SI Appendix.

Revilla & Wiegand. Individual movement behavior, matrix heterogeneity, and the dynamics of spatially structured populations

The demographic submodel. The Iberian lynx is the most endangered wild cat in the world (1). It inhabits only two isolated populations in the south of the Iberian Peninsula (2, 3). Our study system is located in Doñana area, a flat region where croplands cover half of the area, with the remaining fragmented vegetation dominated by Mediterranean scrubland, pine and eucalyptus plantations and marshlands. Doñana National Park is located in the south of this area. Habitat degradation and fragmentation are the main threats for the conservation of the species (1). Its survival depends on our understanding of the dynamics of its metapopulations in the context of landscape management, which in turn depends on how habitat features and landscape patterns promote and/or constrain dispersal among subpopulations (2, 4).

Days are the basic time unit in the model, affecting the movement during dispersal and mortalities, whereas processes acting at other time resolutions are scaled accordingly. The demographic structure is based on the individual-based spatially implicit model presented by Gaona et al. (2) and by Ferreras et al. (4). It reflects our current understanding of the biology of lynx, which is similar to the life cycle of many other species with natal dispersal and a land-tenure territorial system. We stochastically model individual lynxes independently during the birth, dispersal, aging and death processes. Here we describe its structure (2, 4). The main difference with Gaona's et al (2) model is that we consider space explicitly, and hence individual movement, settlement, territoriality and the carrying capacity of subpopulations are directly linked to a landscape map.

Territoriality. The distribution and amount of breeding habitat in the landscape determines the location and potential maximum carrying capacity of each subpopulation. We modeled territories based on the estimates of non-overlapping core areas (5, 6), which yield core area sizes between 4-5 and 12 cells of breeding habitat per core area. We adjusted those values to obtain the maximum carrying capacity currently observed in each subpopulation [see the table below in *Model Parameterization*, (4)].

Reproduction. Only residents above the age of first reproduction and below the age of last reproduction might reproduce (see the table below in *Model Parameterization*). Resident females with an overlapping or neighboring resident male (also within reproductive age) may reproduce once a year with a given probability $p(r) = b_{\mathrm{n}}$. In two populations, where habitat quality is highest, breeding probability is higher $p(r) = b_{\mathrm{n}} + \Delta b_{\mathrm{b}}$ (see the table below in *Model Parameterization*). Reproduction occurs at day 90 of every year (7).

Additionally we used a density dependence function affecting birth probability in those subpopulations holding more than one potential territory (for more details see (2). In such a case, when there is only one resident female ($n_t = 1$), birth probability reaches a maximum value $b_{\max}$. Birth probability decreases linearly from this maximum to the corresponding b at carrying capacity of the patch ($n_{\max}$) following

$$f(n_t) = b_{\max} - \frac{(b_{\max} - b)(n_t - 1)}{(n_{\max} - 1)} \quad , \qquad \textbf{[1]}$$

where $b = b_n$ for standard patches or $b = b_n + \Delta b_b$ for the best patches, n_t is the current number of territories occupied and K_j is the carrying capacity of patch j (see the table below in *Model Parameterization*). Therefore the effective probability of reproduction is

$$p(r) = \begin{cases} b & \text{if} \quad n_t = K_j \\ f(n_t) & \text{if} \quad n_t < K_j \end{cases} \quad , \qquad \textbf{[2]}$$

In the best areas the probability of reproduction considering density dependence is defined only in case that $b < b_{\max}$, otherwise $p(r) = b$.

Litter size is stochastically determined from the observed distribution, ranging from 2 to 4 kittens per litter (see the table below in *Model Parameterization*). Newborn individuals are located at the same spatial coordinates as the mother. We assumed a sex ratio at birth of 0.5 (7).

