuals in 2022 and 8 in 2024. All packs remained together until late summer each year, and in some cases until late December, after which they diminished rapidly, probably following the dispersal of the young. In a single one case a young female remained in contact with the adult pair until breeding the following year.

In the case of the largest pack of wolves, mortality from vehicle collisions was high. Many pups died during the autumn-winter dispersal period: of a total of 63 observations of pups recorded between 2021 and 2024, 8 died from vehicle collisions before winter and 7 of these from the "Monticchie" Nature Reserve area, where the largest group of wolves is present. Here, mortality per cohort ranged from a low of 50 % in 2022-23 to a high of 75 % in 2024; in some areas, mortality from vehicle strikes may therefore wipe out the net productivity of local wolf populations.

Habitat features influencing recolonisation

Municipalities with the presence of wolves in at least one year of the study period were different from those in which the wolf was never present for seven environmental variables (Table 2). In particular, urban areas and meadows were more represented where the presence of the wolf has never been recorded, while arable land, poplar groves, bushland, watercourses and water basins had higher percentages in the municipalities where the wolf was present.

Table 2 – Mean percent values (SE) of the environmental variables with significant differences between municipalities of wolf presence ($N = 28$) and absence ones ($N = 35$) (Student t-test).

Variables	Presence	Absence	t	P
Poplars	3.5 (0.74)	1.5 (0.22)	2.87	0.006
Meadows	7.1 (1.35)	10.8 (1.31)	1.99	0.051
Scrubland	2.0 (0.27)	1.1 (0.16)	2.96	0.004
Watercourses	2.5 (0.49)	1.3 (0.24)	1.30	0.018

Between municipalities with stable occupancy by wolves and sporadic or absence ones, significant differences resulted only for deciduous woods, water basins, and nature reserves; all these variables had higher percentage values in the municipalities with a stable wolf presence (Table 3).

Table 3 – Mean percent values (SE) of the environmental variables with significant differences between municipalities of wolf stable and sporadic presence (Student t-test).

Variables	Stable presence	Sporadic presence	t	P
Arable lands	82.1 (1.72)	62.8 (1.39)	2.05	0.044
Poplars	3.8 (1.17)	2.0 (0.33)	2.08	0.042
Tree crops	1.5 (1.22)	0.1 (0.03)	2.16	0.035
Deciduous woods	2.2 (0.87)	0.9 (0.24)	2.20	0.032
Riparian woods	4.9 (2.05)	2.5 (0.22)	2.10	0.040
Wetlands	0.4 (0.18)	0.1 (0.03)	3.03	0.004
Nature reserve	3.8 (3.13)	0 (0)	2.34	0.023

Five environmental variables entered the model of wolf presence/absence of which four with significant effects (AICc = 64.63); meadows, urban areas, and roads showed negative effects on the probability of wolf presence and urban green areas positive (Table 4). Wetlands had also a positive but not significant effect. The explained deviance (D^2) of the model was 0.39 and the ROC curve showed a good model performance (AUC = 0.89; CL 95 % 0.80-0.96; Figure 3). The model correctly classified 82.5 % of the original cases (75.0 % of the presence and 88.6 % of the absence). No collinearity resulted among the selected variables.

Table 4 – Results of the GLM on the presence (1) and absence (0) of the wolf in the municipalities of the Lodi province.

Variables	Coefficients	SE	Wald	P	Exp(b)	VIF
Meadows	−0.2	0.07	6.52	0.011	0.83	1.4
Urban areas	−0.5	0.18	7.98	0.005	0.61	2.0
Urban green areas	2.7	1.17	5.14	0.023	15.17	3.2
Roads	−1.1	0.43	6.29	0.012	0.34	2.0
Wetlands	1.4	1.09	1.75	0.186	4.24	1.2
Intercept	3.4	1.11	9.09	0.003	29.01	

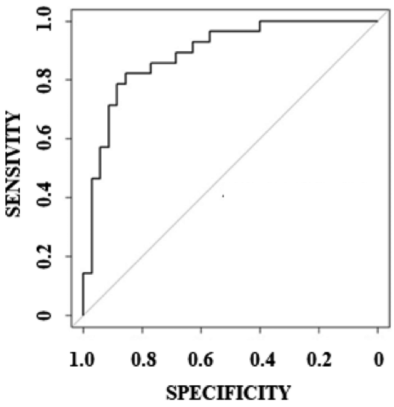

Figure 3 – Roc curve of the GLM for wolf presence/absence in the municipalities of the Lodi province (the grey line represents the curve of a model that classifies the cases randomly).

