# Title:

Predicting spatio-temporal recolonization of reintroduced large herbivore populations and zones of potential human wildlife conflicts: red deer in Corsica

# Running title:

Recolonisation of Corsica by red deer

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# Abstract

1. Trophic rewilding via the (re)introduction of keystone species and ecosystem engineer, such as large herbivores, is increasingly being considered in Europe to support nature recovery and improve the resilience of ecosystems in the face of rapidly changing environmental conditions. Large herbivore presence can however generate issues for local communities, making it important to anticipate likely expansion patterns and identify possible zones of human-wildlife conflicts
2. We used the recently developed integrated Step Selection Function approach to build a predictive, spatially explicit, individual-based model to examine reintroduced Corsican red deer (Cervus elaphus) population expansion in Corsica. We developed the model based on known demographic processes and habitat selection of reintroduced red deer collected during a xx-year intensive field study.
3. During model validation, our model accurately described the recolonization process in the three reintroduction sites, correctly predicting xxx. We then projected dispersers over the entire island for 2050. We predicted xxx. We identified xx as likely spatial barriers slowing the red deer expansion.
4. Synthesis and applications. As the number of trophic rewilding projects increases in Europe, there is a real need to anticipate how the (re)introduced populations are likely to expand their distribution to prevent avoidable human-wildlife conflicts.

**Keywords**

Trophic rewilding, adaptive management, recolonization, spatially explicit individual-based model, red deer

# Introduction

In the face of rapidly changing environmental conditions, increasing level of environmental predictability and dramatic loss of biodiversity, nature recovery has become a priority, with the United Nations for example declaring this decade as the Decade on Ecosystem Restoration to spur global actions to prevent, halt and reverse the degradation of ecosystems. In this context, trophic rewilding, a form of environmental management approach that aims to diversify and complexify ecological interactions through the (re)introduction of keystone species and ecosystem engineers, has gained significant traction in Europe (Pettorelli et al., 2018). Trophic rewilding discussions have primarily focused on the necessity and feasibility of large herbivore (re)introductions, given their significant impacts on ecosystems. Through their presence and activities (e.g., feeding, trampling, urination and defecation), large herbivores indeed directly and indirectly influence ecosystem structure and processes, ultimately leading to changes in ecosystem composition and functioning.

The translocation of large species is, however, not without risks and can lead to conflicts with human populations as large species interact with human activities such as agriculture, logging, hunting, and development. In the United States, for example, the reintroduction of elks, *Cervus canadensis*, was associated with increased costs to local communities as they saw their fences being more damaged, their crops being more depredated, and their livestock catching more disease (Mc Cann et al., 2021; Hegel et al, 2009). One way to prevent the likely increases in human-wildlife conflicts following species translocations is to identify areas likely to be colonized by introduced individuals, so that targeted actions can be strategically deployed early enough to mitigate the risks associated with population expansion. This step is generally done by mapping habitat suitability at landscape scales using approaches such as species distribution modelling, and rarely, individual based modelling (see e.g., Marucco and McIntire 2010).

By spatially simulating individual animals and their interactions with one another and the environment (McLane *et al.*, 2011; Accolla *et al.*, 2021), mechanistic Individual-Based Models (IBMs) can make readily interpretable predictions of emergent population expansion (e.g. Fernández et al, 2006; Philips 2020). However, their reliability strongly depends on how accurately the set of “movement rules” for individuals reflects the true movement of individual animals. Developing such rules heuristically or based on separately defined habitat suitability maps has previously provided interesting insights (e.g. Mims *et al.*, 2019; Philips, 2020), but remains constrained by land cover definition and resolution issues. An alternative approach, based more directly on animal movement, is to develop such rules directly from empirical movement data collected by animal GPS collars (e.g. Crevier et al. 2021).

In this study, we aim to use the recently developed integrated Step Selection Function approach by Signer and colleagues (2023) to build a spatially explicit IBM to predict reintroduced Corsican red deer (*Cervus elaphus*) population expansion in Corsica. The case of the Corsican red deer is particularly interesting as island fauna, in general, has been known to undergo a much higher extinction rate than continental fauna (Wood et al. 2017), and yet research on the consequences of species translocations within islands remains poorly studied. Although previously abundant, the Corsican deer completely disappeared from this highly topographically heterogeneous island in 1970 due to illegal hunting and habitat fragmentation (vineyards). Following its extinction in the wild, a conservation program started in the eighties (Riga et al. 2022), with deer being translocated from Sardinia and raised in natural reserves in Corsica for several years before being released into the wild in 1998. Translocated individuals were released in three very different locations: Moltifau, in the North of the island; San Petru di venacu in the Centre; and Zicavu in the South.