Survival. We stochastically sampled a binomial distribution with a given survival probability S_i for each age-stage class i of individuals (see the table below in *Model Parameterization*,). We distinguished between the different mortality rates of cubs (from birth to 9 months), non-dispersing subadults, dispersing animals and residents (see the table below in *Model Parameterization*,). Survival rates differ when animals are inside and outside the National Park (where they are much lower). We used published annual survival estimates S_i to calculate daily survival rates S_i^d [for a summary see (4, 8)].

During their first year of life, cubs have a survival probability S_c (S_{cNP}) outside (inside) the National Park calculated for a period of 275 days (assuming birth the first day of April, (7)). Dispersal can begin when lynxes are between 9 and 28 months-old (i.e., between January of their second calendar year and September of their third calendar year, (9). Therefore the survival probability of non-dispersing subadults S_s (S_{sNP}) is applied as a function of the amount of time they remain in the natal territory before dispersing.

We considered a basic mortality rate for dispersing individuals that is applied as a per-day mortality while animals move. Additionally we have some evidence that animals that spent on average more time in open habitat suffered an increased mortality risk. We consider an additive increase of the risk of mortality during dispersal when lynxes are moving in a more fragmented matrix. We use a linear increase in the daily mortality risk as a function of the proportion of time dispersing individuals spent in open matrix habitat following

$$m_{jk} = m_d + \rho \cdot m_d \cdot \frac{s_o}{s_k} \quad , \qquad \textbf{[3]}$$

where m_{jk} is the actual daily mortality rate applied to a given dispersing individual j in day k, m_d is the basic daily mortality rate of dispersing individuals, s_o and s_t are the number of steps in open matrix and the total number of steps moved in the current day k, respectively, and ρ is the parameter that defines the increase in mortality risk as a fraction of m_d, which is calculated as

$$m_d = \begin{cases} 1 - S_d^d & \text{if out of the park} \\ 1 - S_{dNP}^d & \text{if inside the park} \end{cases} \quad , \qquad \textbf{[4]}$$

For example, if ρ = 1 and the individual moved only in open matrix, the expected mortality rate m_d is doubled for that individual and day.

We used survival rates for residents outside and inside the National Park, without an increased mortality due to senescence, because due to the overall high mortality rates suffered by individuals at the previous individuals rarely reach the maximum age, and hence any effect of senescence on population parameters is irrelevant. We determined survival stochastically on a daily basis to generate a realistic pattern of empty territories available for moving animals along the year.

At the end of every year the age of all individuals is incremented. Animals reaching the maximum age $A_{\max}$ die deterministically the following year (see the table below in *Model Parameterization*,).

The movement submodel. Individuals disperse from their natal areas when between 8 and 23 months old, lasting from a few weeks to more than a year (9). The behavior and performance of this movement model and the relative importance of the different movement rules have been described elsewhere (10). The landscape is represented by a grid of barrier, open, dispersal and breeding habitats [with a 0.5 km resolution (10)]. Barrier habitat is composed by urban areas and wide water bodies; open habitat is characterized by land uses without cover, whereas dispersal habitat offers protective cover (mostly forested areas). Animals perform a sequence of stochastic movement steps in which they can move to one of the surrounding eight cells, or stay in their current position. However, they cannot move into barrier habitat. Individuals move independently of each other without competing for space (except for settlement, see *The demographic submodel*). Time is modeled in steps of one day, within which individuals move sequentially.

Internal state. Moving lynxes have two goals, finding unoccupied breeding habitat were they can settle and reproduce and minimizing their risk of mortality. Empty territories can be located inside their own natal local population or somewhere else. Searching individuals minimize the time spent in open habitat or in fragmented areas. This is because breeding habitat distribution is associated with dispersal habitat, and hence individuals maximize their search within that type of habitat and because they perceive a higher risk of mortality when moving in more fragmented areas and in open habitat (see *Navigation capacity* and *Survival*).

