PROCEEDINGS B

royalsocietypublishing.org/journal/rspb

Research

Extra-territorial excursions of Eurasian lynx (*Lynx lynx*) during the mating season across Europe

Yutong Liang[1,2], Stephanie Kramer-Schadt[3,4], Jenny Mattisson[5], Elisa Belotti[6,7], Luděk Bufka[7], Dime Melovski[8], Darja Slana[9], Ole Anders[10], Tomma Lilli Middelhoff[10], Henrik Andren[11], Malin Aronsson[11], Jens Persson[11], Jakub Skorupski[12,13], Magdalena Tracz[12], Maciej Tracz[12], Marcin Grzegorzek[12], Roksana Baryło[12], Sarah Bauduin[14], Jean-Michel Vandel[14], Rok Černe[9], Aleksander Trajbarič[9], Martin Duľa[15,16], Miroslav Kutal[15,16], Urša Fležar[9,17], Lan Hočevar[17], Miha Krofel[17], Teresa Oliveira[17], Tomislav Gomerčić[18], Ira Topličanec[18], Jakub Kubala[19], Branislav Tám[20], Jarmila Krojerová-Prokešová[21,22], Raido Kont[23], Rafał Kowalczyk[24], Krzysztof Schmidt[24], John D. C. Linnell[25,26], John Odden[27], Anja Molinari-Jobin[28], Robert W. Mysłajek[29,30], Sabina Nowak[29,30], Michał Figura[29,30], Henryk Okarma[31], Aivars Ornicāns[32], Joe Premier[2,†] and Marco Heurich[1,2,26,†]

[1]Faculty of Environment and Natural Resources, University of Freiburg, Freiburg, Germany
[2]Bavarian Forest National Park, Grafenau, Germany
[3]Leibniz Institute for Zoo and Wildlife Research, Berlin, Germany
[4]Institute of Ecology, Technische Universität Berlin, Berlin, Germany
[5]Norwegian Institute for Nature Research, Trondheim, Norway
[6]Faculty of Forestry and Wood Sciences, Czech University of Life Sciences Prague, Prague, Czech Republic
[7]Šumava National Park Administration, Vimperk, Czech Republic
[8]Macedonian Ecological Society, Skopje, North Macedonia
[9]Slovenia Forest Service, Ljubljana, Slovenia
[10]Harz National Park, Wernigerode, Germany
[11]Grimsö Wildlife Research Station, Swedish University of Agricultural Sciences, Riddarhyttan, Sweden
[12]West-Pomeranian Nature Society, Szczecin, Poland
[13]University of Szczecin, Szczecin, Poland
[14]French Agency for Biodiversity, France
[15]Faculty of Forestry and Wood Technology, Mendel University in Brno, Brno, Czech Republic
[16]Carnivore Conservation Programme, Friends of the Earth Czech Republic, Olomouc, Czech Republic
[17]Biotechnical Faculty, University of Ljubljana, Ljubljana, Slovenia
[18]Faculty of Veterinary Medicine, University of Zagreb, Zagreb, Croatia
[19]Technical University of Zvolen, Slovakia
[20]National Zoological Garden Bojnice, Bojnice, Slovakia
[21]Institute of Vertebrate Biology, Czech Academy of Sciences, Prague, Czech Republic
[22]Faculty of AgriSciences, Mendel University in Brno, Brno, Czech Republic
[23]Institute of Ecology and Earth Sciences, University of Tartu, Tartu, Estonia
[24]Mammal Research Institute Polish Academy of Sciences, Białowieża, Poland
[25]Norwegian Institute for Nature Research, Lillehammer, Norway
[26]University of Inland Norway—Evenstad Campus, Koppang, Norway
[27]Norwegian Institute for Nature Research Oslo, Oslo, Norway
[28]Progetto Lince Italia, Tarvisio, Italy
[29]Institute of Ecology, Warsaw University Faculty of Biology, Warsaw, Poland
[30]Association for Nature ‘Wolf’, Twardorzeczka, Poland
[31]Institute of Nature Conservation Polish Academy of Sciences, Kraków, Poland
[32]Latvian State Forest Research Institute Silava, Salaspils, Latvia

YL, 0009-0001-7447-1302; SK-S, 0000-0002-9269-4446; DM, 0000-0002-1072-6978; HA, 0000-0002-5616-2426; JP, 0000-0003-1405-7561; JS, 0000-0001-6899-701X; MD, 0000-0003-2675-4575; UF, 0000-0001-5865-948X; MK, 0000-0002-2010-5219;

Cite this article: Liang Y *et al*. 2026 Extra-territorial excursions of Eurasian lynx (*Lynx lynx*) during the mating season across Europe. *Proc. R. Soc. B* **293**: 20252235.
https://doi.org/10.1098/rspb.2025.2235

Received: 1 September 2025
Accepted: 24 November 2025

Subject Category:
Ecology

Subject Areas:
behaviour, ecology

Keywords:
foray, extra-home range movement, mating tactics, reproductive strategies, mammalian carnivore

Author for correspondence:
Stephanie Kramer-Schadt
e-mail: kramer@izw-berlin.de

[†]These authors contributed equally to the study.

Electronic supplementary material is available online at https://doi.org/10.6084/m9.figshare.c.8171352.

THE ROYAL SOCIETY
PUBLISHING

TO, 0000-0001-9751-5198; JK, 0000-0003-2051-508X; JK-P, 0000-0002-0067-6196; KS, 0000-0002-9043-291X; JP, 0000-0003-3225-6038; MH, 0000-0003-0051-2930

Extra-territorial mating excursions (i.e. short-term movements beyond established home ranges to seek mating opportunities) represent an underexplored reproductive strategy in felids. Using telemetry data from 125 Eurasian lynx (172 lynx-years, 1995–2023) across Europe, we investigated sex-specific spatio-temporal patterns and drivers of these excursions during the mating season. Overall, 33% of males and 11% of females undertook excursions, with males having higher rates than females. Male excursions mostly occurred in March, coinciding with the peak of the conception period, while females tended to undertake excursions either before or after this peak. The median Euclidean distance travelled beyond the home range was 6.8 km for males and 2.6 km for females, with corresponding median durations of 119 h and 85 h, respectively. Translocated individuals exhibited higher excursion rates than those in established populations, suggesting mate-searching in novel environments. We found no evidence that human influences affected excursion rates or distances. Our findings highlight a mating tactic that is often overlooked and provide new insight into sex-specific and context-dependent movement strategies in Eurasian lynx. By linking extra-territorial excursions to reproduction patterns, our study informs future research on mate-searching behaviour in felids and offers implications for conservation planning, particularly in isolated or reintroduced populations.

1. Introduction

Extra-territorial excursions, or forays, refer to short-term movements beyond an individual's established home range, after which the individual returns (hereafter referred to as excursions). Among birds [1,2] and some mammals (e.g. red fox *Vulpes vulpes* [3], European badger *Meles meles* [4], red squirrel *Sciurus vulgaris* [5]), mating excursions are common and can increase reproductive opportunities by facilitating mate choice, reducing inbreeding risk, and enhancing offspring fitness [6–8]. Despite their potential significance, such excursions are poorly documented in felids, species that are among the most vulnerable apex predators and of high conservation concern [9]. Although male-biased breeding-season excursions have been investigated in a few species, such as pumas (*Puma concolor*) [10], the behavioural patterns and mechanisms driving these finer-scale movements remain unclear. Yet these movements may influence individual fitness and population dynamics, processes central to ecology and evolution [11].

In solitary felids, male reproductive success is closely linked to movement strategies that facilitate access to receptive females. Resident males may defend exclusive territories to monopolize females [12,13], whereas alternative tactics such as intrasexual range overlaps or long-distance excursions also occur [10,14], indicating a degree of behavioural flexibility in mate-searching movements of felids. The choice of mating strategy could be influenced by ecological and social factors, including male social status (e.g. dominant versus subordinate), female distribution, movement costs and the local sex ratio [15,16]. For instance, males are more likely to maintain territoriality when females are spatially predictable and when the risks and energetic costs of defending exclusive mating access to females from competing suitors (i.e. aggressive confrontations, patrolling and marking) are outweighed by the potential to increase their fitness [17]. Excursions may be advantageous for males when females are sparsely or unpredictably distributed. By contrast, females typically exhibit strong site fidelity, driven by the need for a secure food supply and to protect offspring from predation and infanticide [13,18]. Nevertheless, occasional female mating excursions have been documented in pumas [10] and hypothesized in African leopard (*Panthera pardus*) [14], potentially for mate assessment via scent cues [19] or infanticide avoidance through paternity confusion [20].

The Eurasian lynx (*Lynx lynx*; hereafter lynx) is a solitary, territorial felid ranging from western Europe to central Asia. Lynx are polygynous; resident males typically maintain a large home range covering several females [21,22]. During the mating season, both sexes increase movement rates [23–26], including occasional excursions [27,28]. Although female spatial behaviour is mainly driven by prey availability [29], increasing movements could enhance mating opportunities and conception success, especially in low lynx densities or when males have limited control over mating [6,14,30]. Unlike year-round breeding felids such as domestic cats (*Felis catus*), leopards (*Panthera pardus*) and lions (*Panthera leo*), lynx are seasonal, monoestrous breeders with one oestrous per year, typically from February to April in Europe [31–33]. Females are in oestrus for 2–10 days, during which they are sexually receptive and display typical behaviours such as calling and rolling [33,34]. The timing of oestrus may vary geographically, as indicated by regional differences in parturition dates [35]. Intersexual interactions are mainly limited to this seasonal breeding period, constraining mating opportunities and mate choice. Mating excursions by either sex may reflect strategies to increase access to mates, yet their movement patterns remain understudied in lynx.

