University of Kent

Kent Academic Repository

Cisneros-Araujo, Pablo, Garrote, German, Corradini, Andrea, Cagnacci, Francesca, Farhadinia, Mohammad S., Salcedo, Javier, Sarmento, Pedro, Sánchez, Juan Francisco, Palacios, María Jesús, García-Viñás, Juan Ignacio and others (2025) ***Movement phases make a difference in habitat selection: Iberian lynx diversity of responses to human-modified landscapes.*** **Journal of Animal Ecology, 94 (10). pp. 1983-1996. ISSN 0021-8790.**

Downloaded from

https://kar.kent.ac.uk/110597/ The University of Kent's Academic Repository KAR

The version of record is available from

https://doi.org/10.1111/1365-2656.70099

This document version

Publisher pdf

DOI for this version

Licence for this version

CC BY-NC-ND (Attribution-NonCommercial-NoDerivatives)

Additional information

Versions of research works

Versions of Record

If this version is the version of record, it is the same as the published version available on the publisher's web site. Cite as the published version.

Author Accepted Manuscripts

If this document is identified as the Author Accepted Manuscript it is the version after peer review but before type setting, copy editing or publisher branding. Cite as Surname, Initial. (Year) 'Title of article'. To be published in ***Title of Journal*** , Volume and issue numbers [peer-reviewed accepted version]. Available at: DOI or URL (Accessed: date).

Enquiries

If you have questions about this document contact ResearchSupport@kent.ac.uk. Please include the URL of the record in KAR. If you believe that your, or a third party's rights have been compromised through this document please see our Take Down policy (available from https://www.kent.ac.uk/guides/kar-the-kent-academic-repository#policies).

Check for updates

Received: 7 October 2024 | Accepted: 6 May 2025

DOI: 10.1111/1365-2656.70099

Journal of Animal Ecology

RESEARCH ARTICLE

Movement phases make a difference in habitat selection: Iberian lynx diversity of responses to human-modified landscapes

Pablo Cisneros-Araujo[1] | German Garrote[2] | Andrea Corradini[3,4] | Francesca Cagnacci[3,4] | Mohammad S. Farhadinia[5,6] | Javier Salcedo[2] | Pedro Sarmento[7] | Juan Francisco Sánchez[8] | María Jesús Palacios[9] | Juan Ignacio García-Viñás[1] | Santiago Saura[1] | Aitor Gastón[1]

[1]Centro para la Conservación de la Biodiversidad y el Desarrollo Sostenible (CBDS), ETSI Montes, Forestal y del Medio Natural (ETSIMFMN), Universidad Politécnica de Madrid (UPM), Madrid, Spain; [2]Agencia de Medio Ambiente y Agua de Andalucía, Seville, Spain; [3]Animal Ecology Unit, Research and Innovation Centre (CRI), Fondazione Edmund Mach, San Michele all'Adige, Italy; [4]NBFC, National Biodiversity Future Centre, Palermo, Italy; [5]Department of Biology, University of Oxford, Oxford, UK; [6]Durrell Institute of Conservation and Ecology, School of Anthropology and Conservation, University of Kent, Canterbury, UK; [7]Institute for the Conservation of Nature and Forests (ICNF), Beja, Portugal; [8]Asistencia Técnica de la Dirección General del Medio Natural y Biodiversidad de la Junta de Comunidades de Castilla-La Mancha, Toledo, Spain and [9]Dirección General de Medio Ambiente de la Junta de Extremadura, Mérida, Spain

Correspondence
Pablo Cisneros-Araujo
Email: pablo.cisneros.araujo@upm.es

Handling Editor: Catherine L. Parr

Abstract

1. Wildlife conservation requires a comprehensive understanding of habitat and landscape conditions supporting viable and well-connected populations, especially for reintroduction efforts. Habitat selection depends on different life processes and behavioural states driving animal movements. However, habitat modelling often considers all species records together or distinguishes only between locations within and outside home ranges.
2. We considered a more detailed characterization of movements, focusing on five distinct movement phases: home ranges, transient residences, excursions, post-release dispersals and dispersals. Utilizing GPS telemetry data from 124 Iberian lynxes (*Lynx pardinus*), mainly tracked during a reintroduction programme, we examined their habitat selection and adaptation to heterogeneous, human-modified and fragmented landscapes.
3. We developed context-specific mixed-effects habitat selection models for each phase, incorporating two hierarchical selection scales: resident range and path selection functions at the landscape scale, and step selection functions at the local scale.
4. All lynxes consistently avoided intensive non-tree cropland and selected mosaics of natural vegetation, including tree, shrubland and grassland cover. Resident lynxes selected areas with low road and human infrastructure densities locally,

Santiago Saura and Aitor Gastón are co-senior authors.

This is an open access article under the terms of the Creative Commons Attribution-NonCommercial-NoDerivs License, which permits use and distribution in any medium, provided the original work is properly cited, the use is non-commercial and no modifications or adaptations are made.
© 2025 The Author(s). *Journal of Animal Ecology* published by John Wiley & Sons Ltd on behalf of British Ecological Society.

but no such pattern emerged at the landscape scale, likely due to constraints on establishing large home ranges where infrastructures are widespread and intertwined with natural cover.

5. We observed significant differences in habitat selection among non-residential phases. During excursions, lynxes avoided areas with high human infrastructure, whereas during dispersals, this avoidance was less pronounced, indicating high behavioural plasticity. The post-release dispersal phase mirrored dispersals but showed infrastructure avoidance and a higher selection for sheltering features like rugged terrain and shrub cover.
6. Our findings emphasize the importance of distinguishing specific movement phases, and particularly different movement phases outside home ranges, when assessing habitat selection, especially for translocated animals settling in the landscape. This differentiation is essential to (i) identify suitable reintroduction areas with habitat features supporting post-release movements and settlement; (ii) evaluate habitat conditions of temporary stopovers facilitating long-distance dispersals, and (iii) achieve accurate connectivity estimates among populations. True dispersal events, as the primary movements facilitating gene flow and range expansion, should be treated separately in landscape permeability studies to effectively guide related conservation efforts.

KEYWORDS
connectivity, dispersal, habitat selection, Iberian lynx, landscape permeability, movement ecology, reintroduction, rewilding

1 | INTRODUCTION

A thorough understanding of the habitat features that animals select in heterogeneous and dynamic landscapes is highly valuable for effective wildlife conservation. For species requiring population reinforcements to persist or broaden their distribution range, the study of species–habitat relationships is paramount to identify suitable areas for translocations and/or reintroductions (Northrup et al., 2022; Osborne & Seddon, 2012). To maximize the success of reintroduction projects, it is especially relevant to determine landscape features that facilitate connectivity among populations (Zeller et al., 2012). More generally, understanding animals' relationships with anthropogenic land cover features that may hamper their dispersal or pose a risk for their survival (e.g. transport infrastructure and human settlements) is crucial for identifying animal adaptation strategies and improving conservation efforts (Berger-Tal & Saltz, 2014; Thorsen, Hansen, et al., 2022). Habitat selection analyses have hence been widely applied in animal ecology and are continually evolving to address the complexities of habitat-species relationships, considering factors, such as individual-specific responses (Muff et al., 2020), selection scales (DeCesare et al., 2012; Mateo Sánchez et al., 2014) and movement behaviours (Klappstein et al., 2023).

Numerous studies have delved into the variations in habitat selection between residential and non-residential movements (Elliot et al., 2014; Gastón et al., 2016; Palomares et al., 2000; Thorsen, Hansen, et al., 2022; Van Den Bosch et al., 2023), motivated by the need of accurately modelling landscape permeability and connectivity (Blazquez-Cabrera et al., 2016; Goicolea et al., 2021). Resident animals tend to select high-quality habitats to optimize fitness, favouring areas with conditions that best support their survival and reproductive success (Elliot et al., 2014; Palomares et al., 2000). Conversely, non-residential movements require traversing unfamiliar landscapes, often involving more plastic habitat selection—behavioural adjustments to better suit the conditions of their immediate environment—to tolerate less permeable, lower quality habitats (Elliot et al., 2014; Gastón et al., 2016; Palomares et al., 2000; Thorsen, Hansen, et al., 2022; Wong & Candolin, 2015). Exposure to lower quality habitats may increase mortality risks, including conspecific aggression, road mortality or human persecution (Bonte et al., 2012; Stamps, 2001).

While dispersal is the main process driving movements between meta-populations, facilitating gene flow and long-term viability (Clobert et al., 2012; Elliot et al., 2014), non-residential movements also respond to a spectrum of ecological needs. For instance, individuals may establish temporary residences while dispersing through the landscape (Beier, 1995; Zimmermann et al., 2005) or may embark on excursions beyond their home ranges for various purposes, such as finding mates, exploring or foraging (Kelly et al., 2020; Zimmermann et al., 2005), with

13652656, 0, Downloaded from https://besjournals.onlinelibrary.wiley.com/doi/10.1111/1365-2656.70099 by Test, Wiley Online Library on [21/07/2025]. See the Terms and Conditions (https://onlinelibrary.wiley.com/terms-and-conditions) on Wiley Online Library for rules of use; OA articles are governed by the applicable Creative Commons License

different habitat selection patterns during these processes (Hooven et al., 2023). Additionally, translocated individuals in reintroduction areas may undergo behavioural modification, including a greater diversity or prominence of certain movement phases (Cisneros-Araujo et al., 2024), and select different habitat features during their post-release exploratory movements before settling in a residence area (Berger-Tal & Saltz, 2014; Picardi et al., 2022). Despite the diverse processes underlying various non-residential movements, they are often grouped together in ecological research (Gastón et al., 2016; Goicolea et al., 2021; Rio-Maior et al., 2019; Rueda et al., 2021; Vanbianchi et al., 2018) and seldom distinguished in habitat selection analyses (Hooven et al., 2023). This lack of distinction may imply significant biases with yet unassessed implications for our understanding of habitat selection processes and for accurately informing subsequent management and conservation measures (Roever et al., 2014).