Six environmental variables entered the model of wolf stable presence in the municipalities of Lodi province (AICc = 48.24), of which five (Wetlands, Arable lands, Tree crops, Poplars, and Water basins) had positive and significant effects; Urban areas also had a positive but not significant effect (Table 5). The explained Deviance of the model was 0.949 and the ROC analysis showed an excellent discrimination ability of the model (AUC = 0.92; CL95 % = 0.82-0.99; P<0.0001) (Figure 4). The model correctly classified 92.1 % of the total cases (98.0 % of sporadic presence or absence and 71.4 % of regular presence). The variables that entered the model showed no collinearity.

Table 5 – Results of the GLM on the stable presence (1) and sporadic presence (0) of the wolf in the municipalities of the Lodi province.

Variables	Coefficients	SE	Wald	P	Exp(b)	VIF
Wetlands	5.7	1.99	8.34	0.004	2.97	1.2
Urban areas	0.2	0.13	2.91	0.088	1.25	2.0
Arable lands	0.3	0.12	7.63	0.006	1.41	3.2
Tree crops	2.7	1.00	7.36	0.007	1.54	2.0
Poplars	0.5	0.23	5.34	0.021	1.69	1.4
Water basins	1.5	0.65	4.90	0.027	4.34	1.4
Intercept	−30.5	10.84	7.87	0.005	>0.0001	

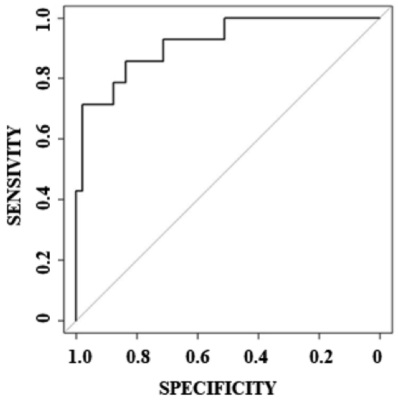

Figure 4 – Roc curve of the GLM for wolf stable presence in the municipalities of the Lodi province (the grey line represents the curve of a model that classifies the cases randomly).

The model predicted a probability of stable presence of the specie > 0.5 in 10 municipalities for a total of 160.22 km^2 and a probability > 0.7 in 6 municipalities (94.5 km^2). The municipalities with the highest probability of stable presence were located along the Po and Adda rivers and on the hills (Figure 5).

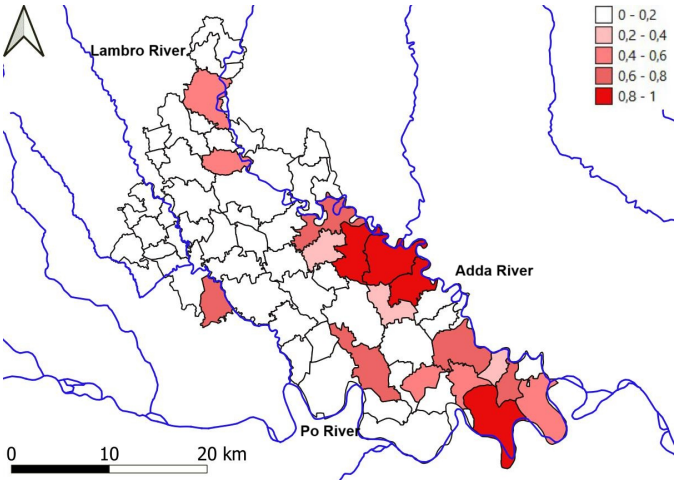

Figure 5 – Presence probability map.

Discussion

Wolf populations have been steadily and rapidly increasing over a large part of their distributional range for about 20 years (Mech, 2017) and during this time they have recovered most of the areas lost between the 18th and 20th centuries mainly due to persecution and competition

with humans (Chapron et al., 2014; Fardone et al., 2025). This first phase of the recolonisation process firstly concerned montane and peri-mountainous areas and then less elevated areas characterized by high wildness in northern Europe (i.e. Northern Poland; Jędrzejewski et al. 2004); in Italy this second phase of wolf population consolidation concerned the Ticino valley, one of the few Italian rivers that provides an ecological corridor between the Alps and the Po Valley (Dondina et al., 2020; Fardone et al., 2025). The expansion of the species is still in rapid progress and the wolf is effectively colonizing the Po Valley, one of the most densely populated areas in Europe.

