Tracking the hidden niches: Movement-based insights into northern lapwing intraspecific variation and conservation

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ABSTRACT

Global monitoring data reveal farmland bird population declines, primarily driven by agricultural intensification, chemical inputs, and climate shifts. The northern lapwing (*Vanellus vanellus*) is a farmland bird that exemplifies this decline across Europe. The aim of this study is to quantify intraspecific variation in habitat selection and evaluate the degree of behavioural variance in resource use among individuals and assess its conservation implications. We tested for: (1) inter-individual differences in resource use; (2) repeatability of habitat preferences; and (3) niche components driving selection patterns. Using Movebank GPS data from 13 individuals (2021-2023) across Europe, we applied step selection functions (SSFs) incorporating biotic and abiotic covariates. Repeatability estimates were derived from mixed-effects models to quantify consistent individual-level selection across resource gradients. We also estimated variation of habitat selection across seasons as well as within- and between-individual variation. Movement data showed high individual heterogeneity in several niche axes (notably glyphosate exposure and human population density), while some axes such as soil nitrogen were relatively homogeneous. Step selection functions indicated that soil water index and the earthworm abundance factor influenced movement, but no single environmental variable explained movement patterns consistently across all individuals. Lapwings tended to move more under certain moon conditions and selected pulses, flowers, vegetables and sugar beet with additional seasonal shifts in preferences. Repeatability analyses suggested that individual consistency in crop selection was generally low, with the highest repeatability for pulses, vegetables, flowers (R=0.31) and much lower or negligible for most other crops. Conservation strategies should focus on maintaining low-intensity farmland and grasslands, particularly in remote areas. Predator control through culling is ineffective due to rapid recolonization; instead, managing nesting habitats and removing predator perching structures in highly used nesting sites is recommended. Establishing dedicated nesting areas (lapwing plots) can further support the species survival.

Keywords

wader, spatial personality, multifunctional landscape, individualised niches, NDVI, tillage, mowing

Introduction

Farmland birds are avian species that breed and forage in, or close to, agricultural landscapes. Adapted to open habitats, they likely benefited historically from the expansion and intensification of agriculture. They contribute to a range of ecosystem services, including seed dispersal, biological pest control, nutrient cycling, maintenance of habitat quality, and cultural services such as recreation. Farmland bird populations are also widely used as indicators of broader biodiversity in agricultural landscapes (Kirk et al., 2020).

Multiple long-term monitoring schemes have shown that most farmland bird species undergo significant population declines. Declines of farmland birds have been documented in all continents and in different ecological contexts and scales (from regional to global). Country-level declines have been reported e.g. for Germany (Kamp et al., 2021), Denmark (Heldbjerg et al., 2018) and Spain (Traba & Morales, 2019). Meanwhile, BirdLife Australia reported a 56% decline in farmland bird populations since 1970. Similarly, the abundance of farmland birds in North America has declined by 74% from 1966 to 2013 (Stanton et al., 2018). The 2024 report of the PanEuropean Common Bird Monitoring Scheme found a decline of 60% of the Farmland Bird Index since 1980. The main causes of the decrease of farmland birds have been identified as the intensification and modernization of agricultural activities (Reif et al., 2024; Rosin et al., 2016, 2020), the application of pesticides (Fuentes et al., 2023), illegal capture and hunting, urbanization (Tscharntke & Batáry, 2023) and climate change. The European Union, in an attempt to mitigate farmland bird declines, introduced the agri-environment schemes (AES) as a measure to increase biodiversity in agricultural landscapes within the Common Agricultural Policy (Sharps et al., 2023).

Natural communities of plants and animals in human-modified landscapes have been shaped by both agricultural activities and climate shifts (Ellis et al., 2021). European agricultural landscapes have changed significantly in the past decades. Biodiversity has declined and landscape structure has become more homogeneous (European Commission, 2021; European Environment Agency, 2025; Harpke et al., 2025; Jeanneret et al., 2021; PECBMS, 2024; van Swaay et al., 2025). The last Common Agricultural Policies (CAP) have introduced the concepts of agro-ecosystems, agri-environment schemes and multifunctional landscapes (Lefebvre et al., 2015; Taylor & Van Grieken, 2015), which represent practical measures for the promotion of species diversity in agricultural landscapes.