Motion capacity. Lynxes have two default movement modes, both defined by the probability distributions of number of steps per day and the autocorrelation in turning angles when moving in unfragmented dispersal habitat. We stochastically determine the number ϕ_{d} of steps from the accumulated density probability function of the total distance moved per period of activity

$$p_{\mathrm{a}}(\phi_{\mathrm{d}}) = (1 + \alpha \cdot \phi_{\mathrm{d}}^{3})^{-1} \quad , \qquad \textbf{[5]}$$

where p_a is the probability obtained and α is a parameter [(10), see the table below in *Model Parameterization*]. The overall degree of autocorrelation θ_d is defined as the probability to move in the same direction as the previous movement step (10). The distribution of turning angles is bimodal, with a higher probability to move in the previous direction and to move back. We estimated the probability to move back as a fraction of the probability to move ahead

$$\theta_{back} = \theta_d \delta \quad , \qquad \textbf{[6]}$$

being the possible range of δ between 0 (no probability to move back) and 1 (the same probability to move back than ahead). The probability to move to any other cell is calculated after θ_d and θ_{back} to sum 1.

In the second movement mode the autocorrelation of the path increases when animals move more steps (more than 3 km h^{-1}). Therefore if $\phi_d / 10.5 > L$ then

$$\theta_l = \theta_t + \Delta\theta_l \quad , \qquad \textbf{[7]}$$

where 10.5 is the average duration of a period of activity (5), L is the threshold parameter defining long distance movements (given by the number of steps per hour L = 6 steps), θ_t is the total probability to keep the previous direction (see Eq. 9), $\Delta\theta_l$ is the increase due to long distance movement, and θ_l is the final autocorrelation observed in long distance movements (10). Lynx use this movement mode to leave the current area after some time.

Navigation capacity. Lynxes can detect the type of habitat within their perceptual range [their 8-cell neighborhood (10)], evaluating the existence of an empty territory whenever they detect a cell of breeding habitat. Open habitat strongly affects movement properties. We use a parameter N_d (= 5 cells of dispersal habitat) defining the threshold below which the lynx perceive its surroundings as fragmented and model the avoidance of open habitat in fragmented areas ($D < N_d$) as

$$\begin{aligned} P_o(O,D) &= \frac{1}{(O+D)}\beta \\ P_d(O,D) &= \frac{1-[OP_o(O,D)]}{D} \end{aligned} \quad , \qquad \textbf{[8]}$$

where $P_\mathrm{o}(O, D)$ and $P_\mathrm{d}(O, D)$ are the probabilities for a given cell of open and dispersal habitat, respectively, to be selected, O and D are the number of cells of open and dispersal habitat within perceptual range and β is the parameter describing the avoidance of open habitat. In this way lynxes select cells of open habitat with the same probability as dispersal habitat if their location is surrounded by more than N_d cells of dispersal habitat, avoiding them if surrounded by less (10). Animals moving in fragmented areas increase the autocorrelation level as

$$\theta_t = \theta_d + \Delta\theta_f \quad , \qquad \textbf{[9]}$$

where $\Delta\theta_f$ is the increase in autocorrelation and θ_t is the total autocorrelation, resulting in faster moves per day in fragmented areas.

Lynxes may explore the open habitat during their periods of activity, but normally return to dispersal habitat as the period passes. We modeled these excursions into open habitat as the probability P_d to move towards the last cell of dispersal habitat visited in the current period of activity (short-term memory) as a function of time

$$P_\mathrm{d}(T) = T\gamma \quad , \qquad \textbf{[10]}$$

where γ defines the return to dispersal habitat. T is the number of hours already moved during the current period of activity, calculated as

$$T = 10.5\frac{\phi_c}{\phi_d} \quad , \qquad \textbf{[11]}$$

where ϕ_c is the current step and ϕ_d is the total number of steps of the current day (stochastically determined after Eq. 1). Once on the way towards the last cell of dispersal habitat the individual moves in this direction until it detects a cell of dispersal habitat and then moves directly to it (10).