This new phase of the wolf's expansion is quite different from previous ones, which had simple explanations linked to socio-cultural factors such as the positive effects of legal protection, the gradual abandonment of the Apennine mountains by man and the consequent increase in natural habitats and prey, and the constant reduction in the number of hunters and poachers in recent decades (Haller and Bender, 2018). The recolonization of the Po Valley, an area where the species became extinct at the end of the 18th century, but from which it had almost disappeared two centuries earlier, presents completely new characteristics, since it is the most densely populated area in Italy and one of the most densely populated in Europe (Livani et al., 2023). The Po Plain is an highly urbanised and infrastructurally developed area, which, at least at first sight, lacks the environmental characteristics suitable for this predator outside of parks and nature reserves. (Zimmermann et al., 2014; Bassi et al., 2015; Zanni et al., 2023; Fardone et al., 2025) Although the recolonisation of the entire European range of the wolf is still in progress, and although some parts of the historical range can only be recovered by reintroduction (e.g. Great Britain) it is clear that if the species were to colonise the Italian Po Valley, it would be able to reclaim the whole of Europe, with the exception of the more densely urban areas.

In the lower Lombardy plains, the first sighting of wondering wolves were from our study area, while in the plains of the neighbouring Emilia-Romagna region (province of Piacenza), the presence of wolves had already been reported since 2012. The diffusion of wolves in our study area do not seems a continuous and progressive phenomenon, but rather a sudden and relatively widespread one. All sighting in 2019 occurred in autumn, all including young individuals in the dispersal phase appearing in relatively distant territories. In the following year a decrease in reports and colonized territories was observed, despite the replication of reproduction in one of the first colonised municipality. Then, between 2021 and 2023, the species spread to all the municipality bordering the Po river to the south, Adda river to the east and hilly areas and the Lambro river along the western boundary of the province. This expansion, during which we recorded at least 4 new reproductions and recurring reproductions are confirmed in first-settlement areas, is followed by a new phase of slight contraction in 2024. The pattern here described seems to reflect a progressive "pulse" process of recolonisation, in which several young individuals settle, albeit for a limited period, in new municipalities, while adult reproducing pairs establish themselves in municipalities that, having been acquired in previous years, have proved more suitable to host adult pairs on a stable basis.

Population metrics

Although the results of our study are also based on opportunistic data collection, they seem to confirm what is known in the literature about wolf populations in Europe. It is therefore likely that some of the following generalizations are largely reliable and useful for understanding wolf population dynamics in densely populated areas. From 2021 to 2024, the average wolf density in the study area was 0.89 ind/km^2 (range = 0.73–1.09 ind/km^2), a lower value than that found in protected areas in Spain (1.7 ind/km^2; Nakamura et al. 2021, 2.9 ind/km^2; Blanco and Cortés 2007), Poland (1.2-1.9 ind/km^2; Myslajek et al., 2018)) and Italy (4.7 ind/km^2; Apollonio et al. 2004) and more like to densities found where the species is culled, such as in Belarus (0.9–1.5 ind/km^2; Okarma et al. 1998), Sweden (<0.01 ind/km^2 Finland and Sweden; Kojola et al., 2006, Dalerum et al., 2019). The litter and pack data also show some similarities with those collected in Europe. Our estimate of an average litter size of 4.8 cubs is compatible with data from Sidorovich et al. (2007), who reported average litter sizes of 4.8-7.7 in Belarus. The estimated size of our packs (8-9 individuals) is also compatible with data from Spain (6.2; Nakamura et al. 2021, 6.5; Barrientos 2000; 9.3 Fernández-Gil et al. 2013), Poland (4-5; Okarma et al. 1998), France (average=3.8, min=2, max=12; Duchamp et al. 2012), Italy (average 4.2, max = 7; Apollonio et al. 2004).

The overall comparison between our population metrics and those available on European populations seems to suggest that some post-reproductive parameters are rather similar, while population density data are more like culled wolf populations. These data suggest that our population is still below carrying capacity and in full demographic expansion, and that it may increase in numbers in the coming years.