The northern lapwing (*Vanellus vanellus*) is a medium sized bird that feeds and breeds in open agricultural habitats, such as lowland wet meadows, marshes and wet grasslands and open habitats with low vegetation and high-water content. Although it is highly popular among the public (NABU, 2024; Sheldon et al., 2004a), it is facing severe declines in Europe (PECBMS, 2024). The monitoring scheme of common birds has found a 62% decline of northern lapwings across Europe (PECBMS, 2024). The species is characterized as Near Threatened (NT) by the IUCN and it is included in the Annex 2 of the Birds Directive, Annex III of the Berne Convention, and Annex II of the Bonn Convention. At a national scale, though, its conservation status varies. For example, in Germany it is under the Federal Species Conservation Regulation (BArtSchV), while in France and Greece, despite being protected by EU law, northern lapwing hunting is permitted (Souchay & Schaub, 2016).

Recent technological advancements in individual tracking devices led to the generation of large datasets of very high spatiotemporal resolution. The combination of ecological niche theory with technologically advanced individual-level observations represents a new frontier in conservation biology and aligns with recent calls for more broad integration across organizational and spatial scales (Jeltsch et al., 2025). The ecological niche of a population can be decomposed to a between-individual and within-individual components (Roughgarden, 1972). Both components are instrumental for the conservation of a species. For instance, tracking data allow the exploration of individual specialization in space use, also known as spatial personalities (Stuber et al., 2022) which in turn leads to individual differences in resource use, also known as individualized niches (Takola & Schielzeth, 2022). The methodologies that are used to collect movement data can be either through GPS tracking devices or through satellites or camera tracking or telemetry. These data are then usually made available through platforms and web-based interactive maps.

The aim of this paper is to quantitatively estimate intraspecific niche variation in northern lapwing in order to inform the conservation of the species. The research questions of our study were: i) Do individuals differ consistently in their resource use patterns? ii) What is the magnitude of the between-individual variation? iii) What are the conservation implications of intraspecific variation in resource use? To address these research questions, we analysed the individual resource use by combining biotic (e.g. earthworms, human presence) and abiotic (e.g. weather, soil and vegetation) drivers. We used step selection functions to quantify how the aforementioned variables affect movement behaviour of each individual, offering a mechanistic understanding of resource use and niche specialisation at the individual level. Subsequently, we used the results of the step selection functions to inform the exploration of consistent behavioural differences through repeatability models. Mechanistic approaches of intraspecific variation can shed light into community dynamics and interspecific interactions (Moran et al., 2022).

Methods

Study area and tracking data

We analysed all northern lapwing movement data that are publicly available for Europe through the Movebank database (dataset ID: 1448409403, curator: Jelle Loonstra). The data covered an area across the Netherlands, Belgium, France, and Spain (Fig. 1) and the tracking period extended from April 2021 to March 2023. The temporal resolution ranged from 0.08 minutes to

5.6 hours. In order to standardize sampling effort across all individuals, we filtered the points with a sampling rate of 180 minutes, considering ±30 seconds of tolerance. The final dataset contained a total of 14,701 data points from 13 individuals, since one was excluded after resampling. The number of observations per individual ranged from 18 to 1,139 steps.

For each recorded position (hereafter used step), we generated a set of 10 random alternative available positions (hereafter available steps) that the individual could possibly move towards (Fig. S1). Each available random point was at most 10 km away from the used one, as a step length of over 10 km was deemed unrealistic. In the case where the birds appeared to remain in the same location for multiple time intervals (inactive or sleeping), the generation of random steps was not possible, thus, we added jitter (0,001 m) to each repeated point. We removed all points (used or available) that were over the sea and England.