To provide novel insights into habitat selection, we investigated this process across five movement phases for a threatened carnivore, the Iberian lynx, *Lynx pardinus* (Temminck, 1827). This medium-sized solitary feline is native to the Iberian Peninsula and specializes in preying on the European rabbit *Oryctolagus cuniculus*. A sharp decline in rabbit numbers, together with poaching, habitat loss and fragmentation (Garrote, Fernández-López, et al., 2020; Guzmán, 2004), resulted in less than a 100 Iberian lynxes remaining in 2 isolated populations (Doñana-Aljarafe and Andujar-Cardeña). In response to this critical scenario, significant conservation efforts were implemented, including active habitat management, mortality mitigation and an extensive captive breeding, translocation and reintroduction programme (Rodriguez & Calzada, 2015; Simón et al., 2012). These measures have yielded substantial success, leading to an exponential recovery of the species, which currently surpasses 2000 individuals (year 2023 data) in 9 populations, 7 of which are reintroduced. Despite this progress, the species still faces challenges arising from habitat fragmentation in highly heterogeneous landscapes with a large share of agricultural and anthropogenic land uses (Gastón et al., 2016). This is particularly important when facing the longer term aim of recovering most of the species historical range in the Iberian Peninsula. Consequently, the primary objective of the ongoing species conservation efforts was to improve the connectivity among Iberian lynx populations and establish a self-sustainable and expanding meta-population (LIFE LYNXCONNECT, 2020).

The identification of suitable reintroduction areas for the Iberian lynx was informed by multiple studies that assessed its habitat requirements within the two populations (Doñana-Aljarafe and Andujar-Cardeña) that persisted over time (Fernández et al., 2003, 2006; Garrote, Fernández-López, et al., 2020; Palomares, 2001; Palomares et al., 2000). Nevertheless, habitat selection depends on availability and habitat use estimates obtained in one area may lead to poor predictions in other areas with different features (Aarts et al., 2013; Osborne & Seddon, 2012). Thus, the analysis of GPS data from multiple Iberian lynx populations revealed that individuals may positively select a wider range of habitats than previously thought, including heterogeneous agricultural areas like non-intensive olive groves with natural vegetation remnants (Gastón et al., 2016). This GPS database was obtained following the first reintroductions and primarily consisted of translocated Iberian lynxes tracked to assess their habituation to reintroduction areas, along with several individuals monitored within their native populations, providing extensive data on their movements and habitat selection (Cisneros-Araujo et al., 2024). These also allowed Gastón et al. (2016) to explore differences in habitat selection within and outside home ranges, demonstrating that during the latter, lynxes were more tolerant to anthropogenic features, which resulted in higher connectivity estimates in subsequent analyses using these improved habitat selection estimates (Blazquez-Cabrera et al., 2016).

Despite these advancements, no study has yet undertaken a comprehensive analysis of GPS movement data for the Iberian lynx that leverages the identification of various types of movements outside home ranges (Cisneros-Araujo et al., 2024). Such an analysis would allow to separately assess the species–habitat selection patterns during each of these movement phases. Among these, it is particularly important to specifically and separately focus on true dispersal events, which are the primary movements contributing to population connectivity and gene flow (Elliot et al., 2014), avoiding potential confusion with the species' habitat selection during other movement phases. Likewise, it is crucial to assess the habitat conditions of temporary stopovers that facilitate long dispersal events among populations. In summary, it remains unexplored how different processes driving Iberian lynx movements (e.g. excursions, dispersals and post-release dispersals) affect the species–habitat relationships and connectivity among populations.

To address these knowledge gaps, we analysed the largest Iberian lynx tracking dataset to date, encompassing GPS locations from 124 individuals across the Iberian Peninsula. Many of these lynxes were tracked during the translocation programme, providing a unique opportunity to study their habitat selection across several movement behaviours that are not commonly captured in stable populations. Instead, these behaviours are more frequently found in reintroduced populations that are not at equilibrium and show a higher diversity of movement tactics (Cisneros-Araujo et al., 2024). We modelled habitat selection and landscape permeability during five distinct movement phases: two residential phases (home ranges and transient residences) and three non-residential phases (excursions, dispersals and post-release dispersals). We accounted for individual variability in habitat responses and incorporated fine and broad habitat selection scales to capture habitat selection at two hierarchical levels, namely second- and fourth-order. We hypothesized that the Iberian lynx's habitat selection patterns would vary across movement phases (Gastón et al., 2016), even among different types of non-residential phases, as they respond to distinct life processes. Specifically, we expected that differences in tolerance and adaptations to anthropogenic features would be observed across movement phases, allowing for the navigation of the fragmented landscape and the settlement in safe and resource-rich areas.

13652656, 0, Downloaded from https://besjournals.onlinelibrary.wiley.com/doi/10.1111/1365-2656.70099 by Test, Wiley Online Library on [21/07/2025]. See the Terms and Conditions (https://onlinelibrary.wiley.com/terms-and-conditions) on Wiley Online Library for rules of use; OA articles are governed by the applicable Creative Commons License

2 | MATERIALS AND METHODS

2.1 | GPS telemetry dataset

We analysed a GPS telemetry dataset from 124 Iberian lynxes, comprising a total of 137,970 locations. The lynxes were collared between 2010 and 2023, with 19 individuals from native populations and 106 individuals following translocation. Of the translocated lynxes, 20 were wild individuals translocated from other populations (1 was also monitored in its natal range), and 86 were from captive breeding programmes. These captive-born individuals had no previous experience in the wild and were mostly subadults (<2 years old; Cisneros-Araujo et al., 2024). Before their release, captive-born lynxes underwent preparatory measures to facilitate their adaptation to life in the wild, including being raised in enclosures with natural vegetation, fed live prey (e.g. rabbits) and kept without human contact to encourage natural behaviour (Life+IBERLINCE, 2016). These measures have been shown to enable captive-born lynxes adopting similar space use and habitat selection patterns to those of free-ranging individuals (Cisneros-Araujo et al., 2024; Gastón et al., 2016). The dataset maintained a balanced sex ratio (62 males and 62 females). The GPS dataset had a sampling rate of 4 h. Methods for pre-processing GPS data are described in Cisneros-Araujo et al. (2024) and in the Supporting Information S1. To conduct subsequent analyses, we followed the methodological schema in Figure 1.

All capture and collaring procedures were conducted by certified technicians and veterinarians authorized by the competent environmental authorities of the regions involved (Junta de Andalucía, Junta de Comunidades de Castilla-La Mancha, Junta de Extremadura in Spain and Instituto da Conservação da Natureza e das Florestas in Portugal). These activities were carried out within the framework of authorized conservation and monitoring programs, specifically LIFE06NAT/E/000209, LIFE10NAT/ES/570 (IBERLINCE) and LIFE19NAT/ES/001055 (LYNXCONNECT), and in compliance with national and regional legal mandates. All capturing and animal handling procedures followed the sanitary and technical guidelines established by the Iberian Lynx Sanitary Advisory Panel (Grupo de Manejo Sanitario del Lince Iberico, 2014) to ensure animal welfare.

2.2 | Classification of movement phases

We separately considered five movement phases for our habitat selection analyses (Table 1; Figure 1). Methods for classifying movement phases are fully described in Cisneros-Araujo et al. (2024) and in the Supporting Information S2. We did not test for sex differences as previous studies have shown that habitat selection in the Iberian lynx is not significantly influenced by sex (Palomares, 2001; Palomares et al., 2000), but rather by the behavioural state of individuals (Gastón et al., 2016; Palomares, 2001; Palomares et al., 2000), highlighting the importance of movement phases in shaping habitat selection.

2.3 | Environmental variables

We considered seven environmental variables that may influence the habitat selection of the Iberian lynx (Fernández et al., 2006; Gastón et al., 2016, 2019; Palomares, 2001; Palomares et al., 2000). The species predominantly inhabits natural vegetation mosaics, which provide both refuge and prey availability, as rabbits find shelter in bushes and forage in grasslands. We characterized mosaics using the (1) tree cover density (2018; 10 m; European Environment Agency, 2020c); (2) shrubland cover (2018; 10 m) obtained from CLC+ Backbone 2018 (European Environment Agency, 2023); and (3) grassland cover density (2018; 10 m; European Environment Agency, 2020a). We also included (4) terrain ruggedness (1 arc-second, ~30 m), obtained according to Riley et al. (1999) from the SRTM digital elevation model (EROS, 2017), as a proxy for refuge (e.g. outcrops). As constraints on the species' presence, we considered (5) cropland cover density, excluding tree crops (2018; 100 m, Copernicus Global Land Service; Buchhorn et al., 2020); (6) roads (OpenStreetMap contributors, 2017); and (7) imperviousness density (European Environment Agency, 2020b). The imperviousness density layer works as a proxy of large human infrastructure and already includes highway density data. Thus, to avoid potential partial redundancy and a high correlation with the imperviousness layer, highways were not included in the roads layer.

All variables with pixels finer than 100 m were aggregated to a 100 m pixel size using the average of pixel values. Tree cover, grassland and imperviousness density layers were averaged to maintain a continuous 0–100 scale, while shrubland, originally a presence/absence binary variable, reflects its percentage cover at 100 m. As a result, all layers (except the roads and terrain ruggedness layer) had values ranging between 0 and 100, indicating the density of each land cover per pixel. Roads were rasterized as a binary variable at 100 m pixel resolution (see Section 2.4.2 for the obtention of road density values using focal means). All pairs of environmental layers had a correlation of <0.45 (Spearman's ρ^2; Spearman, 1961). A summary of the characteristics of environmental variables across movement phases is provided in Table S4.