Historically widespread across Europe, lynx experienced severe population declines due to hunting, persecution, habitat loss and prey depletion [36]. Since the 1970s, reintroduction and reinforcement programmes have aimed to establish populations, restore genetic diversity and connect isolated populations [28,37]. Most established populations, whether remnant or reintroduced, are now stable or increasing [38]. However, translocated individuals often exhibit behavioural and ecological differences. Captive-bred felids may show deficiencies in reproduction and social interactions [39], while reintroduced lynx individuals have demonstrated more cautious movement and fewer excursions in the Iberian lynx [40], or altered habitat preferences in the Eurasian lynx [41]. These behavioural differences may influence fitness, particularly during the mating season when access to mates is critical. Whether translocated lynx adopt bolder strategies to maximize reproductive opportunities or risk-averse tactics to prioritize survival remains unclear. While previous studies have examined post-release movements and habitat use [41–43], movement behaviour related to mate searching remains underexplored. Telemetry data across ecological

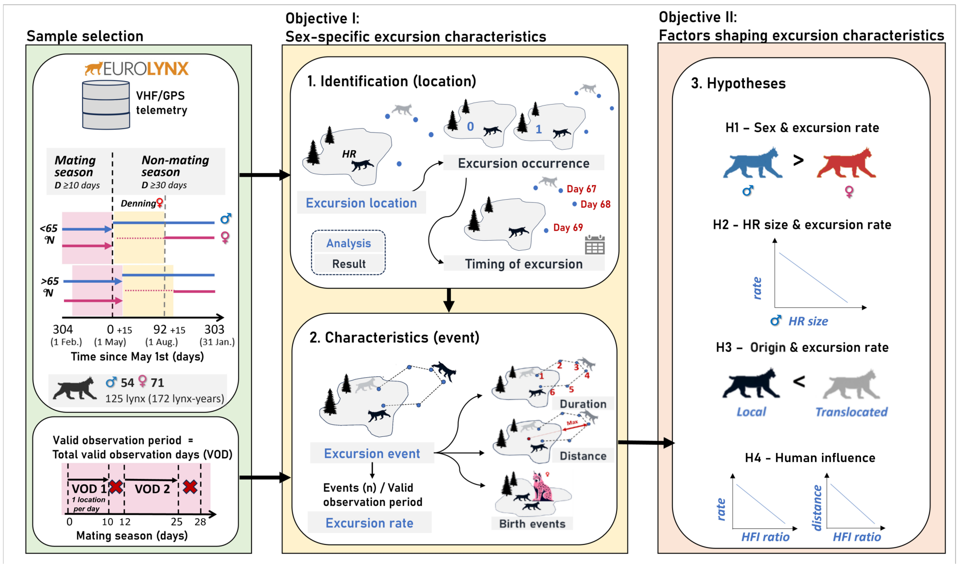

Figure 1. Workflow summarizing sample selection and two objectives: (I) investigating sex-specific excursion characteristics (see §2b(i)–(ii)) and (II) examining factors shaping excursions using generalized linear mixed models (GLMMs; see §2c). We tested four hypotheses, as follows. (H1) Males undertake more excursions than females, reflecting active mate-searching behaviour to maximize reproductive opportunities. (H2) Males with larger home ranges (HR) exhibit fewer excursions than those with smaller ranges, as larger ranges are more likely to encompass home ranges of receptive females, reducing the need for excursions. (H3) Wild-born (local) lynx from established populations undertake fewer excursions than translocated individuals, reflecting their familiarity with local resources and stable home ranges. Conversely, translocated lynx make more excursions due to limited spatial knowledge and the need to adjust to unfamiliar environments. (H4) Both the frequency and excursion distance decline with increasing human influence in the surrounding landscape.

and anthropogenic gradients provides an opportunity to investigate how individual origin and environmental context shape mating-season movement. These insights are essential for understanding the behavioural ecology of reintroduced felids and improving conservation strategies.

Mating excursions primarily rely on information about neighbouring individuals (i.e. scent marking [44], vocalizations [45]) and landscape structure [46,47], as these factors shape individuals' ability to track down mates. However, mate-searching movements and communication modes essential for mating success may be constrained in human-modified landscapes. Roads, settlements and agricultural areas can disrupt the spatial distribution of potential mates [45,48,49]. While lynx typically favour habitats with low human disturbance [50], the extent to which human influence on the landscape affects excursion behaviour remains unknown. This knowledge gap is particularly relevant in Europe, where lynx populations inhabit highly fragmented landscapes and face persistent human influence. Many reintroduced populations in central Europe exhibit reduced genetic diversity and elevated inbreeding levels [51–54], highlighting the urgency of understanding how human-modified landscapes influence mating-related movements in lynx, key to reproductive success and long-term population viability.

Using a large telemetry dataset of 125 lynx monitored over 172 lynx-years between 1995 and 2023 across eight European populations, we investigated spatio-temporal patterns of lynx excursions during the mating season. We examined how these movements were shaped by sex, as well as ecological and anthropogenic factors. We developed four hypotheses (figure 1) to identify the drivers of excursion patterns and providing insights into the mating strategies of Eurasian lynx and their implications for conservation across Europe.

2. Material and methods

(a) Study areas and sample selection

Following the workflow of our study (figure 1), we first compiled GPS and VHF location data on lynx from eight populations across Europe (figure 2). All animal captures and handling received permission from relevant national authorities, with procedures adhering to legal, ethical and safety requirements of the respective jurisdictions (electronic supplementary material, table S1). The telemetry data were previously screened to remove erroneous records, such as biologically implausible movements or collar errors [56].

We conducted all analyses in R version 4.3.0 [57]. We included only resident individuals with established home ranges, identified via stable patterns in net square displacement [58] and semi-variance functions [59] with R packages *amt v.0.2.2.0* and *ctmm v.1.2.0* [60,61]. We focused on residents that were sexually mature by the beginning of the mating season [34], specifically females aged ≥21 months and males aged ≥33 months (with birth dates assumed to be 1 May). Although subadult males can reach sexual maturity, they typically lack established home ranges and were therefore excluded from the analyses.

We defined the mating season as the period when conception typically occurs, based on lynx birth dates across Europe [35] and a gestation of 66–70 days [33]. North of 65°N, the mating season spanned 15 February to 15 May, with 90% of births (peak) between 15 March and 15 April. South of 65°N, it was from 1 February to 30 April, peaking between 1 March and 1 April. We

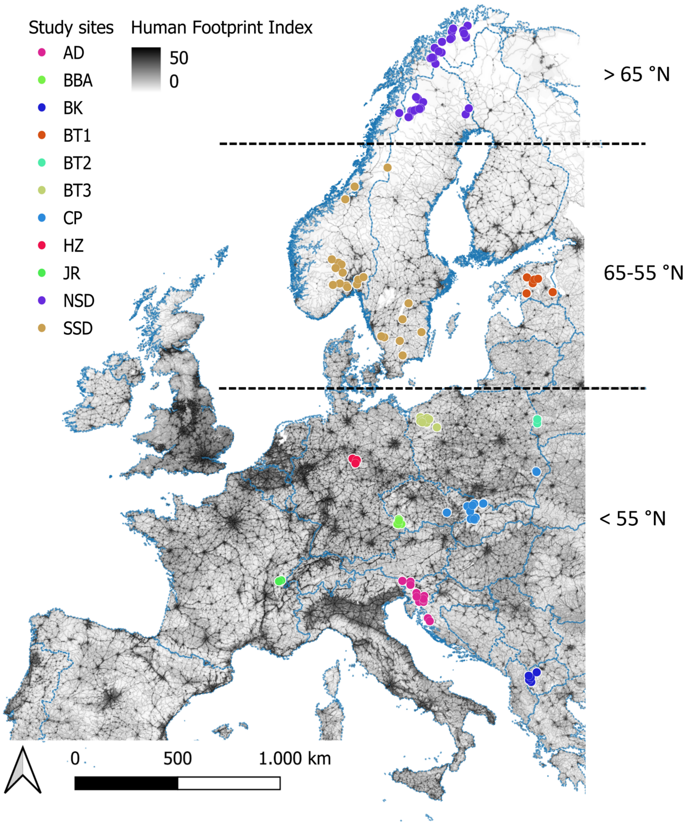

Figure 2. Telemetry data (1995–2023) from 125 lynx across Europe were used to identify excursions. Individuals were grouped into three eco-regions (>65°N, 65–55°N, <55°N) and 11 study sites based on geographic proximity: Alpine-Dinaric (AD), Bohemian–Bavarian–Austrian (BBA), Balkan, Baltic 1 (BT1; Estonia), Baltic 2 (BT2; Białowieża, in eastern Poland), Baltic 3 (BT3; Western Pomerania, in northwestern Poland), Carpathian (CP), Harz (HZ), Jura (JR), Northern Scandinavian (NSD; >65°N) and Southern Scandinavian (SSD; <65°N). Human Footprint Index (HFI) values range from 0 (low impact; white) to 50 (high impact; black) [55].

standardized temporal analyses by defining a lynx-year as the annual cycle beginning at the end of the mating season: 16 May (>65°N) and 1 May (<65°N).