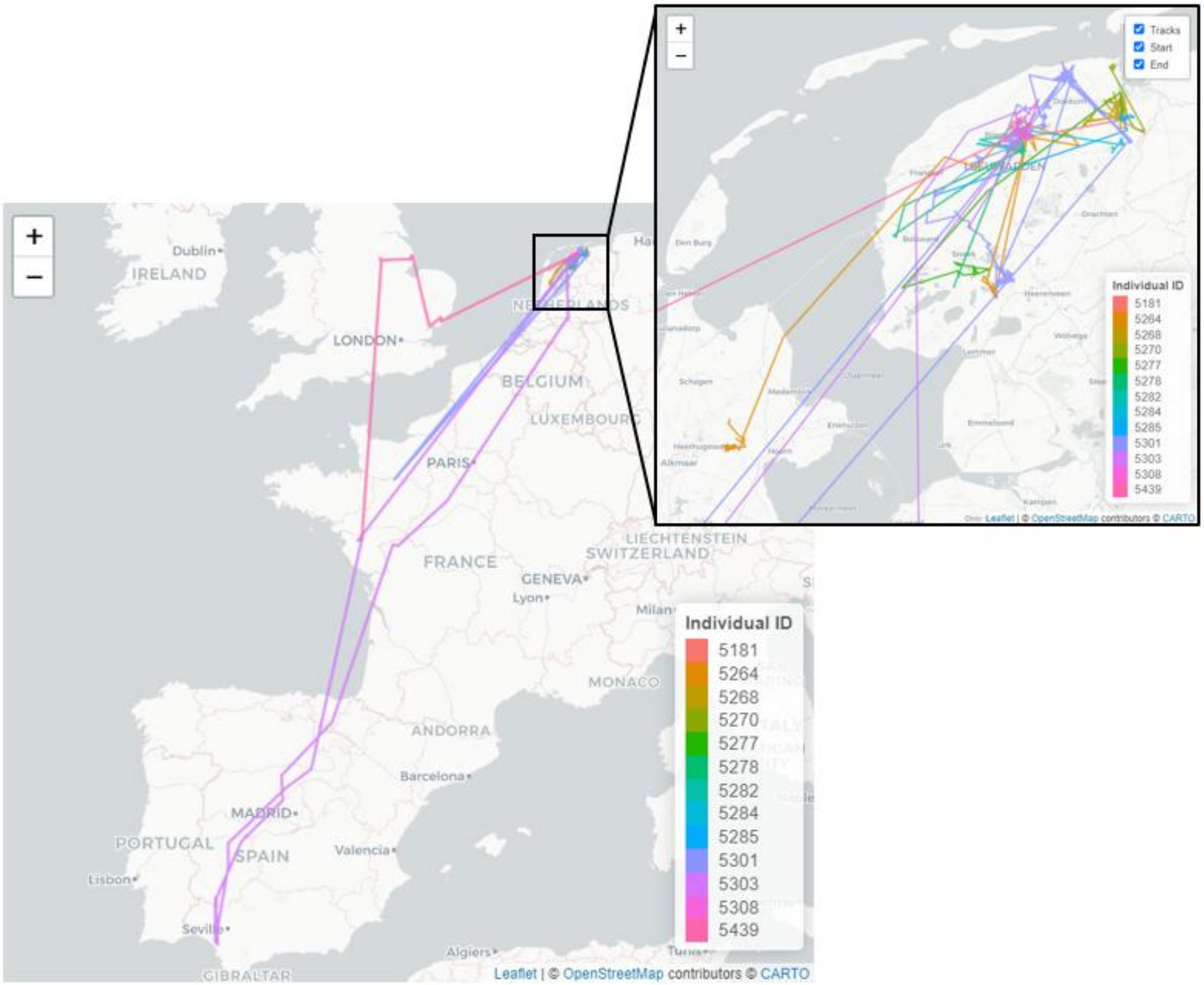

Figure 1. Extend of the study area and GPS recorded positions of all individuals. An interactive version of this plot is provided in the Supplementary files.

Environmental data cube compilation

We compiled a set of environmental variables hypothesized to influence the movement patterns of northern lapwings and to characterize the ecological niche of the species. These variables included abiotic factors (air temperature at 2 meters above the ground, precipitation, wind speed, distance and phase of the moon, Normalized Difference Vegetation Index, crop type), soil factors (soil bulk density, soil water index, soil organic carbon, soil organic carbon stock, soil nitrogen), biotic factors (human population density, human footprint, and earthworm abundance and richness) and landscape management information (cropping intensity, pesticide application rates) (Table S1). For each environmental variable, we used the most recent data available, ensuring that temporal alignment was maintained as closely as possible. In cases where exact temporal matching was not possible, we incorporated environmental data from the closest year, under the assumption that these variables had not changed significantly over time.

Abiotic factors

We extracted ERA5-Land wind data and aligned daily temperature and precipitation values to each used and available observation using the associated timestamp for the corresponding hour of the day. We obtained crop type data from the EU Crop Maps for 2018 and 2022, using the 2018 data to fill in gaps on the 2022 map, particularly in the northern part of the study area. We removed all crops that appeared 30 times or less in the dataset.

We modelled night-time activity using the distance and phase of the moon for each used and available position, calculated with the lunar R package (Lazaridis, 2022), considering the respective timestamp of each observation. NDVI data were extracted for each used and available location from the MODIS Terra Vegetation Indices (250 m resolution) dataset corresponding to the closest available date.

Soil factors

Soil carbon, carbon stock, bulk density and nitrogen content data were extracted for each used and available location from the SoilGrids dataset (Poggio et al., 2021).