2.4 | Habitat selection analyses

We adopted a matched used-available sampling design to study how the habitat selection by the Iberian lynx varied depending on the movement phase at two scales of analysis. First, we conducted analyses at the 'landscape scale' to evaluate the environmental characteristics of resident ranges (resident range selection analysis) and non-residential movement paths (path selection analysis) relative to those that were available in their surrounding landscape. We used the term 'landscape scale' to refer to habitat selection where availability is defined by the broader surrounding landscape relative to each observed movement path (cf. second-order habitat selection; Johnson, 1980). Second, we analysed habitat selection at the 'local scale' to evaluate how the

13652656, 0, Downloaded from https://besjournals.onlinelibrary.wiley.com/doi/10.1111/1365-2656.70099 by Test, Wiley Online Library on [21/07/2025]. See the Terms and Conditions (https://onlinelibrary.wiley.com/terms-and-conditions) on Wiley Online Library for rules of use; OA articles are governed by the applicable Creative Commons License

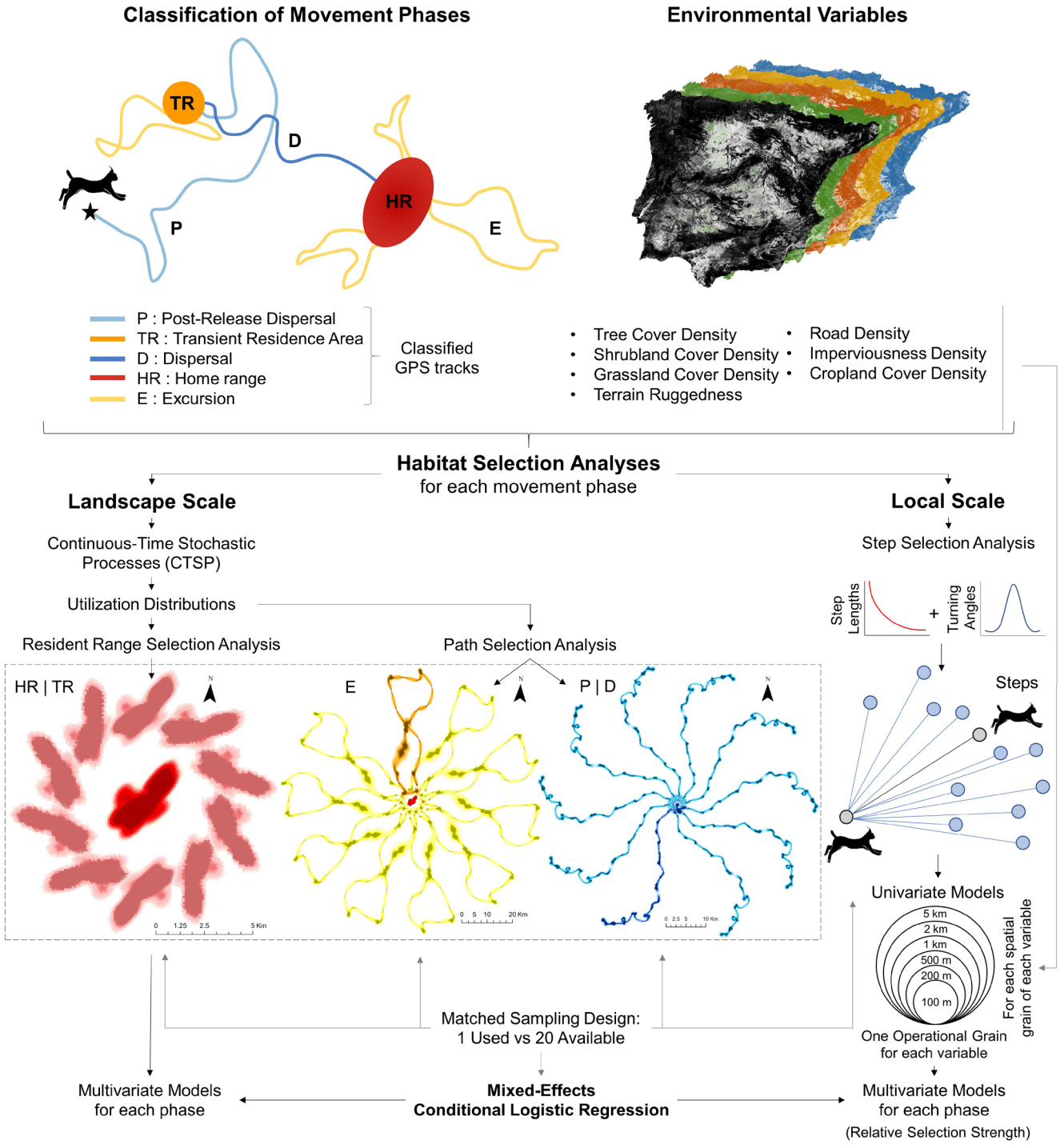


FIGURE 1 Schema of the workflow of methods, which included the classification of movement phases, the estimation of environmental variables and the habitat selection analyses at landscape and local scales. See Figure S1 for an illustrative example of a classified movement path.

lynxes responded to their environment by comparing the habitat characteristics of locations that were selected by the animal with available locations that were reachable but not selected (step selection analysis). Therefore, we refer to habitat selection at the 'local scale' when availability is defined over shorter distances that lynxes can travel between consecutive locations (cf. fourth-order habitat selection; Johnson, 1980). For subsequent movement analyses, we used *R* software (version 4.2.0; R Core Team, 2022), and a list of references of R packages utilized in the analyses is provided in Supporting Information S3.

2.4.1 | Habitat selection at the landscape scale

For habitat selection analysis at the landscape scale, we used two types of selection analyses according to the space-use characteristics

13652656, 0, Downloaded from https://besjournals.onlinelibrary.wiley.com/doi/10.1111/1365-2656.70099 by Test, Wiley Online Library on [21/07/2025]. See the Terms and Conditions (https://onlinelibrary.wiley.com/terms-and-conditions) on Wiley Online Library for rules of use; OA articles are governed by the applicable Creative Commons License

TABLE 1 Summary and description of movement phases.

Movement phases		Description
Residence areas (clusters of GPS locations)	Home range	Residence areas lasting at least 105 days (see Cisneros-Araujo et al., 2024)
	Transient residence	Abandoned residence areas after being used at least 10 days and < 105 days
Non-residential movements	Excursion	Movements away from a residence area but that eventually return to the same residence area
	Post-release dispersal	Movements from the release point to the first residence area or to the end of the monitoring period
	Dispersal	Movements between two residence areas, or lasting at least 10 days and not ending in a residence area before the monitoring ended

of movement phases. For movement phases that showed restricted space use and range residency (i.e. home ranges and transient residences), we used a resident range selection analysis (similar to a path selection analysis but adapted for resident areas; Cushman & Huettmann, 2010). Conversely, for non-residential movement phases showing no restricted space use and directional persistence (i.e. excursions, transitions and post-release dispersals) we used a path selection analysis (Cushman & Huettmann, 2010).

In both cases, we fitted continuous-time stochastic processes (CTSP) to the location series of every individual's movement phase to estimate their utilization distributions (UD), which were considered as 'used' samples in our matched sampling design. We used the *ctmm R* package to fit CTSP, accounting for the autocorrelation among observations in the GPS dataset (Calabrese et al., 2016; Fleming et al., 2018; Noonan et al., 2019). We obtained starting parameter values from semi-variance functions to fit a set of candidate models that varied according to the movement phase.

To estimate the UD for true locations in the resident range selection analysis, we considered the following models: the independent identically distributed (IID) process, which assumes no correlation in positions and velocities; the Ornstein–Uhlenbeck (OU) process, which features correlated positions and restricted space use; the Ornstein–Uhlenbeck Foraging (OUF) process, which, as the OU process, considers range-residency but also takes into account correlated velocities; and a special case of the OUF model (OUf) in which the position and velocity autocorrelation timescales are identical (Calabrese et al., 2016). Among candidate models, we selected the most parsimonious one to estimate the UD by applying optimally weighted and area-corrected autocorrelated kernel density estimators (wAKDE) (Fleming et al., 2018). We repeated this procedure individually for each residence area. From each wAKDE, we used the probability mass function (PMF) to get a raster layer of relative frequencies of use. Next, we artificially generated 'available' UDs for each used distribution, which represent alternative range areas that were available to the animal in the landscape but that were not selected as residence. For this purpose, we placed generated distributions at a distance equal to two times the radius of the 99% wAKDE and rotated them around the actual residence area with a constant angle increment of 18° to get 20 available UDs (see illustration in Figure 1).

To estimate the UD for true locations in the path selection analysis, we considered two candidate models: the Brownian motion (BM) process, which features autocorrelated positions, and the Integrated OU (IOU) process that includes autocorrelated positions and velocities (Calabrese et al., 2016). We only considered paths lasting more than 24 h to facilitate parameter estimation. For each path, we used the CTSP model (BM or IOU, see below) and the Kriging method to obtain the UD, which was derived from all possible trajectories conditioned on the GPS locations that compose each movement path (Fleming et al., 2015). For each path, we prioritized the use of the continuous-velocity IOU process for estimating UDs due to its higher precision (Fleming et al., 2015). We used the BM process for trajectories which could not estimate continuous velocities. From each UD, we again estimated raster layers through the PMF. We matched each path UD with 20 available distributions. The estimation of available samples slightly depended on the movement phase and aimed to represent alternative movement paths that were available to the animal in the landscape. We rotated each path UD by applying a constant angular increment of 17.14° and pivoting around the centroid of the corresponding residence area (excursions) or the start of the path (dispersal and post-release dispersal; see illustration in Figure 1). We report the results on the CTSP used to estimate UD at the landscape scale in Supporting Information S4.

Once used and available UDs were estimated, we multiplied the pixel utilization probabilities of each distribution by each environmental raster layer and summed the returned values. To standardize each environmental variable, we subtracted their mean and divided it by their standard deviation.

We then analysed habitat selection in each movement phase following the approach of Muff et al. (2020). We fitted mixed-effects conditional logistic regression models to the matched used and available set for each phase. In all models, we included all previously mentioned environmental variables as covariates and individual-specific random slopes for each covariate to account for individual variation in habitat selection. To this end, we used the *glmmTMB* R package to fit a Poisson model—with equivalent likelihood to a conditional logistic regression—in which intercepts are modelled as random effects with a fixed variance of 10^6 (Muff et al., 2020).

13652656, 0, Downloaded from https://besjournals.onlinelibrary.wiley.com/doi/10.1111/1365-2656.70099 by Test, Wiley Online Library on [21/07/2025]. See the Terms and Conditions (https://onlinelibrary.wiley.com/terms-and-conditions) on Wiley Online Library for rules of use; OA articles are governed by the applicable Creative Commons License

2.4.2 | Habitat selection at the local scale

We analysed habitat selection at the local scale using step selection functions, which offer a robust framework for assessing fine-scale species interactions with their environment (Fieberg et al., 2021; Muff et al., 2020; Thurfjell et al., 2014; Figure 1). For each observed step, we matched 20 available random steps. To generate random steps, we fitted a Gamma distribution of observed step lengths and a Von Mises distribution of observed turning angles, both based on each movement phase. We only retained steps having a regular 4-h sampling rate for the step selection analyses. The procedures described herein were carried out using the functions in the *amt* R package.