To determine excursion locations during the mating season for each lynx-year, we included individuals with GPS/VHF data with continuous coverage for ≥ 10 days during the mating season, and ≥ 30 days in the preceding non-mating season. This ensured data across different months within a 4–12 month annual home range. We excluded female movements during the denning period (1 May–1 August, <65°N; 16 May–15 August, >65°N) because restricted movements during maternal care [62] do not reflect typical space use. This exclusion ensured comparable home range delineation for females with and without kittens, as it was based on comparable and representative movement behaviour, allowing more consistent identification of excursions across individuals. In total, 125 individuals (71 females, 54 males), comprising 172 lynx-years, met these criteria (figures 1 and 2; electronic supplementary material, table S2). To minimize spatial autocorrelation and sampling bias from differing tracking schedules among individuals, regions and years, we standardized data by selecting one GPS/VHF location per day [63], specifically the position closest to midnight when lynx are normally most active [64]. Consecutive locations were recorded at least 2 h apart, with a median sampling interval of one location per 24 h, ensuring temporal independence and comparability across individuals. A sensitivity analysis was conducted using the all locations (electronic supplementary material, S1).

We divided the study area into three eco-regions (>65°N, Northern Scandinavia; 65–55°N, Southern Scandinavia and the Baltics; <55°N, Central and Southern Europe) to reflect variation in environmental conditions, prey availability, human influence, reproductive timing and sample size (figure 2; electronic supplementary material, table S3). We classified the origin of lynx as either ‘translocated’ (i.e. released into reintroduced populations within 3 years post-release, including ‘wild-caught’ and ‘captive-bred’ individuals) or ‘local’ (i.e. namely wild-born lynx from established populations; electronic supplementary material, table S2). The 3-year window corresponds to ≈ 8 months of potential mate-searching across three mating seasons, aligning with the suggested timeframe to evaluate large carnivore reintroduction success [65]. In total, we included 17 translocated (12 captive-bred, 5 wild-caught) and 108 local lynx.

(b) Data processing

(i) Excursion identification

We defined annual home ranges using local convex hulls (LoCoH) with R package *adehabitatHR* v.0.4.22 [66], because they delineate range limits that follow landscape features individuals rarely cross (e.g. rivers, lakes, mountains or human-made barriers), and have been widely used in excursion studies [10,67]. Other methods, like kernel estimators, often produce overly smoothed boundaries that encompass inaccessible areas [68,69]. For comparison, we additionally estimated home ranges using minimum convex polygon (MCP), kernel density estimation and autocorrelated kernel density estimation (electronic supplementary material, figure S2). We delineated home range boundaries using the 95% isopleth, retaining all locations and considering those outside this boundary as potential extraterritorial forays.

We defined excursions as temporally consecutive locations of an individual lynx, within a given lynx-year, occurring outside its annual home range and beyond a threshold distance based on its maximum movement distance from the home range centroid (electronic supplementary material, S1 and figure S1). Excursions comprised at least two consecutive locations extending over 24 h. This threshold was applied to capture movements long enough to represent deliberate extra-territorial forays, rather than short-term displacements near home-range borders (e.g. boundary patrols and scent-marking at range edges [24–26,70]). By focusing on longer excursions, we aimed to identify movements most likely to be associated with behaviours such as mate searching, which were the focus of this study.

We calculated excursion proportion as the ratio of individuals undertaking at least one excursion to the total number of monitored individuals across years. To compare excursion timing and synchrony, we coded excursion days as 1 and non-excursion days as 0, and estimated the temporal distribution of excursions with density curves of excursion days (= 1) during the mating season for each sex and eco-region.

(ii) Excursion characteristics

For each individual, we calculated excursion rate as the number of excursion events standardized by the valid observation period (days with consistent tracking at a rate of one location per day) (figure 1). We characterized each excursion event using two metrics: (i) duration (i.e. the time elapsed between first and last locations, including travel to and from the home range) and (2) distance (i.e. Euclidean distance from the home range threshold to the farthest location reached; electronic supplementary material, figure S1). We examined the spatio-temporal overlap between excursion events and estimated female conception periods, inferred from confirmed birth events and known gestation lengths (electronic supplementary material, S2).

(iii) Anthropogenic factors

We used the Human Footprint Index (HFI; 1 km² resolution) as a proxy for human influence [55]. This index integrates eight variables representing direct and indirect human influences on the landscape: the extent of built environments, croplands, pasturelands, human population density, night-time lights, railways, roads and navigable waterways (figure 2).

For each lynx with excursion events, we calculated mean HFI: (i) within the home range (hrHFI); (ii) within a buffer extending one home range radius beyond the home range boundary (bHFI), representing surrounding human influence; and (iii) within a buffer around valid excursion locations (exHFI), with buffer size equal to half of the sex-specific average daily distance travelled across eco-regions (electronic supplementary material, figure S3). To evaluate human influence outside home ranges, we used log-transformed bHFI/hrHFI and exHFI/hrHFI; positive values indicated greater, and negative values lower, external human footprint relative to inside the home range.

(c) Statistical analyses

We compared excursion proportion, distance and duration between sexes and across three eco-regions (>65°N, 65–55°N, <55°N). To account for variation among individuals and years, we applied a bootstrap method [71], resampling individuals with replacement within sex-region strata, selecting one year per individual, and estimating sex- and region-specific medians from 1000 replicates to obtain 95% confidence intervals. Relative excursion dates, defined as days since the onset of the mating season, were compared between sexes across eco-regions using the Wilcoxon rank-sum test [72].

We fitted generalized linear mixed-effects models (GLMMs) with *glmmTMB* v.1.1.10 [73], evaluated model diagnostics with *DHARMA* v.0.4.7 [74], and visualized outputs with *ggplot2* v.3.5.1 [75]. We scaled continuous predictors (mean = 0, SD = 1) for interpretability, and all variance inflation factors (VIFs) were below 3 [76]. Random intercepts for individual identity and study site accounted for repeated observations over lynx-years and among study sites. We optimized model fit with the 'BFGS' algorithm to improve convergence and parameter stability. We evaluated model performance using conditional R^2 (lognormal approximation) with *MuMIn* v.1.48.4 [77]. We compared the full model, including all hypothesized predictors, against simpler models using the corrected Akaike information criterion (AICc) [78]. For transparency, we also report the Bayesian information criterion (BIC) and ΔBIC (electronic supplementary material, table S9) to assess the robustness of model selection. Although BIC, with its stronger penalization of model complexity, tended to favour slightly simpler models, both criteria identified similar key predictors, confirming that our conclusions are robust to information-criterion choice.

(i) Excursion rate

We focused on excursions during the mating season. To test how home range size, origin (translocated or local) and human influence affect excursion rate, we fitted a negative binomial model to account for overdispersion. The response variable was the number of excursion events per individual, with the log-transformed valid observation period as an offset. Explanatory variables included home range size, origin and the log-transformed human footprint ratio (bHFI/hrHFI). An interaction between sex and home range size tested whether males with smaller home ranges exhibited higher excursion rates. We also tested, but excluded, an interaction between eco-regions and human footprint ratio, accounting for variation in human influence

Table 1. Excursion proportion, excursion distance and duration are presented as medians with 95% CIs, during the mating season by sex and across eco-regions (North: >65°N, Centre: 65–55°N, South: <55°N). Numbers in parentheses indicate lynx-years (ly) or number of excursion events (*n*), respectively.

excursion	eco-region (°N)	males: median [95% CI]	males sample size	females: median [95% CI]	females sample size
proportion (%)	>65	12 [0, 36]	12 (ly = 24)	7 [0, 18]	26 (ly = 41)
	55–65	18 [0, 47]	10 (ly = 10)	7 [0, 27]	18 (ly = 20)
	< 55	44 [26, 62]	32 (ly = 45)	17 [4, 34]	27 (ly = 32)
distance (km)	> 65	6.8 [1.1,7.4]	3 (*n* = 3)	2.3 [0.1, 8.5]	3 (*n* = 4)
	55-65	10.4 [10.1, 10.8]	2 (*n* = 2)	2.8 [0.7, 11.0]	2 (*n* = 3)
	< 55	5.3 [2.8, 10.1]	16 (*n* = 32)	3.0 [0.2, 30.8]	5 (*n* = 5)
duration (h)	> 65	108 [93, 168]	3 (*n* = 3)	144 [72, 240]	3 (*n* = 4)
	55-65	96 [71,120]	2 (*n* = 2)	74 [72, 96]	2 (*n* = 3)
	< 55	120 [95, 191]	16 (*n* = 32)	96 [72, 168]	5 (*n* = 5)

across the three eco-regions, due to multicollinearity (VIF > 3), convergence issues and limited statistical support. Similarly, an interaction between sex and origin to assess sex-specific translocation effects did not improve model fit and was excluded, particularly given the small number of translocated individuals (males = 8, females = 9). To account for potential biases in home range estimation caused by unequal sample sizes (51–366 locations) [79], we included the total number of tracking locations as a covariate. Where data permitted, we also quantified excursion rates outside the mating season and compared them with mating-season rates (electronic supplementary material, S3) to assess whether excursions occur predominantly during the mating season, as expected under mate-searching behaviour.

(ii) Excursion distance

To evaluate human influence on excursion distance, we employed a gamma mixed-effects model (log link). The response variable was excursion distance; predictors were sex, log-transformed human footprint ratio (exHFI/hrHFI), and their interaction with eco-regions, capturing variation in human footprint across eco-regions. We included the number of excursion locations to adjust for sampling bias. To account for variation in telemetry effort during the mating season, we included number of valid observation days (days with continuous tracking of one location per day covering each excursion) as a fixed effect.