Biotic factors (human population density, human footprint, and earthworm abundance and richness)

We used human population density data from Eurostat for NUTS3 regions (Eurostat, 2025) along with the Global Terrestrial Human Footprint dataset (Mu et al., 2022), which relies on more permanent and rigid factors, such as infrastructure, and night-time lights, which remain relatively stable over time. The earthworm abundance and richness factors (Orgiazzi & Panagos, 2018)~~,~~ were derived from a study on earthworm richness and abundance (Rutgers et al., 2016) and are available upon request from the European Soil Data Centre. Due to the calculation method of the earthworm factor, negative values indicate high earthworm abundance or richness.

Landscape management data (cropping intensity, pesticide application rates)

Cropping intensity was extracted from a fine resolution global dataset (Zhang et al., 2021), while pesticide application rates were extracted from a European database (Porta et al., 2025). We assumed that cropping cycles remain stable over short time periods, thus we used the GCI30 map from 2020 on the data of 2023. Similarly, we assumed that pesticide application rates remained stable between 2018 and 2021.

Data analysis

To address collinearity among the predictor variables, we calculated correlations for every pair of variables and an auxiliary regression with the numerical variables to estimate the Variance Inflation Factor (VIF) for every variable separately (Fig. S2, Table S3). We then built a model for each predictor group (food, weather, soil, humans) to examine intraspecific variation using step selection functions. Inter-individual variation in use patterns of vegetation types was examined with the aid of repeatability models. All analyses were performed in R and all variables were scaled to a mean of 0 and standard deviation of 1.

Individual variation in niche axes

To explore the intraspecific variation among the birds in our sample, we adopted the following workflow. First, we used individual resource utilisation curves (visualised as ridgeline plots and heatmaps) to visually examine within- and between-individual variation for each variable. We then implemented a step-selection function for each individual with the amt R package (Signer, 2018) to estimate the importance of each variable. We fitted the step selection functions with a binary response variable (used vs available), step ID as a random effect and environmental variables, turning angle and step length as fixed effects. One individual (ID: 5284) was excluded from the individual-based SSFs due to insufficient data, but included in all other analyses. Individuals 5308 and 5270 were excluded for the same reason from the weather models of individual-based SSFs. In the case of crop type selection, where the individual-level subsets did not have enough data for individual-level SSDs, we fitted an SSF for all individuals, using *Grassland* as the reference level (because it was the most commonly used crop type) and an interaction between crop type and temperature. We fitted this step selection function with a binary response variable, individual-level effects for temperature, while crop types, turning angle and step length were used as fixed effects. Based on the results of the SSF on crop types, we identified the crop types that have a significant effect on the movement of northern lapwings and subsequently estimated the magnitude of individual differences on crop type selection through the repeatability of usage for each (Stoffel et al., 2017).

To analyse the temporal variation in activity, we used two approaches: nocturnal activity (since some birds tend to be active also at night) and seasonal variation in resource use. The nocturnal activity of northern lapwings was modelled using only the used locations (i.e. the original points of the GPS tags). The response variable in the night models was step length, transformed as *log*(step length + 1). First, we fitted a linear mixed-effects model to test whether nocturnal step length varied with moon distance, including moon distance and moon phase as fixed effects and allowing both the intercept and the slope of moon distance to vary among individuals. To visualise between-individual heterogeneity, we generated individual-specific predicted relationships between moon distance and *log*(step length + 1) (with moon phase held constant at new moon) and contrasted these with the population-level prediction based on fixed effects only. Second, we assessed whether individuals differed in their responses across moon phases by fitting a mixed model with moon phase as a fixed effect and individual-specific random effects for each phase (0+moon_phase|id), while holding moon distance constant at its centred mean (moon_dist = 0) for prediction. We also used step selection functions to explore the crop type selection during night time. Seasonal variability in the drivers of northern lapwing movements was examined by fitting step selection functions for all individuals (due to inadequate size of individual-level subsets), but with random slopes in order to allow for different responses.

Repeatability of resource selection

Repeatability is defined as the proportion of population-level variance that can be attributed to the between-individual differences. Repeatability is an indicator of different phenotypes (or personalities) within a population. A repeatability of 0 indicates that a trait is not consistent across observations, whereas a repeatability of 1 indicates that an individual trait remains consistent across measurements. In the context of habitat selection, high repeatability indicates that the individuals' habitat preferences are consistent over time and across contexts (indicating spatial 'personalities') and low repeatability means that individual preferences vary substantially. Repeatability models included individual ID as a random effect and a crop type as a fixed effect.

