An individual-based model for white storks (*Ciconia ciconia*) in Germany during breeding season

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Abstract

Understanding how habitat selection influences individual fitness is essential for predicting species responses to environmental change. Resource Selection Functions (RSFs) are widely used to quantify habitat preferences, but they often overlook individual variation and rarely link habitat use to demographic outcomes. We combined empirical habitat-selection modelling with a spatially explicit individual-based model (IBM) to investigate how habitat use influences movement, energetic performance, breeding success, and survival of white storks (*Ciconia ciconia*) in Germany. Using breeding-season GPS data from 33 individuals, we fitted matched used-available conditional logistic regression models incorporating vegetation productivity (NDVI), landscape structure, and land-cover classes. The selected model indicated negative selection for NDVI ($\beta = -0.42$) and positive selection for edge density ($\beta = 0.19$), suggesting a preference for open, structurally heterogeneous landscapes. Strong intraspecific variation was observed, with several individuals exhibiting habitat-selection responses that differed from population-level trends. Cross-validation indicated moderate predictive performance, with used locations ranked among the three highest-scoring alternatives in 37-39% of choice sets. Later, we integrated the selected RSF into an IBM simulation of breeding-season movement across five selected years, which includes resource acquisition through movement choices, energetic dynamics, breeding decisions, mortality risk, and breeding-site fidelity. Simulated outcome showed a breeding success ranging from 78.8% to 92.6%, while annual survival ranged from 87.1% to 100%. Individuals occupying more suitable habitats achieved higher cumulative energy balances and higher breeding success. Sensitivity analyses showed that model outcomes were robust to variation in movement and relocation parameters but sensitive to energetic breeding thresholds. Our study demonstrates how RSF-informed IBMs can translate habitat-selection patterns into fitness-related outcomes and improve predictions of species responses to landscape change.

Keywords: Resource selection function, habitat selection, energetic dynamics, RSF-IBM integration, landscape heterogeneity

Introduction

Animal movement is shaped by landscape structure, individual behaviour, and anthropogenic activity. Anthropogenic habitat alteration has been shown to affect the dynamics of many animal species (Cayuela et al., 2020; Gilbert et al., 2016). Human-altered landscapes can disrupt population persistence by limiting the movement and dispersal of individuals, restricting them to unsuitable environments, and thereby affecting fitness and survival (Cayuela et al., 2020). At the same time, movement is not only a response to landscape structure but also a key driver of ecological processes, including foraging efficiency, predator-prey interactions, and species distributions (Schlägel et al., 2020). Understanding how landscape composition shapes animal movement is important for the prediction of population persistence.

Traditionally, habitat selection studies have often assumed ecological equivalence among conspecific individuals (Gomez et al., 2025). This assumption is only valid when differences in resource use among individuals are rare, weak, or ecologically negligible (Bolnick et al., 2003; Des Roches et al., 2017). However, individuals frequently differ in feeding preferences, risk-taking behaviour, and functional roles (Jeltsch et al., 2025), exhibiting individualized niches (Takola, 2026; Takola and Schielzeth, 2022; Trappes et al., 2022). Such variation can strongly affect population responses to environmental change. For example, populations composed of both bold and shy individuals appear more resilient to fragmentation, whereas behaviourally homogeneous groups, particularly those dominated by cautious individuals, experience stronger negative effects (Rohwäder and Jeltsch, 2022). Furthermore, intraspecific trait variation is affecting not only within-species dynamics, but also interspecific interactions (Moran et al., 2022). Individual variation is, therefore, especially relevant when studying the extinction risk of species.

The white stork is a particularly suitable model species for the study of individual variation because it has been studied in detail for multiple decades (Flack et al., 2018, 2016; Schaub et al., 2005; Vaitkuviene et al., 2015). White storks are also among the best-monitored bird species in Europe, supported by long-term GPS tracking and strong citizen-science engagement, which enables robust spatial and temporal analyses (Berthold et al., 2022). In addition, the species functions as an umbrella species whose conservation can benefit a wider variety of species (Pestka et al., 2023). Because it forages extensively in farmland and nests close to human-made structures, the species exemplifies how land-use patterns shape both movement behaviour and habitat use (Standfuß et al., 2022). At the same time, these traits make the species vulnerable to habitat alteration and anthropogenic barriers along movement corridors (Rotics et al., 2016). White storks select foraging habitats according to vegetation structure (Standfuß et al., 2022) and food availability, typically preferring open habitats with low herbaceous cover (Latus et al., 2000; Pestka et al., 2023). In Europe, they show strong preferences for traditionally managed pastures, meadows, and shallow field wetlands (Pestka et al., 2023). Later in the breeding season, from late March to August (Vaitkuviene et al., 2015), they frequently exploit mowed meadows and freshly ploughed fields (Radović and Tepić, 2009). Their behaviour also varies with age, life stage, sex, and previous reproductive success (Vergara et al., 2006; Zurell et al., 2018). Site fidelity is particularly shaped by age and breeding status: adults generally show strong nest-site fidelity during the breeding season (Vergara et al., 2006; Zurell et al., 2018) but reduced fidelity the rest of the year (Berthold et al., 2022; Flack et al., 2016). Although the species declined in Europe from the late 1940s onward, largely because of landscape alteration, agricultural intensification, expanding human settlement, and climate change in the wintering grounds (Itonaga et al., 2011; Pestka et al., 2023), recent population increases in some regions indicate partial recovery (Itonaga et al., 2011). This recovery has been supported by conservation measures such as artificial nesting platforms (Santopaolo et al., 2013) and the establishment of European Stork Villages by EuroNatur (Ferger and Schwaderer, 2016). Nevertheless, the study of habitat preferences remains essential for maintaining and strengthening this positive trajectory.