3. Results

(a) Excursion identification and characteristics

Overall, a higher median proportion of males undertook excursions compared with females (33%, 95% CI = (20, 44) versus 11%, 95% CI = (4, 18)). Males had more excursion events than females (37 versus 12), a greater median excursion distance (6.8 km, 95% CI = (3.4, 10) versus 2.6 km, 95% CI = (0.7, 6.3)), and longer median durations (119 h, 95% CI = (95, 167) versus 85 h, 95% CI = (72, 168)). Consistent sex-specific excursion patterns were observed across eco-regions, except for longer median durations for females in the north (table 1). The highest excursion proportions were recorded in the south (44% in male; 17% in female) compared to other eco-regions. When repeating the analyses using all available locations and the MCP method (electronic supplementary material, table S8), males also showed greater median excursion proportions and distances than females in the south; similar median excursion distances in males were observed across eco-regions.

Male excursions were temporally synchronized around the peak of the mating season, whereas female excursions showed a wider temporal spread throughout the mating season (figure 3A). Males started excursions later than females (Wilcoxon rank-sum test: W = 2835, median difference = 15 days, 95% CI = (8, 21)). For males, the median starting day ranged from mid-March in the south (<55°N) and centre (55–65°N) to mid-April in the north (>65°N), with no evidence of regional differences (figure 3B; electronic supplementary material, table S6). In both the south and north, females tended to initiate excursions earlier than males (median advances of 11 and 38 days, respectively; electronic supplementary material, table S6).

(b) Excursion linked to reproductive success

Among the eight excursions recorded in six females with confirmed parturition dates in the same year, one confirmed parturition was linked to an excursion undertaken by the female during oestrus (one reintroduced in Western Pomerania, Poland) (electronic supplementary material, figure S4). For males, none of the observed excursions could be confidently associated with confirmed conceptions, as no spatial overlap occurred with marked females known to reproduce in the same year. However, given the limited number of individuals with concurrent reproductive data, potential associations cannot be excluded.

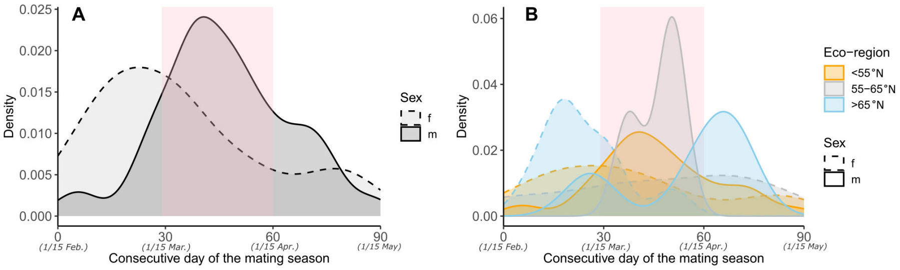

Figure 3. Distribution of excursion days by (A) sex (male = 188, female = 49) and (B) eco-regions (south (<55°N): male = 170, female = 21; centre (55–65°N): male = 6, female = 10; north (>65°N): male = 12, female = 18) from the start of the mating season (south/centre: 1 February–1 May; north: 15 February–15 May). Peak mating periods are highlighted in pink (south/centre: 1 March–1 April; north: 15 March–15 April).

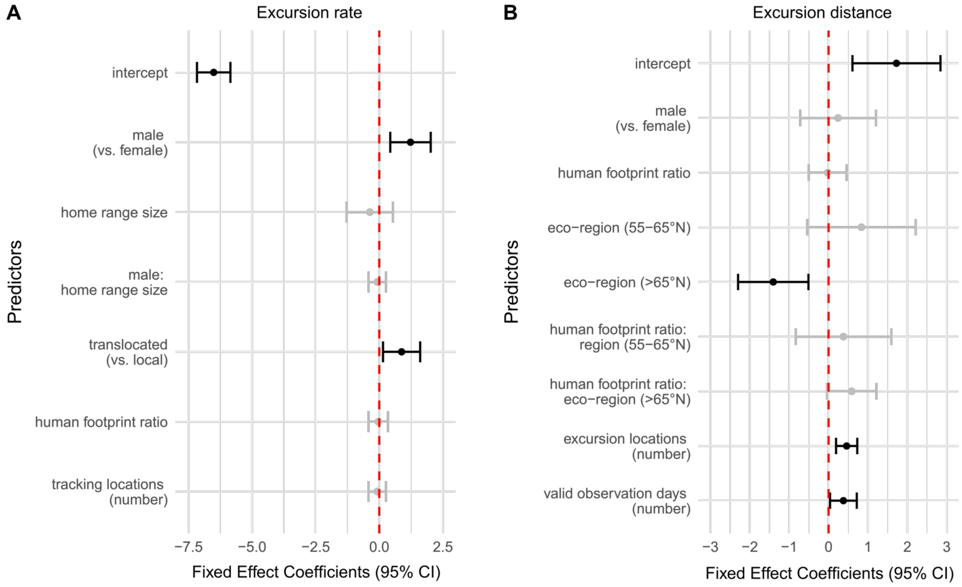

Figure 4. Coefficient plots show mean estimates with 95% confidence intervals (CIs): black, CIs excluding zero; grey, CIs including zero. (A) Negative binomial mixed-effects model estimates excursion rates by sex (male = 54, lynx-year = 79; female = 71, lynx-year = 93), home range size, origin (local (*n* = 109, lynx-year = 147) versus translocated (*n* = 17, lynx-year = 25)), human footprint ratio, and home range size—sex interaction (conditional $R^2 = 0.294$). Random-effect variances (lynx ID, study site) < 0.001. (B) Gamma mixed-effects model estimates excursion distances (male = 21, lynx-year = 37; female = 10, lynx-year = 12) by sex, human footprint ratio, region and their interactions (conditional $R^2 = 0.689$). Random-effect variance: lynx ID = 0.17 (SD = 0.42); study site < 0.001.

(c) Excursion rate and distance

The full excursion rate model (figure 4A) revealed that male lynx exhibited higher excursion rates than females, and translocated individuals showed higher excursion rates than local ones. We found no evidence for effects of home range size or human footprint ratio. The full excursion distance model (figure 4B) revealed no clear evidence for effects of sex or human footprint ratio. Longer excursion distances were associated with a greater number of excursion locations and longer number of valid observation days. Similar findings were observed across all candidate models and those based on MCP home range delineation (electronic supplementary material, table S9). Models using all available location data with 95% LoCoH suggested that excursion rates and distances increased with sampling frequency (electronic supplementary material, table S9, (A) a3 and b3). Both sexes and translocated lynx showed higher excursion rates during the mating season than the non-mating season (electronic supplementary material, S3).

4. Discussion

In this study, we applied telemetry tracking data to investigate sex-specific spatio-temporal patterns in extra-territorial excursions during the mating season of a large, wild-living, solitary felid, the Eurasian lynx, at a continental scale. We found that males undertook more excursions than females, consistent with our prediction. These movements were synchronized with estimated conception timing, which may be explained by mate-searching behaviour beyond home ranges. In line with our expectation, translocated lynx had higher excursion rates than local lynx from established populations. We found no evidence for our hypothesis that males with larger home ranges or areas of higher human influence, measured by the human footprint index, would reduce excursion rates or distance. Our findings thus offer novel insights into the mating strategies of lynx and the potential ecological drivers that may influence excursion behaviours.

Our findings showed that males have higher excursion rates during the mating season, with approximately one third exhibiting excursions. Similar male-biased excursions have been reported in puma [10,80], representing, to our knowledge, the only previously documented case in solitary felids. These male-biased movements probably aim at increasing encounters with receptive females [13], potentially to locate additional mates beyond established home ranges, as observed in other polygynous mammals like European polecat (*Mustela putorius*) [81]. The fact that most individuals did not undertake excursions aligns with lynx reliance on scent-marking to maintain territorial boundaries and communicate social status (e.g. [23,26]). These chemical signals allow individuals to advertise occupancy and reproductive condition without leaving their territories, thereby reducing the need for direct encounters. Excursions may increase risks, exposing individuals to unfamiliar neighbours and potential aggressive interactions, injury or death [26,82]. Notably, male excursions peaked synchronously in the northernmost region, corresponding with regional differences in birth timing [35]. By contrast, the less synchronized movements in central and southern Europe may reflect reproductive plasticity under more variable climates, where extended mating periods and less synchronous female oestrus could be advantageous. Shorter, synchronized excursions in northern populations may reflect adaptation to brief reproductive windows imposed by colder climates and limited prey [83]. While our results highlighted male-driven mating behaviour, regional variation in timing may also reflect differences in female reproductive physiology, which remains to be investigated. In addition, our analysis focused on resident males, leaving the earlier dispersal or roaming phases of subadult life history, when males compete to establish territories and dominance that may shape future mating strategies, as an important topic for future research.

As predicted, females had lower excursion rates than males, with most female excursions occurring outside the peak mating period. This may suggest females primarily mated with resident or visiting males within their home ranges. Increased over-marking activity during the pre-mating and mating seasons [26] probably facilitates such encounters while reducing the energetic costs of extra-range mate-searching. Saving energy and maintaining access to known resources [84,85] is particularly critical for females, given the approaching costs of gestation, lactation and kitten rearing [86]. Despite this, we observed female excursions across multiple study sites (electronic supplementary material, table S5). These results indicate that females occasionally engage in excursions, possibly for mate searching in neighbouring areas when no males are available within their home ranges. This could be especially important in small or isolated populations, where lower lynx density or habitat connectivity may increase the risk of Allee effects [87]. Excursions tended to occur shortly before or after the estimated conception periods in females that reproduced (electronic supplementary material, figure S4). Early movements may serve to advertise reproductive status or initiate copulation during the brief oestrus phase, while later excursions might reflect mate searching when the local male is absent in small populations or has been lost during the mating season, such as in Norway, where the legal hunting season overlaps with this period [88].