Resident vs. dispersing wolves: differences in habitat features

The presence of the wolf is associated with a triad of variables (extent of poplar groves, water basins and scrubland) that define the riparian and floodplain environments in which the species can find shelters, while it is negatively affected by the area of meadows. As this variable is directly correlated with the area of wooded environments, water basins and protected areas, we believe that the figure reflects a wolf choice for natural areas not fragmented by crops such as meadows. Overall, the GLM model confirms the univariate comparison and describes an easily interpretable environmental context, where roads and urban areas, together with meadows, are unfavourable predictors for the wolf, while urban green areas contribute positively and significantly to the model. In the Lodi province, many towns and villages are crossed by rivers and canals which, close to settlements, often preserve green areas and forests that far from towns have been removed. We consider it likely that this variable, which is indeed positively correlated with urban areas ($r = 0.43$, $n = 63$, $p < 0.0001$), makes a positive contribution to the model by describing areas of limited anthropic disturbance in contexts of high population density.

The environmental characteristics that influence the stable *vs.* irregular presence of wolves in municipalities are slightly different. As reported in Table 3, the tree cover in wetlands, guaranteed by natural forests, but also by poplar groves and reforestation, is higher where the wolf has a regular and stable presence; however, the stability of wolf presence also seems to be positively influenced by extensive cropland. In our study area, the alternation between small protected areas and large areas of arable land is a dichotomous phenomenon ($r = 0.46$, $n = 63$, $p < 0.0001$): at the border of the first category, the second suddenly begins without transitional areas with gradually decreasing wildness. The wolf is likely to settle permanently in the small protected areas, even in the proximity of urban areas, where large open areas allow effective control of sources of danger or disturbance. The GLM model largely confirms what was found in the univariate comparison, attributing a positive influence to wetlands and water basins with high tree cover and extensive surrounding crops. Even urban areas, whose effect is not significant, seem to have a positive effect on the stable presence of the species, confirming what was discussed above. The contribution of wetlands and water basins to the model is important because the dynamics of wolf distribution in the study area is also influenced by the availability of food resources.

In Europe, wolf presence and abundance are correlated with the availability of wild ungulates, a trophic resource that is scarce in the study area. Where wild ungulates are scarce, livestock can become a trophic resource of considerable importance for the wolf (Meriggi and Lovari, 1996; Meriggi et al., 2011; Zlatanova et al., 2014). However, in the province of Lodi, as in the whole of the Po Valley, livestock is not left to graze in the open, but is bred and kept in stables, and is therefore not available to wolves. Based on preliminary faecal analyses, the main food resource of the wolf in our area is the coypu *Myocastor coypus* and, to a much lesser extent, the cottontail *Sylvilagus floridanus* (Torretta *com pers*; *M. coypus* = 98 % *S. floridanus* = 2.0 % $n = 28$). Coypus are common in the province of Lodi because of the dense water network and are widespread in wetlands and water basins: the contribu-

tion of these variables to the model may also indicates the presence of food resources, which are fundamental for the survival of the species. The hypothesis that the coypu is a key element in the successful expansion of the wolf in the southern provinces of the Lombardy Region is supported by its density in our study area, which is by far the highest in the region (about 131.9 ind/km^2; Balestrieri et al. 2016, recalculated).

We observed similarities and differences with literature data and recent analyses of the environmental suitability of the entire Po Valley (Dondina et al., 2020; De Feudis et al., 2025; Fardone et al., 2025). Our study confirms the importance of forest cover, even of small size, in providing the presence and stability of wolf packs, but contrary to what has been observed by other authors, in our case a stable presence of the wolf does not seem to be negatively conditioned by anthropogenic elements such as roads, motorways and railways. Good tolerance to human settlements has also been found in Tuscany, particularly in the areas recently colonized by wolves; this can be explained by the increase in the wolf population and the reduction of more natural areas not yet occupied where dispersing wolves can settle (Zanni et al., 2023). The environmental choices of local wolf populations, also due to the ecological plasticity of the species are highly variable, but in most published studies roads, urban areas and crops reduce the connectivity of populations by acting as important barriers to wolf dispersal (Jędrzejewski et al., 2004; Rodríguez-Freire and Crecente-Maseda, 2008; Dondina et al., 2020; De Feudis et al., 2025). In our case, despite the high incidence of mortality due to vehicle collisions, the expansion of the road network does not seem to affect the habitat choices when wolves stabilize their presence. If other environmental conditions are met, the wolf still settles near road networks, despite their negative influence on reproduction that curbs its spreading.