Then, we assessed the spatial grain at which each environmental variable best matched Iberian lynx selection at the local scale. For this purpose, we considered a gradient of spatial grains for each environmental variable, obtaining spatial layers using focal means with six radii (100, 200, 500, 1000, 2000 and 5000 m), each representing a specific Iberian lynx grain of interaction with its environment. We extracted the values of each variable's spatial grain at the end location of each step for both used and available locations. We standardized extracted values by subtracting the mean and dividing by the standard deviation of each variable. Then, we used mixed-effects conditional logistic regression (Muff et al., 2020) with individual-specific random slopes to fit univariate models for every spatial grain. Among each variable's univariate models, we selected the model with the lowest AICc score, from which we designated the variable's operational spatial grain—that is the grain that best represented the Iberian lynx habitat selection.

Next, we fitted phase-specific multivariable habitat models using mixed-effects conditional logistic regression (Muff et al., 2020) to account for variations in habitat selection among individuals. We included standardized environmental variables at their operational grain as covariates. For all environmental covariates, we added a quadratic term to allow for non-linear relationships. After fitting multivariable models, we used the relative selection strength (Avgar et al., 2017; Fieberg et al., 2021) to quantify the magnitude of selection of each environmental variable during each movement phase. To achieve this, we used the phase-specific models to make population-level predictions across the range of each covariate, while keeping the remaining covariates fixed at their means. As a reference for comparison, we used a hypothetical location represented by the means of each environmental variable calculated only from the available locations of each model. Last, we compared the predictions of each covariate with the predictions at the reference location to obtain relative selection strengths for each environmental variable and each movement phase.

3 | RESULTS

Iberian lynxes exhibited all five movement phases considered in the classification (Table 2). Only 6% of all lynxes ($n = 7$) did not establish any residence area during the monitoring period (256 days, SD = 213).

3.1 | Habitat selection at the landscape scale

Analyses at the landscape scale revealed several differences in the Iberian lynx habitat selection depending on the movement phase (Figure 2; Table S1). Transient residences were established in areas characterized by significantly lower road density than in the available landscape, which was not found for home ranges. Despite this difference, transient residences and home ranges mostly shared habitat choices at the landscape scale. For instance, both types of residences showed a significant selection of areas with non-dominance of the shrub cover, which was not observed during non-residential phases.

Considering movements outside residence areas, excursion paths went through areas with fewer roads and human infrastructure density than in the available landscape. Despite showing an overall negative selection, dispersal paths did not show a significant avoidance of these anthropogenic features. Post-release dispersal paths resembled dispersal events but showed significant avoidance of roads (90% confidence). No substantial differences were found among non-residential phases for terrain ruggedness and vegetation (tree, shrubland and grassland) cover density variables, all showing non-significant habitat selection. Nonetheless, low tree cover areas were preferred during excursions (90% confidence). Additionally, non-tree croplands were consistently avoided during both residential and non-residential movement phases, highlighting a shared pattern in habitat avoidance.

3.2 | Habitat selection at the local scale

Univariate models supported a 100 m grain size for all environmental variables except for the imperviousness and road density variables,

TABLE 2 Summary of Iberian lynx movement phases. No. and % of individuals refer to the total number and percentage of individuals that experienced each phase.

Movement phase	No. of locations	No. of 4-h steps	No. of events	No. of individuals	% of individuals
Home ranges	85,752	57,033	77	72	58
Transient residences	10,822	6126	77	47	38
Excursions	13,652	8978	539	91	73
Post-release dispersals	9509	6809	73	71	70
Dispersals	4776	3051	56	43	35

13652656, 0, Downloaded from https://besjournals.onlinelibrary.wiley.com/doi/10.1111/1365-2656.70099 by Test, Wiley Online Library on [21/07/2025]. See the Terms and Conditions (https://onlinelibrary.wiley.com/terms-and-conditions) on Wiley Online Library for rules of use; OA articles are governed by the applicable Creative Commons License

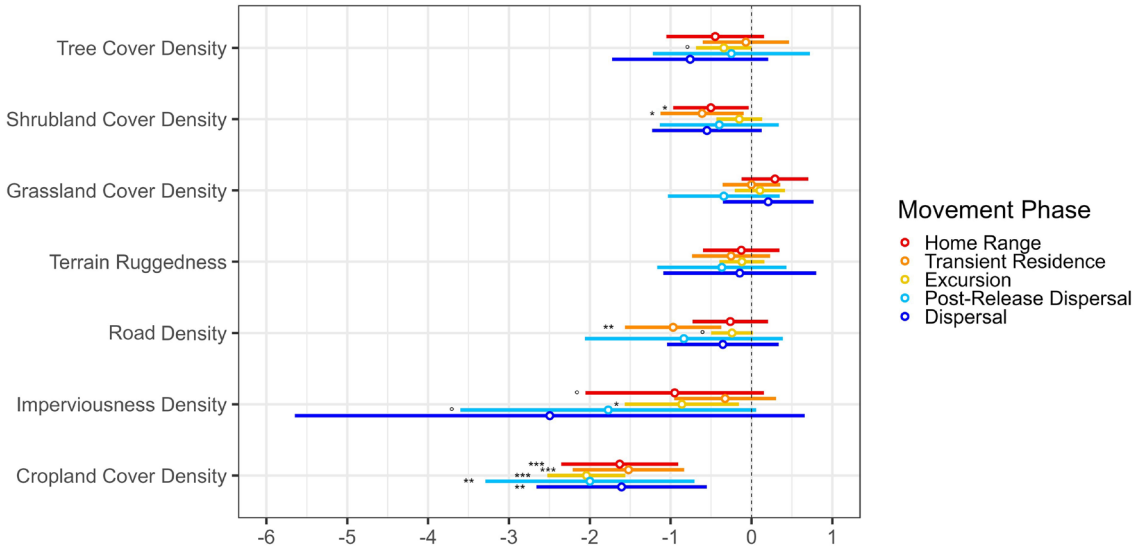


FIGURE 2 Coefficients (circles) of each environmental variable with 95% confidence intervals (horizontal brackets) for each movement phase-specific model at the landscape scale. Codes for the levels of significance of coefficients are: *p*-values < 0.001 ('***'), < 0.01 ('**'), < 0.05 ('*') and < 0.01 ('°').

which were selected at 500 and 1000 m, respectively (Figure 3; Table S2). Empirical distributions of step lengths (Gamma) and turning angles (von Mises) are illustrated in Figure S2. Croplands and anthropogenic variables exhibited linear negative responses while natural vegetation and terrain ruggedness variables displayed quadratic responses across movement phases (Figure 3). Model summaries are reported in Table S3.

Models at the local scale showed notable differences and some similarities in Iberian lynx habitat selection across movement phases (Figure 3). For instance, lynxes consistently selected low-to-medium tree cover densities across all movement phases but showed a significantly stronger tendency towards higher tree densities within their home ranges (Figure 3a). Resident lynxes also selected low-to-medium shrubland cover, while non-residential lynxes tended to favour higher shrubland densities, particularly during post-release dispersal (Figure 3b). Likewise, grasslands were selected at low-to-medium covers, but dispersing lynxes preferred slightly higher densities (Figure 3c). Importantly, dispersing lynxes selected terrain with medium ruggedness, while resident lynxes preferred flatter areas (Figure 3d).

Distinct patterns emerged in response to roads, differing significantly between residential and non-residential phases. Non-residential lynxes showed a non-significant gradual negative trend, while residents exhibited a steep negative response (Figure 3e). The response to imperviousness density was similar to roads, but residential lynxes avoided this cover more intensively. In contrast to roads, lynxes significantly avoided areas with large human infrastructure (including highways) while taking excursions. Lynxes dispersing after being released significantly avoided this cover too but showed more tolerance to higher densities. Conversely, dispersing individuals did not show a significant avoidance of large infrastructures (Figure 3f). Last, areas dominated by non-tree crops were consistently avoided in all movement phases. Despite this strong avoidance, lynxes had some tolerance for areas with a low cover of cropland, particularly during excursions and residential phases (Figure 3g).

4 | DISCUSSION

Our findings supported our hypothesis that the Iberian lynx's habitat selection patterns would vary across movement phases, even among non-residential phases. Generally, lynxes favoured areas with low-to-medium densities of trees, shrubs and grasslands, though specific density choices varied by movement phase. For instance, lynxes particularly favoured features providing refuge during post-release dispersals compared with residential phases, showing a shift in habitat selection. Moreover, lynxes avoided human infrastructure more strongly during residential phases and showed weaker avoidance during non-residential movements, especially during dispersals, evidencing their remarkable dispersal plasticity. These differences were more apparent at the local scale, while responses to habitat features at the landscape scale were limited, possibly due to high interindividual variability and the relatively fine-grained heterogeneity of the landscape. These findings underscore the importance of considering specific movement phases and selection scales in habitat selection, landscape permeability and connectivity studies, especially for reintroduced populations and translocated individuals.

4.1 | Selection of mosaiced and low-disturbance habitats during residency

Residential habitat selection patterns were characterized by the choice of low-to-medium densities of trees, shrublands and grasslands.