We found no evidence that males with larger home ranges exhibited fewer excursions, suggesting that male movement strategies are shaped not only by mate availability within home ranges, but also by other ecological or demographic factors associated with home range size. In the low-density population in Northern Scandinavia (the north eco-region, > 65 °N), males maintained large annual home ranges yet exhibited low excursion proportion (8%; electronic supplementary material, table S4), possibly because these ranges already encompassed most available mates, making further excursions unlikely to increase mating success given the low probability of encountering scattered extra-territorial females. During the short mating period, however, ranges contracted and centred on fertile females, reducing the need for excursions [84]. Conversely, in a high-density, high-turnover population in northwest Anatolia, males held small territories overlapping several female home ranges, suggesting territorial monopolization may offer greater advantages under such conditions [89]. These differences imply that males adjust their mating strategies to local conditions, balancing the costs of defending territories against the potential benefits of extra-range mate searching. This trade-off is probably further shaped by the spatio-temporal distribution of receptive females, reflected in the operational sex ratio (i.e. sexually active males per receptive female) and synchrony of oestrus. When the ratio is less male-biased and female receptivity is asynchronous, monopolization may be more feasible than seeking additional mates through excursions [90,91].

As predicted, translocated lynx had higher excursion rates than local individuals in established populations. In western Pomerania (Poland), translocated captive-bred lynx exhibited particularly high excursion proportions (80% in males, 43% in females), with some travelling over 80 km (male) and 30 km (female) beyond their established home ranges before returning. These extensive mating-season movements may reflect a lack of, or unfamiliarity with, local social structures or reproductive cues [80]. Alternatively, individual variation in exploratory tendencies could increase mate searching while simultaneously increasing risk exposure [92,93]. Furthermore, we found no sex differences in excursion rates among translocated lynx, possibly indicating active mate searching by both sexes, although small sample sizes could have limited statistical power. This pattern aligns with observations in reintroduced Iberian lynx, where weak territoriality and unstable spatial organization persisted during the early post-release years [94,95], probably due to unfamiliar environments and low conspecific density [37]. While some excursions may involve exploration for prey or shelter, their concentration during the mating season suggests mate searching as the primary driver. Supporting this, all translocated wild-caught males in the Dinaric population undertook mating-season excursions, with one-third exceeding 20 km. Together, these findings highlight pronounced individual variation in excursion behaviour among translocated lynx, which has important implications for evaluating reproductive outcomes. Variation in movement strategies may influence the likelihood of encountering mates and, ultimately, successful reproduction in reintroduced populations.

There is broad evidence that human-modified landscapes and activities limit exploratory movements in large mammals [96,97]. During extra-territorial mate searches, lynx rely on social cues such as scent marking and vocalization [26,45], and traffic noise could mask vocal signals near roads and forest edges [45]. As scent marks occur mainly in continuous forest structures (e.g. juvenile conifers, moss-covered rocks) and occasionally on low-use human structures (e.g. buildings, forest roads) [23,98], disruptions to these cues may constrain excursions. In our data, however, we detected no effect of human-footprint ratio on excursion rate or distance. In a sensitivity analysis using all available locations (increasing the proportion of daytime records, particularly in regions with higher sampling rates), excursion rate appeared negatively associated with human footprint ratio (electronic supplementary material, table S9). Potential ecological mechanisms, such as time-specific avoidance of human features or constraints imposed by habitat edges, remain hypotheses and require targeted analyses beyond our current scope. Alternatively, this pattern may reflect regional differences in sampling effort rather than a true ecological relationship, highlighting the importance of using a standardized dataset for comparing individuals and regions.

Although excursions during the mating season support the hypothesis of mate-searching as an alternative mating tactic in lynx, several limitations should be considered. First, despite overall male-biased excursion rates, no male excursions were recorded in the Jura Mountains or Estonia (electronic supplementary material, table S5), probably due to small sample sizes (electronic supplementary material, table S4). Second, re-running analyses using MCP-based home-range borders (in place of LoCoH) and recalculating excursion metrics using all available locations, yielded consistent male-biased patterns in the southern eco-region, thereby confirming our conclusions were not driven by analytical choices (electronic supplementary material, table S8). In the central and northern eco-regions, smaller and sex-imbalanced samples (≈2:1 females:males) widened confidence intervals, reducing precision rather than introducing systematic bias; we therefore interpreted regional differences cautiously. Third, estimates involving the Human Footprint Index (HFI; 2009) also warrant caution due to the temporal mismatch with some of the telemetry records (1995–2023). Furthermore, while we assessed spatio-temporal overlap between excursions and conception events, limited genetic and birth data precluded robust links to reproductive success. Although our study cannot confirm whether excursions directly led to reproduction, their potential conservation importance requires attention. If such movements facilitate mating outside kin clusters (e.g. those in the Carpathians [99] and Finland [100]), they may promote genetic exchange and buffer inbreeding. This role could be particularly critical where local mates are absent or removed during the mating season, helping maintain reproduction rates and population resilience. Given the positive correlation between geographic and genetic distances [101], excursions could support long-term population viability and connectivity, particularly in small, newly established populations, or populations with high anthropogenic mortality.

5. Conclusion

Our study found evidence of male-biased extra-territorial excursions in Eurasian lynx during the mating season, probably to maximize mating opportunities and facilitate encounters with receptive females. This pan-European analysis provides new insight into mating strategies in felids and highlights their potential role in reducing founder effects by increasing the likelihood of mating encounters, particularly in small or newly established populations. Recognizing these patterns is important for conservation, as such excursions may heighten exposure to anthropogenic risks, including road mortality, poaching and human–wildlife conflict, especially in the human-dominated landscapes of central and southern Europe. From a monitoring perspective, these behaviours have direct implications for lynx population surveys. They should inform the design of camera-trap studies in combination with spatial capture–recapture, the primary felid monitoring approach in Europe [102], and are likely to be relevant to other felids with similar movement behaviours. Where possible, surveys should avoid the mating season, especially in areas undergoing reinforcement through translocation. If surveys must be conducted during this period, analyses should explicitly account for extra-territorial movements to reduce bias in population estimates.

Ethics. All animal captures and handling were conducted in compliance with relevant national and European animal welfare regulations and permits; detailed information is provided in electronic supplementary material, table S1.

Data accessibility. The code and processed data used for the analyses are available from the Zenodo repository [103].

Supplementary material is available online [104].

Declaration of AI use. We have not used AI-assisted technologies in creating this article.

Authors' contributions. Y.L.: conceptualization, data curation, formal analysis, investigation, methodology, project administration, resources, software, validation, visualization, writing—original draft, writing—review and editing; S.K.-S.: conceptualization, methodology, supervision, writing—review and editing; J.M.: resources, writing—review and editing; E.B.: resources, writing—review and editing; L.B.: resources, writing—review and editing; D.M.: resources, writing—review and editing; D.S.: resources, writing—review and editing; O.A.: resources, writing—review and editing; T.L.M.: resources, writing—review and editing; H.A.: resources, writing—review and editing; M.A.: resources, writing—review and editing; J.Pe.: resources, writing—review and editing; J.S.: resources, writing—review and editing; Mag.T.: resources, writing—review and editing; Mac.T.: resources, writing—review and editing; M.G.: resources, writing—review and editing; R.B.: resources, writing—review and editing; S.B.: resources, writing—review and editing; J.-M.V.: resources, writing—review and editing; RČ.: resources, writing—review and editing; A.T.: resources, writing—review and editing; M.D.: resources, writing—review and editing; M.Ku.: resources, writing—review and editing; U.F.: resources, writing—review and editing; L.H.: resources, writing—review and editing; M.Kr.: resources, writing—review and editing; T.O.: data curation, resources, writing—review and editing; T.G.: resources, writing—review and editing; I.T.: resources, writing—review and editing; J.K.: resources, writing—review and editing; B.T.: resources, writing—review and editing; J.K.-P.: resources, writing—review and editing; R.Kon.: resources, writing—review and editing; R.Kow.: resources, writing—review and editing; K.S.: resources, writing—review and editing; J.D.C.L.: resources, writing—review and editing; J.O.: resources, writing—review and editing; A.M.-J.: resources, writing—review and editing; R.W.M.: resources, writing—review and editing; S.N.: resources, writing—review and editing; M.F.: resources, writing—review and editing; H.O.: resources, writing—review and editing; A.O.: resources, writing—review and editing; J.Pr.: conceptualization, data curation, methodology, supervision, writing—review and editing; M.H.: conceptualization, funding acquisition, methodology, project administration, supervision, writing—review and editing.

All authors gave final approval for publication and agreed to be held accountable for the work performed therein.

Conflict of interest declaration. We declare we have no competing interests.

