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# Born to be wild: Captive-born and wild Iberian lynx (*Lynx pardinus*) reveal space-use similarities when reintroduced for species conservation concerns

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ABSTRACT

An ambitious conservation programme to save the Iberian lynx from extinction conducted several reintroductions aiming to restore its historical range. The urgency due to the delicate conservation status prompted translocating captive-born and wild individuals, while preventing an early assessment of how both groups combined their space-use and differed in post-release movements. To address this issue, we conducted a comprehensive movement ecology analysis using GPS data of 161 Iberian lynxes from 9 populations. First, we classified five movement phases within individuals' trajectories: residence areas (stable and transient), excursions, post-release dispersals, and transitions between residences. Second, we used continuous-time movement models to estimate range size and daily speeds and measured the distance travelled during extra-territorial movements. Finally, we conducted comparative analyses to evaluate differences between captive-born, wild translocated, and wild non-translocated individuals across phases, sex, age-class and populations. Most individuals in all groups established home ranges, supporting the reintroduction main goal. Yet, contrary to the species' natural pattern, captive-born subadults did not show intersexual home range size differences, which emerged after experiencing free-ranging, when becoming adults. More differences emerged for non-residential behaviours. Captive-born lynxes were more prone to post-release dispersal, to slower post-release movements and to having smaller transient residences, indicating cautious behaviour. Our study supports using captive-born individuals for reintroductions, while prioritizing wild individuals for reinforcements in highly competitive populations. Further, we suggest relevant metrics for planning translocations and connectivity management, and we demonstrate how an integrated ex-situ and reintroduction initiative can substantially contribute to restoring an endangered species' distribution range.

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## 1. Introduction

With the intention of preventing, halting, and reversing the degradation of ecosystems on every continent and in every ocean, the United Nations has designated the Decade on Ecosystem Restoration (2021–2030; UNEP, 2019). Central to restoration strategies are conservation translocations of native species (IUCN/SSC, 2013). Translocations can have several goals, including the reinforcement of populations of threatened species, or the reintroduction of a species in areas where it has gone extinct (IUCN/SSC, 2013). Despite their crucial role, it is imperative to closely evaluate the translocation efforts to optimize their success in restoring native species distribution and abundance (Thomas et al., 2023). This is particularly relevant for carnivores, whose key role as predators can produce cascading effects on their ecosystems (Evans et al., 2022).

One notable case of carnivore translocations is the Iberian lynx, *Lynx pardinus* (Temminck, 1827). At the beginning of the 2000s, the Iberian lynx was one of the most endangered mammal species globally. With fewer than 100 individuals remaining in two isolated populations in Spain (Doñana-Aljarafe and Andujar-Cardeña, Fig. 1), the species faced severe threats due to habitat loss and fragmentation, human persecution, and a sharp decline in its primary prey, the European rabbit, *Oryctolagus cuniculus* (Garrote et al., 2020; Guzmán, 2004). Accordingly, it was classified as Critically Endangered (Arx et al., 2008), prompting various conservation efforts to prevent the species from its imminent extinction. These measures included mitigating major mortality causes like wildlife-vehicle collisions, disease, and poaching; enhancing carrying capacity by actively managing the habitat to aid rabbit recovery; and increasing population size or re-establishing populations by an intense reintroduction and translocation programme (Rodriguez and Calzada, 2015; Simón et al., 2012). Most translocated individuals originated from an ambitious ex-situ breeding programme based on four breeding centres. Releases of individuals reared in captivity and of others captured in the wild were strategically combined with the goal of enhancing genetic diversity and reinforcing or re-establishing viable populations. To this end, captive-born individuals were genetically profiled (Godoy et al., 2023; Kleinman-Ruiz et al., 2019; Life+IBERLINCE, 2016). Reintroduced captive-born felids have generally lower survival rates than wild-caught ones (Jule et al., 2008), but pre-release training can improve their chances of survival (Walker et al., 2022). Therefore, cubs underwent preparatory measures to avoid human conditioning and promote their hunting and social skills before reintroduction (Life+IBERLINCE, 2016). This remarkable conservation programme has resulted in a substantial increase in Iberian lynx numbers, leading to downgrading the risk to Endangered (Rodriguez and Calzada, 2015). Presently, there are nine stable populations (seven of which are from reintroduced individuals) spread across Spain and Portugal (Fig. 1), with over 1600 individuals and a net increase of 1500 % over 20 years (MITECO and ICNF, 2022). Nowadays, the challenge is to interconnect these populations of mixed origin (i.e. captive-bred and wild) and strive to extend their space-use further to cover the historical distribution range (LIFE LYNXCONNECT, 2020).

Understanding the space-use properties of post-release movements is fundamental for validating the effectiveness of translocations, i.e. checking whether released individuals settled in restricted areas, so establishing a spatially stable population (Berger-Tal and Saltz, 2014; Sarkar et al., 2016); and for implementing adaptative management of reintroductions – e.g., deciding what individuals to release and where, with respect to the historical distribution range (Letty et al., 2007; Thomas et al., 2023). Reintroduced individuals typically begin exploring new areas until the benefit of resource exploitation outweighs the benefit of further exploration (Berger-Tal and Saltz, 2014). Overall, the exploration time invested can vary greatly and depends on the characteristics of each individual (Picardi et al., 2021), with some travelling long distances during this process, which can increase mortality risks and reduce the chances of settling inside the desired reintroduction area (Berger-Tal and Saltz, 2014; Rueda et al., 2021). Conversely, others may become familiar with resource-abundant locations in the novel environment and start revisiting them over time, leading to the formation of home ranges (Ranc et al., 2022).

Studying post-release movement is especially important for a large-scale reintroduction programme like the one on the Iberian lynx that aimed at restoring the species distribution range from two relic-isolated populations. The doom conservation status of the Iberian lynx at the onset of the conservation programme imposed a further complication, i.e. the combination of ex-situ and wild individuals for translocations,

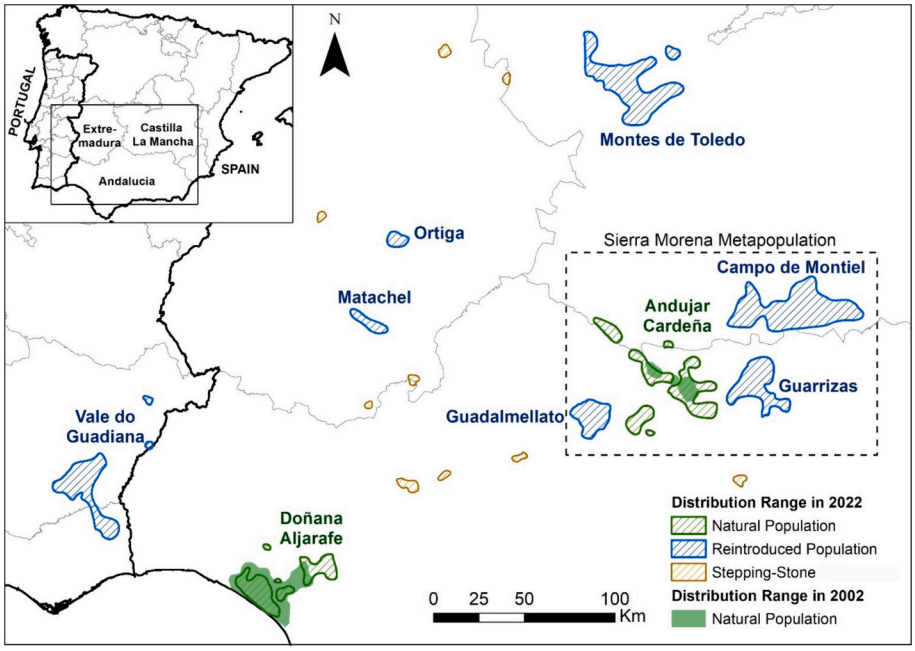



**Fig. 1.** Expansion of the Iberian lynx distribution range from 2002 to 2022. Four populations already function as interconnected subpopulations forming the Sierra Morena metapopulation (dashed line; Godoy et al., 2023). However, we refer here to them as "populations" according to their status at the moment of reintroduction. Stepping-stones are natural settlement areas recently colonized by the species.