Red deer are highly adaptable, occupying a range of habitats including forests, grasslands, and alpine meadows (Alves et al., 2014). Their habitat preference can vary with season and geographic location and is influenced by the presence of both food and cover (ref). In general, they are known to seek cover in forested areas, and forage in open clearings. In topographically variable environments, red deer tend to move to higher elevations during the summer for better forage while occupying lower elevations during winter to avoid deep snow and harsh conditions (Dagtekin et al 2023). In Sardinia, the Corsican red deer has been shown to select areas with natural forests and/or Mediterranean maquis close to water sources; their tolerance to humans and roads has been previously described as low (Puddu et al. 2009). Because of this, we expected landcover type, topography, season and anthropogenic activity to strongly influence their movements, and therefore the connectivity of the landscape. We first calibrated and validated our model using data on 19 individuals from the three translocation sites; we then used this model to predict the potential future red deer recolonization to guide red deer conservation and management decisions. This included identifying critical areas for red deer establishment, which will be fundamental for future sources in the deer recolonization process of Corsica as a whole.

# Material and methods

## *Study location and animal data*

Corsican red deer were released into the wild in Corsica in three localities between 1998 and 2018 (Figure 1): Moltifau (North), San Petru di venacu (Centre) and Zicavu (South). Moltifau is broadly characterized by shallow and arid soils on gneiss and granite bedrocks; the landscape combines open and wooded countryside, with grasslands and maquis covering the gentler slopes and forests growing on the steeper slopes. San Petru di venacu, in the Massif du Rotondo, is part of the geological series known as the "Medium-grained granite of central Corsica"; the area is characterized by mountain valleys covered by oaks, beeches, bushes, and scrubs. Zicavu, in the Plateau du Coscione, is a mid-mountainous site characterized by its Euro-Siberian physiognomy and features beech, fir, larch, and alder trees. The hilly and rugged landscape hosts numerous springs, streams, and marshes (LIFE financial instrument of the European Union, 2014, 2015).

Nineteen individuals (13 females and 6 males) were GPS collared to gather information on the animals' survival, dispersion, and habitat use in the three previously described localities (North site: 2F and 2M; Centre: 5F and 4M; South: 6F). The devices collected data for 5 years, between December 15th of 2015 until January 9th of 2020. Animals’ locations were recorded twice a day – at 10 a.m. and 10 p.m. for a median of 25 months.

## *Overall approach*

We followed Potts and colleagues (2022) in developing an initial step selection function, using this function to parameterise an IBM, identifying discrepancies between the IBMs predictions and empirical patterns, and then refining the step selection function. We iterate through this process until we arrive at a satisfactory IBM. IBM evaluation was based on the model’s ability to replicate patterns observed in GPS-tracked red deer; namely home range size and the spatial distribution of deer activity.

Movement data analysis

We used step-selection functions (SSF), contrasting each observed step with 15 randomly generated steps. To obtain random steps, we sampled the length and angle of random steps from the distribution of observed steps. We used slope and distance to roads as continuous variables, and sex, landcover and season as categorical variables. Elevation and landcover values were extracted from the Shuttle Radar Topography Mission (Jarvis et al., 2008) and the 2018 CORINE Land Cover inventory (https://doi.org/10.2909/960998c1-1870-4e82-8051-6485205ebbac), respectively. We reclassified land covers as artificial, agricultural, forest, scrub, bare and wetland. Distance to roads was calculated from a Corsican Road map (need the ref for this data which we received from the Corsica team).

We fit the SSF using a conditional logistic regression model using the amt package in the R. We first used variance inflation factors (VIF) and pairwise correlations to test for multicollinearity of variables with thresholds of 10 and 0.70, respectively. We then developed a theoretically-derived saturated model of which factors influence deer movement, this provided the structure of our initial step selection function. This model included landscape variables of landcover, slope, and the distance to roads; the individual variables of sex ; the temporal variable of season; and step specific variables of the log length of a step and the cosine of the turning angle of a step relative to a previous step. We treated each individual as a separate strata to account for individual variation among deer. Starting with this saturated model we performed step-wise model selection using AIC to find the best model. The best model from the first round (see Table x) of model selection generated implausibly large home ranges when the coefficients were applied to the IBM (see below); we thus added the variable of log distance to release site to the best model and repeated the step-wise model selection process a second time (see Table x).

