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Nonparametric spatial regression of survival probability: visualization of population sinks in Eurasian Woodcock

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Abstract. Both evolutionary ecologists and wildlife managers make inference based on how fitness and demography vary in space. Spatial variation in survival can be difficult to assess in the wild because (1) multisite study designs are not well suited to populations that are continuously distributed across a large area and (2) available statistical models accounting for detectability less than 1.0 do not easily cope with geographical coordinates. Here we use penalized splines within a Bayesian state-space modeling framework to estimate and visualize survival probability in two dimensions. The approach is flexible in that no parametric form for the relationship between survival and coordinates need be specified a priori. To illustrate our method, we study a game species, the Eurasian Woodcock *Scolopax rusticola*, based on band recovery data (5000 individuals) collected over a >50 000-km^2 area in west-central France with contrasted habitats and hunting pressures. We find that spatial variation in survival probability matches an index of hunting pressure and creates a mosaic of population sources and sinks. Such analyses could provide guidance concerning the spatial management of hunting intensity or could be used to identify pathways of spatial variation in fitness, for example, to study adaptation to changing landscape and climate.

Key words: Bayesian state-space modeling; bivariate radial spline; capture–mark–recapture; capture–recovery; Eurasian Woodcock; generalized additive models (GAM); hunting management; Leslie matrix; population growth rate; Scolopax rusticola; *smooth function; sustainability of wildlife exploitation.*

INTRODUCTION

Population biologists are often interested in how the demography of their study species varies across space (e.g., Post 2005, Quintana-Ascencio et al. 2009, Saracco et al. 2010). Indeed, demography and fitness measures are closely linked, making spatial variation in demographic parameters of crucial importance to answer questions related to local adaptation, range limits, habitat choice, and dispersal, particularly in a context of ever more rapidly changing climate and human land use (Hirzel and Le Lay 2008). In addition, wildlife managers generally want to assess the effect of, or identify the need for, management actions (Schwartz et al. 2010). The spatial location of hunting-free reserves, for example, is subject to a number of socioeconomic pressures, and a sounder scientific basis might facilitate more directed decisions. Survival probability is the key demographic parameter here, because it is both driving a substantial part of the variation in population growth rate, and is impacted on by exploitation. Yet characterizing its variation over space often remains a methodological challenge.

An often used method to assess spatial variation in survival probability is multisite capture–recapture schemes, in which individuals are marked across a selection of isolated "sites" and are subsequently reencountered in these or more sites. Multistate capture–recapture models (Hestbeck et al. 1991) are then used to infer how the survival probability varies between sites. This study design, however, is relevant only in a limited number of situations, because sites have to be clearly separated, e.g., habitat fragments (Githiru and Lens 2006) or breeding colonies (Péron et al. 2010). In most cases, however, the population will be continuously, and sometimes sparsely, distributed across the landscape. Therefore, a sound method to assess continuous (as opposed to site-specific) spatial variation in capture–recapture model parameters seems required (Saracco et al. 2010). Here we introduce a method for attaining spatially explicit estimates of survival probability based on splines, i.e., the fitting of piecewise regressions (Ruppert et al. 2003). The approach is based on state-space modeling of band recovery and mark–recapture data, and is implemented in a Bayesian

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framework using Markov chain Monte Carlo (MCMC) algorithms with WinBUGS (Spiegelhalter et al. 2003).

To illustrate our approach, we analyze data from the Eurasian Woodcock *Scolopax rusticola*, a forest-dwelling game bird, for which large sample sizes of banding and recovery records are available (Ferrand et al. 2008). How survival varies in space in this population can constitute evidence for the additive nature of hunting mortality. The "additive hypothesis" implies that the hunting-related mortality adds to other, natural sources of mortality (Burnham and Anderson 1984). Therefore, areas of high and low hunting intensity should exhibit low and high survival probability, respectively. The "compensatory hypothesis," on the other hand, states that an increase in one source of mortality is compensated via a decrease in other sources (Burnham and Anderson 1984). These two situations obviously correspond to two theoretical points on a gradient of possible responses to exploitation: it is likely that both additive and compensatory mortality co-occur, at least up to a threshold of hunting pressure after which compensation mechanisms become insufficient (Williams et al. 2002). We will also show that spatial variation in survival probability can produce a mosaic of population sources and sinks across the landscape (Pulliam 1988, Novaro et al. 2000, Schwartz et al. 2010).