without knowing their respective space-use behaviour. The two available studies on post-release behaviour in single lynx populations - Vale do Guadiana, Portugal (Fig. 1; Sarmento et al., 2019); Matachel, Extremadura, Spain (Fig. 1; Rueda et al., 2021) - indicated that several individuals among the reintroduced ones made exploratory movements before settling in a specific area, a common process in other lynx species (Buderman et al., 2018; Vandel et al., 2006). However, Sarmento et al. (2019) reported that home ranges of captive-born individuals did not vary in size between males and females, which contradicts the natural pattern observed in wild populations, where male home ranges are significantly larger to increase female encounters (Ferreras et al., 1997; Gil-Sánchez et al., 2011; Sandell, 1989). Conversely, Rueda et al. (2021) found that the captive-born individuals re-establishing the population showed the 'natural' difference in home range size between sexes. These contrasting results raise a set of questions: (1) what prevalent post-released movement and space-use patterns occurred in the reintroduced Iberian lynxes across many populations; (2) whether these patterns differed between captive-born and wild individuals, so affecting their adaptation to the environment. Answering these questions is key for designing future translocations, informing decisions about the suitability of captive-born individuals for reintroductions and reinforcements, as well as determining the optimal location, size and configuration of future reintroduction areas and their distance from existing populations. This is especially relevant in light of the ongoing Iberian lynx recovery project (LIFE LYNXCONNECT, 2020), aiming at enhancing the establishment of a meta-population through new reintroductions in 'stepping-stone' areas (Fig. 1).

We fill this gap by testing whether Iberian lynx space-use and movement patterns differed in captive-born and wild individuals forming new or reinforcing existing populations; and by discussing the conservation consequences of these differences in light of the restoration of a viable species distribution range. For this purpose, we used a large (161 lynxes from nine populations) and long-term (2008–2023) GPS tracking database of captive-born (73 %) and wild individuals (27 %), the latter being either captured and translocated (10 % of the total), or collared and released on site (17 % of the total). We considered five movement and space-use patterns (SU) that could occur in reintroduced Iberian lynx including both captive-born and wild individuals (Fig. 2A): reintroduced captive-born lynxes could establish sedentary ranges similarly to wild individuals, with males having larger home ranges than females (SU1) (Ferreras et al., 1997; Gil-Sánchez et al., 2011); alternatively, with males and females showing similar home range sizes (SU2)

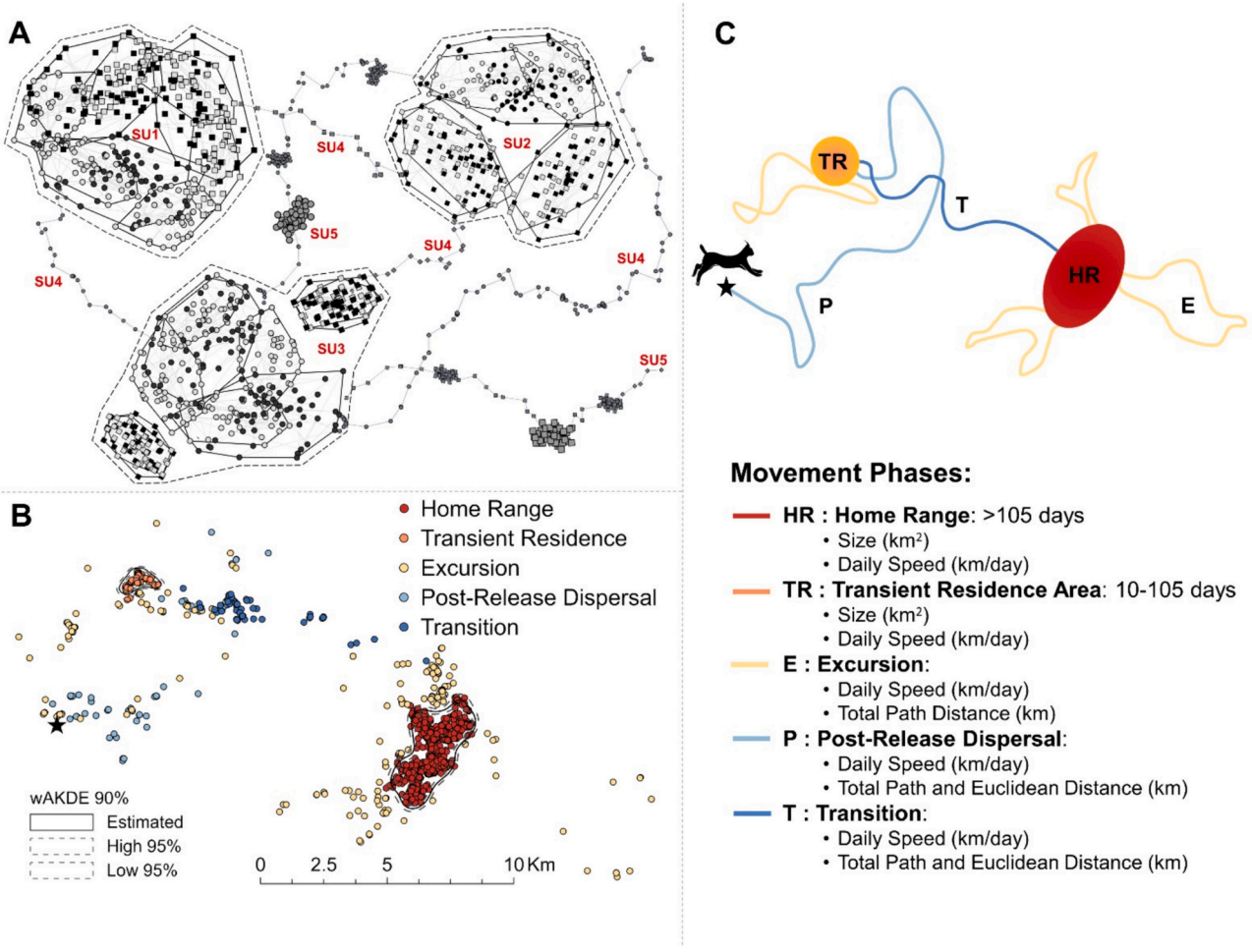



**Fig. 2.** (A) Conceptualization of how individual movement and space-use of reintroduced Iberian lynx may emerge as populations' distribution pattern, ultimately re-establishing a viable species distribution range. Dots are single relocations (squares for captive-born and circles for wild individuals; black for males, light grey for females, and dark grey when sexes are not distinguished). Solid black lines represent conceptual home ranges, light grey lines the individual movements within them, while dashed black lines represent the emerging population distribution. Dark grey lines indicate dispersal and nomadic patterns. For the space-use (SU) letter codes, see the main text. Adapted from Mueller and Fagan (2008). Note that females' home ranges are encompassed within males' territory, as per the Iberian lynx prevalent mating system (Ferreras et al., 1997). (B) Illustrative example of the movement phases of an Iberian lynx movement path. Points represent relocations and colours indicate the movement phase they belong to. Black solid lines represent the 90 % wAKDE and dashed lines indicate their respective 95 % CI. The black star represents the first point of the movement path. (C) Schema of a space-use tactic, i.e. the combination of several movement phases in an Iberian lynx movement path. Lines represent the movement path of each non-residential phase and ellipsoids the areas of residential phases.

