# 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. 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 (Accolla et al., 2021; McLane et al., 2011), mechanistic individual-based models can make readily interpretable predictions of emergent population expansion (e.g. Fernández et al, 2006; Philips 2020). However, their reliability 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 provided previous insights (e.g. Mims *et al.*, 2019; Philips, 2020). 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 predictive, spatially explicit, individual-based model to examine 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 (Mandas et al, 2017), 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 (ref). Their habitat preference can vary with season and geographic location and is influenced by the presence of both food and cover (Borowski and Ukalska, 2008). 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: 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 December 31st of 2020. Animals’ locations were recorded twice a day – at 10 a.m. and 10 p.m. for a minimum of 24 months.

## Environmental data

Elevation and landcover values are 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. Distance to roads was calculated from a Corsican Road map (need the ref for this data which we received from the Corsica team).

## Movement data analysis

We followed Potts et al. (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. Briefly a step selection analysis defines each “step” in an animals movement (over 12 hours in this case) in terms of its characteristics (e.g. distance travelled or some features of the area where the step begins, ends or passes through). The step selection function is fit to identify the characteristics of true steps, for each animal, from among a number of randomly generated steps (15 in our case).

We initially developed a theoretically-derived saturated model of what factors influence deer movement , this provided the structure of our initial step selection function. This model included environmental 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. The model included both main effects and theory-based interaction terms (see supplementary for full details). We then applied step-wise model selection with AIC to simplify the model, and once the best model was found this was used as the initial step selection function

The full details of model selection results and SSF to IBM iteration are provided in the supplementary material. Briefly, the best model from the first round of model selection generated implausibly large home ranges we thus added the variable log distance to release site to the best model and repeated the model selection process.

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

## Individual Based Model

The presentation of our individual-based model follows the standard Overview, Design concepts, and Details (ODD) protocol (Grimm *et al.*, 2006, 2020).

**Overview**

***Purpose and patterns***This IBM aims to simulate the reintroduction and movement of reintroduced red deer on Corsica. We evaluate this model through its ability to replicate patterns observed in GPS-tracked red deer. These include step length, home range size, and the spatial distribution of deer activity.

***Entities, state variables, and scales***There are three entities present in this IBM: environment patches, deer agents, and deer release site agents.

*Patches* are 1ha representations of the landscape of Corsica with state variables:

* Landcover class: Artificial, Agricultural, Forest, Scrub, Bare, Wetland.
* Slope: in x units calculated by x method
* Distance to road: the Euclidean distance to the nearest x type road, in meters.
* n-visits: the number of visits by deer to the patch
* movement-prob: the probability an individual deer moves to the patch

*Deer* are agents representing individual deer. They are split into mature deer (≥ 1 year old) and immature deer (< 1 year old). Deer are characterised by state variables:

* age: the age of the deer (in ticks)
* sex: male or female
* mature: whether they are mature or not
* offspring: for mature deer, whether they have offspring
* mother’s ID: for immature deer, their mother’s WHO ID
* independence-countdown: a numerical variable to count down in ticks until an immature offspring deer is mature
* release-site-x: the x coordinate of the release site (for released deer) or the home range centre (for birthed deer)
* release-site-y: the y coordinate of the release site (for released deer) or the home range centre (for birthed deer)

*Deer release sites* are agents representing the release sites of individual deer which were originally reintroduced onto Corsica. Their state variables are:

* the sex of the deer to be released (male/female)
* the release time (in ticks)

Global variables also present in this IBM include:

* the simulated date-time
* the season (summer/winter)
* focal-deer (WHO ID)
* the target-patches (list of patches).

date-time and season are used to track whether it is summer or winter for the purpose of modelling deer movement. Summer begins on 15th April, whilst winter begins on 15th October. target-patches are a list of patches which a deer could potentially move towards, whilst focal-deer is used by the target patches to calculate movement-prob (see *move-mature*).

***Process overview and scheduling***Each tick represents a 12-hour period, as this is the temporal resolution of the GPS tracking data. During each tick, five sub-models execute in the below order:

1. *deer-release* simulates the initial reintroductions of deer onto Corsica
2. *birth* simulates the birth of deer
3. *move-mature* simulates the movement of mature deer, informed by the SSF outputs
4. *move-immature* simulates the movement of immature deer
5. *death* simulates the death of adult deer and any associated offspring

*move-adult* is executed prior to *move-offspring* to ensure offspring follow their mother. In addition, *death* is executed in ID order to ensure mothers die before offspring.

In addition, a *patch-count* procedure is executed by patches to update their n-visits variable, should a deer visit the patch.