STATE-SPACE JOINT MODELING OF BAND RECOVERY AND CAPTURE–RECAPTURE DATA

Survival probability $\phi_{i,t}$ of individual i between year t and $t+1$ was not directly measured in the field, but was assessed through the observations of this individual, live or dead. The observations were obviously incomplete, in that not all live individuals were recaptured and not all dead individuals were reported as such. To analyze these data, we made explicit the distinction between the observation (detected or not) and the state of individuals (alive or dead) by developing a state-space model (Gimenez et al. 2007, Royle 2008, Schofield and Barker 2008). The incorporation of a spatial structure in survival is made much more convenient when survival is separated from nuisance parameters.

We considered three states: "alive and available to capture," "newly dead and available to recovery," and "long dead and not available," and denoted by $\mathbf{S}_{i,t}$ the random state vector taking values (1,0,0), (0,1,0), (0,0,1), if, at time t, individual i was in state alive, newly dead, or long dead, respectively. The observations "not seen," "recaptured alive," and "recovered dead" were then generated from these underlying states. We denoted by $\mathbf{O}_{i,t}$ the random observation vector taking values (1,0,0), (0,1,0), (0,0,1) if, at time t, individual i was not seen, recaptured alive or recovered dead. We also introduced model parameters as follows: given that individual i was alive a time t, it may survive to time $t+1$ with survival probability $\phi_{i,t}$ and be recaptured with recapture probability $p_{i,t}$. Given that individual i is dead at time t, it may have died from hunting and be reported as such with recovery probability $r_{i,t}$. The state-space model is then described by the state equations that specified the state of the individuals at time $t+1$, given their state at time t:

$$\mathbf{S}_{i,t+1} \mid \mathbf{S}_{i,t} \sim \text{multinomial}\left(1, \mathbf{S}_{i,t}\begin{bmatrix} \phi_{i,t} & 1-\phi_{i,t} & 0 \\ 0 & 0 & 1 \\ 0 & 0 & 1 \end{bmatrix}\right) \tag{1}$$

and by the observation equations, which specified the observation of the individuals at time t given their state at time t:

$$\mathbf{O}_{i,t} \mid \mathbf{S}_{i,t} \sim \text{multinomial}\left(1, \mathbf{S}_{i,t}\begin{bmatrix} 1-p_{i,t} & p_{i,t} & 0 \\ 1-r_{i,t} & 0 & r_{i,t} \\ 1 & 0 & 0 \end{bmatrix}\right). \tag{2}$$

NONPARAMETRIC AND SEMIPARAMETRIC SPATIAL REGRESSION OF SURVIVAL PROBABILITY

The survival probability $\phi_{i,t}$ of individual i banded in location $\mathbf{x}_i = (x_i, y_i)$ from time t to $t+1$ was modeled as follows:

$$\text{logit}(\phi_{i,t}) = \log\left(\frac{\phi_{i,t}}{1-\phi_{i,t}}\right) = f(\mathbf{x}_i) + \varepsilon_i \tag{3}$$

where f is a nonparametric regression function, $\mathbf{x}_i$ is the dimension-two vector containing coordinates, and ε_i are individual random effects independently and identically distributed as $N(0, \sigma_\varepsilon)$. Time dependence and age dependence in $\phi_{i,t}$ are omitted for clarity, but were eventually included in the model using fixed effects. The interest of the method is to use a function f allowing a description of the data that is sufficiently unconstrained to capture spatial variation of unknown shape (i.e., no predetermined form as in parametric regression), but also allowing a sufficiently autocorrelated fit so that irregularities in the data are smoothed. We obtained these properties by using a bivariate spline function and by penalizing rough fits (Ruppert et al. 2003, Gimenez et al. 2006, Gimenez and Barbraud 2009).