(Sarmento et al., 2019); or with captive-born lynxes having smaller ranges and slower movements than wild lynxes due to cautious behaviour (SU3) (Sih et al., 2004; Spiegel et al., 2017). We also considered that reintroduced lynxes could display post-release dispersal during the first phases after the release and then nomadic behaviour without establishing sedentary ranges (SU4), or establishing several transient residence areas (SU5). Either or a combination of these movement patterns would then emerge in the populations' distribution pattern of the species (Fig. 2A; see Mueller and Fagan, 2008). To test which space-use patterns have contributed to the Iberian lynx populations' re-establishment, first, we identified the movement phases (stable residence areas, excursions, post-release dispersal, transient residence areas, and related transitions between residence areas) composing the space-use tactics of each individual; second, we computed a set of movement and space-use metrics to characterize these phases; third, we compared such metrics across movement phases accounting for individual characteristics (i.e., sex; age class; captive-born, wild translocated or wild non-translocated), and populations (see also Table S1 for a summary of questions and methodological approaches).

## 2. Materials and methods

### 2.1. GPS telemetry dataset

We used a large GPS telemetry dataset of 161 Iberian lynxes from nine populations that were collared between 2008 and 2023 in the context of three consecutive conservation projects (LIFE06NAT/E/000209, LIFE10NAT/ES/570 IBERLINCE and LIFE19NAT/ES001055 LYNXCONNECT). We followed the Iberian Lynx Sanitary Advisory Panel guidelines when capturing and collaring lynxes (Grupo de Manejo Sanitario del Lince Iberico, 2014). Each lynx was collared by certified technicians and veterinarians in charge of the monitoring of each studied population. The GPS-based dataset movement paths derive from the collaring of 81 males and 80 females, belonging to two age classes: 26 adults (≥2 years old) and 133 subadults (<2 years old; Beltran and Delibes, 1993). The paths varied in terms of tracking duration time (from 16 to 1101 days) and sampling rate (every 4 h (92 %), 6 h (2 %), 8 h (0.4 %), 12 h (4 %) and 24 h (1 %)). We regularised the animal tracks showcasing irregular sampling rate to a 24 h sampling rate. We manually removed obvious unrealistic locations (e.g., in the breeding centre or above water bodies) using *ArcGIS Pro*. Additionally, we followed Bjørneraas et al. (2010) to remove finer-grain outliers resulting from unrealistic movements – i.e., with step distances (Δ, μ), speeds (α), and turning angles (θ) exceeding predefined thresholds considered biologically realistic for the Iberian lynx. To do so, we computed the movement parameters for a moving window of five locations (i.e., considering two locations before and after the focal location) and removed the locations that would lead to the following extreme values: $\Delta = 16{,}000$ m; $\mu = 14{,}000$ m; $\alpha = 4000$ m/h; $\theta = -0.97$ (166°-194° turning angle), chosen according to previous GPS data screenings on solitary felids (Farhadinia et al., 2020b; Johansson et al., 2018). Besides the Iberian lynx location data, we collected 558 GPS samples from fixed locations to calibrate the measurement error of the GPS collars. We found a User Equivalent Range Error varying from 11.85 to 12.88 m. To conduct subsequent data analyses, we followed the methods described in Table S1.

### 2.2. Step one: classification of individual movement phases

We characterized the space-use tactics adopted by individual Iberian lynxes by classifying each movement path into several movement phases. To do so, we applied the SeqScan algorithm to each individual movement path (Damiani et al., 2016, 2018) using the MigrO QGIS plugin (Damiani et al., 2015; QGIS Development Team, 2016). In brief, for each individual, the algorithm identifies spatiotemporal clusters of GPS locations (residence areas) to then identify the movement paths that start and finish in the same cluster (excursions) and the paths that connect two consecutive clusters (transitions). The parameters needed to identify the clusters are: the minimum number of neighbouring locations ($N$) situated inside a distance threshold ($\varepsilon$), and a presence threshold ($\delta$) to define the minimum duration (in days) of a cluster. For our case study, we estimated the set of parameters for each individual. First, we estimated the $\varepsilon$ distance as the median step length of each lynx movement path. Second, we determined the optimal threshold presence $\delta$ at 10 days after conducting a sensitivity analysis to identify the duration that allowed for the identification of relevant transient residence areas (Fig. S1). Last, for each location, we obtained the number of neighbour locations inside a distance and a time window defined by $\varepsilon$ and $\delta$, respectively. We thus estimated $N$ as the average number of neighbours of all the locations of the movement path.

We classified four main movement phases: (1) **Residence areas**, (i.e. "clusters"), which are portions of space in which an animal resides for at least ten consecutive days despite short periods of absence. (2) **Excursions**, which are displacements away from the residence area but looping back to the same area. We only considered excursions that lasted >24-h. (3) **Transitions**, which are the displacement events from one residence area to another. In this case, we also considered as transition events when an individual departed from one residence area but did not finish in any other one before the monitoring ended. To ensure that those were transitions (and not excursions), only movements longer than ten days were retained, as 95 % of the monitored excursions lasted less than that. In the case of a translocated or reintroduced lynx, we also classified (4) **post-release dispersals**, which are the movement paths defined from the point of release to the first residence area, or to the end of the monitoring period. We then classified the residence areas into two categories based on time spent within each: (1.a) **home ranges**, which are areas that lasted >105 days (Fig. S2); (1.b) **transient residence areas**, which are clusters that lasted <105 days and more than ten days. Any other residence areas lasting <105 days without evidence of being abandoned before the monitoring ended were generically labelled as "residence areas". A summary schema and an example of classification are shown in Fig. 2B–C.

We identified the different space-use tactics adopted by lynxes by combining the phases composing each individual's movement path. Then, we calculated the frequency of each space-use tactic in reintroduced captive-born, wild translocated and wild non-translocated individuals. Likewise, to evaluate the settlement of released individuals in reintroduced populations, we calculated the rate of home range establishment of captive-born and translocated wild lynxes over time since release. To disentangle the influence of lynx densities in home range establishment, we repeated this procedure but considered only lynxes reintroduced within the first two years of each population.

### 2.3. Step two: movement metrics

To characterize Iberian lynx movement and space-use patterns, we obtained a set of movement metrics that were estimated from continuous-time movement models (residence area sizes and speeds) or directly measured from empirical trajectories (distances). For subsequent movement analyses, we further used *R* software (version 4.2.0, R Core Team, 2022).

#### 2.3.1. Movement models

We fitted continuous-time stochastic process (CTSP) to the location series of each individual movement path of each phase to estimate residence area sizes and average daily speeds while accounting for the autocorrelation present in GPS data (Calabrese et al., 2016; Fleming et al., 2018; Noonan et al., 2019). Candidate models differed depending on the movement phase used to fit the CTSP models. For movement phases that showed range-residency (i.e. home range and transient residence), we considered these models: the Independent Identically Distributed process (IID) 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) which, as the OU process, also 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). On the contrary, for excursions, transitions, and post-release dispersals, which are movement phases that show directional persistence and no range-residency, we considered two models: the Brownian Motion (BM) process which features autocorrelated positions, and the Integrated Ornstein–Uhlenbeck (IOU) process that includes autocorrelated positions and velocities (Calabrese et al., 2016). We obtained starting parameter values from semi-variance functions to fit the candidate models. Then, we fitted candidate models and selected the most parsimonious model according to the lowest second-order Akaike's information criterion score (AICc). To carry out this procedure, we used the *ctmm R* package (Calabrese et al., 2016).