Conclusions

1. The colonisation of densely urbanised lowland areas is a case study for the wolf, which is once again threatened in several parts of Europe by the expected downgrading of its conservation status. In fact, the reconquest of densely urban areas may be the final stage in the recolonisation of the historic European range and the beginning of a possible new phase of coexistence between humans and a large carnivore.

2. The low densities found in the province of Lodi, which are closer to those of culled populations than those of protected ones, suggest that the population is below carrying capacity and that the expansion of the species in the lowlands is well underway and may increase in the coming years.

3. The presence of wolves is mainly influenced by the extent of natural or artificial forest formations, while the stability of a population is also favoured by wetlands, abandoned reservoirs and the presence of green areas close to inhabited ones; residual protected areas consisting of wetlands and forests where it is easier to find refuge, favour its settlement even close to human settlements. Moreover, wetlands and water basins also support abundant populations of coypu, a species that, according to preliminary analyses, constitutes almost the entire diet of the wolf in our study area

4. Contrary to other reports, the wolf does not appear to be negatively affected by the presence of a dense network of motorways, roads and railways, even thought mortality of young wolves can reach up to 75 % of annual productivity. Mortality from vehicle strikes is increasing and may be linked to the use of rodenticides in agriculture: indeed, recent research shows that almost all wolves hit by vehicles tested positive for warfarin and other anticoagulants (Musto et al., 2024).

5. On the basis of the data collected, we believe that the species will continue to expand in the Province of Lodi until it reaches the Milan area, which is now close to the northernmost urban areas reached by the wolf. The metropolitan belt surrounding Milan and its motorway network can be considered as a dispersal sink preventing the species from rapidly reaching the Alps by reconnecting with the existing populations.

6. In the absence of culling and with relatively low levels of social conflict, the recovery of the Lodi Plain is currently dependent on mortality from vehicle collisions. As juvenile mortality by collisions appears to be high in areas with a stable presence of the wolf, mitigating this impact through the creation of culverts and protected passages could represent a limited, economically sustainable approach that would guarantee population productivity, promote juvenile dispersal and ultimately the conservation of new wolf populations in the lowlands of Europe.

References

Akaike, H. 1973 Information Theory and an Extension of the Maximum Likelihood Principle. In: Petrov, B.N. and Csaki, F., Eds., International Symposium on Information Theory, 267-281.

Anderson, D.R., Burnham, K.P. and Thompson, W. 2000. Null Hypothesis Testing: Problems, Prevalence, and an Alternative. Journal of Wildlife Management. 64. 912-923. 10.2307/3803199.

Anderson, D.R., Link WA, Johnson DH, Burnham KP. 2001. Suggestion for presenting the results of data analyses. Journal of Wildlife Management 65:373–378.

Apollonio, M., Mattioli, L., Scandura, M. Mauri, L., Gazzola, A. and Avanzinelli, E. 2004. Wolves in the Casentinesi Forests: insights for wolf conservation in Italy from a protected area with a rich wild prey community. Biological Conservation 120: 249-260. https://doi.org/doi10.1016/j.biocon.2004.02.021.

Balestrieri, A., Zenato, M., Fontana, E., Vezza, P., Caronni, F.E. and Prigioni, C. 2016. An indirect method for assessing the abundance of introduced pest Myocastor coypus (Rodentia) in agricoltural landscapes. Journal of Zoology 298:37-45.

Barrientos, L.M. 2000.Tamaño y composición de diferentes grupos de lobos en Castilla y León. Galemys, 12:249-256.

Bassi, E.; Willis, S.G.; Passilongo, D.; Mattioli, L.; Apollonio, M. 2015. Predicting the Spatial Distribution of Wolf *Canis lupus* Breeding Areas in a Mountainous Region of Central Italy. PLoS ONE 10. e0124698.