Studying how animals interact with their environment can help identify key habitat requirements (Cornelsen et al., 2024). Resource Selection Functions (RSFs) are widely used to quantify habitat-use relationships by modelling relative selection probability. Combined with remote sensing, RSFs can support conservation planning, land-use assessment, and ecological risk analysis. However, RSFs are often not transferable to different spatiotemporal contexts due to intraspecific variation (Boyce et al., 2002). Individual-Based Models (IBMs) offer a mechanistic framework for representing ecological systems as collections of interacting individuals. Instead of relying on population averages, IBMs assign traits, behaviours, and decision rules to individuals and allow larger-scale ecological patterns to emerge from these interactions (Bolliger, 2007; Stadtländer, 2012). This makes them especially suitable for linking individual variability and behavioural processes to population- and ecosystem-level outcomes. For example, IBMs have outperformed density-based models in explaining stream trout habitat selection (Railsback et al., 2003). More recent applications have extended IBMs toward scaling individual energetics to community coexistence (Szangolies et al., 2024), predicting animal distributions under global change (Gomez et al., 2025), and incorporating behavioural variation such as risk-taking and foraging personalities in fragmented landscapes (Dammhahn et al., 2022; Rohwäder and Jeltsch, 2022). Thus, the combination of RSFs and IBMs can provide data-driven resource selection models that take into account intraspecific variation and can facilitate the prediction of population viability.

This study develops and evaluates a spatially explicit, RSF-informed individual-based model for white storks in Germany during the breeding season. The model integrates empirically derived movement preferences, dynamic resource availability, energetic state, breeding decisions, mortality risk, and breeding-site fidelity into a single mechanistic simulation framework. We first use RSFs to identify key habitat-selection variables and then integrate these empirical selection patterns into an IBM. This framework links individual foraging behaviour to modelled outcomes, namely breeding status (breeder or non-breeder) and mortality.

Methodology

Data collection and processing

White stork data

We used the MPIAB white stork tracking dataset (1991–2017) from the Movebank data repository (Berthold et al., 2022; Kays et al., 2022; Kranstauber et al., 2011). From this dataset, we extracted a subset corresponding to the white stork breeding season (March-August) for the years 1992 to 2012. We included only individuals for which all recorded locations during at least one complete breeding season fell within Germany (Figure 1). No additional filtering by breeding status or age class was applied. The resulting subset included 33 individuals and 1,302 location records. According to the dataset metadata, age classes consisted of 3 adults, 12 first-winter juveniles, 1 juvenile, and 17 individuals of unknown age.

NDVI and NDWI

Monthly Normalised Difference Vegetation Index (NDVI) and Normalised Difference Water Index (NDWI) were derived in Google Earth Engine from Landsat 5 TM and Landsat 7 ETM+ Collection 2 Level-2 surface-reflectance imagery after masking clouds, shadows, and snow and applying standard reflectance calibration. We generated median composites for July and August, and index values were extracted within a 250 m buffer around each used and available point to represent local vegetation productivity and surface-water availability during the breeding season. Additionally, we derived continuous July–August NDVI and NDWI layers for

2012, 2018, and 2024 from Landsat 8 OLI and Landsat 9 OLI-2 imagery. All raster layers were exported as GeoTIFFs and used as environmental inputs in the individual-based model to simulate white stork habitat selection under changing landscape conditions.

Land cover and landscape metrics

Land-use and land-cover (LULC) data were obtained from the GLC_FCS30D global dataset at 250 m spatial resolution for July in 1990, 1995, 2000, 2001, and 2012 (Zhang et al., 2024). Each RSF year (1992–2012) was matched to the closest available LULC year. All raster files were projected to WGS 84 (EPSG:4326) prior to analysis. Landscape metrics including Shannon Diversity Index (SHDI), Shannon Evenness Index (SHEI), Patch Density (PD), and Edge Density (ED) were calculated following FRAGSTATS (Kevin McGarigal et al., 2015; McGarigal , Kevin and Marks , Barbara J., 1995) and implemented in R (R Core Team, 2026) using the 'landscapemetrics' (Hesselbarth et al., 2019) and 'terra' (Hijmans et al., 2020) packages. To support both statistical modelling and simulation, metrics were derived using two complementary approaches. For resource selection analysis, metrics were calculated directly at observation locations using the 'landscapemetrics' package, providing localised estimates of landscape composition and configuration. For the individual-based model (IBM), spatially continuous raster layers of the same metrics were generated using a moving-window approach applied to land cover rasters projected to an equal-area coordinate system (EPSG:3035) at 250 m resolution.

A fixed window representing a 1200 m spatial context (11 × 11 cells; approximately 756 ha) was used to compute class-based diversity (SHDI, SHEI), patch density using 8-neighbour connectivity (PD), and edge density based on adjacency between land cover classes (ED), normalised by area. Both approaches ensure a consistent representation of landscape structure, with point-based metrics used for statistical inference and raster-based metrics providing spatially explicit inputs for simulation.

Resource selection functions of white storks

A used-available points sampling framework was implemented to construct the Resource Selection Functions (RSFs). Observed breeding-season GPS locations of individual white storks were treated as used points, while available points were generated to represent accessible but unused habitat. For each used location, ten available points (10:1 ratio) were randomly sampled within an annular buffer of 1-50 km to approximate the individual's potential movement space. Available points were assigned the same year and breeding-season period as their corresponding used point to maintain temporal consistency and all metadata (bird ID, tag ID, year, and month) were retained. Used and available points were coded as 1 and 0, respectively, and exported for environmental variable extraction. The 'sf' package (Pebesma, 2016) in R was used for creating the used-available points.