#### 2.3.2. Residence area size

We used the best fit range-resident movement models to estimate the size of residence areas by applying optimally weighted and area-corrected autocorrelated kernel density estimators (wAKDE) (Fleming et al., 2018). We considered the residence area as the area encompassing the 90 % isopleths of wAKDE.

#### 2.3.3. Daily movement speeds

We used a continuous-time speed estimation approach (Noonan et al., 2019) based on CTSP models, to obtain estimates of average daily speeds with 95 % confidence intervals. This approach simulates movement paths conditional on the data with a finer sampling resolution and reduces biases caused by coarse sampling rates, positional error and path directionality (Noonan et al., 2019). To estimate continuous-time speeds, we only used the movement paths whose fitted CTSP models featured autocorrelated velocities – i.e., IOU process for non-residential phases, and OUF and OUf processes for residential phases.

#### 2.3.4. Total path and Euclidean distances

Beyond the metrics derived from CTSP, we also included two further descriptive metrics directly derived from the empirical observations: the total path covered by excursions, transitions and post-release dispersals, expressed as the beeline distance between consecutive locations for each movement path (only for regular trajectories with 4-h sampling rate, i.e. 92 % of the locations), and the Euclidean distance between the first and last location of each dispersal and transition movement paths (regardless of the sampling rate).

### 2.4. Step three: movement metrics differences across phases, populations and groups of individuals

To evaluate the differences in the characteristics of movement and space-use across phases, individuals and populations, we conducted comparative analyses on all metrics. First, we used the *meta()* function of the *ctmm* package, in which individual estimates are modelled with a $\chi 2$ distribution and each group of metrics with an inverse Gaussian (IG) function. The $\chi 2$-IG approach allowed us to account for individual estimation uncertainties and downweigh uncertain estimates in relation to more certain ones to obtain accurate group-level estimates (Fleming et al., 2021). Using this approach, we tested whether the size of residence areas and average daily speeds differed across movement phases also accounting for sex and origin (wild non-translocated vs. wild translocated vs. captive-born), at the individual level. We also used the *meta()* function to assess the variation of home range sizes between populations, population types (natural or reintroduced) and age classes. Likewise, to disentangle the potential influence of high lynx densities, we compared the size of residence areas of all lynxes vs. the size of those released within two years from the first reintroduction only. To assess differences in the metrics across movement phases, and individual or population characteristics, we used F-tests and effect sizes with CIs, as returned by the *meta()* function. We defined effect sizes as the ratio between mean group variable estimates (residence area sizes and speeds; Fleming et al., 2021). Therefore, we considered significant differences whenever the ratio 95 % CIs did not cross 1.

Second, we also tested the differences of total path distance and Euclidean distance (i.e., the empirically determined metrics not estimated with the *ctmm* package), with a Wilcoxon test and manually calculated the ratios with 95 % CIs of the mean using a non-parametric bootstrap. We report the measures of significance (*p*-values) of each test and effect sizes in Tables S2 of the Supplementary material.

## 3. Results

### 3.1. Movement phases and space-use tactics

Iberian lynxes displayed a wide diversity of space-use tactics based on different combinations of movement phases (Fig. 2B–C; S3; for a summary of each movement phase see Table S3). We observed a greater variety of space-use tactics in captive-born lynxes (total $n_{\text{space-use tactics}} = 22$, within 118 lynxes) than in wild translocated (total $n_{\text{space-use tactics}} = 9$, within 17 lynxes) and non-translocated (total $n_{\text{space-use tactics}} = 10$, within 28 lynxes) individuals. The most frequent tactic for captive-born individuals (29 %) was composed of a post-release dispersal followed by the establishment of a residence area from which excursions were made (Fig. S3B). For wild individuals, the most common tactic was home range establishment with related excursions (29 % non-translocated; 22 % translocated; Fig. S3AC), previously including a post-release dispersal if the individual was translocated (22 %; Fig. S3C). Home ranges were present in most space-use tactics, especially in wild non-translocated individuals (75 %, or 100 % considering unclassified residence areas). Nonetheless, also the space-use tactic of translocated wild lynxes and captive-born individuals commonly included home ranges (56 %, or 89 % with residence areas; and 47 %, or 80 % with residence areas, respectively).

The rate of individuals establishing home ranges was always slightly higher for wild individuals regardless of the period threshold considered (Fig. 3A). After 6 months of monitoring, all wild individuals had settled in a home range. For the same period, 81 % of captive-born individuals had established a home range; and >90 % after a year of monitoring (Fig. 3A).

Fully nomadic patterns were absent in wild non-translocated Iberian lynxes, although several individuals made transitions between residence areas (32 %). Only two translocated wild lynxes were completely nomadic: one kept dispersing after release, while another one dispersed after establishing a transient residence area. Instead, captive-born individuals were more prone to nomadism with 10 % of them dispersing after release and 11 % after establishing transient residence areas. Twelve (19 %) captive-born individuals did not establish a home range after 6 months of monitoring (4 individuals after 9 months; Fig. 3A), indicating that a few individuals were nomadic for extensive periods.

### 3.2. Characteristics of movement and space-use

#### 3.2.1. Size of residence areas

Average home range sizes varied strongly both in natural (13.82 $km^2$, min. 2.49 – max. 61.5) and reintroduced populations (11.51 $km^2$, min. 1.04 – max. 71.62) (Fig. 3B). We found no differences in the home range size between wild non-translocated, wild translocated and captive-born males, nor between wild non-translocated, wild