13652656, 0, Downloaded from https://besjournals.onlinelibrary.wiley.com/doi/10.1111/1365-2656.70099 by Test, Wiley Online Library on [21/07/2025]. See the Terms and Conditions (https://onlinelibrary.wiley.com/terms-and-conditions) on Wiley Online Library for rules of use; OA articles are governed by the applicable Creative Commons License

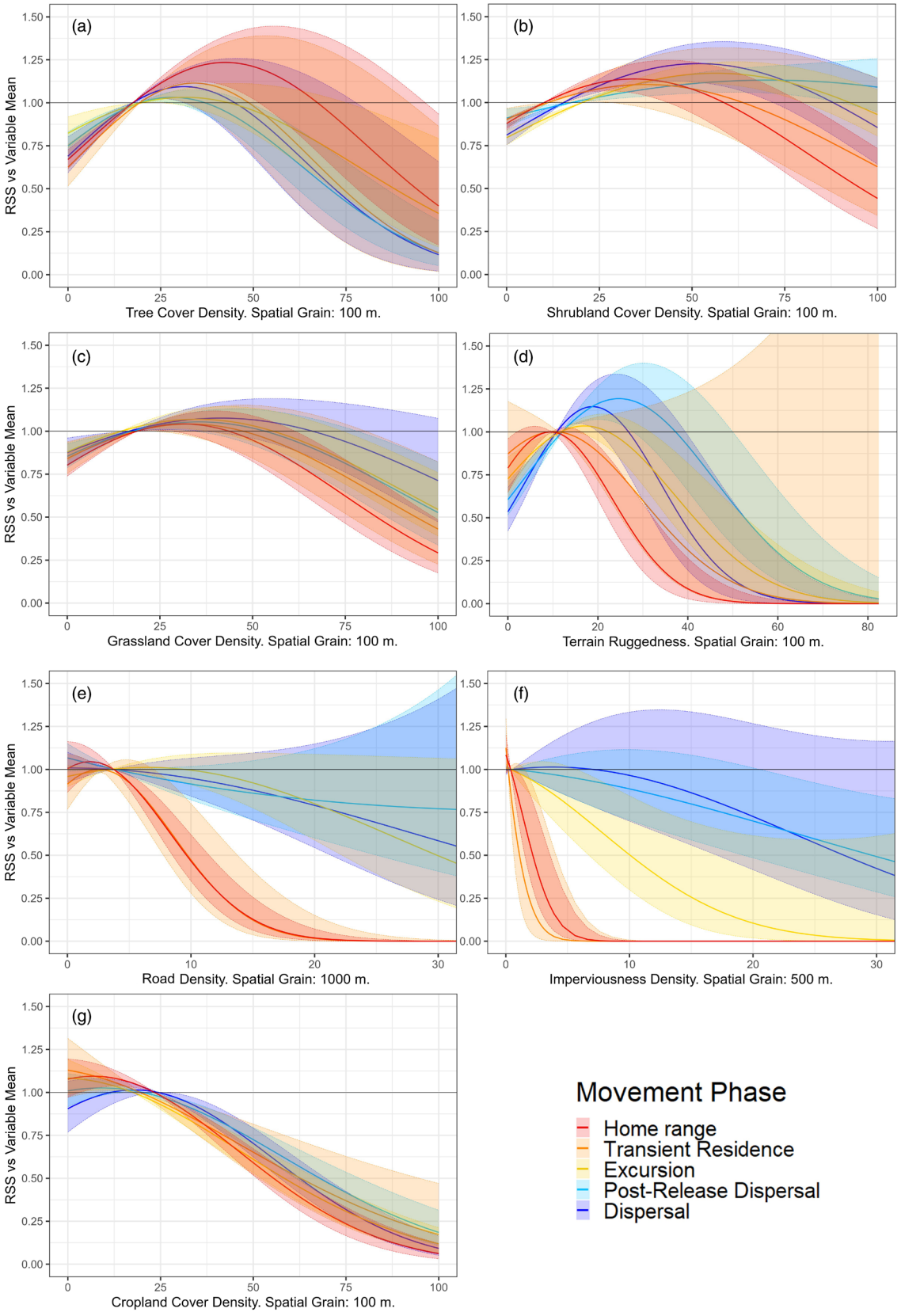


FIGURE 3 Curves of the relative selection strength of environmental variables of each phase-specific habitat model at the local scale. Solid lines and ribbons represent the mean relative selection strength and 95% CIs, respectively. Reference for the relative selection strength is a hypothetical location with a value equal to the mean of the corresponding variable estimated only from available locations (see Section 2.4.2). Environmental variables are shown as follows: (a) tree cover density, (b) shrubland cover density, (c) grassland cover density, (d) terrain ruggedness, (e) road density, (f) imperviousness density and (g) cropland cover density.

13652656, 0, Downloaded from https://besjournals.onlinelibrary.wiley.com/doi/10.1111/1365-2656.70099 by Test, Wiley Online Library on [21/07/2025]. See the Terms and Conditions (https://onlinelibrary.wiley.com/terms-and-conditions) on Wiley Online Library for rules of use; OA articles are governed by the applicable Creative Commons License

This suggests a marked affinity for areas with intermixed natural vegetation covers (Gastón et al., 2016, 2019; Palomares, 2001) where transitions between woody vegetation and grasslands are frequent. Lynxes may be positively selecting these areas because of their association with high rabbit densities (Fernández et al., 2003). Rabbits are also benefitted by flatter terrain and tall vegetation covers in these mosaiced habitats (Calvete et al., 2004; Palomares, 2001). Tall vegetation provides enough space for grass growth, and its roots facilitate the excavation of rabbit warrens (Palomares, 2001, 2003). Therefore, the lynx's preference for rabbit-abundant areas may mediate its positive selection of low rugged terrain and significant tree cover within home and transient ranges.

Lynxes established home ranges in areas with infrastructure densities similar to those of the available landscape. This tendency to show lower infrastructure avoidance is probably a result of the highly heterogeneous landscape where infrastructures are common and intertwine natural cover, making it difficult to reveal habitat selection patterns at broad scales of analysis. This pattern reflects the inherent challenges associated with establishing large home ranges (average size: 11.6 km^2, 95% CI: 9.1–14.6; Cisneros-Araujo et al., 2024) in a landscape with extensive infrastructure. Conversely, during the establishment of transient residences, roads were avoided, a pattern potentially attributed to their smaller average size (4.0 km^2, 95% CI: 2.6–6.0; Cisneros-Araujo et al., 2024), allowing their establishment in areas with minimal road overlap. Moreover, the avoidance of roads can be attributable to the cautious behaviour observed in translocated individuals post-release (Cisneros-Araujo et al., 2024), with roads limiting their space use in transient residences.

Nevertheless, at the local scale, resident Iberian lynxes did exhibit a strong aversion to infrastructure (Gastón et al., 2016). This behaviour suggests that despite the challenges of establishing home ranges in areas with minimal anthropogenic influence, lynxes adapted to human-dominated landscapes by learning the locations of infrastructure and actively avoiding them within their residence areas (Bouyer et al., 2015; Thorsen, Bischof, et al., 2022). This result underscores the essential role of spatial memory in shaping their residential movements (Ranc et al., 2022), especially for individuals settling in a novel environment, as the greatest majority of individual lynxes here considered (Cagnacci, 2023).

Lynxes consistently avoided high densities of non-tree cover croplands at both spatial scales, indicating a clear avoidance of such environments when settling residence or navigating the landscape. This pattern of avoidance aligns with previous habitat selection studies on the Iberian lynx (Gastón et al., 2016; Palomares et al., 2000). However, it is necessary to emphasize that agricultural tree covers, such as olive groves, may be positively selected by lynxes as long as there is enough natural vegetation providing refuge (Garrote, Bueno, et al., 2020; Gastón et al., 2016).

Generally, we observed common habitat selection patterns in both types of residence areas (transient and permanent), suggesting that prevailing habitat conditions may not be the primary factor leading to the abandonment of transient residences and that lynxes do not settle for low-quality habitat when inhabiting an area temporarily. Alternative factors, such as intraspecific competition (Ferreras et al., 1997, 2004) or absence of mating conspecifics (Kanda et al., 2019; Vogt et al., 2014) could potentially be triggering the abandonment of transient residences and should be carefully evaluated in future research.

4.2 | Variabilities among non-residential movements

Our results showed a significant avoidance of human infrastructure during excursions as well as post-release dispersals, although to a lesser extent. However, no significant response to human infrastructure was observed during dispersals, highlighting the functional disparity in the responses to environmental variables between non-residential phases (Hooven et al., 2023). This dispersal plasticity and tolerance to human features has been observed in multiple carnivores (Abrahms et al., 2017; Barry et al., 2020; Elliot et al., 2014; Gastón et al., 2016) and may be due to several factors, such as dispersers moving through unfamiliar environments (e.g. lacking awareness of corridor areas with higher quality habitats; Barry et al., 2020), adopting higher risk behaviours (Barry et al., 2020; Cote et al., 2010; Stamps, 2001) or selecting areas with higher human influence to avoid intraspecific conflict and injury from other lynxes (Farhadinia et al., 2020; Smith, 1993; Zimmermann et al., 2005), despite these areas being less favourable on other factors.

Nevertheless, dispersers may have adapted to unfamiliar environments by prioritizing refuge availability (Bouyer et al., 2015). This adaptation is evident in their increased selection of rugged terrain, where there is typically an increased availability of resting sites (Filla et al., 2017; Signer et al., 2019). This pattern is also consistent with their marked selection of medium and high densities of shrubland, another important source of refuge for lynxes (Palomares et al., 2000). Prioritizing refuge during dispersal may also be linked to energy management, with lynxes selecting resting sites to recover before resuming their journey (Farhadinia et al., 2020). Interestingly, their heightened selection of shrubland and rugged terrain was particularly pronounced during the post-release dispersal phase, possibly indicating that they might act more cautiously by seeking more shelter in response to the stress associated with the handling and translocation process, or the exposure to an unknown environment.

4.3 | Implications for landscape permeability modelling and conservation

Considering the higher behavioural plasticity of dispersers in response to human infrastructure, most landscape permeability models may underestimate the connectivity of the species even if movements within and outside home ranges are considered (Blazquez-Cabrera et al., 2016; Gastón et al., 2016). Consequently, as dispersal represents one of the primary processes facilitating connectivity (Clobert et al., 2012; Elliot et al., 2014), we advocate

13652656, 0, Downloaded from https://besjournals.onlinelibrary.wiley.com/doi/10.1111/1365-2656.70099 by Test, Wiley Online Library on [21/07/2025]. See the Terms and Conditions (https://onlinelibrary.wiley.com/terms-and-conditions) on Wiley Online Library for rules of use; OA articles are governed by the applicable Creative Commons License

for their exclusive use in the estimation of landscape resistance surfaces for modelling functional connectivity. Failing to classify non-residential movements may result in biased conclusions on how populations are effectively connected and thus may potentially lead to unreliable connectivity planning (Elliot et al., 2014).