Resource selection was analysed using a matched used-available design implemented as conditional logistic regression in R using the 'survival' package (Therneau, 2026). The binary response variable (used) is distinct observed locations (denoted with 1) from randomly generated available locations (denoted with 0) within each choice set, with matched strata defined by set_id to account for the sampling design. Predictor variables included one vegetation index (either NDVI or NDWI), one landscape metric (ED, PD, SHDI, or SHEI), and land cover class (LULC_class) as a categorical factor. To avoid multicollinearity and overparameterisation, models were restricted to combinations including a single vegetation variable and a single landscape metric. Population-level models were fitted, including a clustering term for individual bird_ID to account for repeated observations per individual. Competing model structures were compared using Akaike's Information Criterion (AIC), and the best-supported model was selected for further analysis. To quantify intraspecific variability in habitat selection, the selected model structure was subsequently fitted separately for each individual using conditional logistic regression with matched strata, allowing estimation of individual-specific coefficients for the selected predictors. Only individuals with sufficient data (minimum number of choice sets and used observations) were retained for per-individual modelling.

White stork individual-based model

The individual-based model STRIDE was developed to simulate white stork movement, energy budget, breeding decisions, and home-range dynamics across multiple breeding seasons in a spatially explicit landscape. Each bird was represented as an autonomous agent initialised at a known nest location (the first recorded GPS location for that individual) and linked to an individual-specific RSF derived from the empirical habitat selection analysis. The environment consisted of annual raster layers of land cover, NDVI, NDWI, and fragmentation metrics, aligned to a common grid and sampled at each candidate movement location. Habitat suitability was evaluated by combining the individual-specific RSF with behavioural constraints, allowing birds to select among candidate steps at each time step according to the relative suitability of surrounding cells.

The model operated at a fixed temporal resolution of 30 min and simulated daytime activity only, from 05:00 to 20:00, during the breeding season from 1 March to 31 August. At each step, birds moved according to behaviour-specific movement kernels defined by step length, directional persistence, and the spatial extent of movement. Three behavioural modes were represented: non-breeding, breeding, and prospecting. These modes differed in movement distance, turning behaviour, candidate search breadth, and attraction to the breeding centre. During breeding, movement remained centred on the breeding site, whereas non-breeding and prospecting individuals ranged more widely. Prospecting was triggered later in the season or after breeding failure, enabling individuals to explore alternative areas with potentially higher habitat suitability.

Movement decisions were linked to energetic consequences by assigning each land-cover type a baseline food value modified by NDVI, NDWI, and fragmentation-derived habitat quality. Food resources were depleted locally by foraging and renewed periodically, such that habitat quality varied through time. At each movement step, individuals gained energy from food intake and lost energy through physiological maintenance, foraging, and flight, with movement distance directly affecting energetic expenditure. Daily net energy balance was tracked for each bird, and cumulative energy status determined survival. Mortality occurred when the cumulative energy deficit exceeded a predefined threshold of 60% of the daily energetic requirement.

Breeding decisions were modelled as state-dependent outcomes of sustained energetic performance. Between days 15 and 45 of the season, individuals could enter breeding behaviour if recent energy balance exceeded a surplus threshold of 30% relative to the daily energetic requirement. Final breeding success was then evaluated from the net energetic balance accumulated over the final 30 days of the season. Individuals meeting this requirement were classified as successful breeders, whereas those that attempted breeding but failed to meet the threshold were classified as failed breeders. Individuals that never met the breeding-entry condition remained non-breeders. Breeding status therefore, emerged from cumulative foraging success rather than from a fixed rule.

The model also incorporated dynamic breeding-site fidelity and home-range shifting. Successful breeders retained their breeding centre and began the following season from that location, such that breeding success increased site loyalty. In contrast, failed breeders and non-breeders could enter prospecting mode and evaluate whether an alternative site offered sufficient improvement in habitat suitability to justify a shift. A breeding centre was shifted only when the alternative site exceeded the current centre by a minimum threshold in RSF-derived suitability and was sufficiently distant to prevent trivial relocations. If no better site was found, the individual retained its existing centre for the following season. Home-range shifts thus emerged from repeated breeding failure, prospecting behaviour, and individual evaluation of alternative habitat quality.

The model was run sequentially across years using year-specific environmental layers, allowing individuals to experience changing landscape conditions through time. At the end of each simulated season, bird states, energetic outcomes, breeding status, home-range shifts, and full step-level movement trajectories were recorded. A full ODD description of the model (Grimm et al., 2010) and a vODD (Szangolies et al., 2024) are provided in the Supplementary Material.

Model validation and Sensitivity analysis

Model validation for the RSF was conducted using multiple complementary procedures to assess predictive discrimination, parameter robustness, and transferability of the final conditional logistic regression RSF. First, leave-one-bird-out cross-validation was applied to evaluate generalisation across individuals. In each iteration, all observations from one bird were withheld, the model was refitted using the remaining birds, and habitat scores for the excluded bird were calculated from the fitted coefficients. Within each matched choice set, candidate locations were ranked by predicted score, and performance was quantified as the proportion of sets in which the used location ranked first among the three highest-ranked locations and by mean rank. Second, bird-blocked 5-fold cross-validation was performed by partitioning individuals into five non-overlapping groups, ensuring that all observations from a given bird occurred exclusively in either training or testing data. The same ranking metrics were calculated for each fold. Third, in-sample ranking performance was assessed by fitting the final model to the full dataset and evaluating the rank of used locations within their original matched sets. Finally, coefficient stability was examined using a cluster bootstrap (200 iterations), resampling birds with replacement to preserve within-individual dependence. For each bootstrap sample, the model was refitted, and empirical confidence intervals were derived for NDVI and ED_scaled coefficients.

Sensitivity analyses were conducted to evaluate the robustness of the individual-based model (IBM) to key behavioural and movement parameters. Three parameters were systematically assessed: the minimum site-improvement threshold for home-range shifting (MIN_BETTER_SITE_SCORE = 0.00, 0.05, 0.10, and 0.20), the minimum shift distance required for relocation (MIN_SHIFT_DISTANCE_M = 1000, 3000, and 10000 m), and the energetic surplus required for breeding initiation (BREED_MIN_EXCESS = 0.10, 0.30, and

0.50). For each parameter value, simulations were repeated using three independent random replications across five landscape years (2000, 2001, 2012, 2018, and 2022), while all other model settings remained unchanged.