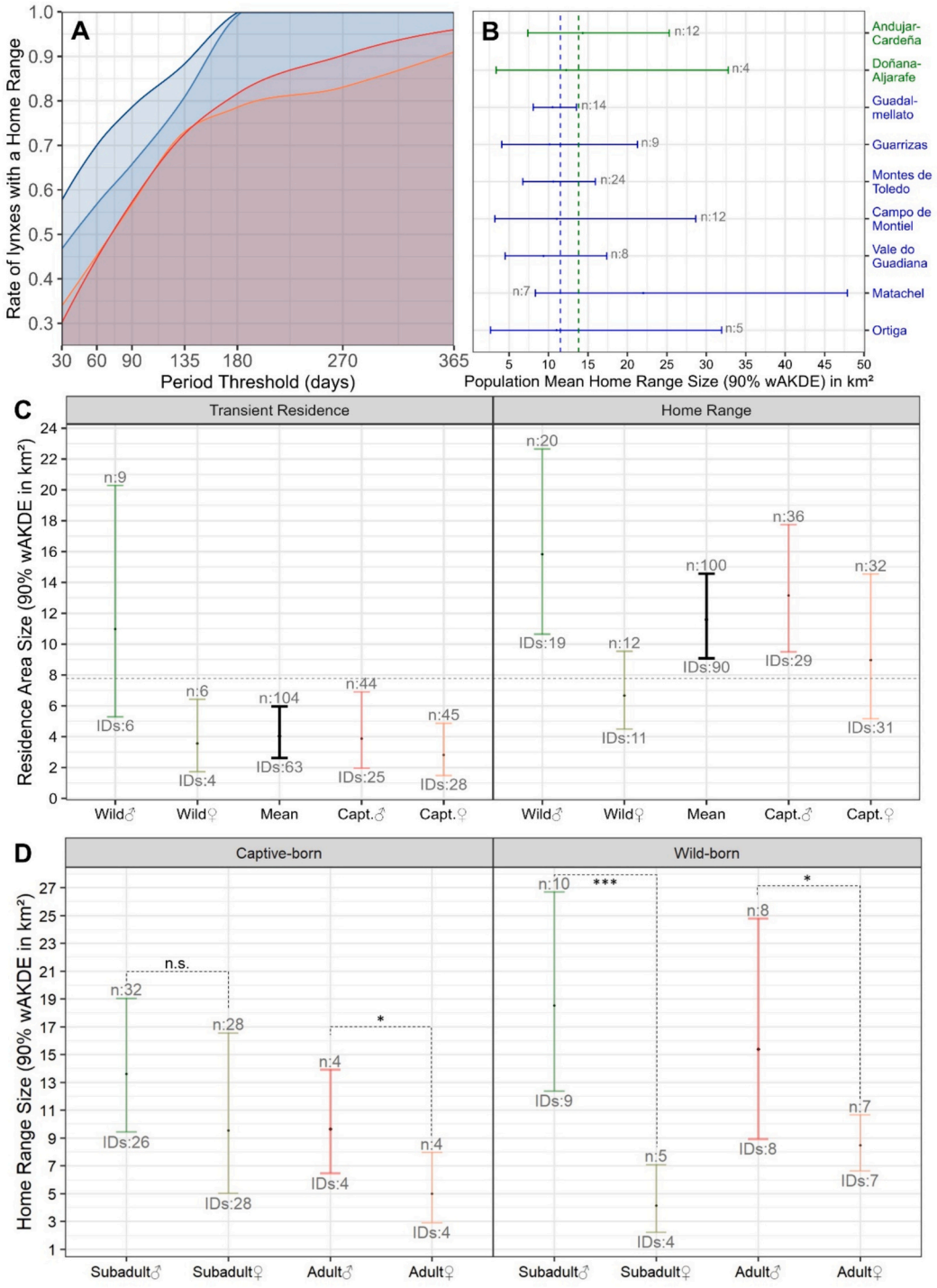



**Fig. 3.** Size and rate of establishment of residence areas: (A) Cumulative rate of translocated Iberian lynxes that established a home range (HR) within several period thresholds (days) according to origin and time since population re-establishment: all relocated individuals; and individuals released within the first 2 years since their population re-establishment. Solid lines are represented using smoothed non-parametric curves. Individuals were only included in the analysis if their monitoring period exceeded each specific period threshold, i.e. the sample size decreases as the duration is longer. (B) Mean HR size (90 % wAKDE) of each population. Natural populations appear in green and reintroduced ones in blue. The dashed vertical lines represent the mean HR size for all natural (green) and reintroduced populations (blue). (C) Mean residence area sizes and 95 % CI (90 % wAKDE of transient residences (left) and HRs (right)) according to movement phase, sex and origin: wild non-translocated ("Wild:noTrans"), wild translocated ("Wild:Trans") or captive-born. The horizontal solid and dashed grey lines represent the overall mean value and 95 % CI, respectively. (D) Mean HR sizes and 95 % CI (90 % wAKDE) according to origin, sex and age class. Codes for the levels of significance of coefficients are: *p*-values <0.001 ('***'), <0.05 ('*'), and ≥ 0.05 ('n.s.'). In C and D, the number of individuals (IDs), and total sample size of wAKDE (n) are reported on top and below the vertical brackets. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

translocated and captive-born females (Fig. 3C).

Nevertheless, in wild individuals (translocated and non-translocated), female home ranges were significantly smaller than those of males, for both age classes (*F*-test *p*-values: <0.01, Fig. 3C–D). Adult captive-born individuals showed a significant home range size difference between sexes as well (*F*-test *p*-value: 0.03; Fig. 3D). However, when considering only subadults, the home ranges of captive-born individuals were not significantly different between sexes (*F*-test *p*-value: 0.18), as opposed to wild translocated and non-translocated subadults (*F*-test *p*-values: <0.05; Fig. 3D).

Transient residence areas were on average significantly smaller than home ranges (*F*-test *p*-value: <0.0001; Fig. 3C). Captive-born males established transient residence areas significantly smaller than those of translocated and non-translocated wild males (*F*-test *p*-values: <0.05; Fig. 3C). This pattern was consistent for lynxes translocated within two years from the first reintroduction of each population (Fig. S4).