Spline functions are the sum of K piecewise regressions, connected at breakpoints or knots $(\boldsymbol{\kappa}_k)_{k=1,\ldots,K}$, where $\boldsymbol{\kappa}_k$ is a dimension-two vector containing coordinates. Because we dealt with geographical coordinates (the individual banding location $\mathbf{x}_i$), we needed the fit to be insensitive to a change in orientation of the axes (rotational invariance), which we obtained by using the distance function C, defined as $C(\mathbf{u}, \mathbf{v}) = ||\mathbf{v}-\mathbf{u}||^2 \log||\mathbf{v}-\mathbf{u}||$, where $||\mathbf{r}|| = \sqrt{\mathbf{r}^\top\mathbf{r}}$ is the norm of vector $\mathbf{r}$ (more detail in Appendix A). The bivariate radial spline function is then written as follows:

$$f(\mathbf{x}_i) = \beta_0 + \beta_1 \cdot x_i + \beta_2 \cdot y_i + \sum_{k=1}^{K} b_k \cdot C(\kappa_k, \mathbf{x}_i) \tag{4}$$

where β_0, β_1, β_2, and $(b_k)_{k=1,\dots,K}$ are parameters to be estimated. Random data irregularities generally make the use of Eq. 4 of little interest if some amount of smoothing is not applied. Smoothing is equivalent to offsetting the jumps in the first-order derivative of f, which in turn, is equivalent to penalizing the knots contributing to these jumps; thus the term penalized splines or P-splines. Such penalization is performed by putting a constraint on the norm of vector $(b_1, \cdots, b_K)$, which renders the criterion to be minimized exactly similar to the fitting criterion of a linear mixed model (Appendix A), with β-elements as fixed effects, and b-elements as random effects distributed as $N(0, \sigma_b)$. This penalization has two advantages: (1) it makes the implementation of P-splines straightforward in standard computer packages as long as random effects can be handled, and (2) a data-driven optimal estimate of the amount of smoothing is obtained as a by-product as $\lambda = \sigma_\varepsilon/\sigma_b$ (Appendix A). The final step in building P-splines was to choose the number and position of knots $\boldsymbol{\kappa}_k$ (detail in Appendix A).

The same semiparametric spatial regression model structure was applied to recovery probability $r_{i,t}$:

$$\text{logit}(r_{i,t}) = f'(\mathbf{x}_i) + \varepsilon'_i. \tag{5}$$

Hereafter, parameters with a prime refer to the model for the recovery probabilities.

Due to the life history of Eurasian Woodcocks, our model was also slightly more complex than what was just presented, in that the spatial regression was applied to the winter period only: $\phi_{i,t}$ and $r_{i,t}$ corresponded to winter (October–February) survival and recovery probabilities. Overall survival probability was the product of $\phi_{i,t}$ and of $\xi_{i,t}$, the summer survival (Appendix B; see Gauthier and Lebreton 2008). We did not use recoveries occurring on the breeding grounds; recovery probability $r_{i,t}$ applied only to the winter period (Appendix B).

MODEL SELECTION AND INFERENCE

Bayesian inference

We used the MCMC algorithm as implemented in WinBUGS 1.4 (Spiegelhalter et al. 2003) to integrate the resulting multidimensional likelihood function. We generated two chains of length 20 000, discarding the first 5000 as a burn-in, and assessed the convergence of the chains using the Gelman-Rubin criterion (Brooks and Gelman 1998). The R package R2WINBUGS (Sturtz et al. 2005) was used to call WinBUGS and export results into the R environment (R Development Core Team 2010).

The priors for the hyperparameters σ_b^2 and σ_ε^2, as well as $\sigma_b'^2$ and $\sigma_\varepsilon'^2$, were uniform on [0, 8]. The β- and β′-elements were assigned normal priors with mean 0 and variance 100. The use of larger prior variances would occasionally induce numerical instabilities (supposedly linked to survival probability reaching its upper or lower boundary). Parameters used to describe the fixed effects (on the logit scale) of age, sex, and year were given normal priors with mean 0 and variance 10 000. We also incorporated the fixed effect of direct (same year as banding) and indirect (subsequent years) recovery on recovery probability (Appendix B), to which we gave a normal prior with mean 0 and variance 10 000.