Funding. Scholarship from Prof. Dr Klaus Riepe und Ellen Riepe-Brunnström Stiftung to Y.L. Norwegian Institute for Nature Research (160022/F40); Research Council of Norway (251112, 281092, 156810); the Norwegian Directorate for Nature Management; Nature Protection Divisions of the County Governor's Offices in Innlandet, Viken, Vestfold & Telemark, Trøndelag, Nordland, and Troms & Finnmark. EU Interreg IV Objective 3 Czech Republic–Bavaria programme (19) and German Federal Environmental Foundation (Deutsche Bundesstiftung

Umwelt, 33059-01). German Federal Environmental Foundation (2015–2018) and MAVA Foundation through the Balkan Lynx Recovery Programme (2018–2022). Slovenian Research and Innovation Agency (J1-50013, P4-0059) and the European Commission (LIFE Lynx, LIFE16 NAT/SL/000634). Operational Programme Environment via the State Environmental Fund of the Czech Republic; the Nature Conservation Agency of the Czech Republic (9028766, 2011–2014); Institutional Research Plan (RVO: 68081766). Danube Transnational Programme SaveGREEN (DTP3-314-2.3); Operational Programme Environment (CZ.05.4.27/0.0/0.0/20_139/0012815); National Science Centre (2024/55/B/NZ9/02690; 2024/55/B/NZ9/02958). Polish Ministry of Education and Science, 'Implementation Doctorate' (DWD/5/0413/2021) to M.F. Project POIS.02.04.00-00-0143/16 'Return of the lynx to north-western Poland', EU Cohesion Fund (Operational Programme Infrastructure and Environment, 2014–2020) and the Minister of Science under the Regional Excellence Initiative (2024–2027).

Acknowledgements. We obtained telemetry data from the EUROLYNX network (www.eurolynx.org; paper no. 9 in the EUROLYNX series). Data curation was supported by the Regina Bauer Stiftung. We thank all EUROLYNX members for their stimulating discussions, field personnel, interns, civil servants and students, at all involved sites for their assistance in the fieldwork of capturing and monitoring lynx, as well as Moritz Wenzler and Maik Henrich methodological support.

References

1. Pedersen MC, Dunn PO, Whittingham LA. 2006 Extraterritorial forays are related to a male ornamental trait in the common yellowthroat. *Anim. Behav*. **72**, 479–486. (doi:10.1016/j.anbehav.2006.02.010)
2. Schlicht L, Valcu M, Kempenaers B. 2015 Male extraterritorial behavior predicts extrapair paternity pattern in blue tits, *Cyanistes caeruleus*. *Behav. Ecol*. **26**, 1404–1413. (doi:10.1093/beheco/arv076)
3. Iossa G, Soulsbury CD, Baker PJ, Harris S. 2008 Body mass, territory size, and life-history tactics in a socially monogamous canid, the Red Fox *Vulpes vulpes*. *J. Mammal.* **89**, 1481–1490. (doi:10.1644/07-MAMM-A-405.1)
4. Kelly DJ, Gaughran A, Mullen E, MacWhite T, Maher P, Good M, Marples NM. 2020 Extra territorial excursions by european badgers are not limited by age, sex or season. *Sci. Rep.* **10**, 9665. (doi:10.1038/s41598-020-66809-w)
5. Lane JE, Boutin S, Gunn MR, Coltman DW. 2009 Sexually selected behaviour: red squirrel males search for reproductive success. *J. Anim. Ecol*. **78**, 296–304. (doi:10.1111/j.1365-2656.2008.01502.x)
6. Debeffe L *et al*. 2014 A one night stand? Reproductive excursions of female roe deer as a breeding dispersal tactic. *Oecologia* **176**, 431–443. (doi:10.1007/s00442-014-3021-8)
7. Griffith SC, Owens IPF, Thuman KA. 2002 Extra pair paternity in birds: a review of interspecific variation and adaptive function. *Mol. Ecol*. **11**, 2195–2212. (doi:10.1046/j.1365-294x.2002.01613.x)
8. Pontzer H, Kamilar JM. 2009 Great ranging associated with greater reproductive investment in mammals. *Proc. Natl Acad. Sci. USA* **106**, 192–196. (doi:10.1073/pnas.0806105106)
9. Macdonald D, Loveridge A. 2010 *The biology and conservation of wild felids*. Oxford, UK: Oxford University Press.
10. Allen ML, Wittmer HU, Houghtaling P, Smith J, Elbroch LM, Wilmers CC. 2015 The role of scent marking in mate selection by female pumas (*Puma concolor*). *PLoS One* **10**, e0139087. (doi:10.1371/journal.pone.0139087)
11. Nathan R, Getz WM, Revilla E, Holyoak M, Kadmon R, Saltz D, Smouse PE. 2008 A movement ecology paradigm for unifying organismal movement research. *Proc. Natl Acad. Sci. USA* **105**, 19052–19059. (doi:10.1073/pnas.0800375105)
12. Caro TM, Collins DA. 1987 Male cheetah social organization and territoriality. *Ethology* **74**, 52–64. (doi:10.1111/j.1439-0310.1987.tb00921.x)
13. Sandell M. 1989 The mating tactics and spacing patterns of solitary carnivores. In *Carnivore behavior, ecology, and evolution* (ed. JL Gittleman), pp. 164–182. Boston, MA: Springer. (doi:10.1007/978-1-4757-4716-4_7)
14. le Roex N, Mann GKH, Hunter LTB, Balme GA. 2022 Relaxed territoriality amid female trickery in a solitary carnivore. *Anim. Behav*. **194**, 225–231. (doi:10.1016/j.anbehav.2022.09.022)
15. Clutton-Brock TH. 1989 Review lecture: mammalian mating systems. *Proc. R. Soc. Lond. B* **236**, 339–372. (doi:10.1098/rspb.1989.0027)
16. Sandell M, Liberg O. 1992 Roamers and stayers: a model on male mating tactics and mating systems. *Am. Nat.* **139**, 177–189. (doi:10.1086/285319)
17. Palomares F, Lucena-Pérez M, López-Bao JV, Godoy JA. 2017 Territoriality ensures paternity in a solitary carnivore mammal. *Sci. Rep*. **7**, 4494. (doi:10.1038/s41598-017-04820-4)
18. Wolff JO, Peterson JA. 1998 An offspring-defense hypothesis for territoriality in female mammals. *Ethol. Ecol. Evol*. **10**, 227–239. (doi:10.1080/08927014.1998.9522854)
19. Andersson M, Simmons LW. 2006 Sexual selection and mate choice. *Trends Ecol. Evol*. **21**, 296–302. (doi:10.1016/j.tree.2006.03.015)
20. Wolff JO, Macdonald DW. 2004 Promiscuous females protect their offspring. *Trends Ecol. Evol*. **19**, 127–134. (doi:10.1016/j.tree.2003.12.009)
21. Breitenmoser-Würsten C, Zimmermann F, Molinari-Jobin A, Molinari P, Capt S, Vandel JM, Stahl P, Breitenmoser U. 2007 Spatial and social stability of a Eurasian lynx *Lynx lynx* population: an assessment of 10 years of observation in the Jura Mountains. *Wildlife Biol.* **13**, 365–380. (doi:10.2981/0909-6396(2007)13[365:SASSOA]2.0.CO;2)
22. Schmidt K, Jędrzejewski W, Okarma H. 1997 Spatial organization and social relations in the Eurasian lynx population in Bialowieza Primeval Forest, Poland. *Acta Theriol*. **42**, 289–312. (doi:10.4098/at.arch.97-30)
23. Allen ML, Hočevar L, de Groot M, Krofel M. 2017 Where to leave a message? The selection and adaptive significance of scent-marking sites for Eurasian lynx. *Behav. Ecol. Sociobiol*. **71**, 136. (doi:10.1007/s00265-017-2366-5)
24. Jędrzejewski W, Schmidt K, Okarma H, Kowalczyk R. 2002 Movement pattern and home range use by the Eurasian lynx in Białowieża Primeval Forest (Poland). *Ann. Zool. Fenn.* **39**, 29–41. http://www.jstor.org/stable/23735800
25. Sunde P, Kvam T, Moa P, Negård A, Overskaug K. 2000 Space use by Eurasian lynxes *Lynx lynx* in central Norway. *Acta Theriol.* **45**, 507–524. (doi:10.4098/AT.arch.00-50)
26. Vogt K, Zimmermann F, Kölliker M, Breitenmoser U. 2014 Scent-marking behaviour and social dynamics in a wild population of Eurasian lynx *Lynx lynx*. *Behav. Process*. **106**, 98–106. (doi:10.1016/j.beproc.2014.04.017)
27. Breitenmoser U, Kavczensky P, Dötterer M, Breitenmoser-Würsten C, Capt S, Bernhart F, Liberek M. 1993 Spatial organization and recruitment of lynx (*Lynx lynx*) in a re-introduced population in the Swiss Jura Mountains. *J. Zool*. **231**, 449–464. (doi:10.1111/j.1469-7998.1993.tb01931.x)
28. Krofel M *et al*. 2025 Multidisciplinary monitoring and stakeholder engagement support large carnivore restoration in human-dominated landscape. *Ecol. Appl*. **35**, e70052. (doi:10.1002/eap.70052)
29. Schmidt K. 2008 Behavioural and spatial adaptation of the Eurasian lynx to a decline in prey availability. *Acta Theriol*. **53**, 1–16. (doi:10.1007/bf03194274)
30. Sullivan JD, Ditchkoff SS, Collier BA, Ruth CR, Raglin JB. 2017 Breeding behavior of female white-tailed deer relative to conception: evidence for female mate choice. *Ecol. Evol.* **7**, 2395–2402. (doi:10.1002/ece3.2845)