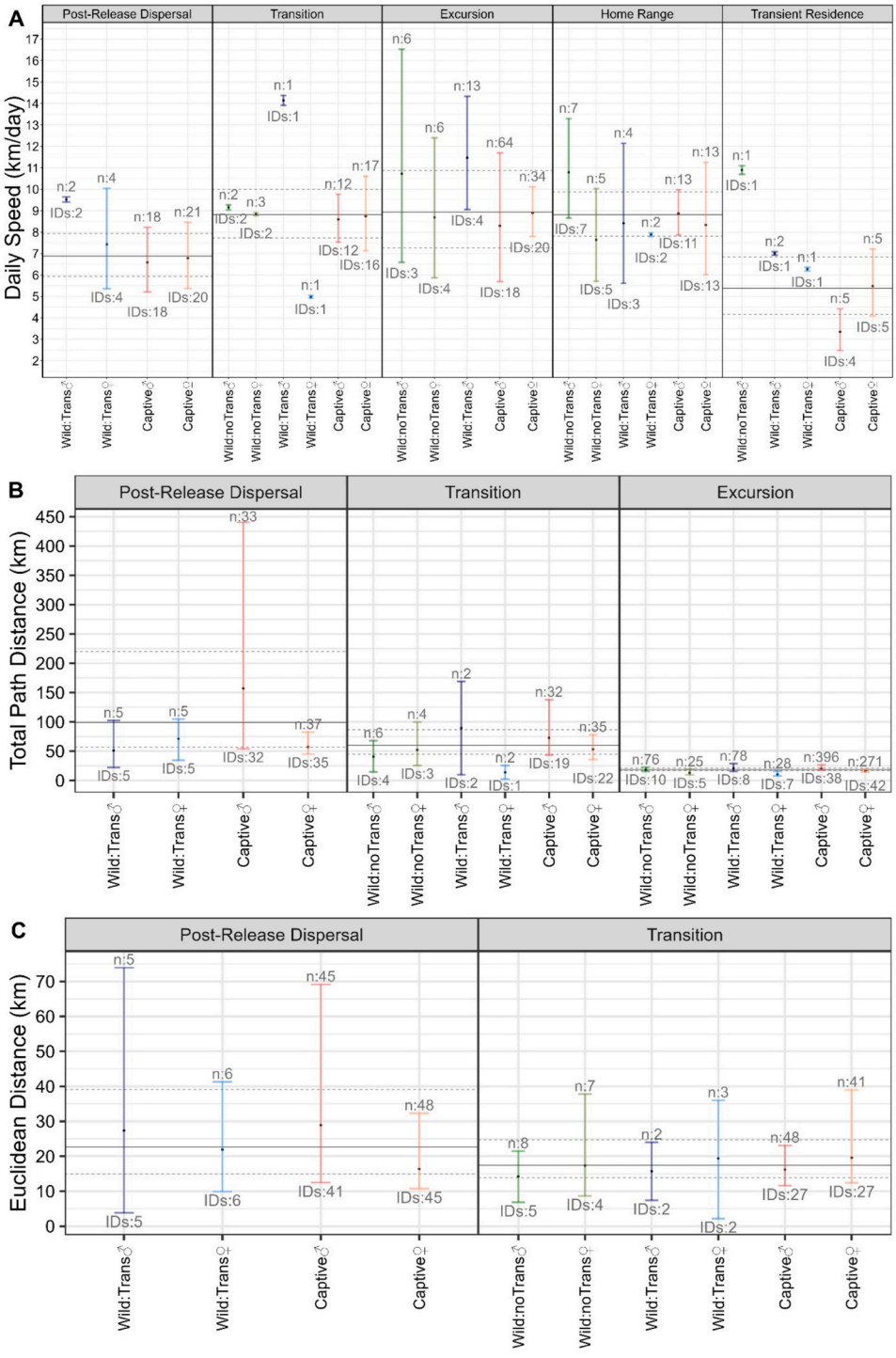



**Fig. 4.** Daily speeds and distances travelled across movement phases (mean and 95 % CI): (A) Daily movement speeds (km/day); (B) total path distances (km); and (C) Euclidean distances (km) according to movement phases, sex and origin: wild non-translocated ("Wild:noTrans"), wild translocated ("Wild:Trans") or captive-born. When only two samples are available (n:2), they are both reported. The horizontal solid and dashed grey lines represent the mean value and the 95 % CI of each phase, respectively. The sample size (n) and number of individuals (IDs) are reported on top and below the vertical brackets, respectively.

However, the mean number of transient areas did not differ between the translocated wild (0.66) and captive-born (0.2) males (Wilcoxon test *p*-value: 0.098). Females instead showed similar transient residence sizes and numbers for all origins (Fig. 3C).

### 3.2.2. Daily speeds

Movement speeds were stable throughout transitions, excursions and home ranges (Fig. 4A), but lynxes travelled significantly slower during the post-release dispersal (*F*-test *p*-values: <0.05) and the transient residence (*F*-test *p*-values: <0.005) phases. Captive-born males travelled significantly slower than wild males during transient residence (*F*-test *p*-values: <0.0001) and post-release dispersal (*F*-test *p*-value: 0.0017) phases (Fig. 4A). Females did not show differences among origins in their daily speeds.

### 3.2.3. Distances travelled during extra-territorial movements

Iberian lynxes covered considerable distances when dispersing, travelling for an average total path distances of 59.88 km (95 % CI: 44.99–88.07) during transitions and 98.89 km (95 % CI: 56.53–220.38) during post-release dispersal events, and with up to 2381 km travelled during the latter (440 days post-release dispersal; Fig. 5A). While compared across all groups of individuals, both total path (Wilcoxon test *p*-value; 0.09) and Euclidean distances (Wilcoxon test *p*-value; 0.25) travelled during transitions and post-release dispersal events were not significantly different (Fig. 4B–C). However, excursions were on average significantly shorter than transitions (Wilcoxon *p*-value <0.0001) and post-release dispersals (Wilcoxon test *p*-value <0.0001).

We did not find significant differences in the total path and Euclidean distances travelled between males and females (Fig. 4B–C). Females travelled shorter distances during excursions than males for non-translocated wild individuals (Wilcoxon test *p*-value: 0.047) and captive-born individuals (Wilcoxon test p-value: <0.005). For translocated wild individuals this difference was not significant (Wilcoxon test *p*-value: 0.05). We also did not find significant differences between wild non-translocated, wild translocated, and captive-born lynxes in the total path and Euclidean distances travelled during transitions and post-release dispersals (Fig. 4B–C).

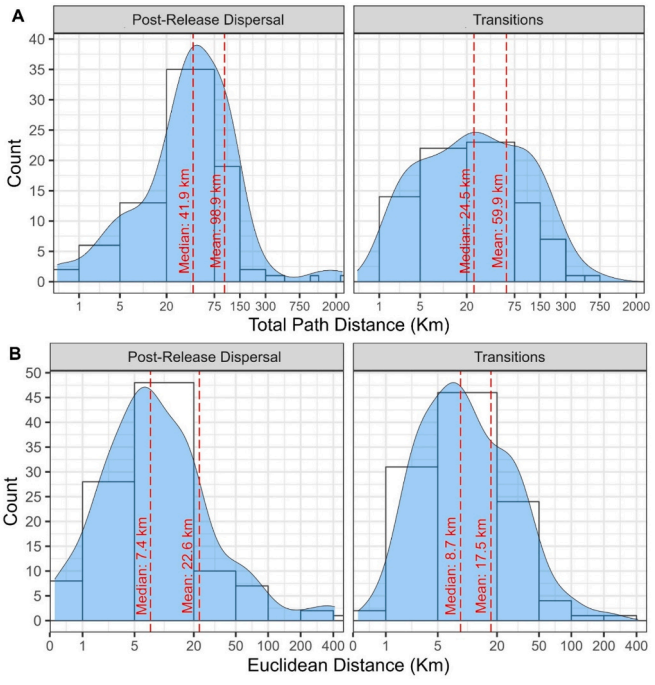



**Fig. 5.** Histogram and density plot of the (A) total path distances and (B) Euclidean distances travelled. Note that distances are transformed using the expression log(1 + distance) for readability.

## 4. Discussion

Our findings revealed that both reintroduced captive-born and wild Iberian lynxes presented space-use patterns functional to shaping the populations that have re-defined the species distribution range, laying the foundation for the success of the reintroduction projects. Residency behaviour, in particular, emerged across both groups of translocated individuals. Nevertheless, the lack of intersexual home range size difference in captive-born subadults, which is contrary to the species' natural pattern, and the distinct extraterritorial movements observed in captive-born individuals highlight the necessity of conducting close monitoring of translocated lynx to evaluate their post-release movements and long-term adaptation during future population reinforcements and reintroductions. Consequently, our study emphasizes the importance of considering these factors when developing conservation strategies for the Iberian lynx and provides quantitative indications on how to blend the translocation of captive-born and wild individuals.

### 4.1. Space-use and populations' distribution patterns

Residence areas, especially home ranges, were included in most of the space-use tactics adopted by reintroduced lynxes, as expected for a territorial felid (Sandell, 1989). Our findings showed that wild individuals settled at a higher rate in home ranges than captive-born ones (Fig. 3A). Nevertheless, most reintroduced lynxes, regardless of origin, also established home ranges indicating that they successfully adapted to their new environment (Berger-Tal and Saltz, 2014; Sarkar et al., 2016). This is further supported by the high survival rates of reintroduced individuals (81 % for wild- and 60 % for captive-born in populations where lynxes from both origins were released; WWF, 2019), which were overall higher than those reported in other *Felidae* reintroduction projects (Jule et al. (2008) for a review: 62 % for wild- and 45 % for captive-born as an overall average) and similar to those reported in other carnivore translocations (Thomas et al. (2023) for a review: 70 % for wild- and 64 % for captive-born).