Indicator variables for the selection of effects

Was this spatial structure justified by the data compared to the null model in which parameters were spatially invariant? We used a model selection approach to address this question in the Bayesian framework (Kuo and Mallick 1998). A two-mode variable that we term "indicator" (0/1) described the presence/absence of a given effect in each simulation of the MCMC chains (Royle and Dorazio 2008:70 ff.). We included indicator variables for all parameters occurring in the spline part of function f, and considered that if at least one of the indicators was equal to one in more than 95% of the posterior sampled values (i.e., the corresponding parameter had to be included in the model), the spatial model was selected over the null model (model with no spatial variation). The performance of this approach remaining to be evaluated, we also relied on the Deviance Information Criterion, DIC (Spiegelhalter et al. 2003).

APPLICATIONS

To illustrate the use of nonparametric and semiparametric spatial regression of survival in a management context, we analyzed capture–recapture–recovery data from the Eurasian Woodcock (*Scolopax rusticola*) population wintering in France. Briefly, on the wintering grounds most woodcocks commute daily between nighttime feeding grounds (mainly meadows) where banding occurs using pole-hanged nets and flashlights, and daytime roost sites in forests, where hunting occurs (Duriez et al. 2005). Woodcocks are marked with metal bands. Recovered bands are reported to the woodcock network group at the Office National de la Chasse et de la Faune Sauvage (French Hunting and Wildlife Service). More detail on field methods can be found in Gossmann et al. (1994) and Ferrand et al. (2008). Here we used data collected between October 1989 and February 2009 (20 years, which is almost the maximum recorded longevity of that species, and more than 10 times the average life span in the population). The study area was restricted to the subset between 0° and 2° E and 46.5° and 49.5° N, France, from which we randomly selected 5000 individuals out of 6693 to reduce the computational burden.

This area encompassed four qualitatively contrasted units. (1) The Northeast corresponds to the intensively cultivated Beauce, and is also partly urbanized. Woodcock habitat is only relictual in this area; accordingly, banding and recovery records were sparse there. (2) The Southeast corresponds to the forested Sologne. The area holds favorable woodcock habitat but is also renowned for its hunting estates. Dense records of banding and recovery occurred there. (3) The Southwest encompasses the Regional Park of Loire Anjou Touraine, which holds a mosaic of moist forests and grazing and hay meadows, constituting probably the best woodcock habitat in the study area. (4) The Northwest includes agricultural land of less intensive nature (hedged farmland), where banding and recovery records were also densely distributed.

The sampling design specific to the woodcock data made it compulsory to refine capture–recapture–recovery multistate models. We present these developments in Appendix B. Most importantly, survival had to be modeled on a monthly basis: monthly winter survival is the fifth root of overall winter survival.

Hunting pressure and additive mortality

If hunting mortality is at least partially additive to other sources of mortality, spatial variation in hunting pressure should be proportional to spatial variation in winter survival probability.

The local hunting pressure on woodcocks was measured through a proxy that we term the local hunting pressure index (HPI). The computation of that index was based on the fact that, although woodcocks are generally site faithful, they may disperse long distances during severe winters (Gossmann et al. 1994). Thus, during average weather, woodcocks are subjected to the local hunting pressure, but after cold spells, many woodcock are out of their usual location and are subjected to a different hunting pressure. HPI for a given location was then the proportion of birds banded in that location that were recovered dead within a 10 km radius. HPI is a reliable proxy for local hunting pressure only if band reporting rate (the rate at which hunted individuals are reported as such) is roughly invariant across banding locations (discussed in *Discussion: General applicability and interest of the method*). We computed HPI over the 20 years of data available, using only locations where at least 20 woodcocks had been banded over that period. We focused thereby on the temporal average of local hunting pressure. Then we visually compared the spatial variation in survival and in HPI. If the maps indicated a cross-correlation between survival and HPI, we tried the following semiparametric model, in which hunting pressure effect was directly incorporated as

$$\mathrm{logit}(\phi_{i,t}) = \alpha \cdot H_i + f(\mathbf{x}_i) + \varepsilon_i \qquad (6)$$