Besides differentiating movement phases, the incorporation of other key factors in habitat selection—such as selection scales, non-linear habitat responses, interindividual variability and environmental heterogeneity across the species range—allowed our study to provide detailed and robust habitat selection estimates that are highly valuable for the effective management of Iberian lynx habitats. Specifically, the identification of precise habitat selection thresholds for each environmental variable and movement phase is instrumental for developing habitat conservation and restoration measures within stable populations, as well as for identifying suitable areas for future reintroductions. In planning reintroductions, managers should consider not only residential habitat selection patterns but also account for lynx habitat requirements during the post-release dispersal phase. For instance, selecting release sites in areas with abundant refuges (e.g. shrub and rocky cover) may be essential to support the short-term adaptation of translocated individuals. Additionally, outreach programmes should be implemented in the surroundings of release and reintroduction areas, as lynxes showed lower infrastructure avoidance during non-residential movement phases.

Our findings underscore the importance of movement phase-specific habitat selection models to disentangle species–habitat relationships and develop targeted conservation and restoration measures for the Iberian lynx and other carnivores. These findings hold particular relevance for ongoing conservation efforts (project LIFE LYNXCONNECT), offering valuable guidance for enhancing population connectivity and identifying suitable areas for future reintroductions aimed at expanding and recovering the species' historical range.

AUTHOR CONTRIBUTIONS

Pablo Cisneros-Araujo: Conceptualization; methodology; formal analysis; data curation; writing—original draft; writing—review and editing; visualization; project administration; funding acquisition; resources; investigation; software. **German Garrote**: Conceptualization; data curation; writing—review and editing; project administration; funding acquisition; resources; investigation; supervision. **Andrea Corradini**: Conceptualization; methodology; writing—review and editing; investigation. **Francesca Cagnacci**: Conceptualization; methodology; writing—review and editing; resources; investigation; supervision. **Mohammad S. Farhadinia**: Conceptualization; methodology; writing—review and editing. **Javier Salcedo**, **Pedro Sarmento**, **Juan Francisco Sánchez** and **María Jesús Palacios**: Data curation; resources; writing—review and editing; funding acquisition. **Juan Ignacio García-Viñás**: Supervision; funding acquisition; writing—review and editing. **Santiago Saura**: Conceptualization; writing—review and editing; project administration; resources; investigation; supervision. **Aitor Gastón**: Conceptualization; methodology; writing—review and editing; project administration; funding acquisition; resources; investigation; supervision.

ACKNOWLEDGEMENTS

We would like to thank all partners from current and past Iberian lynx LIFE projects (LIFE06NAT/E/000209, LIFE10NAT/ES/570 IBERLINCE and LIFE19NAT/ES001055 LYNXCONNECT), particularly to Junta de Andalucía (JA), Junta de Extremadura (JuntaEx), Gobierno de Castilla-La Mancha (JCCM) and Instituto da Conservaçaõ da Natureza e das Florestas (ICNF), for sharing the species telemetry data. We also thank the UPM for funding Pablo Cisneros-Araujo's PhD grant, and Panthera Corporation for funding several GPS collars through the Small Cat Action Fund. Andrea Corradini and Francesca Cagnacci contributed to this work partly under the support of NBFC to Fondazione Edmund Mach, funded by the Italian Ministry of University and Research, PNRR, Missione 4 Componente 2, 'Dalla ricerca all'impresa', Investimento 1.4, D.D. 1034 17/06/2022, Project CN00000033. This manuscript reflects only the authors' views and opinions, neither the European Union nor the European Commission can be considered responsible for them.

CONFLICT OF INTEREST STATEMENT

The authors declare that they have no known competing financial interests or personal relationships that could have influenced the work reported in this article.

DATA AVAILABILITY STATEMENT

The data used in this study are guarded by the JA, JuntaEx, JCCM and ICNF, but restrictions apply to their availability, which were used here under licence, and so are not publicly available. Data are however available from the owners if requested with justification of use.

STATEMENT ON INCLUSION

Our study comprises authors from various countries, including scientists and conservationists from Spain and Portugal, where the study was conducted. Several conservationists from key partners of the ongoing species conservation project (LIFE LynxConnect) actively participated in the research and evaluation of obtained results. Results of this study have been and will be shared among partners of the LIFE project, as well as among other relevant stakeholders in the conservation of the Iberian lynx.

ORCID

Pablo Cisneros-Araujo https://orcid.org/0000-0001-8326-931X

REFERENCES

Aarts, G., Fieberg, J., Brasseur, S., & Matthiopoulos, J. (2013). Quantifying the effect of habitat availability on species distributions. *Journal of Animal Ecology*, *82*(6), 1135–1145. https://doi.org/10.1111/1365-2656.12061

Abrahms, B., Sawyer, S. C., Jordan, N. R., McNutt, J. W., Wilson, A. M., & Brashares, J. S. (2017). Does wildlife resource selection accurately inform corridor conservation? *Journal of Applied Ecology*, *54*(2), 412–422. https://doi.org/10.1111/1365-2664.12714

Avgar, T., Lele, S. R., Keim, J. L., & Boyce, M. S. (2017). Relative selection strength: Quantifying effect size in habitat- and step-selection inference. *Ecology and Evolution*, *7*(14), 5322–5330. https://doi.org/10.1002/ece3.3122

13652656, 0, Downloaded from https://besjournals.onlinelibrary.wiley.com/doi/10.1111/1365-2656.70099 by Test, Wiley Online Library on [21/07/2025]. See the Terms and Conditions (https://onlinelibrary.wiley.com/terms-and-conditions) on Wiley Online Library for rules of use; OA articles are governed by the applicable Creative Commons License

Barry, T., Gurarie, E., Cheraghi, F., Kojola, I., & Fagan, W. F. (2020). Does dispersal make the heart grow bolder? Avoidance of anthropogenic habitat elements across wolf life history. *Animal Behaviour*, *166*, 219–231. https://doi.org/10.1016/j.anbehav.2020.06.015

Beier, P. (1995). Dispersal of juvenile cougars in fragmented habitat. *The Journal of Wildlife Management*, *59*(2), 228. https://doi.org/10.2307/3808935

Berger-Tal, O., & Saltz, D. (2014). Using the movement patterns of reintroduced animals to improve reintroduction success. *Current Zoology*, *60*(4), 515–526. https://doi.org/10.1093/czoolo/60.4.515

Blazquez-Cabrera, S., Gastón, A., Beier, P., Garrote, G., Simón, M. Á., & Saura, S. (2016). Influence of separating home range and dispersal movements on characterizing corridors and effective distances. *Landscape Ecology*, *31*(10), 2355–2366. https://doi.org/10.1007/s10980-016-0407-5

Bonte, D., Van Dyck, H., Bullock, J. M., Coulon, A., Delgado, M., Gibbs, M., Lehouck, V., Matthysen, E., Mustin, K., Saastamoinen, M., Schtickzelle, N., Stevens, V. M., Vandewoestijne, S., Baguette, M., Barton, K., Benton, T. G., Chaput-Bardy, A., Clobert, J., Dytham, C., … Travis, J. M. J. (2012). Costs of dispersal. *Biological Reviews*, *87*(2), 290–312. https://doi.org/10.1111/j.1469-185X.2011.00201.x

Bouyer, Y., San Martin, G., Poncin, P., Beudels-Jamar, R. C., Odden, J., & Linnell, J. D. C. (2015). Eurasian lynx habitat selection in human-modified landscape in Norway: Effects of different human habitat modifications and behavioral states. *Biological Conservation*, *191*, 291–299. https://doi.org/10.1016/j.biocon.2015.07.007

Buchhorn, M., Smets, B., Bertels, L., Roo, B. D., Lesiv, M., Tsendbazar, N.-E., Herold, M., & Fritz, S. (2020). Copernicus global land service: Land cover 100m: Collection 3: Epoch 2018: Globe (version V3.0.1) [dataset]. *Zenodo*. https://doi.org/10.5281/ZENODO.3518038

Cagnacci, F. (2023). Memory pays off. *Nature Ecology & Evolution*, *7*(3), 316–317. https://doi.org/10.1038/s41559-022-01968-9

Calabrese, J. M., Fleming, C. H., & Gurarie, E. (2016). Ctmm: An R package for analyzing animal relocation data As a continuous-time stochastic process. *Methods in Ecology and Evolution*, *7*(9), 1124–1132. https://doi.org/10.1111/2041-210X.12559

Calvete, C., Estrada, R., Angulo, E., & Cabezas-Ruiz, S. (2004). Habitat factors related to wild rabbit conservation in an agricultural landscape. *Landscape Ecology*, *19*(5), 533–544. https://doi.org/10.1023/B:LAND.0000036139.04466.06

Cisneros-Araujo, P., Garrote, G., Corradini, A., Farhadinia, M. S., Robira, B., López, G., Fernández, L., López-Parra, M., García-Tardío, M., Arenas-Rojas, R., Del Rey, T., Salcedo, J., Sarmento, P., Sánchez, J. F., Palacios, M. J., García-Viñás, J. I., Damiani, M. L., Hachem, F., Gastón, A., & Cagnacci, F. (2024). Born to be wild: Captive-born and wild Iberian lynx (*Lynx pardinus*) reveal space-use similarities when reintroduced for species conservation concerns. *Biological Conservation*, *294*, 110646. https://doi.org/10.1016/j.biocon.2024.110646

Clobert, J., Baguette, M., Benton, T. G., & Bullock, J. M. (Eds.). (2012). *Dispersal ecology and evolution*. Oxford University Press. https://doi.org/10.1093/acprof:oso/9780199608898.001.0001

Cote, J., Clobert, J., Brodin, T., Fogarty, S., & Sih, A. (2010). Personality-dependent dispersal: Characterization, ontogeny and consequences for spatially structured populations. *Philosophical Transactions of the Royal Society, B: Biological Sciences*, *365*(1560), 4065–4076.