Results

Data description

Our dataset included information on the movement of 13 northern lapwings, over the course of 2 years (2021-2023) in western Europe. We used GPS tracking data to derive used and available steps (n = 40,777 points) and remote sensing techniques to characterize the environmental space selected by the individuals.

Individual variation in niche axes

We detected both between-individual and within-individual variation in resource use patterns, through a visual inspection of individual resource utilisation curves and heatmaps. For example, individuals showed different patterns in their exposure to herbicides (glyphosates) and human population density (Fig. 2). In other cases, such as the soil nitrogen, the patterns were more homogeneous (Fig. S5).

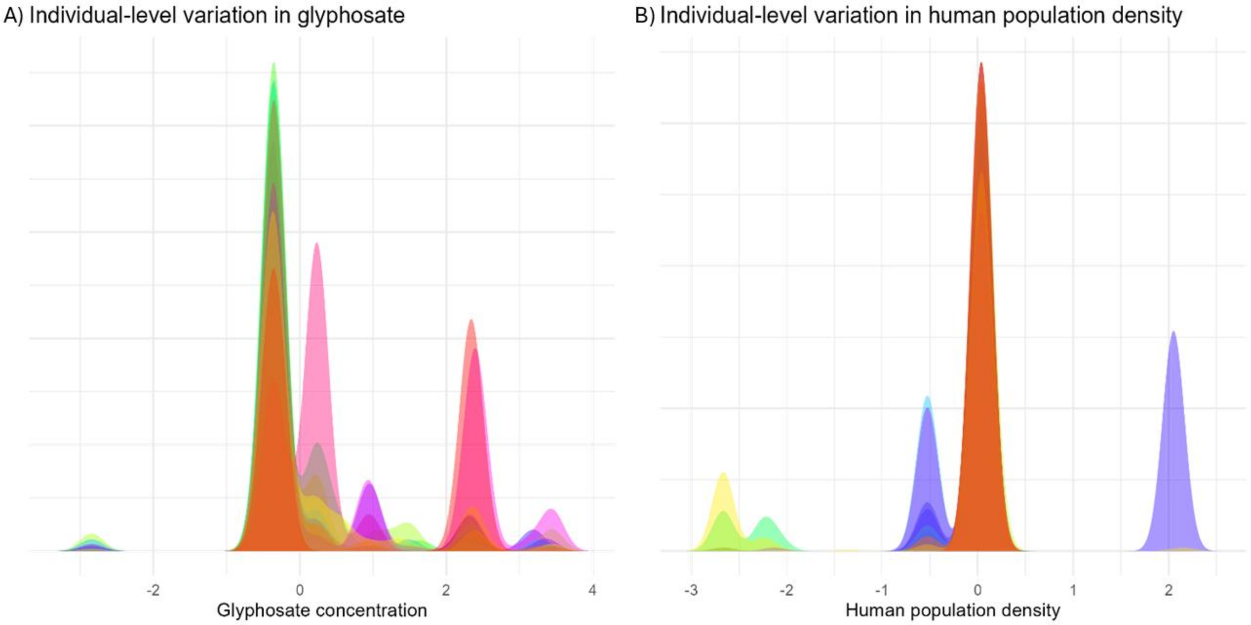

Figure 2. Individual resource utilisation curves for glyphosate (A) and human population density (B).

We used step selection functions to describe resource use variation by northern lapwings in relation to various biotic and abiotic variables (Table S2). The step selection functions indicated that the soil water index and the earthworm abundance factor were significantly affecting the movement patterns. Overall, none of the tested variables was significantly associated with the movement patterns of all northern lapwings (Fig. 3), however, some variables had significant coefficients for certain individuals, indicating differentiation in their impact. For example, in the case of individual-level step selection functions, the NDVI had either a significantly positive (IDs: 5439, 5264, 5285), a significantly negative (IDs: 5303, 5268, 5301) or a non-significant effect on the movement patterns of lapwings (Tables S4-S7).

Northern lapwings tended to move more during full-moon nights compared to new-moon nights (Fig. S3). In addition, earth-moon distance was positively correlated with step length (estimate = 0.20, S.E. = 0.09) and positively correlated with full and waxing moon (estimate = 1.17, S.E. = 0.54 and estimate = 0.97, S.E. = 0.56 correspondingly), indicating that northern lapwings tend to be more active when the moon is less bright but fuller, though there was high between-individual variation. During the night, individuals were strongly choosing pulses-flowers-vegetable and sugar beet crops while avoiding potato crops, artificial land and shrubland (Fig. S4).