Individual Based Model

To predict red deer expansion in Corsica, the island was divided in non-overlapping 1h patches associated with the following state variables: landcover class; average slope; average distance to the road; probability that an individual deer moves to the patch. – equivalent to the gap between GPS recordings

In our IBM, female and male deer are either mature (≥ 1 year old) or immature (< 1 year old). Other state variables associated to deer include their age, reproductive status for mature female (ie, with or without offspring), mother’s identity (for immature deer), and the coordinates of the release site (for those initial deer who are introduced in the landscape). In our model, deer do not interact beyond immature deer following their mother’s movements and sharing their location until they mature. All movement behaviour of deer is probabilistically determined at the patch-level for each deer based on variables identified in the SSF, while population dynamics are determined by probabilistic birth and death rates.

The model begins on 16th December 2015 at 10:00 – the time of the first deer GPS detection. Deer are introduced to the model at release-site locations and times according to their real reintroductions on Corsica (Supplementary Information). All input variables dictating deer movement are presented in table 1 (SSF output). Survival and birth rates were based on red deer life history and local expert opinion. Local expert opinion suggested that a survival rate of 97% and 6 – 7 fawns per 10 female deer. We aimed to replicate the latter by applying a birth probability of 65% to all female deer regardless of whether they had a fawn or not, but only allowing deer without an offspring to subsequently give birth. The max lifespan was assumed to be 14 years (Pérez-Barbería, Carranza and Sánchez-Prieto, 2015).

The max distance a deer can move in a 12-hour tick (their max step length) is 2.60km, which is the 99.9 percentile of the GPS data. The relative probability for a deer to move from their current patch x to patch z is given by:

where |z – x| ≤ max step length

|z – x| represents the Euclidean distance between patches x and z, meaning only patches within the max step distance are considered. Zi represents the deer- and patch-level main and interactive variables influencing deer movement as identified in the SSF, whilst βi represents the effect size for each variable. β is determined by sampling from a normal distribution with a mean equal to the effect size and standard deviation equal to the standard error of the associated SFF variable output (Table 1). The denominator term sums the probabilities of all patches within the max step length, and is used to calculate a relative probability for each target patch that the deer will move towards it (the *movement-prob*). Based on each patch’s movement probability, a patch is then probabilistically selected which the deer moves to. To do this, a random float between 0-1 is first generated. Then, each target patch’s *movement-prob* is summed onto a cumulative probability one-by-one. If a patch’s movement-prob increases the cumulative probability above the random float value, then that patch becomes the selected patch. Once a patch is selected; the deer individual then moves towards it.

Individual-based model validation

[other validation approaches]

To validate that the IBM was simulating deer with accurate habitat preferences we compared habitat suitability models trained on the observed deer data and the simulated deer data. In each case we calculated the number of observed deer visits for each 100m pixel, and then standardised this value to between 0 and 1 to generate a “visit rate” per pixel. We then trained random forest models to predict this visit rate from the landscape variables (elevation, slope, distance to roads and land cover type). Finally, we used this model to predict potential visit rates in the presence of deer (i.e. expected habitat suitability) across Corsica. Finally we visually inspected the results of this process to as applied to both the observed and simulated data.

# Results

We considered 25,584 steps, with a median of 1147 steps per deer (range = 29–1497 steps); median step-lengths was 240m. Our final model included landscape variables of land cover, slope, distance to roads, individual variables of sex and distance from release site, temporal variables of season, and step-specific variables of step length and turning angle. This final model suggested deer avoided roads and selected for areas of agricultural, bare and scrub cover (Figure 2).

We validated the results of the IBM built on the results of this model in x ways: xxx, xxx, and by comparing habitat selection between the real and simulated deer. [text on the results of the other validations]. The habitat preferences of the simulated deer were qualitatively similar to the observed deer, with preferences for moderate slopes and elevations for example (Fig x). The resulting habitat suitability maps of Corsica were also qualitatively similar, though both are unrealistically narrow (Fig x).