Cushman, S. A., Chase, M., & Griffin, C. (2010). Mapping landscape resistance to identify corridors and barriers for elephant movement in southern Africa. In S. A. Cushman & F. Huettmann (Eds.), *Spatial complexity, informatics, and wildlife conservation* (pp. 349–367). Springer Japan. https://doi.org/10.1007/978-4-431-87771-4

DeCesare, N. J., Hebblewhite, M., Schmiegelow, F., Hervieux, D., McDermid, G. J., Neufeld, L., Bradley, M., Whittington, J., Smith, K. G., Morgantini, L. E., Wheatley, M., & Musiani, M. (2012). Transcending scale dependence in identifying habitat with resource selection functions. *Ecological Applications*, *22*(4), 1068–1083. https://doi.org/10.1890/11-1610.1

Elliot, N. B., Cushman, S. A., Macdonald, D. W., & Loveridge, A. J. (2014). The devil is in the dispersers: Predictions of landscape connectivity change with demography. *Journal of Applied Ecology*, *51*(5), 1169–1178. https://doi.org/10.1111/1365-2664.12282

EROS. (2017). *Shuttle Radar Topography Mission (SRTM) 1 arc-second Global [Tiff]*. U.S. Geological Survey. https://doi.org/10.5066/F7PR7TFT

European Environment Agency. (2020a). *Grassland 2018 (raster 10 m), Europe, 3-yearly, Aug. 2020 (version 01.00) [GeoTIFF]*. European Environment Agency. https://doi.org/10.2909/60639D5B-9164-4135-AE93-FB4132BB6D83

European Environment Agency. (2020b). *Imperviousness density 2018 (raster 10 m), Europe, 3-yearly, Aug. 2020 (version 01.00) [GeoTIFF]*. European Environment Agency. https://doi.org/10.2909/3BF542BD-EEBD-4D73-B53C-A0243F2ED862

European Environment Agency. (2020c). *Tree cover density 2018 (raster 10 m), Europe, 3-yearly, Sep. 2020 (version 02.00) [GeoTIFF]*. European Environment Agency. https://doi.org/10.2909/486F77DA-D605-423E-93A9-680760AB6791

European Environment Agency. (2023). *Corine land cover change CLC+ backbone 2018 (raster 10 m), Europe, 3-yearly, Feb. 2023 (version 01.00) [GeoTIFF]*. European Environment Agency. https://doi.org/10.2909/CD534EBF-F553-42F0-9AC1-62C1DC36D32C

Farhadinia, M. S., Michelot, T., Johnson, P. J., Hunter, L. T. B., & MacDonald, D. W. (2020). Understanding decision making in a food-caching predator using hidden Markov models. *Movement Ecology*, *8*(1), 1–13. https://doi.org/10.1186/s40462-020-0195-z

Fernández, N., Delibes, M., & Palomares, F. (2006). Landscape evaluation in conservation: Molecular sampling and habitat modeling for the Iberian lynx. *Ecological Applications*, *16*(3), 1037–1049.

Fernández, N., Delibes, M., Palomares, F., & Mladenoff, D. J. (2003). Identifying breeding habitat for the Iberian lynx: Inferences from a fine-scale spatial analysis. *Ecological Applications*, *13*(5), 1310–1324. https://doi.org/10.1890/02-5081

Ferreras, P., Beltrán, J. F., Aldama, J. J., & Delibes, M. (1997). Spatial organization and land tenure system of the endangered Iberian lynx (*Lynx pardinus*). *Journal of Zoology*, *243*(1), 163–189. https://doi.org/10.1111/j.1469-7998.1997.tb05762.x

Ferreras, P., Delibes, M., Palomares, F., Fedriani, J. M., Calzada, J., & Revilla, E. (2004). Proximate and ultimate causes of dispersal in the Iberian lynx *Lynx pardinus*. *Behavioral Ecology*, *15*(1), 31–40. https://doi.org/10.1093/beheco/arg097

Fieberg, J., Signer, J., Smith, B., & Avgar, T. (2021). A 'how to' guide for interpreting parameters in habitat-selection analyses. *Journal of Animal Ecology*, *90*(5), 1027–1043. https://doi.org/10.1111/1365-2656.13441

Filla, M., Premier, J., Magg, N., Dupke, C., Khorozyan, I., Waltert, M., Bufka, L., & Heurich, M. (2017). Habitat selection by Eurasian lynx (*Lynx lynx*) is primarily driven by avoidance of human activity during day and prey availability during night. *Ecology and Evolution*, *7*(16), 6367–6381. https://doi.org/10.1002/ece3.3204

Fleming, C. H., Fagan, W. F., Mueller, T., Olson, K. A., Leimgruber, P., & Calabrese, J. M. (2015). Estimating where and how animals travel: An optimal framework for path reconstruction from autocorrelated tracking data. *Ecology*, *97*(3), 576–582. https://doi.org/10.1890/15-1607.1

Fleming, C. H., Sheldon, D., Fagan, W. F., Leimgruber, P., Mueller, T., Nandintsetseg, D., Noonan, M. J., Olson, K. A., Setyawan, E., Sianipar, A., & Calabrese, J. M. (2018). Correcting for missing and irregular data in home-range estimation. *Ecological Applications*, *28*(4), 1003–1010. https://doi.org/10.1002/eap.1704

Garrote, G., Bueno, J. F., Ruiz, M., De Lillo, S., Martin, J. M., Moral, M., & Simón, M. A. (2020). Breaking barriers: Iberian lynx *Lynx pardinus* Temminck, 1827 (Mammalia: Carnivora: Felidae) colonizing olive groves. *Journal of Threatened Taxa*, *12*(2), 15221–15228. https://doi.org/10.11609/jott.4829.12.2.15221-15228

13652656, 0, Downloaded from https://besjournals.onlinelibrary.wiley.com/doi/10.1111/1365-2656.70099 by Test, Wiley Online Library on [21/07/2025]. See the Terms and Conditions (https://onlinelibrary.wiley.com/terms-and-conditions) on Wiley Online Library for rules of use; OA articles are governed by the applicable Creative Commons License

Garrote, G., Fernández-López, J., Rojas, E., López, G., & Simón, M. A. (2020). Planning the peninsula-wide recovery of the Iberian lynx: Identification of favourable habitat areas. *Mammalia*, *84*(5), 413–420. https://doi.org/10.1515/mammalia-2019-0052

Gastón, A., Blázquez-Cabrera, S., Ciudad, C., Mateo-Sánchez, M. C., Simón, M. A., & Saura, S. (2019). The role of forest canopy cover in habitat selection: Insights from the Iberian lynx. *European Journal of Wildlife Research*, *65*(2), 30. https://doi.org/10.1007/s10344-019-1266-6

Gastón, A., Blázquez-Cabrera, S., Garrote, G., Mateo-Sánchez, M. C., Beier, P., Simón, M. A., & Saura, S. (2016). Response to agriculture by a woodland species depends on cover type and behavioural state: Insights from resident and dispersing Iberian lynx. *Journal of Applied Ecology*, *53*(3), 814–824. https://doi.org/10.1111/1365-2664.12629

Goicolea, T., Gastón, A., Cisneros-araujo, P., García-viñas, J. I., & Mateo-sánchez, M. C. (2021). Deterministic, random, or in between? Inferring the randomness level of wildlife movements. *Movement Ecology*, *9*, 1–14.

Grupo de Manejo Sanitario del Lince Iberico. (2014). Manual Sanitario del Lince Ibérico. https://www.lynxexsitu.es/ficheros/documentos_pdf/85/Manual_Sanitario_Lince_Ib_2014.pdf

Guzmán, J. N. (Ed.). (2004). *El lince ibérico (Lynx pardinus) en España y Portugal: Censo-diagnóstico de sus poblaciones*. Ministero de Medio Ambiente.

Hooven, N. D., Springer, M. T., Nielsen, C. K., & Schauber, E. M. (2023). Influence of natal habitat preference on habitat selection during extra-home range movements in a large ungulate. *Ecology and Evolution*, *13*(2), e9794. https://doi.org/10.1002/ece3.9794

Johnson, D. H. (1980). The comparison of usage and availability measurements for evaluating resource preference. *Ecology*, *61*(1), 65–71. https://doi.org/10.2307/1937156

Kanda, C. Z., Oliveira-Santos, L. G. R., Morato, R. G., De Paula, R. C., Rampim, L. E., Sartorello, L., Haberfeld, M., Galetti, M., & Cezar Ribeiro, M. (2019). Spatiotemporal dynamics of conspecific movement explain a solitary carnivore's space use. *Journal of Zoology*, *308*(1), 66–74. https://doi.org/10.1111/jzo.12655

Kelly, D. J., Gaughran, A., Mullen, E., MacWhite, T., Maher, P., Good, M., & Marples, N. M. (2020). Extra territorial excursions by European badgers are not limited by age, sex or season. *Scientific Reports*, *10*(1), 9665. https://doi.org/10.1038/s41598-020-66809-w

Klappstein, N. J., Thomas, L., & Michelot, T. (2023). Flexible hidden Markov models for behaviour-dependent habitat selection. *Movement Ecology*, *11*(1), 30. https://doi.org/10.1186/s40462-023-00392-3

LIFE LYNXCONNECT. (2020). LIFE 3.0—LIFE project public page. https://webgate.ec.europa.eu/life/publicWebsite/index.cfm?fuseaction=search.dspPage&n_proj_id=7639

Life+IBERLINCE. (2016). Protocolo de Liberaciones del Lince Ibérico. http://www.iberlince.eu/images/docs/3_InformesLIFE/ProtocoloLiberaciones_M.Iberlince.pdf

Mateo Sánchez, M. C., Cushman, S. A., & Saura, S. (2014). Scale dependence in habitat selection: The case of the endangered brown bear (*Ursus arctos*) in the Cantabrian range (NW Spain). *International Journal of Geographical Information Science*, *28*(8), 1531–1546. https://doi.org/10.1080/13658816.2013.776684

Muff, S., Signer, J., & Fieberg, J. (2020). Accounting for individual-specific variation in habitat-selection studies: Efficient estimation of mixed-effects models using Bayesian or frequentist computation. *Journal of Animal Ecology*, *89*(1), 80–92. https://doi.org/10.1111/1365-2656.13087

Noonan, M. J., Fleming, C. H., Akre, T. S., Drescher-Lehman, J., Gurarie, E., Harrison, A.-L., Kays, R., & Calabrese, J. M. (2019). Scale-insensitive estimation of speed and distance traveled from animal tracking data. *Movement Ecology*, *7*(1), 35. https://doi.org/10.1186/s40462-019-0177-1