Sensitivity outputs included survival, breeding success, failed breeding attempts, non-breeding frequency, number of shifting individuals, cumulative energetic balance, breeding-site loyalty, and home-range shift distance. Mean responses and standard deviations across replicate runs were calculated to assess parameter sensitivity and overall model stability. This framework allowed assessment of whether emergent IBM dynamics remained robust under realistic variation in behavioural thresholds and movement constraints.

Results

Summary statistics from the MoveBank dataset

After all filtering, the final analytical sample comprised 33 white storks, representing 10 years, 10 breeding seasons, and 1302 GPS locations were retained for analysis. Tracking effort ranged from 2 to 235 points per bird, with a median of [29 ± 7.97] fixes per individual. If calculated at the seasonal level, tracking effort ranged from 2 to 218 fixes per bird-season, with a median of 28.5. Temporal coverage was highest in July-August, whereas March-April contributed the fewest observations.

Resource selection patterns of white storks

After filtering and excluding invalid strata, the final RSF dataset contained 1302 matched choice sets, comprising 1302 used points and 12976 available points, corresponding to a used:available ratio of [1:9.97] after exclusions. The retained land-cover classes included rainfed cropland, herbaceous cropland, closed deciduous broad-leaved forest, closed evergreen needle-leaved forest, marsh, impervious surface and deep water bodies after rare classes were removed from the analysis. Diagnostic checks confirmed that multicollinearity among predictors was low (VIF < 5).

A total of 8 candidate RSFs were compared (Table 1). The final model selected for interpretation and subsequent IBM parameterisation was m_ndvi_ED_scaled, which included NDVI, Edge density (ED), and LULC classes. In the main text, this model should be treated as the RSF with NDVI + ED_scaled + LULC_class. Model selection was based on Akaike's Information Criterion, and the retained model had an AIC of 6150, with a ΔAIC of 2.15 relative to the best model. This model was retained because, in addition to exhibiting a competitive AIC, it provided a more ecologically meaningful representation of habitat selection patterns. In addition, there was limited variability and reduced ecological interpretability of NDWI within the habitats actually used by the birds. Consequently, the model containing NDVI was considered more robust and biologically realistic despite not having the absolute minimum AIC.

At the population level, habitat selection was negatively associated with NDVI ($\beta = -0.4216$, OR = 0.656, 95% CI = [-0.9129, 0.0698]) and positively associated with ED_scaled ($\beta = 0.1856$, OR = 1.2039, 95% CI = [0.1228, 0.2485]) (Figure 2). These results indicate that white storks selected less green habitats and preferred more edge-dense landscapes during the breeding season. Relative to the reference land-cover class, rainfed cropland, the strongest positive selection was observed for impervious surface, whereas the strongest avoidance was observed for deep water bodies and marsh. Habitat classes showing weak or neutral responses included open deciduous needle-leaved forest, closed deciduous broad-leaved forest, closed evergreen needle-leaved forest and herbaceous cropland. Overall, these results indicate that white storks preferentially used low vegetation sites and avoided deep water areas.

Bird-specific responses showed strong variation among individuals. Variation was observed for both NDVI and ED_scaled with bird-specific slopes ranging from -2.586 to 6.911 for NDVI and from -0.131 to 0.870 for ED_scaled. Most individuals followed the same direction of response as the population-level effect, although six individuals showed contrasting responses for NDVI and two individuals showed contrasting responses for ED_scaled. Overall, the strength of intraspecific heterogeneity in habitat selection was substantial.

RSF model validation

Validation results indicated that the RSF performed moderately in predicting observed habitat use. Cross-validation showed that used locations were ranked higher than expected by chance, with mean ranks of 5.11 (k-fold), 5.19 (LOBO), and 5.21 (ranking validation), and top-rank frequencies of 11.6%, 11.4%, and 14.2%, respectively. Top-3 accuracies ranged between 37.2% and 38.5% across validation procedures (Figure S1). Bootstrap resampling indicated that the coefficient for NDVI was variable and not robust, with a confidence interval of [-1.28, 0.41], whereas ED_scaled showed a relatively stable positive effect with a confidence interval of [0.04, 0.34]. Overall, the RSF showed moderate predictive discrimination and limited to acceptable coefficient robustness.

Individual-based model

Across the five simulation years (2000, 2001, 2012, 2018, and 2022), the IBM simulated 33 birds in 2000, 31 birds in 2001 and 2012, and 27 birds in 2018 and 2022. At the end of the season, 31 (93.9%) birds remained alive in 2000, all 31 (100%) birds remained alive after the simulation year 2001; for 2012, 27 birds (87.09%) were alive; in 2018, 26 (96.29%) birds remained alive; and in 2022, 25 (96.15%) birds remained alive. The number of birds classified as successful breeders was 26 (78.79%) in 2000, 28 (90.32%) in 2001, 26 (83.87%) in 2012, 25 (92.59%) in 2018 and 24 (92.30%) in 2022 (Figure 3). Cumulative energy balance had a mean of 1840.76 units in 2000, 2047.31 units in 2001, 1851.06 units in 2012, 2107.16 units in 2018, and 2113.36 units in 2022, while the mean number of simulated steps per bird was 5540.79, 5888, 5173.55, 5685.296, and 5666.42, respectively.

Simulated movement trajectories showed heterogeneous spatial patterns across years. In 2012, tracks were relatively more wide-ranging, whereas in 2018 they were concentrated. Breeding individuals generally remained more nest-centred, with trajectories concentrated around local foraging areas, whereas non-breeding individuals ranged more widely across the landscape. Differences between breeders and non-breeders were clear, and interannual differences in track structure were most apparent in 2012 and 2022 (Figure 4 & 5).