# Discussion

We

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# Authors contributions

Study conceived and planned by xxx. Field data collected by xx. Xxx contributed substantively to the manuscript ideas. xxx conducted all analyses. xxx led paper writing. All authors reviewed drafts and approved manuscript for submission.

# Acknowledgments

TBD

# Data accessibility

Data and reproducible code are available on Github (<https://github.com/J-Cos/DeerMovement_paper>).

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TABLES

See excel tables

FIGURES

Figure 1. Study site. Corsican red deer have been released in Corsica in Moltifau (North), San Petru di venacu (Centre) and Zicavu (South) between 1998 and 2018. Out of these, nineteen individuals (13 females and 6 males) have been GPS collared to gather information on the animals' survival, dispersion, and habitat use (North site: 2F and 2M; Centre: 5F and 4M; South: 6F). The devices collected data for 5 years, between December 15th of 2015 until December 31st of 2020.

SUPPLEMENTARY INFORMATION

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| --- | --- | --- | --- | --- | --- |
| Table 1A: variables characterising the initially reintroduced deer. Sex, their release coordinates, and their release tick are values assigned to state variables of the reintroduced deer in the simulation. | | | | | |
| Sex | Name | Release area | Release coordinates | Date-time of first GPS recording | Release tick |
| M | Roberto | North Corsica | 42.49983 9.07655 | 16/12/2015 10:00 | 0 |
| F | Barbara | North Corsica | 42.49983 9.07655 | 16/12/2015 10:00 | 0 |
| F | Sara | North Corsica | 42.49983 9.07655 | 17/12/2015 22:00 | 3 |
| F | Giulia | Center of Corsica | 42.24787 9.16314 | 16/03/2016 10:00 | 182 |
| M | Dioniggi | Center of Corsica | 42.24787 9.16314 | 16/03/2016 10:00 | 182 |
| M | Lucio | Center of Corsica | 42.24787 9.16314 | 16/03/2016 10:00 | 182 |
| F | Raphaelle | Center of Corsica | 42.24933 9.16592 | 19/03/2016 10:00 | 188 |
| F | Victoria | Center of Corsica | 42.24933 9.16592 | 19/03/2016 10:00 | 188 |
| M | Lisandru | Center of Corsica | 42.24933 9.16592 | 19/03/2016 10:00 | 188 |
| F | Aurelia | Center of Corsica | 42.24933 9.16592 | 19/03/2016 10:00 | 188 |
| F | Romane | Center of Corsica | 42.24933 9.16592 | 19/03/2016 10:00 | 188 |
| F | Mattea | Center of Corsica | 42.24933 9.16592 | 19/03/2016 10:00 | 188 |
| F | Antonia | Center of Corsica | 42.24933 9.16592 | 19/03/2016 10:00 | 188 |
| F | Sabrina | Center of Corsica | 42.24787 9.16314 | 20/03/2016 10:00 | 190 |
| F | Vanina | Center of Corsica | 42.24933 9.16592 | 20/03/2016 22:00 | 191 |
| F | Violetta | South Corsica | 41.88473 9.22153 | 01/04/2016 10:00 | 214 |
| F | Sapara | South Corsica | 41.88473 9.22153 | 01/04/2016 10:00 | 214 |
| F | Lama | South Corsica | 41.88473 9.22153 | 01/04/2016 10:00 | 214 |
| F | Cavallara | South Corsica | 41.88473 9.22153 | 01/04/2016 10:00 | 214 |
| M | Petru | South Corsica | 41.88473 9.22153 | 01/04/2016 10:00 | 214 |
| F | Latonaccia | South Corsica | 41.88473 9.22153 | 01/04/2016 10:00 | 214 |
| F | Luvana | South Corsica | 41.88473 9.22153 | 01/04/2016 10:00 | 214 |
| F | Chisaccia | South Corsica | 41.88473 9.22153 | 01/04/2016 10:00 | 214 |
| F | Lia | Center of Corsica | 42.26662 9.17083 | 22/02/2018 10:00 | 1598 |
| F | Stella | Center of Corsica | 42.26662 9.17083 | 08/12/2018 10:00 | 2176 |
| M | Banditu | North Corsica | 42.47735 9.18355 | 12/04/2019 10:00 | 2426 |