31. Andrews CJ, Thomas DG, Yapura J, Potter MA. 2019 Reproductive biology of the 38 extant felid species: a review. *Mammal Rev*. **49**, 16–30. (doi:10.1111/mam.12145)
32. Axnér E, Payan-Carreira R, Setterlind P, Åsbrink J, Söderberg A. 2013 Collection of field reproductive data from carcasses of the female Eurasian lynx (*Lynx lynx*). *Theriogenology* **80**, 839–849. (doi:10.1016/j.theriogenology.2013.06.015)
33. Painer J, Jewgenow K, Dehnhard M, Arnemo JM, Linnell JDC, Odden J, Hildebrandt TB, Goeritz F. 2014 Physiologically persistent Corpora lutea in Eurasian lynx (*Lynx lynx*) - longitudinal ultrasound and endocrine examinations intra-vitam. *PLoS One* **9**, e90469. (doi:10.1371/journal.pone.0090469)
34. Jewgenow K, Painer J, Amelkina O, Dehnhard M, Goeritz F. 2014 Lynx reproduction: long-lasting life cycle of corpora lutea in a feline species. *Reprod. Biol*. **14**, 83–88. (doi:10.1016/j.repbio.2014.03.002)
35. Mattisson J *et al*. 2022 Timing and synchrony of birth in Eurasian lynx across Europe. *Ecol. Evol*. **12**, e9147. (doi:10.1002/ece3.9147)
36. Breitenmoser U. 1998 Large predators in the alps: the fall and rise of man's competitors. *Biol. Conserv.* **83**, 279–289. (doi:10.1016/S0006-3207(97)00084-0)
37. Linnell JDC, Breitenmoser U, Breitenmoser-Würsten C, Odden J, von Arx M. 2009 Recovery of Eurasian lynx in Europe: what part has reintroduction played? In *Reintroduction of top-order predators* (eds MW Hayward, MJ Somers), pp. 72–91. Oxford, UK: Blackwell Publishing. (doi:10.1002/9781444312034)
38. Kaczensky P, Ranc N, Hatlauf J, Payne JC, Boitani L. 2024 *Large carnivore distribution maps and population updates 2017–2022/23. In Report to the European Commission Under Contract no. 09.0201/2023/907799/SER/ENV.D.3: 'Support for coexistence with large carnivores', B.4 Update of the Distribution Maps, 133*. IUCN/SSC Large Carnivore Initiative for Europe (LCIE) and Istituto diEcologia Applicata (IEA).
39. Jule KR, Leaver LA, Lea SEG. 2008 The effects of captive experience on reintroduction survival in carnivores: a review and analysis. *Biol. Conserv*. **141**, 355–363. (doi:10.1016/j.biocon.2007.11.007)
40. Cisneros-Araujo P *et al*. 2024 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**, 110646. (doi:10.1016/j.biocon.2024.110646)
41. Topličanec I, Gomerčić T, Černe R, Krofel M, Pop IM, Kubala J, Tám B, Blašković S, Sindičić M. 2022 Early post-release behaviour of Eurasian lynx translocated to the transboundary region of the Dinaric Mountains. *J. Vertebr. Biol*. **71**, 22064. (doi:10.25225/jvb.22064)
42. Skorupski J, Tracz M, Tracz M, Śmietana P. 2022 Assessment of Eurasian lynx reintroduction success and mortality risk in North-West Poland. *Sci. Rep*. **12**, 12366. (doi:10.1038/s41598-022-16589-2)
43. Vandel JM, Stahl P, Herrenschmidt V, Marboutin E. 2006 Reintroduction of the lynx into the Vosges mountain massif: from animal survival and movements to population development. *Biol. Conserv*. **131**, 370–385. (doi:10.1016/j.biocon.2006.02.012)
44. Kokko H, Rankin DJ. 2006 Lonely hearts or sex in the city? Density-dependent effects in mating systems. *Phil. Trans. R. Soc. B* **361**, 319–334. (doi:10.1098/rstb.2005.1784)
45. Krofel M, Kos I. 2009 Recording the Eurasian lynx (*Lynx lynx*) vocalization sequences on Snežnik plateau, Slovenia Beleženje sekvenc oglašanja evrazijskega risa (*Lynx lynx*) na Snežniški planoti. *Nat. Slov*. **11**, 71–72. (doi:10.14720/ns.11.1.71-72)
46. Norris DR, Stutchbury BJM. 2001 Extraterritorial movements of a forest songbird in a fragmented landscape. *Conserv. Biol.* **15**, 729–736. (doi:10.1046/j.1523-1739.2001.015003729.x)
47. Ramos AG, Nunziata SO, Lance SL, Rodríguez C, Faircloth BC, Gowaty PA, Drummond H. 2014 Habitat structure and colony structure constrain extrapair paternity in a colonial bird. *Anim. Behav*. **95**, 121–127. (doi:10.1016/j.anbehav.2014.07.003)
48. Giuntini S, Pedruzzi L. 2023 Sex and the patch: the influence of habitat fragmentation on terrestrial vertebrates' mating strategies. *Ethol. Ecol. Evol*. **35**, 269–298. (doi:10.1080/03949370.2022.2059787)
49. Lane JE, Forrest MNK, Willis CKR. 2011 Anthropogenic influences on natural animal mating systems. *Anim. Behav*. **81**, 909–917. (doi:10.1016/j.anbehav.2011.02.003)
50. Ripari L *et al*. 2022 Human disturbance is the most limiting factor driving habitat selection of a large carnivore throughout Continental Europe. *Biol. Conserv*. **266**, 109446. (doi:10.1016/j.biocon.2021.109446)
51. Bull JK, Heurich M, Saveljev AP, Schmidt K, Fickel J, Förster DW. 2016 The effect of reintroductions on the genetic variability in Eurasian lynx populations: the cases of Bohemian–Bavarian and Vosges–Palatinian populations. *Conserv. Genet*. **17**, 1229–1234. (doi:10.1007/s10592-016-0839-0)
52. Mueller SA, Reiners TE, Middelhoff TL, Anders O, Kasperkiewicz A, Nowak C. 2020 The rise of a large carnivore population in Central Europe: genetic evaluation of lynx reintroduction in the Harz Mountains. *Conserv. Genet*. **21**, 577–587. (doi:10.1007/s10592-020-01270-w)
53. Mueller SA *et al*. 2022 Genome-wide diversity loss in reintroduced Eurasian lynx populations urges immediate conservation management. *Biol. Conserv*. **266**, 109442. (doi:10.1016/j.biocon.2021.109442)
54. Sindičić M, Polanc P, Gomerčić T, Jelenčič M, Huber Đ, Trontelj P, Skrbinšek T. 2013 Genetic data confirm critical status of the reintroduced Dinaric population of Eurasian lynx. *Conserv. Genet*. **14**, 1009–1018. (doi:10.1007/s10592-013-0491-x)
55. Venter O *et al*. 2016 Global terrestrial Human Footprint maps for 1993 and 2009. *Sci. Data* **3**, 160067. (doi:10.1038/sdata.2016.67)
56. Urbano F, Cagnacci F, InitiativeEC. 2021 Data management and sharing for collaborative science: lessons learnt from the euromammals initiative. *Front. Ecol. Evol.* **9**, 727023. (doi:10.3389/fevo.2021.727023)
57. R Core Team. 2023 R: a language and environment for statistical computing. Vienna, Austria: R Foundation for Statistical Computing.
58. Bunnefeld N, Börger L, van Moorter B, Rolandsen CM, Dettki H, Solberg EJ, Ericsson G. 2011 A model-driven approach to quantify migration patterns: individual, regional and yearly differences. *J. Anim. Ecol*. **80**, 466–476. (doi:10.1111/j.1365-2656.2010.01776.x)
59. Fleming CH, Calabrese JM, Mueller T, Olson KA, Leimgruber P, Fagan WF. 2014 From fine-scale foraging to home ranges: a semivariance approach to identifying movement modes across spatiotemporal scales. *Am. Nat.* **183**, E154–67. (doi:10.1086/675504)
60. Calabrese JM, Fleming CH, Gurarie E. 2016 ctmm: anrpackage for analyzing animal relocation data as a continuous-time stochastic process. *Methods Ecol. Evol*. **7**, 1124–1132. (doi:10.1111/2041-210x.12559)
61. Signer J, Fieberg J, Avgar T. 2019 Animal movement tools (amt): R package for managing tracking data and conducting habitat selection analyses. *Ecol. Evol.* **9**, 880–890. (doi:10.1002/ece3.4823)
62. Dalpiaz N *et al*. 2025 Variability in the movement and foraging behaviour of female Eurasian lynx during the denning season across Europe. *Oikos* **e11502**. (doi:10.1002/oik.11502)
63. Noonan MJ *et al*. 2019 A comprehensive analysis of autocorrelation and bias in home range estimation. *Ecol. Monogr*. **89**, 1344. (doi:10.1002/ecm.1344)
64. Heurich M *et al*. 2014 Activity patterns of Eurasian lynx are modulated by light regime and individual traits over a wide latitudinal range. *PLoS One* **9**, e114143. (doi:10.1371/journal.pone.0114143)
65. Hayward MW *et al*. 2007 The reintroduction of large carnivores to the Eastern Cape, South Africa: an assessment. *Oryx* **41**, 205–214. (doi:10.1017/s0030605307001767)
66. Calenge C, Fortmann-Roe S. 2023 adehabitatHR: home range estimation. R package version 0.4.21. (doi:10.32614/cran.package.adehabitathr). See https://CRAN. R-project.org/package=adehabitatHR.