Cumulative net energy balance varied among individuals and across years (Figure 6). The overall distribution of energy budget was centred around 2127.61 units in 2000, 2136.56 units in 2001, 2123.28 units in 2012, 2174.56 units in 2018, and 2279.45 in 2024, indicating that 2022 had the highest energetic performance and 2012 the lowest. Birds classified as successful breeders had higher cumulative energy balances than non-breeders, with mean values of [2208 ± 41.9 for breeders across all years] versus [518 ± 130 for non-breeders across all years], respectively. Similarly, surviving birds had higher cumulative energy balances than birds that died during the simulation, with values of [2096 ± 51] versus [-8.22 ± 0.71]. Overall, these results suggest that more favourable habitat conditions supported higher energetic performance.

Breeding and survival outcomes varied across the five simulation years. In 2000, 26 (78.79%) birds were classified as successful breeders, 3 (9.09%) as failed breeders, 1 (3.03%) as non-breeders, and 2 (6.06%) died. Corresponding values were 28 (90.32%), 2 (6.45%), 0 (0%), and 0 (0%) in 2001, 26 (83.87%), 0 (0%), 1 (3.22%), and 4 (12.90%) in 2012, 25 (92.59%), 1 (3.7%), 0 (0%), and 1 (3.7%) in 2018, and 24 (92.30%), 1 (3.84%), 0 (0%), and 1 (3.84%) in 2022. Breeding success was highest in 2022, whereas survival was lowest in 2012. In general, breeding status tracked energetic condition, with breeders showing higher cumulative energy balances than non-breeders and birds that died.

Differences among yearly environmental layers were reflected in simulated movement, energy balance, breeding success, and survival. Years characterised by higher habitat suitability were associated with higher energy gain, higher breeding frequency, and lower mortality. These patterns were broadly consistent with the RSF results, which indicated selection for edge-rich, moderately vegetated, and heterogeneous landscapes. Overall, birds performed better in landscapes characterised by higher edge density and lower NDVI, suggesting that the IBM reproduced the broad habitat-performance relationships identified by the empirical RSF.

Sensitivity analysis of the IBM

Sensitivity analysis showed that the IBM remained comparatively stable for MIN_SHIFT_DISTANCE_M and MIN_BETTER_SITE_SCORE. For a 1000 m threshold in MIN_SHIFT_DISTANCE_M, the number of successful breeders ranged from 24 to 27 individuals across years and replicates, which slightly increased with the threshold and reached a maximum of 28 individuals at both 3000 m and 10000 m thresholds. The number of deceased birds and shifters ranged from 0 to 4 and from 0 to 2, respectively, across all tested thresholds of MIN_SHIFT_DISTANCE_M (Fig. S3). Mean cumulative energy also remained relatively stable, ranging from approximately 1793 to 2216 across simulations.

Similarly, variation in MIN_BETTER_SITE_SCORE from 0.05 to 0.20 produced only minor differences in model outputs. The number of successful breeders remained between 24 and 28 individuals across all tested thresholds, while deceased birds and shifters ranged from 0 to 4 and from 0 to 2, respectively (Fig. S4). Mean cumulative energy also showed limited variation, ranging from approximately 1793 to 2216. This indicates that moderate changes in the threshold for selecting a better breeding site had little influence on overall model dynamics.

In contrast, BREED_MIN_EXCESS produced a much stronger sensitivity response. At a threshold of 0.10, successful breeders ranged from 25 to 31 individuals across years and replicates, while deceased birds remained between 0 and 4 individuals and shifters between 0 and 1 individual. At the intermediate threshold of 0.30, successful breeders remained relatively similar, ranging from 24 to 28 individuals. However, at the highest threshold of 0.50, successful breeders declined sharply to 3 to 18 individuals, while deceased birds increased to

1 to 9 individuals, and shifters increased up to 7 individuals (Fig. S5). Mean cumulative energy also declined strongly, the mean cumulative energy ranged from approximately 1845 to 2161 at BREED_MIN_EXCESS = 0.10 and from 1793 to 2216 at BREED_MIN_EXCESS = 0.30 and from 798 to 1714 at BREED_MIN_EXCESS = 0.50.

Overall, the IBM was robust to changes in movement distance and better-site selection thresholds, but sensitive to the breeding-energy requirement. This suggests that the model is not unstable under moderate behavioural parameter variation, while still responding strongly to biologically meaningful energetic constraints.

Discussion and Conclusion

This study presents a spatially explicit mechanistic model of white stork movement in Germany during the breeding season. Our results show that breeding-season habitat use by white storks was mainly driven by NDVI, edge density and land-cover class. We selected the model with NDVI, edge density, and land cover class as the most parsimonious, although the alternative NDWI model had a slightly lower AIC. The model containing NDVI was retained because NDVI has been shown to affect habitat selection of white storks (Zurell et al., 2018). At the population level, white storks selected areas with lower NDVI and higher edge density, however individual responses varied significantly. Our results show that breeding season performance depends on both landscape structure and individual variation in habitat selection.

The negative association with NDVI implies that white storks used relatively open or less green habitats during the breeding season. This pattern agrees with previous findings, which state that white storks prefer open habitats with low herbaceous cover and often forage in pastures, meadows, mowed fields, and ploughed fields (Alonso et al., 1991; Latus et al., 2000; Pestka et al., 2023; Standfuß et al., 2022). The avoidance of deep-water bodies and marsh also suggests that suitable habitat is not defined by water availability alone (Martin Moritzii et al., 2001). Instead, accessible foraging conditions appear to be more important than wetness itself. NDVI is therefore ecologically relevant, but its effect should be interpreted as context-dependent. The positive response to impervious surfaces should be interpreted cautiously. It may reflect opportunistic use of human-modified foraging areas rather than preference for built habitat itself. This is consistent with studies showing that white storks can exploit anthropogenic food sources, including landfill-associated resources, when these are available (Gilbert et al., 2016; López-García and Aguirre, 2023; Tryjanowski et al., 2018). The high preference of white storks for high edge density indicates that they selected structurally heterogeneous landscapes during the breeding season. This finding is consistent with the role of farmland mosaics and multifunctional landscapes (Barros et al., 2019). The resource selection functions suggest that landscape configuration contributed to habitat use beyond land cover identity alone.