The natural space-use pattern in solitary felids is characterized by males establishing relatively large home ranges that encompass multiple, smaller female home ranges to increase their mating success (polygamy) (SU1 in Fig. 2A; tiger *Panthera tigris*: Goodrich et al., 2010; leopard *Panthera pardus*: Snider et al., 2021; see also Sandell, 1989). This difference in home range size between males and females is also characteristic of the Iberian lynx mating system as observed in relic populations pre-reintroduction (Ferreras et al., 1997; Gil-Sánchez et al., 2011), as well as in non-translocated and translocated wild individuals (this study). Instead, captive-born individuals seemed to establish the space-use sexual bias only as adults (Fig. 3C–D), suggesting that age conditioned their space-use choices (shifting from SU2 to SU1 space-use pattern, Fig. 2A). As solitary male felids need larger-than-females' home ranges to pursue reproduction, this may be linked to fitness. To support this hypothesis, follow-up work should investigate the reproductive success rate of reintroduced wild vs. captive-born individuals. Alternatively, the age-dependent space-use pattern could be linked to a lack of experience of captive animals in free-ranging movements and a learning process in defining a home range responding to individual needs (Ranc et al., 2022; Stoinski et al., 2003). This is also supported by the delayed establishment of home ranges in captive vs. wild translocated individuals (Fig. 3A).

Rueda et al. (2021) indicated a tendency for home ranges from reintroduced populations being smaller than in natural populations. We instead recorded a generally high individual variability of home range size within and across populations (Fig. 3B). This variability could be caused by several extrinsic and intrinsic factors, such as the availability of food resources (rabbit density), the environmental context (habitat types, connectivity, disturbance), the occurrence of conspecifics, and individual spatial learning and memory capabilities (Cagnacci, 2023).

### 4.2. Extra-territorial movement behaviours

Several reintroduced Iberian lynxes established transient residence areas while dispersing after their release (SU5 in Figs. 2A; S3B–C). Overall, transient residence areas were smaller than home ranges (Fig. 3C), a pattern previously observed in other large felids such as wild pumas, *Puma concolor* (Beier, 1995). One exception were male wild lynxes, which established larger transient residence areas than captive-born males, and similar in size to home ranges. This pattern was also observed for lynxes released in the first stages of reintroduced populations, indicating that the density of conspecifics (Benson et al., 2006; Ferreras et al., 1997) was not the determining factor behind the smaller area sizes of captive-born males. Again, this could be associated with a steeper learning process to get acquainted with new environments for captive than for wild individuals. We also observed that captive-born males moved slower than wild ones inside transient residences and during post-release dispersal. Dispersing solitary felids usually show less mobility than their home range defending conspecifics (Farhadinia et al., 2020b). Slow explorative behaviours together, with smaller range sizes, are associated with shy personalities (Sih et al., 2004; Spiegel et al., 2017). Indeed, Úbeda et al. (2021) reported that in breeding facilities captive-born Iberian lynxes exhibited significantly less impulsive, or more shy, behaviour than wild individuals. This is an important finding, as cautious behaviours can increase survival rates, which is desirable for the success of reintroductions, particularly during their first stages (Smith and Blumstein, 2008). Conversely, bolder behaviours may increase individual fitness through higher reproductive success (Smith and Blumstein, 2008). A comprehensive evaluation of the behavioural responses of wild and captive-born individuals when released in new environments should consider the context encountered, and in particular the effect of human disturbance (Schell et al., 2021).

Reintroduced captive-born individuals were more prone to post-release dispersal than wild individuals (Fig. S3B–C) and some were nomadic for extensive periods (patterns SU4 and SU5 in Figs. 2A, 3A). Two of these individuals travelled extraordinary total path distances up to 8 and 15 times the average observations, respectively. Additionally, another captive-born male was found 930 km away from its point of release in Vale do Guadiana, Portugal (Fig. 1). These are the longest dispersal events ever recorded for the species, highlighting its great dispersive capabilities, comparable to other *Lynx* species (Poole, 1997; Zimmermann et al., 2005), and possibly indicating an attempt to return to their place of origin (Linnell et al., 1997; Miller et al., 2011).

The distances travelled during transitions were similar between translocated and wild non-translocated individuals (Fig. 4B–C). This indicates that the release in a foreign area did not influence translocated individuals to travel longer distances when transitioning between residence areas. Besides, we found that the distance travelled during transitions was comparable to that reported by Ferreras et al. (2004) during natal dispersal, indicating that these transitions share movement characteristics with the species' natural dispersal events. Moreover, the lack of differences in the distance travelled during transitions between males and females (Fig. 4B–C) is consistent with earlier findings on dispersal distances of *Lynx* species being similar between sexes (Ferreras et al., 2004; Poole, 1997; Rueda et al., 2021; Zimmermann et al., 2005). This indicates that both males and females are capable of covering substantial distances during dispersals and establishing residence areas tens of kilometers away from their place of departure (Figs. 4B–C, 5). This process may allow the natural colonization of new areas and the creation of stepping stones that could potentially form new populations in the future, favouring the connectivity of the metapopulation and further widening the species distribution range.

### 4.3. Implications for conservation

Wild and captive-born Iberian lynxes shared several features of space-use and movement patterns leading to residency, ultimately supporting population re-establishment. This finding endorses the utilization of captive-born individuals for population reintroductions, as recently pointed out (Thomas et al., 2023), and supports the effectiveness of husbandry schemes and pre-release training of captive-born lynxes. The ongoing ex-situ breeding programme continues to yield more captive-born individuals and the establishment of new populations is becoming a primary conservation objective for enhancing the genetic viability of the species (Pacín et al., 2023). To get closer to the objective of re-establishing the historical distribution range, we propose employing the newly bred captive offspring for the reintroduction of these new populations (Rueda et al., 2021; Schaub et al., 2009).

However, we found several behavioural differences that managers should consider in future translocations. Given that ex-situ management will be an inevitable component for the conservation of many felids (Farhadinia et al., 2020a), including the Iberian lynx, we recommend that reintroduced individuals are closely tracked using GPS to monitor their movements and their settlement in the desired reintroduction area. Moreover, we recommend monitoring the movements of reintroduced captive-born individuals also years after their release to evaluate their long-term adaptation. When genetic reinforcements are needed in stable populations where competition is high (Kleinman-Ruiz et al., 2019; Simón et al., 2012), we recommend prioritizing the translocation of wild individuals as they may compete more successfully to establish territories than their more cautious captive-born counterparts.

Moreover, the space-use and movement metrics (e.g. home range and transient residence sizes, dispersal distances) used in this study, specifically measured across wild and captive-born individuals and demographic groups, are highly valuable for planning the establishment of new populations. Indicating the size, location and distribution of desired residence areas and stepping stones can strongly support the management of connectivity in order to establish a viable and self-sustainable metapopulation that secures the recovery of the Iberian lynx.

This approach can represent a valid tool whenever a reintroduction programme is put in place, especially for projects involving the captive breeding of felids such as the Texas ocelot (*Leopardus pardalis*; Recover Texas Ocelots, 2023), the Scottish wildcat (*Felis silvestris*; SWAforLIFE, 2019) or the Arabian leopard (*Panthera pardus nimr*; Panthera, 2019). The study of potential movement tactics expected by translocated animals and how these movements would emerge as newly established or expanded populations can support conservation planning and adaptive conservation at the project's onset. Checking whether the movement behaviour of reintroduced animals matches the expectation can indicate, for example, potential issues in the release design; or potential for successful sexual selection.

## 5. Conclusion

The unique opportunity to study the emergence of space-use of reintroduced individuals across multiple populations at the distribution range scale empirically proved how a combination of movement tactics, highly variable across individuals, contributed to population distribution. Our study also highlights the effectiveness of a comprehensive reintroduction initiative, primarily centred on translocating individuals born in captivity. In the context of the current emphasis on ecosystem restoration, our findings demonstrate that integrated ex-situ and reintroduction programs can play a significant role in restoring the distribution range of endangered species.