67. Hansen KW, Jordan NR, Claase MJ, Suraci JP, McNutt JW, Dhruv A, Wilmers CC. 2024 Experimental modification of African wild dog movement and behavior using translocated conspecific scent. *Biol. Conserv*. **294**, 110645. (doi:10.1016/j.biocon.2024.110645)
68. Getz WM, Fortmann-Roe S, Cross PC, Lyons AJ, Ryan SJ, Wilmers CC. 2007 LoCoH: nonparameteric kernel methods for constructing home ranges and utilization distributions. *PLoS One* **2**, e207. (doi:10.1371/journal.pone.0000207)
69. Worton BJ. 1995 A convex hull-based estimator of home-range size. *Biometrics* **51**, 1206. (doi:10.2307/2533254)
70. Krofel M, Hočevar L, Allen ML. 2017 Does human infrastructure shape scent marking in a solitary felid? *Mamm. Biol*. **87**, 36–39. (doi:10.1016/j.mambio.2017.05.003)
71. Davison AC, Hinkley DV. 1997 *Bootstrap methods and their application*. Cambridge, UK: Cambridge University Press. (doi:10.1017/cbo9780511802843)
72. Mann HB, Whitney DR. 1947 On a test of whether one of two random variables is stochastically larger than the other. *Ann. Math. Statist.* **18**, 50–60. (doi:10.1214/aoms/1177730491)
73. Brooks ME, Kristensen K, van Benthem KJ, Magnusson A, Berg CW, Nielsen A, Skaug HJ, Mächler M, Bolker BM. 2017 glmmTMB balances speed and flexibility among packages for zero-inflated generalized linear mixed modeling. *R J.* **9**, 378. (doi:10.32614/RJ-2017-066)
74. Hartig F. 2022 DHARMa: residual diagnostics for hierarchical (multi-level / mixed) regression models. R package version 0.4.6. See https://CRAN.R-project.org/package=DHARMa.
75. Wickham H. 2016 *Ggplot2: elegant graphics for data analysis*, pp. 189–201. New York, NY: Springer International Publishing. (doi:10.1007/978-3-319-24277-4_9)
76. Zuur AF, Ieno EN, Elphick CS. 2010 A protocol for data exploration to avoid common statistical problems. *Methods Ecol. Evol*. **1**, 3–14. (doi:10.1111/j.2041-210x.2009.00001.x)
77. Bartoń K. 2022 MuMIn: multi-model inference. R package version 1.46.0. See https://CRAN.R-project.org/package=MuMIn.
78. Anderson DR, Burnham KP. 2002 Avoiding pitfalls when using information-theoretic methods. *J. Wildl. Manage.* **66**, 912. (doi:10.2307/3803155)
79. Börger L, Franconi N, De michele G, Gantz A, Meschi F, Manica A, Lovari S, Coulson T. 2006 Effects of sampling regime on the mean and variance of home range size estimates. *J. Anim. Ecol*. **75**, 1393–1405. (doi:10.1111/j.1365-2656.2006.01164.x)
80. Belden RC, McCown JW. 1996 *Florida panther reintroduction feasibility study*. Florida Game and Fresh Water Fish Commission. Final report, study no. 7507.
81. Lodé T. 2001 Mating system and genetic variance in a polygynous mustelid, the European polecat. *Genes Genet. Syst*. **76**, 221–227. (doi:10.1266/ggs.76.221)
82. Mattisson J, Segerström P, Persson J, Aronsson M, Rauset GR, Samelius G, Andrén H. 2013 Lethal male–male interactions in Eurasian lynx. *Mamm. Biol*. **78**, 304–308. (doi:10.1016/j.mambio.2012.11.006)
83. Mattisson J, Odden J, Nilsen EB, Linnell JDC, Persson J, Andrén H. 2011 Factors affecting Eurasian lynx kill rates on semi-domestic reindeer in northern Scandinavia: can ecological research contribute to the development of a fair compensation system? *Biol. Conserv*. **144**, biocon.2011.09.004. (doi:10.1016/j.biocon.2011.09.004)
84. Aronsson M, Low M, López-Bao JV, Persson J, Odden J, Linnell JDC, Andrén H. 2016 Intensity of space use reveals conditional sex-specific effects of prey and conspecific density on home range size. *Ecol. Evol*. **6**, 2957–2967. (doi:10.1002/ece3.2032)
85. López-Bao JV, Rodríguez A, Delibes M, Fedriani JM, Calzada J, Ferreras P, Palomares F. 2014 Revisiting food-based models of territoriality in solitary predators. *J. Anim. Ecol*. **83**, 934–942. (doi:10.1111/1365-2656.12226)
86. Oftedal OT, Gittleman JL. 1989 Patterns of energy output during reproduction in carnivores. In *Carnivore behavior, ecology, and evolution* (ed. JL Gittleman), pp. 355–378. Boston, MA: Springer. (doi:10.1007/978-1-4613-0855-3_14)
87. Stephens PA, Sutherland WJ, Freckleton RP. 1999 What is the Allee effect? *Oikos* **87**, 185. (doi:10.2307/3547011)
88. Nilsen EB, Brøseth H, Odden J, Linnell JDC. 2012 Quota hunting of Eurasian lynx in Norway: patterns of hunter selection, hunter efficiency and monitoring accuracy. *Eur. J. Wildl. Res*. **58**, 325–333. (doi:10.1007/s10344-011-0585-z)
89. Mengüllüoğlu D, Edwards S, Hofer H, Berger A. 2021 Female and male Eurasian lynx have distinct spatial tactics at different life-history stages in a high-density population. *Ecol. Evol*. **11**, 10432–10445. (doi:10.1002/ece3.7846)
90. Eberle M, Kappeler PM. 2004 Sex in the dark: determinants and consequences of mixed male mating tactics in Microcebus murinus, a small solitary nocturnal primate. *Behav. Ecol. Sociobiol*. **57**, 77–90. (doi:10.1007/s00265-004-0826-1)
91. Weladji RB, Body G, Holand Ø, Meng X, Nieminen M. 2017 Temporal variation in the operational sex ratio and male mating behaviours in reindeer (*Rangifer tarandus*). *Behav. Process*. **140**, 96–103. (doi:10.1016/j.beproc.2017.04.011)
92. Smith BR, Blumstein DT. 2008 Fitness consequences of personality: a meta-analysis. *Behav. Ecol*. **19**, 448–455. (doi:10.1093/beheco/arm144)
93. Belgrad BA, Griffen BD. 2018 Personality interacts with habitat quality to govern individual mortality and dispersal patterns. *Ecol. Evol*. **8**, 7216–7227. (doi:10.1002/ece3.4257)
94. Rueda C, Jiménez J, Palacios MJ, Margalida A. 2021 Exploratory and territorial behavior in a reintroduced population of Iberian lynx. *Sci. Rep*. **11**, 14148. (doi:10.1038/s41598-021-93673-z)
95. Sarmento P, Carrapato C, Eira C, Silva JP. 2019 Spatial organization and social relations in a reintroduced population of Endangered Iberian lynx *Lynx pardinus*. *Oryx* **53**, 344–355. (doi:10.1017/s0030605317000370)
96. Tucker MA *et al*. 2018 Moving in the anthropocene: global reductions in terrestrial mammalian movements. *Science* **359**, 466–469. (doi:10.1126/science.aam9712)
97. Tucker MA *et al*. 2023 Behavioral responses of terrestrial mammals to COVID-19 lockdowns. *Science* **380**, 1059–1064. (doi:10.1126/science.abo6499)
98. Bouyer Y, Gervasi V, Poncin P, Beudels-Jamar RC, Odden J, Linnell JDC. 2015 Tolerance to anthropogenic disturbance by a large carnivore: the case of Eurasian lynx in south-eastern Norway. *Anim. Conserv*. **18**, 271–278. (doi:10.1111/acv.12168)
99. Krojerová-Prokešová J, Turbaková B, Jelenčič M, Bojda M, Kutal M, Skrbinšek T, Koubek P, Bryja J. 2019 Genetic constraints of population expansion of the Carpathian lynx at the western edge of its native distribution range in Central Europe. *Heredity* **122**, 785–799. (doi:10.1038/s41437-018-0167-x)
100. Holmala K, Herrero A, Kopatz A, Schregel J, Eiken HG, Hagen SB. 2018 Genetic evidence of female kin clusters in a continuous population of a solitary carnivore, the Eurasian lynx. *Ecol. Evol*. **8**, 10964–10975. (doi:10.1002/ece3.4562)
101. Schmidt K, Ratkiewicz M, Konopiński MK. 2011 The importance of genetic variability and population differentiation in the Eurasian lynx *Lynx lynx* for conservation, in the context of habitat and climate change. *Mammal Rev*. **41**, 112–124. (doi:10.1111/j.1365-2907.2010.00180.x)
102. Palmero S, Premier J, Kramer-Schadt S, Monterroso P, Heurich M. 2023 Sampling variables and their thresholds for the precise estimation of wild felid population density with camera traps and spatial capture–recapture methods. *Mammal Rev*. **53**, 223–237. (doi:10.1111/mam.12320)
103. Liang Y *et al*. 2025 Extra-territorial excursions of Eurasian lynx (*Lynx lynx*) during the mating season across Europe. Zenodo. (doi:10.5281/zenodo.17492205)
104. Liang Y *et al*. 2025 Supplementary material from: Extra-territorial excursions of Eurasian lynx (*Lynx lynx*) during the mating season across Europe. Figshare. (doi:10.6084/m9.figshare.c.8171352)