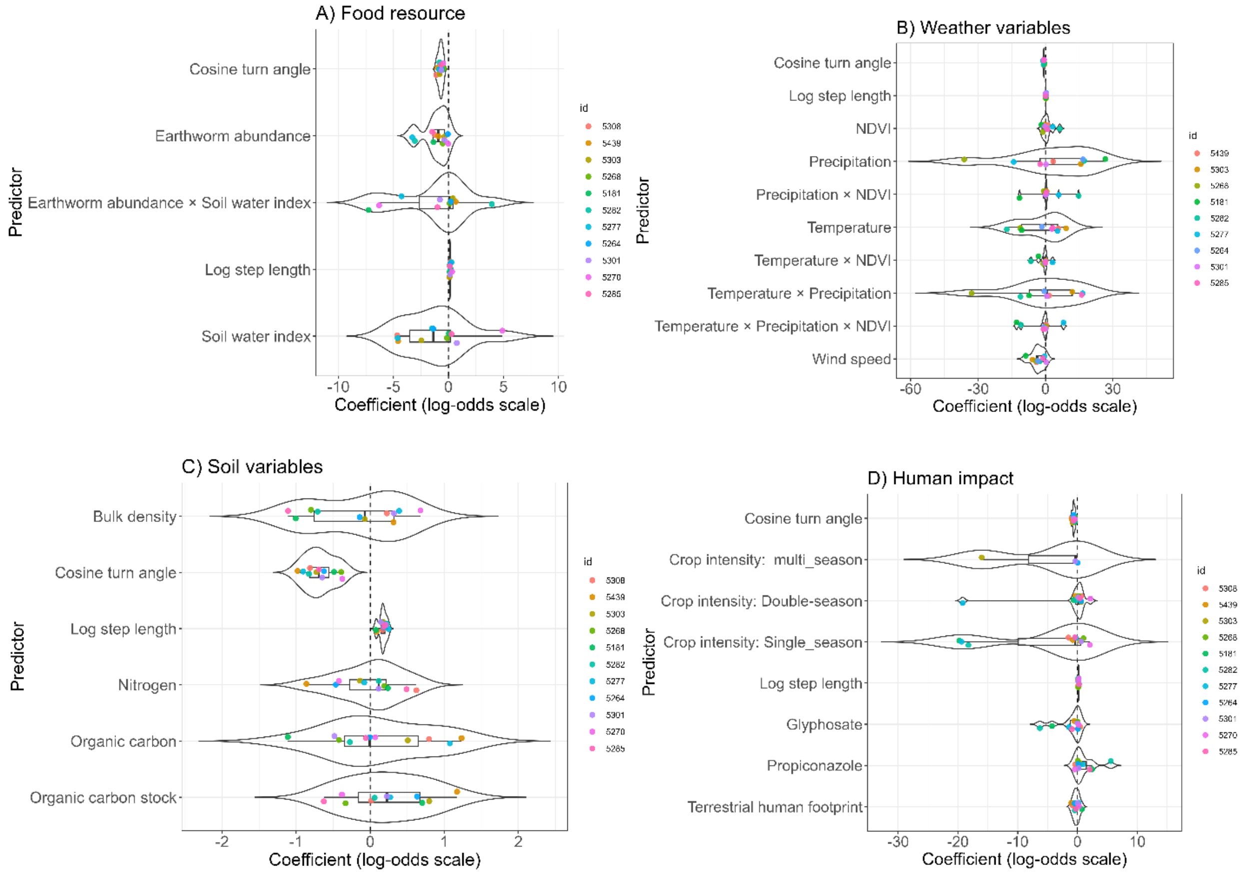

Figure 3. Model estimates for the A) food resource B) weather C) soil D) human impact models.

We also detected seasonal variation for all models (Fig. S7). Northern lapwing preferences varied across seasons in the visitation rates of crop types, while individual variation in the use patterns of all resources was lowest during summer.

Repeatability of resource selection

We used a step selection function to identify the important crop types across all data. The step selection function had significant effects for barley, maize, sugar beet, pulses-vegetables-flowers and grasslands. We then fitted a repeatability model for each of these crops (Fig. S8). The highest repeatability was observed in the category of pulses, vegetables and flowers (R=0.31, 95% CI: 0, 0.5), followed by sugar beet (R=0.09, 95% CI: 0, 0.28), and grasslands (R=0.007, 95% CI:0, 0.01). All other crop types, including maize, barley, potatoes, grassland, and water, showed negligible repeatability estimates (R< 0.01) with confidence intervals overlapping zero (Fig. 4). Repeatability for grasslands and water was also negligible, indicating uniform use patterns between all individuals.