where H_i corresponded to the HPI at the banding location of individual i. The slope of the regression α was a new parameter to be estimated. Other notations are as in Eq. 3. We then used the model selection method described in the previous section to determine whether any spatial variation in survival remained to be observed after having accounted for the effect of HPI. If spatial variation was selected, this meant that HPI was not the sole driver of spatial variation and that some other variables (e.g., habitat) played a role. Parameter α was given a uniform prior distribution on [−2, 0]. In the following, we call model 1 the model without the effect of HPI ($\alpha = 0$, as in Eq. 3) and model 2 the model with HPI effect (with parameter α to be estimated, as in Eq. 6).

In addition, we also examined the posterior mean of $\bar{\rho}$, the average over individuals of $\rho_i = f'(\mathbf{x}_i)/f(\mathbf{x}_i)$, where f' and f represent, respectively, the location-specific component of recovery and survival probabilities. Although known to be plagued by sampling and process biases (Burnham and Anderson 1984, Servanty et al. 2010), this measure of the spatial cross correlation between survival probability and the probability of dying from hunting may bring supporting information on the level of additivity.

Sources and sinks within a population

We expected that survival should vary in space, partly due to hunting pressure. Then the question arose whether low-survival areas were indeed sustainable, i.e., whether enough individuals survived for the local stock to keep its current level. Values were generated from the posterior distribution of survival, averaged over years, and plugged into a two-age-class matrix population model (post-breeding pulse formulation). We assumed that all females had the same fecundity irrespective of their wintering location, partly because we lacked precise data on breeding success and partly because some level of mixture is supposed to occur on the breeding grounds between birds wintering in different locations. We used 1.8 offspring per female as value for fecundity (Hoodless and Coulson 1998, Ferrand et al. 2008). We computed the location-specific population growth rate as the largest eigenvalue λ_i of the population matrix in location $\mathbf{x}_i$. We thereby obtained a sample of values from the posterior distribution of λ_i. We then draw a map of spatial variation in population growth rate, illustrating how local drops in survival probability created population sinks.

RESULTS

Spatial variation selected against the null model

In the model without HPI effect (model 1), all indicator variables had a mean > 0.25 across simulation outcomes, and several had a mean > 0.95. The DIC of the model with spatial component was 4822.8, compared to 11 603.6 if the spatial component was removed. Thus, the use of the spline functions in both survival and recovery probabilities was very likely to improve model fit: survival and recovery probabilities varied in space. In the model with HPI effect (model 2), all indicator variables still had a mean > 0.25 across simulation outcomes, but overall the means were lower, indicating a probably smaller, but still important, spatial variation: some yet unidentified variables drove variation that added to the one caused by HPI.