Blanco, J.C. and Cortés, Y. 2007. Dispersal patterns, social structure and mortality of wolves living in agricultural habitats in Spain. J. Zool. 273:114-124. 10.1111/j.1469-7998.2007.00305.x

Boitani L., P. Kaczensky, F. Alvares, H. Andrén, V. Balys, J.C. Blanco, G. Chapron, S. Chiriac, D. Cirovic, N. Drouet-Houguet, C. Groff, D. Huber, Y. Iliopoulos, O. Ionescu, I. Kojola, M. Krofel, M. Kutal, J. Linnell, A. Majic, P. Mannil, F. Marucco, D. Melovski, D. Mengüllüoğlu, J. Mergeay, S. Nowak, J. Ozolins, A., Perovic, G. Rauer, I. Reinhardt, R. Rigg, V. Salvatori, B. Sanaja, L. Schley, M. Shkvyria, P. Sunde, K., Tirronen, A. Trajce, I. Trbojevic, A. Trouwborst, M. von Arx, M. Wolfl, D. Zlatanova and L. Patkó. 2022. Assessment of the conservation status of the Wolf *Canis lupus* in Europe. Council of Europe Publishing: Strasbourg, France.

Boyce, M.S., Vernier, P.R., Nielsen, S.E, Schmiegelow. K.A. 2002. Evaluating resource selection functions. Ecological Modelling 157: 281-300. https://doi.org/l0.1016/S0304-38000200200-4.

Burnham, K.P., Anderson, D.R., 2002. Model Selection and Multimodel Inference: A Practical Information-Theoretic Approach, 2nd ed. Springer-Verlag, New York, USA.

Chapron, G., Kaczensky, P., Linnell, J.D., Von Arx, M., Huber, D., Andr´en, H., Boitani, L., 2014. Recovery of large carnivores in Europe's modern human-dominated landscapes. Science 346 (6216), 1517–1519. https://doi.org/l0.1126/science.1257553.

Comincini, M. 1991. La bestia feroce. Quando I lupi mangiavano i bambini nell'Italia padana. Diakronia Ed. Milano. Pp 190.

Dalerum, F., Liam O. K.,. Selby C., Pirk W. W. 2020. Relationships Between Livestock Damages and Large Carnivore Densities in Sweden. Front. Ecol. Evol. 7. https://doi.org/doi10.3389/fevo.2019.00507.

De Feudis, C. Torretta, E., Orioli, V., Tirozzi, O., Bani, L. Meriggi, A. and Dondina, O. 2025. Dispersal and settlement dynamics of wolves in a lowland ecological corridor in northern Italy: Effects of resource availability and human disturbance. Biological Conservation. 302. 110936. https://doi.org/doi10.1016/j.biocon.2024.110936.

Dondina O, Orioli V, Torretta E, Merli F, Bani L, Meriggi A 2020 Combining ensemble models and connectivity analyses to predict wolf expected dispersal routes through a lowland corridor. PLoS ONE 152: e0229261. https://doi.org/doi10.1371/journal.pone.0229261.

Duchamp, C., Boyer, J., Briaudet, P. E., Leonard, Y., Moris, P., Bataille, A., and Marboutin, E. 2012. A dual frame survey to assess time-and space-related changes of the colonizing wolf population in France. Hystrix-Italian Journal of Mammalogy, 23: 14-28.

DUSAF https://www.geoportale.regione.lombardia.it/news/-asset_publisher/80SRlLUddraK/content/dusaf-7.0-uso-e-copertura-del-suolo-2023. (Accessed December 10, 2024).

Fardone, L., Forlani, M. Canova, L., De Luca, M. and Meriggi, A. 2025. Can the wolf *Canis lupus* thrive in highly anthropized lowlands? First habitat suitability analysis of the Po Plain, Italy. Animals 15, no. 4 (2025): 546.

Fernández-Gil, F. Álvares, C. Vilá, A. Ordiz, ,N. 2013. Los Lobos de la Península Ibérica Propuestas para el diagnóstico de sus poblaciones. ASCEL, Palencia, Spain.

Fox, J., Marquez M.M. and Bouchet-Valat, M. 2024. Rcmdr: R Commander. R package version 2.9-5, https://github.com/RCmdr-Project/rcmdr.

Haller, A. and Bender, O. 2018. Among rewilding mountains: grassland conservation and abandoned settlements in the Northern Apennines. Landscape Research. 43. 1068–1084. 10.1080/01426397.2018.1495183.

Herzog, S. 2018. Return of grey wolf *Canis lupus* to Central Europe: challenges and recommendations for future management in cultural landscapes. Annals of Forest Research. 61. 203-209. 10.15287/afr.2018.1190.