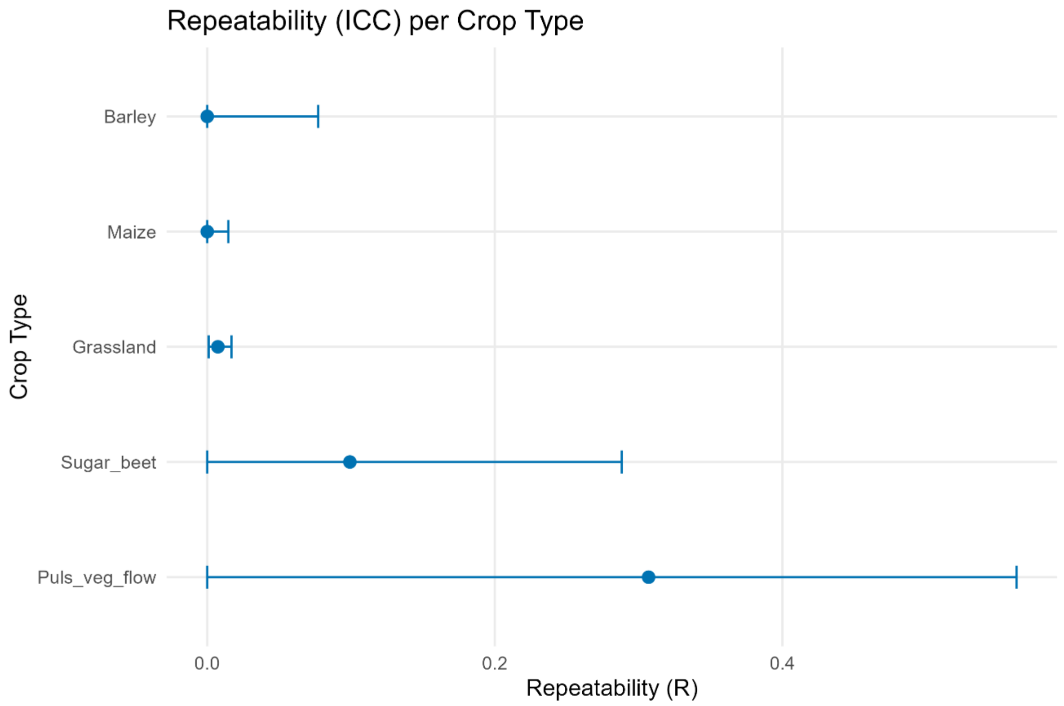

Figure 4. Repeatability of choosing each crop type across all northern lapwings in our study (n=13 individuals).

Discussion

In this study we analysed over 40,000 GPS locations of 13 northern lapwing individuals from 2021 to 2023. We used step selection functions and repeatability models to associate lapwing movement with abiotic and biotic variables and estimate intraspecific niche variation. Overall, northern lapwings selected primarily grasslands, barley and maize, however there was high between-individual heterogeneity in the selection of sugar beet and pulses-vegetables-flowers, confirming previous observations from the UK that northern lapwings are feeding on sugar beet during the night (Sheldon et al., 2004b).

The main biotic variables that we tested were earthworm abundance and human presence. Earthworms are an important component of the northern lapwing diet (Sheldon et al., 2004a). A recent study analysed dietary habits of northern lapwings in the Netherlands and Germany using metabarcoding techniques and found that earthworms were not a major part of the species' trophic niche (Lagendijk et al., 2025). Our study showed that northern lapwings tended to select areas with high earthworm abundance (marginally significant negative values in Fig. 3 indicate a positive association, see also *Biotic factors (human population density, human footprint, and earthworm abundance and richness)*), but no significant effect of the interaction between earthworms and soil water content. Previous studies have found, similar to ours, that lapwings show low tolerance to the presence of humans (Roche et al., 2016). However, the individual resource utilisation curves revealed that one individual actually preferred human presence very strongly.