## CRediT authorship contribution statement

**Pablo Cisneros-Araujo:** Writing – review & editing, Writing – original draft, Visualization, Software, Resources, Project administration, Methodology, Investigation, Funding acquisition, Formal analysis, Data curation, Conceptualization. **German Garrote:** Writing – review & editing, Supervision, Resources, Project administration, Investigation, Funding acquisition, Data curation, Conceptualization. **Andrea**

**Corradini:** Writing – review & editing, Visualization, Methodology, Investigation, Conceptualization. **Mohammad S. Farhadinia:** Writing – review & editing, Methodology, Conceptualization. **Benjamin Robira:** Writing – review & editing, Software, Methodology. **Guillermo López:** Writing – review & editing, Resources, Data curation. **Leonardo Fernández:** Writing – review & editing, Resources, Data curation. **Marcos López-Parra:** Writing – review & editing, Resources, Data curation. **Maribel García-Tardío:** Writing – review & editing, Resources, Data curation. **Rafael Arenas-Rojas:** Writing – review & editing, Resources, Data curation. **Teresa del Rey:** Writing – review & editing, Resources, Data curation. **Javier Salcedo:** Writing – review & editing, Resources, Funding acquisition, Data curation. **Pedro Sarmento:** Writing – review & editing, Resources, Data curation. **Juan Francisco Sánchez:** Writing – review & editing, Resources, Data curation. **María Jesús Palacios:** Writing – review & editing, Resources, Data curation. **Juan Ignacio García-Viñás:** Writing – review & editing, Supervision, Funding acquisition. **Maria Luisa Damiani:** Writing – review & editing, Software. **Fatima Hachem:** Writing – review & editing, Software. **Aitor Gastón:** Writing – review & editing, Supervision, Resources, Project administration, Methodology, Investigation, Funding acquisition, Conceptualization. **Francesca Cagnacci:** Writing – review & editing, Supervision, Resources, Project administration, Methodology, Investigation, Conceptualization.

## 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.

## Data availability

Data used in this study are guarded by JA, JuntaEx, JCCM and ICNF but restrictions apply to their availability and are not publicly available. Data are available if requested with justification of use.

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## Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.biocon.2024.110646.

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# Update


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Corrigendum

# Corrigendum to "Born to be wild: Captive-born and wild Iberian lynx (Lynx pardinus) reveal space-use similarities when reintroduced for species conservation concerns" [Biol. Conserv. 294 (2024) 110646]

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The authors inform about a correction made to Fig. 3, which is shown below:

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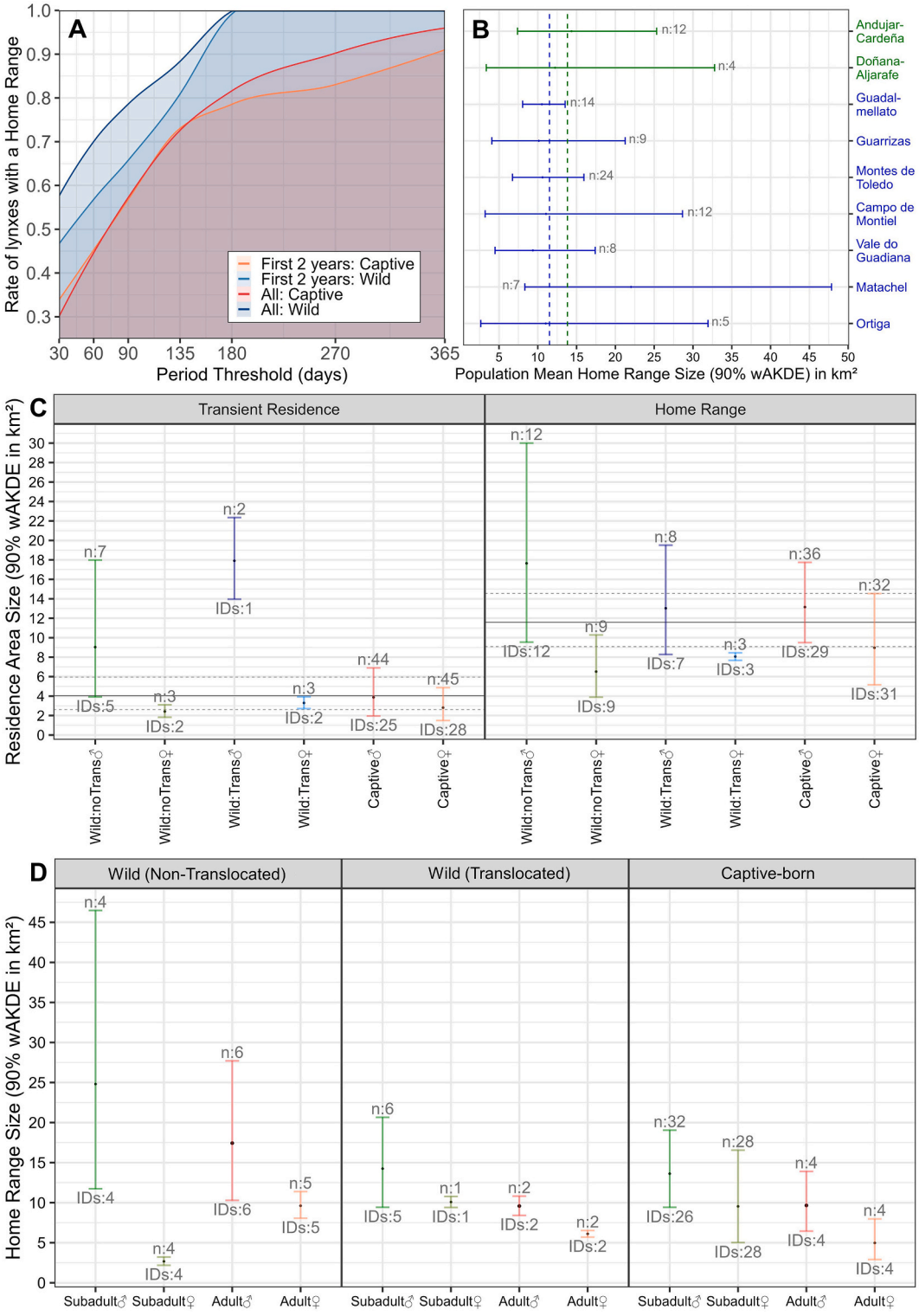



Fig. 3. Size and rate of establishment of residence areas: (A) Cumulative rate of translocated Iberian lynxes that established a home range (HR) within several period thresholds (days) according to origin and time since population re-establishment: all relocated individuals; and individuals released within the first 2 years since their population re-establishment. Solid lines are represented using smoothed non-parametric curves. Individuals were only included in the analysis if their monitoring period exceeded each specific period threshold, i.e. the sample size decreases as the duration is longer. (B) Mean HR size (90 % wAKDE) of each population. Natural populations appear in green and reintroduced ones in blue. The dashed vertical lines represent the mean HR size for all natural (green) and reintroduced populations (blue). (C) Mean residence area sizes and 95 % CI (90 % wAKDE of transient residences (left) and HRs (right)) according to sex and origin: wild non-translocated ("Wild:noTrans"), wild translocated ("Wild:Trans") or captive-born. The horizontal solid and dashed grey lines represent the overall mean value and 95 % CI, respectively. (D) Mean HR sizes and 95 % CI (90 % wAKDE) according to origin, sex and age class. In C and D, the number of individuals (IDs), and total sample size of wAKDE (n) are reported below and on top of the vertical brackets. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

The authors would like to apologise for any inconvenience caused.