Jèdrzejewski, W; Niedzialkowska, M; Nowak, S; and Jèdrzejewska, B. 2004. Habitat variables associated with wolf *Canis lupus* distribution and abundance in northern Poland. Diversity and Distribution 10: 225-233. http://dx.doi.org/doi10.1111/j.1366-9516.2004.00073.x.

Jędrzejewski, W., Jędrzejewska, B., Zawadzka, B., Borowik, T., Nowak, S., and Mysłajek, R.W. 2008. Habitat suitability model for Polish wolves based on long-term national census. Animal Conservation, 115: 377-390.

Kojola, I; Aspi, J; Hakala, A; Heikkinen, S; Ilmoni, C., and Ronkainen, S. 2006. Dispersal in an expanding wolf population in Finland. Biological Conservation 87: 281-286. http://dx.doi.org/doi10.1016/j.biocon.2021.109075.

La Morgia, V., Marucco, F., Aragno, P., Salvatori, V., Gervasi, V., De Angelis, D., Fabbri, E., Caniglia, R., Velli, E., Avanzinelli, E., Boiani, M.V., Genovesi, P., 2022. Stima della distribuzione e consistenza del lupo a scala nazionale 2020/2021. Relazione tecnica realizzata nell'ambito della convenzione ISPRA-Ministero della Transizione Ecologica "Attivita ' di monitoraggio nazionale nell'ambito del Piano di Azione del lupo".

Livani, M. Petracchini, L., Benetatos, C., Marzano, F., Billi, A., Carminati, A., Doglioni, C., Petricca, P., Maffucci, R., Codegone, G., Rocca, V., Verga, F. and Antoncecchi, I. 2023. Subsurface geological and geophysical data from the Po Plain and the northern Adriatic Sea north Italy. Earth System Science Data 15:4261–4293. https://doi.org/doi10.5194/essd-15-4261-2023

Mech, L.D. 2017. Where can wolves live and how can we live with thew? Biological Conservation, 210:310-317

Meggiorini D., Frignani E., Giachello S., Cevenini D., Avanzi G., Balasini L., Bonatti M., Castagna A., Cecere F., D'Ambrosio G., Fratta D., Lupi G., Maffezzoli L., Pavesi A., Rossetti L. and Salandini C. 2024. The return of the wolf *Canis lupus* in the central Po Plain, preliminary investigation on the ecology of the species in the province of Mantua. 10.13140/RG.2.2.25954.34248.

Meriggi, A., Lovari, S. 1996. A review of wolf predation in Southern Europe - Does the wolf prefer wild prey to livestock?. Journ. Appl. Ecol. 336:1561-1571 [10.2307/2404794]

Meriggi, A., Brangi, A., Schenone, L., Signorelli, D. and Milanesi, P. 2011. Changes of wolf *Canis lupus* diet in Italy in relation to the increase of wild ungulate abundance. Ethology Ecology and Evolution – Ethol. Ecol. Evol. 23: 195-210. 10.1080/03949370.2011.577814.

Meriggi, A., Dagradi, D., Dondina, O., Perversi, M. Milanesi, P., Lombardini, M. and Repossi, A. 2015. Short-term response of wolf feeding habits to changes of wild and domestic ungulate abundance in Northern Italy. Ecology Ethology and Eviolution, 27: 389-411.

Meriggi, A., Torretta, E. and Dondina, O. 2020. Recent Changes in Wolf Habitat Occupancy and Feeding Habits in Italy: Implications for Conservation and Reducing Conflict with Humans. In Problematic Wildlife II; Angelici, F.M. and Rossi, L., Eds.; Springer International Publishing: Cham, Switzerland, pp. 111–138.

Molinari-Jobin, A., Kéry, M., Marboutin, E., Molinari, P., Koren, I., Fuxjager, C., Breitenmoser, U., 2012. Monitoring in the presence of species misidentification: the case of the Eurasian lynx in the Alps. Anim. Conserv. 15:266–273. https://doi.org/doi10.1111/j.1469-1795.2011.00511.x.