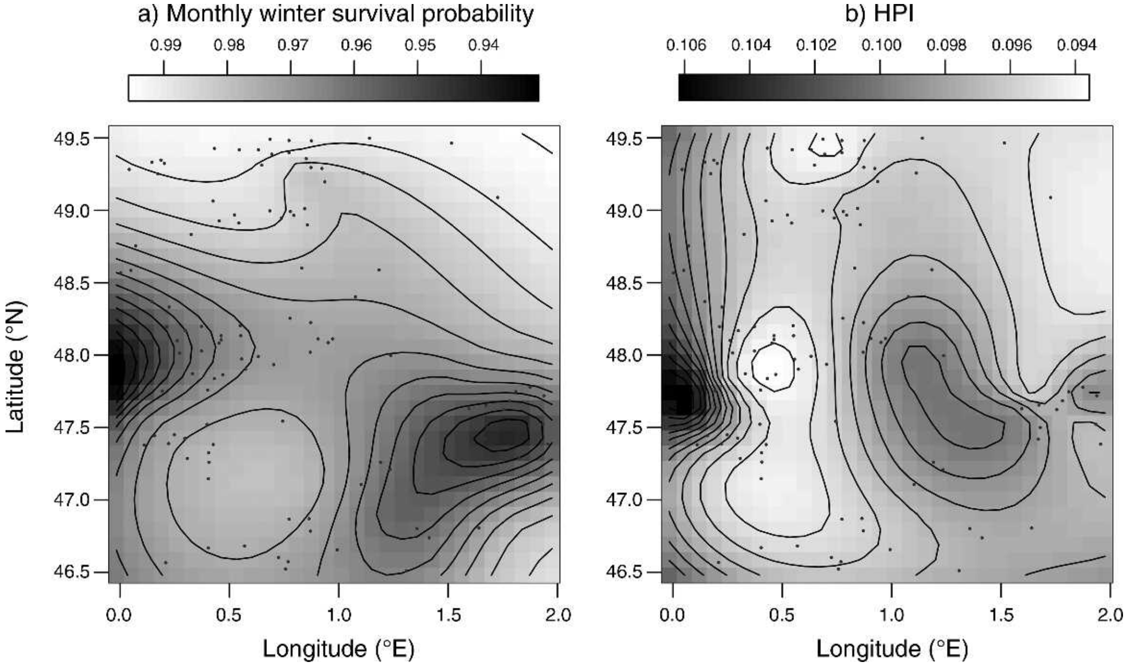

FIG. 1. (a) Spatial variation in mean monthly winter survival probability (averaged over years) of Eurasian Woodcock *Scolopax rusticola*, based on band recovery data (5000 individuals) from a $>$50 000-km^2 area in west-central France. (b) Spatial variation in hunting pressure index HPI, the proportion of birds banded in a location that were recovered dead within a 10-km radius (see *Applications: Hunting pressure and additive mortality* for computation of this index). Dots indicate banding locations with respect to latitude and longitude. Isolines correspond to the grayscale tick marks in the keys. Corresponding maps of standard deviation are provided in Appendix C: Fig. C1.

Spatial variation in winter survival and recovery probabilities

In the model without HPI effect (model 1), the comparison of the survival map and the HPI map indicated a match between the spatial variations in these two variables (Fig. 1). This suggested that local hunting pressure cross-correlated with survival probability, which we tested formally using model 2. On the opposite, the spatial cross-correlation parameter $\overline{\rho}$ was not different from 0 (95% credible interval: −1.81, 2.02). A value of $\overline{\rho}$ significantly different from zero was expected if survival and recovery probabilities were consistently cross-correlated across the range. Accordingly, the match of the survival map with the map for recovery probabilities was poor (Fig. 2 vs. Fig. 1a). In the model with HPI effect (model 2), the estimate of α was −0.53 (95% credible interval: −1.34, −0.04). Some spatial variation in winter survival probability remained after correcting for HPI; it is mapped in Appendix D: Fig. D1.

Population growth rate

Parameter values used in this section are from model 1. The mean of yearly survival probability of adult woodcocks varied spatially between 0.47 and 0.67 (computed as the fifth power of the values presented in Fig. 1, multiplied by the estimate for summer survival probability). The mean of yearly juvenile survival varied spatially between 0.35 and 0.65. Low-survival parts of the woodcock range were not sustainable without immigration from areas with low hunting (Fig. 3).

DISCUSSION

The match between survival and HPI: potential implications for hunting management

Survival and HPI variations were observed to match in space, and accordingly we detected a spatial (as opposed to temporal) cross-correlation between these variables. In other words, the higher the HPI, the lower the survival. This suggests the additivity of hunting mortality over other sources of mortality. However, a sampling covariance of unknown magnitude exists between HPI and survival (Burnham and Anderson 1984). This sampling bias on the estimate of the correlation coefficient between survival and recovery probability originates from the fact that individuals have to be dead in order to be recovered. The lack of strong spatial cross-correlation between survival and overall (as opposed to local; see next section) recovery probabilities may nevertheless suggest that the sampling covariance is small in our case.