The individual-based model facilitated the link between habitat use and survival. The cumulative energy balance proved a suitable mechanism to establish this link. Successful breeders had significantly higher energy balances than non-breeders, indicating higher foraging performance and more effective resource use. Our model can be used throughout the distribution of the species, in order to predict population viability.

However, there are some limitations in our study. Available points were sampled within a 1 to 50 km annular buffer, which approximated accessible habitat but may not match the true movement range of every bird. Land cover layers were matched to the closest available year, which may have introduced temporal mismatch between tracking locations and environmental predictors. Lastly, we omitted the possibility of adaptive behaviour plasticity and we assumed that individuals do not change their behavioural patterns over short periods of time.

The main contribution of this study is the direct use of empirical RSF coefficients in a spatial IBM. Instead of treating all birds as ecologically equivalent, the model allowed individual-specific habitat selection to influence movement, energy gain, breeding outcome, mortality risk and home-range shifting. This links observed habitat selection to fitness-relevant outcomes and predicted population viability, which is a necessary step towards integrating individual-based models in global change Ecology (Jeltsch et al., 2025).

Our study has multiple conservation implications, as it showcases the importance of open, edge-rich and accessible farmland around breeding sites. Maintaining mowed meadows, traditionally managed pastures, ploughed fields and small-scale cropland–grassland mosaics should support efficient foraging. Deep water bodies and marshes should not automatically be treated as suitable foraging habitat unless prey is accessible and vegetation structure allows storks to forage. At the same time, the positive response to impervious surfaces should not be read as support for artificial food sources. Landfills and other anthropogenic feeding sites may attract storks, but they can also expose birds and nestlings to pollutants and other risks (Bjedov et al., 2023; López-García and Aguirre, 2023). Conservation should therefore prioritise natural and agricultural foraging habitats rather than artificial subsidies.

CRediT authorship contribution statement

Jannatul Ferdous: Conceptualisation, Methodology, Software, Formal analysis, Investigation, Data curation, Validation, Visualisation, Writing - original draft, Writing -review & editing.

Ronny Peters: Supervision, Writing - review & editing.

Uta Berger: Supervision, Writing - review & editing.

Elina Takola: Supervision, Conceptualisation, Methodology, Formal analysis, Project administration, Visualisation, Writing - original draft, Writing - review & editing.

Ethics declaration

Our research did not include invasive research on human or animal subjects.

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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Supplementary material

A supplementary material section is available for the present publication. It contains the full model ODD for the STRIDE model and a visual ODD (vODD), along with the validation visualisations for the RSF and the sensitivity analysis visualisations for the STRIDE.

Data availability

For reproducibility, transparency, repeatability, and shareability (Huettmann and Arhonditsis, 2023), the data and code used in this study are publicly available at ZENODO with a doi: https://doi.org/10.5281/zenodo.20796971. The repository includes the datasets, model code, and supporting documentation needed to reproduce the analyses and results.

Declaration of Generative AI and AI-assisted technologies

During the preparation of this work, the authors used the GPT-5 AI model to assist with code development, debugging, and improving the language and readability of the manuscript. The authors reviewed, verified, and edited the content as needed, and take full responsibility for the framework, code validity, and the final content of the publication.

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Figures & Tables

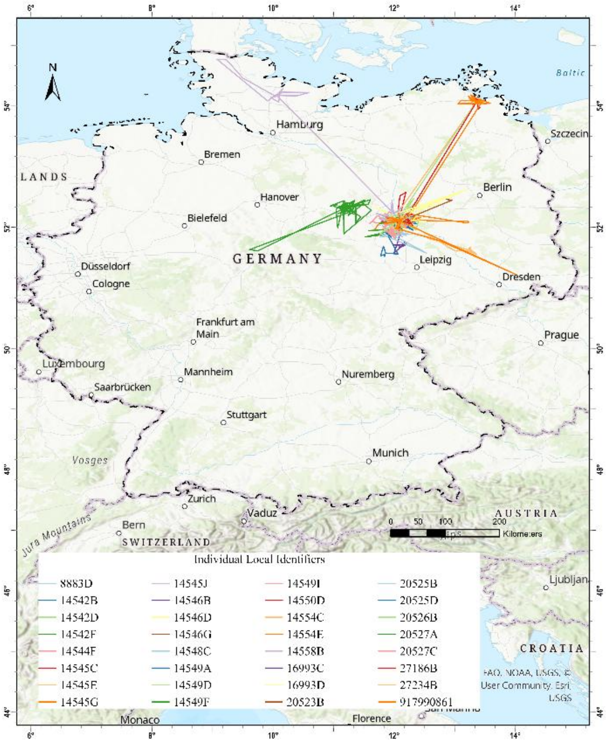

Figure 1. The geographic context and spatial coverage of the input tracking data. The map shows raw movement trajectories of tracked white storks relative (subset of MPIAB white stork data) to the German national boundary. Lines represent individual empirical trajectories.