Dispersal and settlement rules. For every individual we stochastically assigned a date to begin dispersal following the distribution of dispersal probability *p*(*d*) observed in the field [modified from (9)]

$$p(d) = -1.55 + 2.62\left(1 - e^{-0.115t}\right) \quad , \qquad \textbf{[12]}$$

where *t* is the age of the individual in months. Dispersing lynxes move until they die or settle. The distribution and amount of breeding habitat in the landscape determines the carrying capacity of each subpopulation (see *The Demographic Submodel*, above). Females settle in empty breeding habitat with a minimum size (depending on the subpopulation). Males settle in areas where there is a resident female. No overlapping is permitted between the territories of individuals of the same sex. All dispersing individuals move simultaneously, hence permitting competition for empty territories among them, whereas empty potential territories are generated on a daily basis (see *The Demographic Submodel*, above). When two dispersing individuals of the same sex arrive to the same empty area during the same year, an age-based preference ranking is applied to determine which one obtains the territory. The preference ranking was 4>5>6>7>3>8>9 years old and 4>5>6>7>3>2>8>9 years old for males and females, respectively [see (2)]. Following these rankings, resident individuals older than the maximum reproductive rate also can be outcompeted. Outcompeted individuals become floaters, which move searching for a new territory following the same rules as dispersing subadults.

Model parameterization. The submodels are parameterized with field data obtained in Doñana metapopulation during the same period of time as the movement data analyzed by Revilla et al. (10).

Table 1. Parameters of the demographic and movement submodels.

Model Parameter	Symbol	Field Estimate
Maximum carrying capacities (number of resident females)		
Reserva Biologica (population 1)	K_{RB}	4
Coto del Rey (population 2)	K_{CR}	3
Marismillas (population 3)	K_{MA}	2
Acebuche (population 4)	K_{AC}	2
Hato Raton (population 5)	K_{HR}	1
Torrecuadros (population 6)	K_{TO}	1
Puebla (population 7)	K_{PU}	1
Moguer (population 8)	K_{MO}	1
Average litter size (cubs/litter) [*p* for 2, 3 and 4 cubs]		3.0 [0.1; 0.8; 0.1]
Maximum longevity (yr)	$A_{\max}$	13
Age of first reproduction (yr)		
females	r_f	2
males	r_m	3
Age of last reproduccion [females=males (yr)]	$r_{\max}$	9
Dispersal probability	$d(\mathrm{t})$	Eq. 12
Reproductive rate (annual *p*)		
probability of reproduction	b_{n}	0.6
probability of reproduction in best areas (Coto del Rey and Torrecadros)	b_{b}	0.8
densitity dependent maximum probability of reproduction	$b_{\max}$	0.95

Survival rates (annual *p*)		
cubs inside National Park	S_{cNP}	0.50
cubs outside National Park	S_{c}	0.45
subadults inside National Park	S_{sNP}	0.77
subadults outside National Park	S_{s}	0.60
dispersers inside National Park	S_{dNP}	0.70
dispersers outside National Park	S_{d}	0.25
additional mortality risk in open habitat	ρ	5.8*
residents inside National Park	S_{rNP}	0.90
residents outside National Park	S_{r}	0.70
Movement parameters		
Motion capacity		
steps per day	α	0.00027
autocorrelation in dispersal habitat (*p*)	θ_d	0.26
long-distance threshold (steps per hour)	L	6
increase in movement autocorrelation in lon-distance movements (*p*)	$\Delta\theta_l$	0.27
bimodal distribution of turning angles (*p*)	δ	0.65
Navigation capacity		
fragmentation threshold (cells)	N_d	5
increase in movement autocorrelation in fragmented areas (*p*)	$\Delta\theta_f$	0.10
avoidance of open habitat (*p*)	β	0.8
probability to return to dispersal habitat (*p*)	γ	0.09

*This parameter was estimated using maximum likelihood, adjusting for the time moving, the connectivity values and the total mortality rate.

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