Northrup, J. M., Vander Wal, E., Bonar, M., Fieberg, J., Laforge, M. P., Leclerc, M., Prokopenko, C. M., & Gerber, B. D. (2022). Conceptual and methodological advances in habitat-selection modeling: Guidelines for ecology and evolution. *Ecological Applications*, *32*(1), e02470. https://doi.org/10.1002/eap.2470

OpenStreetMap contributors. (2017). OpenStreetMap [Dataset]. https://www.openstreetmap.org/

Osborne, P. E., & Seddon, P. J. (2012). Selecting suitable habitats for reintroductions: Variation, change and the role of species distribution modelling. In J. G. Ewen, D. P. Armstrong, K. A. Parker, & P. J. Seddon (Eds.), *Reintroduction biology* (1st ed., pp. 73–104). Wiley. https://doi.org/10.1002/9781444355833.ch3

Palomares, F. (2001). Vegetation structure and prey abundance requirements of the Iberian lynx: Implications for the design of reserves and corridors. *Journal of Applied Ecology*, *38*(1), 9–18. https://doi.org/10.1046/j.1365-2664.2001.00565.x

Palomares, F. (2003). Warren building by European rabbits (*Oryctolagus cuniculus*) in relation to cover availability in a sandy area. *Journal of Zoology*, *259*(1), 63–67. https://doi.org/10.1017/S0952836902002960

Palomares, F., Delibes, M., Ferreras, P., Fedriani, J. M., Calzada, J., & Revilla, E. (2000). Iberian lynx in a fragmented landscape: Predispersal, dispersal, and postdispersal habitats. *Conservation Biology*, *14*(3), 809–818. https://doi.org/10.1046/j.1523-1739.2000.98539.x

Picardi, S., Coates, P., Kolar, J., O'Neil, S., Mathews, S., & Dahlgren, D. (2022). Behavioural state-dependent habitat selection and implications for animal translocations. *Journal of Applied Ecology*, *59*(2), 624–635. https://doi.org/10.1111/1365-2664.14080

R Core Team. (2022). *A language and environment for statistical computing. (version 4.2.0) [computer software]*. R Foundation for Statistical Computing.

Ranc, N., Cagnacci, F., & Moorcroft, P. R. (2022). Memory drives the formation of animal home ranges: Evidence from a reintroduction. *Ecology Letters*, *25*(4), 716–728. https://doi.org/10.1111/ele.13869

Riley, S. J., De Gloria, S. D., & Elliot, R. (1999). A terrain ruggedness that quantifies topographic heterogeneity. *Intermountain Journal of Sciences*, *5*(1–4), 23–27.

Rio-Maior, H., Nakamura, M., Álvares, F., & Beja, P. (2019). Designing the landscape of coexistence: Integrating risk avoidance, habitat selection and functional connectivity to inform large carnivore conservation. *Biological Conservation*, *235*, 178–188. https://doi.org/10.1016/j.biocon.2019.04.021

Rodriguez, A., & Calzada, J. (2015). *Lynx pardinus*: The IUCN Red List of threatened species 2015: e.T12520A174111773 [Dataset]. https://doi.org/10.2305/IUCN.UK.2015-2.RLTS.T12520A174111773.en

Roever, C. L., Beyer, H. L., Chase, M. J., & Van Aarde, R. J. (2014). The pitfalls of ignoring behaviour when quantifying habitat selection. *Diversity and Distributions*, *20*(3), 322–333. https://doi.org/10.1111/ddi.12164

Rueda, C., Jiménez, J., Palacios, M. J., & Margalida, A. (2021). Exploratory and territorial behavior in a reintroduced population of Iberian lynx. *Scientific Reports*, *11*, 1–12. https://doi.org/10.1038/s41598-021-93673-z

Signer, J., Filla, M., Schoneberg, S., Kneib, T., Bufka, L., Belotti, E., & Heurich, M. (2019). Rocks rock: The importance of rock formations as resting sites of the Eurasian lynx *Lynx lynx*. *Wildlife Biology*, *2019*, 1–5. https://doi.org/10.2981/wlb.00489

Simón, M. A., Gil-Sánchez, J. M., Ruiz, G., Garrote, G., Mccain, E. B., Fernández, L., López-Parra, M., Rojas, E., Arenas-Rojas, R., Del Rey, T., García-Tardío, M., & López, G. (2012). Reverse of the decline of the endangered Iberian lynx. *Conservation Biology*, *26*(4), 731–736.

Smith, J. L. D. (1993). The role of dispersal in structuring the Chitwan tiger population. *Behaviour*, *124*(3–4), 165–195.

Spearman, C. (1961). *The proof and measurement of association between two things*. Appleton-Century-Crofts.

13652656, 0, Downloaded from https://besjournals.onlinelibrary.wiley.com/doi/10.1111/1365-2656.70099 by Test, Wiley Online Library on [21/07/2025]. See the Terms and Conditions (https://onlinelibrary.wiley.com/terms-and-conditions) on Wiley Online Library for rules of use; OA articles are governed by the applicable Creative Commons License

Stamps, J. (2001). 16. Habitat selection by dispersers: Integrating proximate and ultimate approaches. In J. Clobert, E. Danchin, A. A. Dhondt, & J. D. Nichols (Eds.), *Dispersal* (pp. 110–122). Oxford Academic.

Thorsen, N. H., Bischof, R., Mattisson, J., Hofmeester, T. R., Linnell, J. D. C., & Odden, J. (2022). Smartphone app reveals that lynx avoid human recreationists on local scale, but not home range scale. *Scientific Reports*, *1*, 1–13. https://doi.org/10.1038/s41598-022-08468-7

Thorsen, N. H., Hansen, J. E., Støen, O.-G., Kindberg, J., Zedrosser, A., & Frank, S. C. (2022). Movement and habitat selection of a large carnivore in response to human infrastructure differs by life stage. *Movement Ecology*, *10*(1), 52. https://doi.org/10.1186/s40462-022-00349-y

Thurfjell, H., Ciuti, S., & Boyce, M. S. (2014). Applications of step-selection functions in ecology and conservation. *Movement Ecology*, *2*(1), 4. https://doi.org/10.1186/2051-3933-2-4

Van Den Bosch, M., Kellner, K. F., Gantchoff, M. G., Patterson, B. R., Barber-Meyer, S. M., Beyer, D. E., Erb, J. D., Isaac, E. J., MacFarland, D. M., Moore, S. A., Norton, D. C., Petroelje, T. R., Price Tack, J. L., Roell, B. J., Schrage, M., & Belant, J. L. (2023). Habitat selection of resident and non-resident gray wolves: Implications for habitat connectivity. *Scientific Reports*, *13*(1), 20415. https://doi.org/10.1038/s41598-023-47815-0

Vanbianchi, C., Gaines, W. L., Murphy, M. A., & Hodges, K. E. (2018). Navigating fragmented landscapes: Canada lynx brave poor quality habitats while traveling. *Ecology and Evolution*, *8*(22), 11293–11308. https://doi.org/10.1002/ece3.4605

Vogt, K., Zimmermann, F., Kölliker, M., & Breitenmoser, U. (2014). Scent-marking behaviour and social dynamics in a wild population of Eurasian lynx *Lynx lynx*. *Behavioural Processes*, *106*, 98–106. https://doi.org/10.1016/j.beproc.2014.04.017

Wong, B. B., & Candolin, U. (2015). Behavioral responses to changing environments. *Behavioral Ecology*, *26*(3), 665–673.

Zeller, K. A., McGarigal, K., & Whiteley, A. R. (2012). Estimating landscape resistance to movement: A review. *Landscape Ecology*, *27*(6), 777–797. https://doi.org/10.1007/s10980-012-9737-0

Zimmermann, F., Breitenmoser-Würsten, C., & Breitenmoser, U. (2005). Natal dispersal of Eurasian lynx (*Lynx lynx*) in Switzerland. *Journal of Zoology*, *267*(4), 381–395. https://doi.org/10.1017/S0952836905007545

SUPPORTING INFORMATION

Additional supporting information can be found online in the Supporting Information section at the end of this article.

Table S1: Summaries of the mixed-effects conditional logistic models fitted at the landscape scale for each movement phase, including the estimated coefficients, standard errors and codes for the significance levels *p*-values <0.001 ('***'), <0.01 ('**'), <0.05 ('*'), <0.1 ('.').

Table S2: AICc scores for univariate models at the local scale for each environmental variable. The operational spatial grain, indicated by the lowest AICc score, is highlighted in bold. AICc scores are colour-coded from darker blue (lowest AICc) to lighter blue (highest AICc).

Table S3: Summaries of the mixed-effects conditional logistic models fitted at the local scale for each movement phase, including the variable operational spatial grain (m), estimated coefficients, standard errors and codes for the significance levels *p*-values: <0.001 ('***'), <0.01 ('**'), <0.05 ('*'), and <0.1 ('.').

Table S4: Mean and standard errors of environmental variables at the end location of each used step for different movement phases.

Figure S1: Illustrative example of the movement phases along an Iberian lynx movement path. Points represent GPS locations and colours indicate the movement phase they belong to. Black solid lines represent the 90% home range area estimate and dashed lines indicate their respective 95% CI (see Cisneros-Araujo et al. (2024) for details on its estimation). The black star represents the first point of the movement path.

Figure S2: Curves of the Gamma step length (A) and Von Mises turning angle (B) distributions used to generate random steps for the phase-specific habitat selection models (SSF) at the local scale.

How to cite this article: Cisneros-Araujo, P., Garrote, G., Corradini, A., Cagnacci, F., Farhadinia, M. S., Salcedo, J., Sarmento, P., Sánchez, J. F., Palacios, M. J., García-Viñás, J. I., Saura, S., & Gastón, A. (2025). Movement phases make a difference in habitat selection: Iberian lynx diversity of responses to human-modified landscapes. *Journal of Animal Ecology*, *00*, 1–14. https://doi.org/10.1111/1365-2656.70099

13652656, 0, Downloaded from https://besjournals.onlinelibrary.wiley.com/doi/10.1111/1365-2656.70099 by Test, Wiley Online Library on [21/07/2025]. See the Terms and Conditions (https://onlinelibrary.wiley.com/terms-and-conditions) on Wiley Online Library for rules of use; OA articles are governed by the applicable Creative Commons License