**Design Concepts**

***Basic principles*** The basic principle of the IBM is to simulate red deer reintroduction into Corsica. The proximate aim of the IBM is to replicate red deer population dynamics and movement, whilst the ultimate aim is to explore and predict areas of potential human-deer conflict.

***Emergence*** All movement behaviour of deer emerges from the model and is probabilistically determined at the patch-level for each deer based on variables identified in the SSF. Population dynamics also emerge from the model and are determined by probabilistic birth and death rates.

***Adaptation*** Deer do not adapt.

***Fitness*** Deer do not calculate fitness.

***Prediction*** Deer do not directly predict the consequences of their decisions.

***Sensing***The patch a deer is located on can sense patches and their associated state variables within their maximum step length. This is needed so that patches can calculate the relative probability of each deer moving onto them.

***Interaction*** Deer do not interact beyond immature deer following their mothers (see ***Collectives***).

***Stochasticity*** The next patch an individual deer selects to move to is chosen probabilistically based on the SSF. Whether a deer gives birth or dies is also determined probabilistically based on expert knowledge.

***Collectives*** Immature deer follow their mother’s movements and share their location until they mature.

***Observation*** For evaluation and analysis, the home range sizes, the step lengths, and the spatial distribution of n-visit values were exported.

**Details**

***Initialisation*** 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 (table x).

|  |  |  |  |  |  |
| --- | --- | --- | --- | --- | --- |
| Table x: 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 |

***Input*** All input variables dictating deer movement are presented in table x (SSF output). Annual birth and survival probabilities were 65% and 97%, respectively, and were based on expert opinion. The max lifespan was x. The max distance a deer can move in a 12-hour tick (their max step length) is 8.65km, obtained from analysing the raw GPS outputs.

***Sub-models*** The below sub-models are executed to simulate deer reintroduction, birth, movement, and death.

1. *deer-release* This simulates the initial reintroductions of deer onto Corsica. For each release site, if the current time is equal to the release site’s release time, the release site will produce a single mature deer with no mother or offspring. This deer’s sex will match the sex of the release site (which represents the sex of the real deer released), and their age is 731 (i.e., one year old and mature). The release site xy coordinates of the deer will match those of the release site agent.
2. *birth* For mature female deer with no offspring, a single immature offspring is produced if a random float between 0 – 1 exceeds the probability of not giving birth over 12 hours. The probability to not give birth at the 12-hour timestep is the 730.5 root of the annual probability to not give birth. 730.5 is the average number of 12-hour steps in a year, assuming an average of 365.25 days per year. All offspring start as immature and with a random sex. The offspring’s independence-countdown is randomly assigned as either 730 or 731 so that, on average, 730.5 ticks (365.25 days) pass until an immature offspring matures (see *move-immature*). Finally, the mother will set her offspring variable to ‘yes’ to indicate 1) that she has an offspring and cannot reproduce, and 2) to allow for the patch-count procedure to correctly record her offspring.
3. *move-mature* This procedure simulates mature deer movement to a new patch. 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 (termed ‘target-patches’). 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 (SSF table x). The denominator term sums the probabilities of all target patches 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-prob, 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. One a patch is selected; the deer individual then faces and moves towards it. To allow for the n-visits procedure to register that a deer has visited the patches en route to the selected patch, the individual moves forward 100m at a time until the selected patch is reached. Once the deer reaches the selected patch, the procedure stops.

1. *move-immature* This procedure moves immature, offspring deer. Each immature offspring will change their heading to face their mother and jump to her location, as if they have followed her. If the new location is the furthest location the offspring deer has visited from its mother’s release site, then it updates its *release-site* xy variables with the new location.

In addition, the individual’s independence-countdown decreases by one. Should this mean the independence-countdown decreases to zero or lower, the immature deer matures. They set their mother variable as ‘none’ and their mature variable as ‘yes’. Finally, their mother sets her offspring variable to ‘no’ so that she can now reproduce again.

1. *Death* Adult deer die due to both intrinsic and extrinsic causes. If deer exceed their max lifespan, they are assumed to die from intrinsic senescence. Should deer not die from intrinsic senescence, then each mature deer is assumed to die from extrinsic causes if a random float between 0 – 1 exceeds the 12-hour survival probability. Like *birth*, the 12-hour survival probability is scaled from the annual survival probability by taking the 730.5 root. Immature deer do not follow this rule because the birth probability is measured in the field by the number of offspring surviving at one-year old, but immature deer will die if their mother dies.
2. *Patch-count* this procedure is triggered when a mature deer visits a new patch. The new patch will add one to their patch-count variable, to record the mature deer visiting the patch. Should the mature deer have an immature offspring, then they will add two onto their n-visits variable, to record both the visit by the mature deer and their immature offspring.

# Results

Xxx

# 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 will be made available via a digital repository.

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