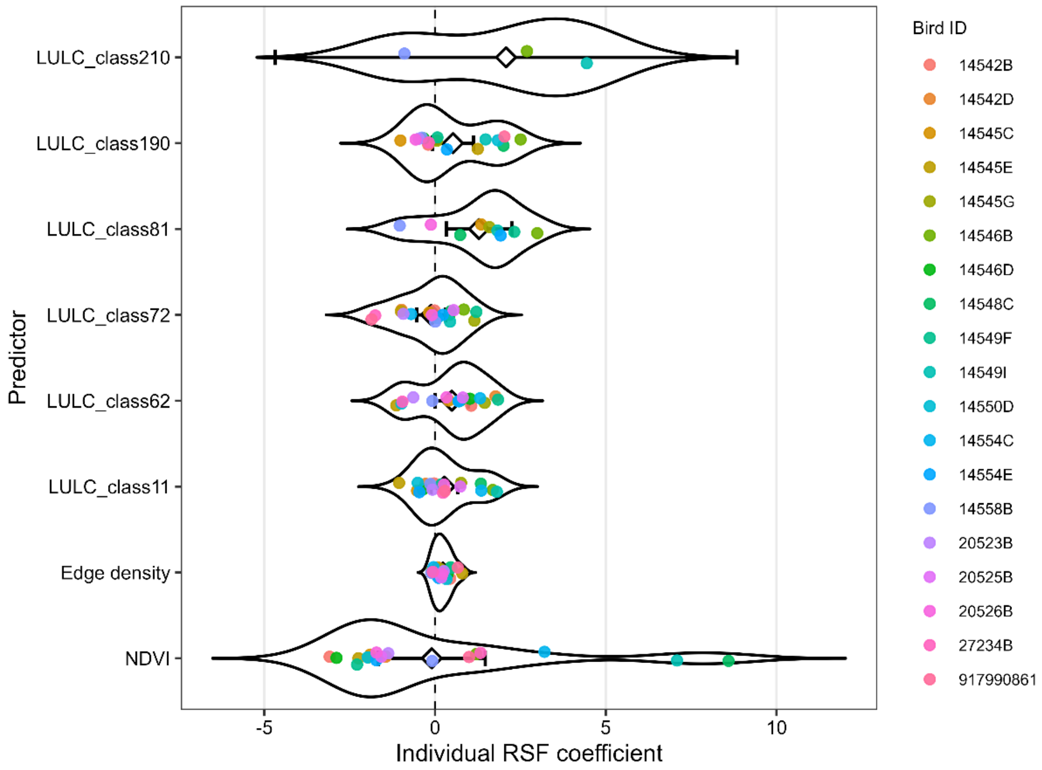

Figure 2. Individual variation in resource selection coefficients from per-bird conditional logistic RSF models using the raw data. Violin plots show the distribution of bird-specific coefficients for NDVI, edge density, and land-cover classes in the selected RSF model. Points represent individual birds, diamonds indicate mean coefficients, and horizontal bars show 95% confidence intervals.

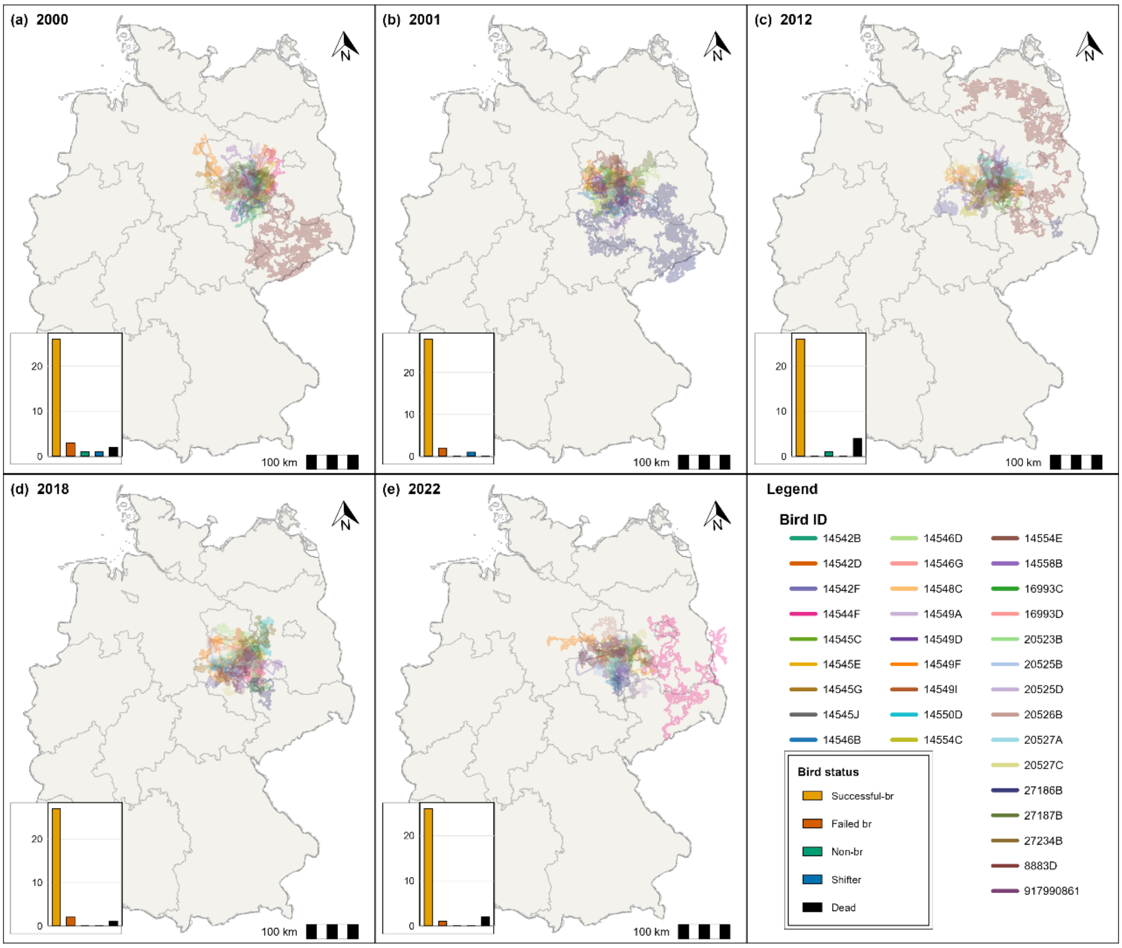

Figure 3. White stork simulated movement for the years 2000, 2001, 2012, 2018 and 2022 in Germany. Barplots show the number of birds per final status (successful breeder, failed breeder, non-breeder, range shifter, dead). Each line colour corresponds to an individual ID.