Myslajek, R.W., Tracz, M., Tomczak, P., Szewczyk, M. Niedzwiecka, N. and Nowak, S. 2018. Spatial organization in wolves *Canis lupus* recolonizing north-west Poland. Large territories at low population density. Mammalian Biology 92: 37-44

Musto, C. Cerri, J. Capizzi, D. Fontana MC. Rubini S. Merialdi G. Berzi G. Ciuti F. Santi A. Rossi A. Barsi F. Gelmini L. Fiorentini L. Pupillo G. Torreggiani C. Bianchi A. Gazzola A. Prati P. Sala G. Apollonio M. Delogu M. Biancardi A. Uboldi L Moretti A. and Garbarino, C. 2024. First evidence of widespread positivity to anticoagulant rodenticides in grey wolves *Canis lupus*. Science of the Total Environment 915: 1-11.

Nakamura, M; Rio-Maior, H; Godinho, R; Petrucci-Fonseca, F; Alvares, F. 2021. Source-sink dynamics promote wolf persistence in human-modified landscapes: Insights from long-term monitoring. Biological Conservation 256. http://dx.doi.org/doi10.1644/05-MAMM-A-061R2.1.

Okarma, H., Jędrzejewski, W., Schmidt, K., Śnieżko, S., Bunevich, A. and Jędrzejewska, B. 1998. Home Ranges of Wolves in Białowieża Primeval Forest, Poland, Compared with Other Eurasian Populations, Journal of Mammalogy 79:842–852. https://doi.org/doi10.2307/1383092.

Quinn, G.P. and Keough, K.J. 2002 Experimental Design and Data Analysis for Biologists. Cambridge University Press, London.https://doi.org/doi10.1017/CBO9780511806384.

Rodríguez-Freire, M. and Crecente-Maseda, R. 2008. Directional Connectivity of Wolf *Canis lupus* Populations in Northwest Spain and Anthropogenic Effects on Dispersal Patterns. Environ Model Assess 13:35–51. https://doi.org/doi10.1007/s10666-006-9078-y.

Roy, P.D. 2002. The Regions of Italy: A Reference Guide to History and Culture. Pp: 465. Bloomsbury Academic, ISBN 0313307334, 9780313307331

Sidorovich, VE., Stolyarov, VP., Vorobei, NN., Ivanova, N.V., and Jędrzejewska, B. 2007. Litter size, sex ratio, and age structure of gray wolves, *Canis lupus*, in relation to population fluctuations in northern Belarus. Canadian Journal of Zoology. https://doi.org/doi10.1139/Z07-001.

Swets, J.A. 1988. Measuring the accuracy of diagnostic systems. Science 240:1285-1293. doi: 10.1126/science.3287615. PMID: 3287615.

Torretta, E., Brangi, A., and Meriggi, A. 2024. Changes in Wolf Occupancy and Feeding Habits in the Northern Apennines: Results of Long-Term Predator–Prey Monitoring. Animals, 14: 735

Yee, T.W. and Mitchell, N.D. 1991. Generalized additive models in plant ecology. Journal of Vegetation Science https://doi.org/doi10.2307/3236170.

Zanni, M.; Brogi, R.; Merli, E.; Apollonio, M. 2023. The wolf and the city: insights on wolves' conservation in the anthropocene. Anim. Cons. 26: 766-780.

Zimmermann, B.; Nelson, L.; Wabakken, P.; Sand, H.; Liberg, O. 2014. Behavioral responses of wolves to roads: Scale-dependent ambivalence. Behav. Ecol. 2014:1353–1364.

Zlatanova, D., Atidzhe, A. Albena, V. and Genov, P. 2014. Adaptive Diet Strategy of the Wolf *Canis lupus* L. in Europe: a Review. Acta Zoologica Bulgarica. 66. 439-452.

Zuur, A., Ieno, E., and Smith, G. 2007. Analysing Ecological Data. 10.1007/978-0-387-45972-1.

Zuur, A., Ieno, E., Walker, N., Saveliev, A. and Smith, G. 2009. Mixed Effect Models and Extensions in Ecology With R. 10.1007/978-0-387-87458-6.

Zuur, A., Ieno, E., and Elphick, C. 2010. A protocol for data exploration to avoid common statistical problems. Methods Ecol Evol 1: 3-14. Methods in Ecology and Evolution. 1. 3 - 14. 10.1111/j.2041-210X.2009.00001.x.

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Supplemental information

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

Supplementary Data (SD) Appendix A.
Supplementary Data (SD) Appendix B.