The main abiotic variables that we tested, beyond crop types and pesticides, were related to soil water content, crop intensity, soil composition, climate and moon luminosity. Propiconazole is a fungicide while glyphosate is a herbicide for weed control. For example, propiconazole is commonly used in cereal crops (especially wheat and barley) (European Food Safety Authority (EFSA) et al., 2017), while glyphosate is commonly used in wheat, maize or rapeseed crops (Antier et al., 2020). Although the overall effect of propiconazole on the birds' movements was low and non-significant, there were three individual step selection functions (IDs: 5285, 5301 and 5439) where propiconazole had a significantly positive estimate. Regarding diurnal activity, our results show that northern lapwings do not always remain inactive during the night. On the contrary, we have shown that northern lapwings tend to be more active (longer steps) in nights with full moon than in nights with new moon, confirming previous observations (Milsom et al., 1990), but their activity was negatively correlated with moon luminosity (measured as the distance between Earth and Moon), likely due to higher predation risk in bright nights. The moon model showed a positive significant relationship between full moon and step length, but with a high standard error. In addition, a large amount of the model's variance was explained by between-individual variation, indicating that activity during night hours differs significantly among individuals. The highest variance explained by among-individual differences was in the moon model, which, in combination with the wide confidence interval of activity during full moon, indicates that not all individuals are equally active at night.

Fine-scale observations are instrumental for the effective design of species conservation measures. Field observations of occupancy rates have shown that, for northern lapwings, the effectiveness of AES for lapwings can be enhanced by the presence of water, which is an integral part of the species ecological niche (Hawkes et al., 2025). AES have proved to be beneficial for northern lapwings, since they provide foraging and breeding sites (Chamberlain et al., 2009; O'Brien & Wilson, 2011). However, when designing conservation interventions, it is important to take into account that northern lapwings show preference for an intermediate level of crop management, such as planting or rolling (Fraixedas et al., 2020; McCallum et al., 2018). In other words, they tend to avoid non-managed and natural areas (even with low vegetation), while, in the present study, they also avoid areas where there is multi-seasonal planting. Interestingly, our results confirm previous findings that lapwings select for medium cropping intensity or tilled areas (Düttmann et al., 2018; Horvat & Denac, 2019; McCallum et al., 2018) and improved grasslands (Düttmann et al., 2018), but see (Taylor & Grant, 2004), although this is not the case for restored meadows (Berg et al., 2002). In addition, nesting site selection is not always driven by the perceived vegetation composition or the presence of wetlands (McCallum et al., 2018), implying that there might be more complex and intrinsic factors for breeding habitat selection (Berg et al., 2002).

Although northern lapwings are considered a well-studied species, there are still key gaps in our understanding of the underlying mechanisms of their population declines. Moreover, lapwings appear to be well studied in Europe, but not throughout the range of their distribution (Phoswa & Downs, 2025). To this day, there are two main bodies of studies on northern lapwings: habitat selection and breeding success. The relationship between these two, across ecological contexts and scales, is the missing link. Future research can focus on linking fine-scale movement and habitat use with fitness outcomes across countries and continents (also known as the ‘think globally, measure locally’ principle).

Conservation recommendations

Based on the results of our study and the literature search, we suggest the following conservation measures for the protection of the northern lapwing:

1. Habitat management

- Northern lapwings avoid humans (densely populated areas) and human infrastructure, thus conservation measures should target habitat in remote areas (present study).
- The presence of even small (e.g. size of 10x10 meters) water bodies (rivers, lakes) is a very important resource for northern lapwings (present study).
- Spring tillage benefits northern lapwings, but they tend to avoid autumn tillage (Milsom, 2005; Sheldon et al., 2004a).
- Plant spring crops when doing crop rotations particularly roots and cereals (Sheldon et al., 2004a).
- Fewer machinery operations during breeding season (Schekkerman et al., 2009)
- Habitat management interventions supported by expert advice (Hunt et al., 2023). Lapwing conservation requires an active involvement of the land managers (McCallum et al., 2018).
- Liming is likely beneficial for northern lapwing breeding (McCallum et al., 2018).
- Northern lapwings select for fields with single- or double-season cropping intensity (present study).

2. Predation

- Culling is a sub-optimal solution because predators like foxes can be replaced very fast from neighboring populations (Porteus et al., 2024). Eliminating one predator does not decrease predation overall (Teunissen et al., 2008).

- Northern lapwings are active also during nights with intermediate moon light (present study).

3. Supporting breeding success

- Avoiding mowing and grass harvesting reduces chick mortality (Schekkerman et al., 2009).
- Ground nests are more threatened by horses rather than cattle (Mandema et al., 2013).
- Set aside areas for lapwing nesting (aka lapwing plots) (Chamberlain et al., 2009).
- Provision of nesting sites should be coupled with limited nest destruction and establishment of cropland-grassland mosaics (Milsom, 2005).
- Lapwings choose to nest away from potential predator perching spots (e.g. hedges) (McCallum et al., 2018), thus the removal of vegetation (such as shrubs) can reduce predation (Hunt et al., 2023).

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