The survival surface (Fig. 1a) clearly indicated that the zone between ∼1.5° and 2° E and 47° and 48° N was a low-survival area, in which monthly survival probability dropped to an unsustainable 0.92–0.94. This zone corresponded to a peak in the HPI (Fig. 1b). Moreover,

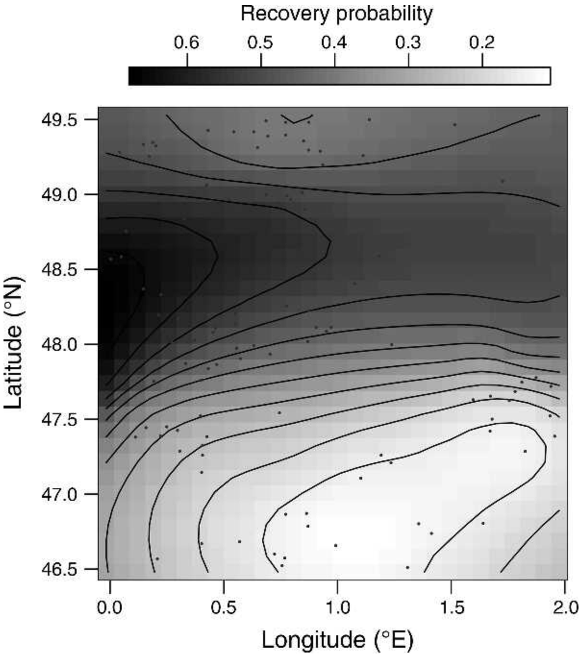

FIG. 2. Spatial variation in mean band recovery probability (averaged over years; all birds in the study were banded). Dots indicate banding locations with respect to latitude and longitude. Isolines correspond to the grayscale tick marks in the key. The corresponding map of standard deviation is provided in Appendix C: Fig. C2.

it can be roughly matched to the location of the Sologne, a region renowned for its hunting estates. The zone that borders our study area on the west was also characterized by a match between high HPI and low survival. In contrast, the area between ~0.25° and 0.6° E and 46.5° and 47° N exhibited high survival and relatively low HPI. This zone roughly corresponds to the Regional Park of Loire Anjou Touraine, where a mixed landscape of forests and wet grazing and hay meadows likely holds prime woodcock habitat.

The French-wintering woodcock population has been stable or slightly increasing over the study period (Ferrand et al. 2008). Local extinctions, to our knowledge, are never reported. Overall, our results are thus congruent with the hypothesis that highly hunted estates are sinks (Fig. 3), but that these subpopulations remain stable because juvenile birds produced in eastern and northern Europe distribute themselves across both high- and low-survival wintering areas. Moreover, individuals do not seem to modify their wintering locations based on the hunting pressure encountered during their first winter, although the latter assertion remains to be tested in more detail (but see Gossmann et al. 1994).

The mismatch between survival and recovery probabilities

HPI (Fig. 1b) corresponded to local recoveries (within 10 km of the banding location), whereas (overall) recovery probability (Fig. 2) corresponded to both local and nonlocal recoveries. The lack of a strong spatial cross-correlation between overall recovery and survival, although HPI did affect survival, suggests that the two types of recoveries correspond to different processes. Indeed, nonlocal recoveries mostly occur in a different, southern area, where woodcocks migrate to when the weather is harsh (G. Péron, Y. Ferrand, F. Gossmann, C. Bastat, M. Guenezan, and O. Gimenez, *unpublished data*). Fig. 2 might thereby indicate a spatial pattern in the propensity to migrate during severe winters. However, caution is needed with this interpretation, given the large standard deviation of the posterior distribution of recovery probability (Appendix C: Fig. C2).

General applicability and interest of the method

The method is based on the assumption that the location at banding is a relevant explanatory variable (Royle and Dubovsky 2001, Doherty et al. 2002). In woodcocks, we can safely assume that the banding location lies in the area where an individual will spend most of its winters (Gossmann et al. 1994).