Figure 4. Activity density map by final simulated state representing the Spatial distribution of simulated stork activity across final behavioural states. Points represent gridded movement activity, with colour intensity showing weighted activity as the summed number of steps per grid cell on a log-scaled gradient. Facets separate individuals by final state: dead, failed breeder, non-breeder, shifter, and successful breeder.

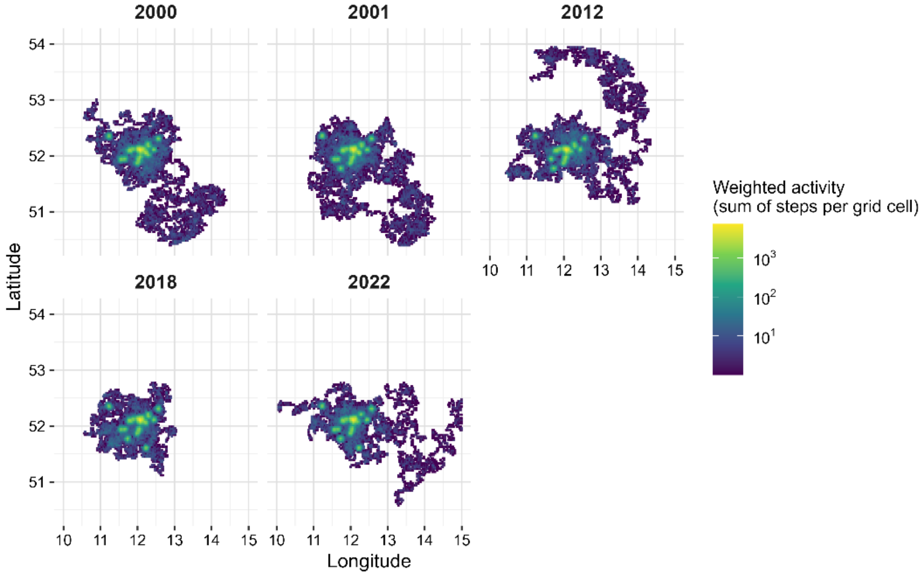

Figure 5. Activity density map by simulation year showing the spatial distribution of simulated white stork activity across selected years. Points represent gridded movement activity, with colour intensity indicating weighted activity as the summed number of steps per grid cell on a log-scaled gradient. Facets show year-specific differences in the concentration and spatial spread of simulated movement activity across the study landscape.

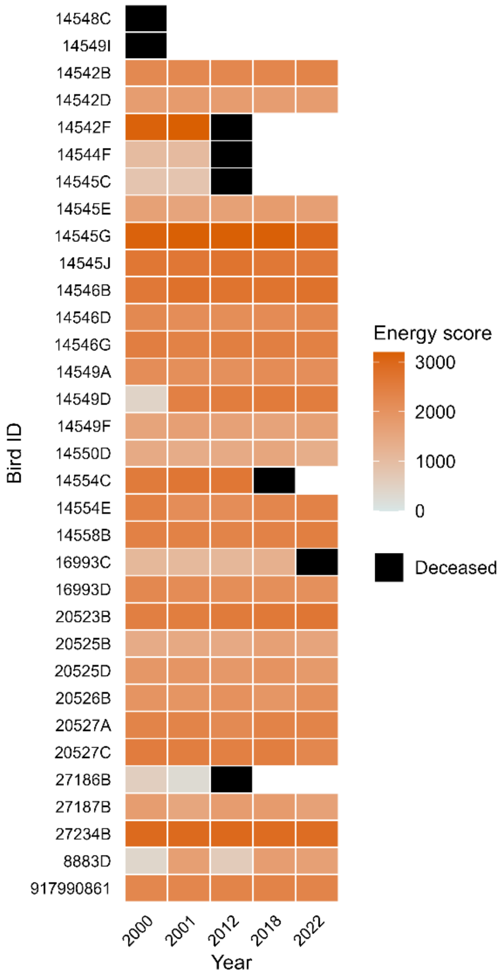

Figure 6. Heatmap for the Annual energy budget of individual simulated white storks showing the cumulative yearly energy score for each individual across simulation years. Tile colour indicates the cumulative energy budget, with higher values representing greater retained energy by the end of the annual simulation. Black cells indicate individuals who died before completing the corresponding simulation year.

Model Predictors	AIC
NDWI + ED_scaled + LULC_class	6148.29
NDVI + ED_scaled + LULC_class	6150.44
NDWI + SHEI_scaled + LULC_class	6172.12
NDVI + SHEI_scaled + LULC_class	6174.02
NDWI + SHDI_scaled + LULC_class	6174.41
NDVI + SHDI_scaled + LULC_class	6176.25

NDWI + PD_scaled + LULC_class	6177.17
NDVI + PD_scaled + LULC_class	6178.93

Table 1. Model parsimony based on AIC.

Simulated year	Successful breeders (%)	Failed breeders (%)	Non-breeders (%)	Dead (%)	Mean cumulative energy	Number of home range shifts
2000	78.79	9.09	3.03	6.06	1840.76	1
2001	90.32	6.45	0	0	2047.31	1
2012	83.87	0	3.22	12.90	1851.06	0
2018	92.59	3.70	0	3.70	2107.16	0
2022	92.30	3.84	0	3.84	2113.36	0

Table 2. Percentage of individuals per final status per year.