The main advantage of the method is that there are no a priori hypotheses, either on the factors at stake in the variation in survival, or on the way survival should vary in space. Indeed, many exploited species, from seafood (Leaf et al. 2007) to bushmeat (Mockrin 2010), are

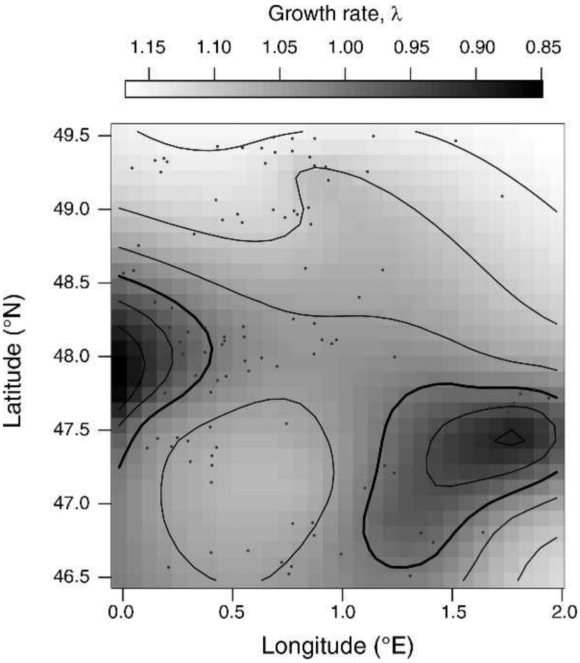

FIG. 3. Spatial variation in mean population growth rate, λ (averaged over years). Dots indicate banding locations with respect to latitude and longitude. The bold line represents the limit between sinks and sources ($\lambda = 1$). Isolines correspond to the grayscale tick marks in the key. A corresponding map of standard deviation is provided in Appendix C: Fig. C3.

typically difficult to monitor, and sometimes little is known about their habitat requirements and local sustainable yield. These species nevertheless often constitute important economic or livelihood enhancement resources, and capture–recovery data can sometimes be easily obtained, taking advantage of the exploitation. Decision-makers could then use the results of spatial survival analyses to target management actions: e.g., set limitations to exploitation in the parts of the range where survival is found to be unsustainably low, and/or use the variation in survival to refine knowledge about habitat requirements. High-survival areas can also act as sources that refill exploitation areas with dispersing offspring (Pulliam 1988, Novaro et al. 2000), and thereby deserve targeted management, such as enhancing their connectivity.

Although the objectives are similar, our spatial regression model is technically different from the conditional autoregressive (CAR) model of survival probability (Royle and Dubovsky 2001, Saracco et al. 2010). Differences in methodology that may impact on biological inference are as follows. (1) Smoothing is data driven in P-spline models, whereas CAR models require that the resolution of the autocorrelation is determined a priori by fixing the cell size of the overlying grid. (2) CAR models may be more sensitive to data scarcity (cells with no direct neighbor). (3) In CAR models, a single parameter (σ_ϕ in Saracco et al. 2010) measures the magnitude of spatial variation, whereas in P-spline models the smoothing parameter λ is more difficult to interpret. Kriging (e.g., Ruppert et al. 2003:242 ff.) is a third methodological option for performing a bivariate nonparametric regression.

Whatever the method used, it can often be interesting to first account for all previously known sources of variation in survival, and then use the nonparametric spatial regression approach to explore the structure of the remaining variation and search for previously overlooked explanatory variables. This is the procedure that we followed when fitting model 2. Results from this model suggested that a substantial part of the spatial variation was not explained by HPI (because the model selection procedure for model 2 favored the model with spatial structure in addition to the effect of HPI). This approach, although seductive from a biological point of view (as it can be extended to include other covariates such as habitat features), presented several drawbacks. First, we suspect that because HPI was not corrected for spatial variation in reporting rate (the probability that hunters report bands), its variation may have been a buffered version of the variation in actual hunting pressure. Second, as recently highlighted by Hodges and Reich (2010), the semiparametric formulation of model 2 renders this model sensitive to potential colinearity between the fixed effect of HPI and the spatial structure of the remaining variation.

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APPENDIX A

Nonparametric and semiparametric spatial regression of survival probability index (*Ecological Archives* E092-141-A1).

APPENDIX B

Capture–recapture–recovery models for the French-wintering Woodcock population index (*Ecological Archives* E092-141-A2).

APPENDIX C

Standard deviation from the posterior distribution of the survival probability, hunting pressure index, recovery probability, and growth rate index (*Ecological Archives* E092-141-A3).

APPENDIX D

Spatial variation in survival after removing the effect of hunting pressure index (*Ecological Archives* E092-141-A4).