Modeling spatial variation in avian survival and residency probabilities

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Abstract. The importance of understanding spatial variation in processes driving animal population dynamics is widely recognized. Yet little attention has been paid to spatial modeling of vital rates. Here we describe a hierarchical spatial autoregressive model to provide spatially explicit year-specific estimates of apparent survival (ϕ) and residency (π) probabilities from capture–recapture data. We apply the model to data collected on a declining bird species, Wood Thrush (*Hylocichla mustelina*), as part of a broad-scale bird-banding network, the Monitoring Avian Productivity and Survivorship (MAPS) program. The Wood Thrush analysis showed variability in both ϕ and π among years and across space. Spatial heterogeneity in residency probability was particularly striking, suggesting the importance of understanding the role of transients in local populations. We found broad-scale spatial patterning in Wood Thrush ϕ and π that lend insight into population trends and can direct conservation and research. The spatial model developed here represents a significant advance over approaches to investigating spatial pattern in vital rates that aggregate data at coarse spatial scales and do not explicitly incorporate spatial information in the model. Further development and application of hierarchical capture–recapture models offers the opportunity to more fully investigate spatiotemporal variation in the processes that drive population changes.

Key words: capture–recapture; CAR model; Cormack-Jolly-Seber; Hylocichla mustelina; MAPS program; mist netting; residency; spatial autoregressive model; spatial ecology; survival estimation; transient model; Wood Thrush.

INTRODUCTION

Capture–recapture models are commonly used to estimate vital rates of animal populations, particularly survival (Sandercock 2006). The general capture–recapture model used to study survival is the Cormack-Jolly-Seber (CJS) model (Lebreton et al. 1992), which provides estimates of *apparent* survival probability; i.e., the probability that an individual survives and remains in the sampled population. Estimates of apparent survival probability deriving from these models can often be biased low for vagile animal populations, such as birds, where nonresident individuals (e.g., passage migrants, dispersing birds, "floaters" [sensu Brown 1969]) may make up a large proportion of the capture–recapture sample. These nonresidents, collectively referred to as "transients" in the literature, include all individuals that have zero probability of being alive and in the population on sampling occasions subsequent to their initial capture (Pradel et al. 1997). Modifications of the CJS model have been developed to provide apparent survival rate estimates that are closer to true survival rates of residents (Pradel et al. 1997, Nott and

DeSante 2002, Hines et al. 2003). There is also intrinsic ecological interest in estimating proportions of residents and transients in local populations; however, little attention has been given to this subject.

Spatial modeling of capture–recapture data has also received little attention. Most studies that have considered "spatial effects" on survival have been within a metapopulation (i.e., discrete subpopulation) context (e.g., Hokit and Branch 2003, Ozugal et al. 2006) or have compared survival rates among broad contiguous regions (e.g., Saracco et al. 2008). Explicit incorporation of spatial effects into capture–recapture models would facilitate identification of scales of spatial pattern in demographic processes and lend insight into drivers of population changes. Furthermore, capture–recapture models are notoriously "data-hungry"; spatial models can improve precision of estimates of demographic parameters in cases where data from individual study areas are sparse by leveraging the spatial relatedness in parameter estimates of adjoining study locations (Ghosh and Rao 1994).

Here we describe a hierarchical model for producing spatially explicit year-specific estimates of apparent survival and residency probabilities from capture–recapture data. The model adapts the state–space formulation of the CJS model described by Royle (2007) and further by Royle and Dorazio (2008). We apply the model to capture–recapture data for a

declining bird species, Wood Thrush (*Hylocichla muste-lina*), that were collected as part of a broad-scale constant-effort mist netting program, the Monitoring Avian Productivity and Survivorship (MAPS) program (DeSante and Kaschube 2007).

THE MODEL

We adopted a hierarchical formulation of the "transient" CJS model (Pradel et al. 1997) based on $i = 1, \ldots, N$ individual encounter histories, $j = 1, \ldots, M$ sampling locations, and $t = 1, \ldots, T$ sampling occasions (Royle and Dorazio 2008: Chapter 11). Because CJS models are conditional on first capture, we distinguish time of first capture for individual i as $t = f_i$. We developed the model in terms of two latent state variables, residency state, $R(i, j, t)$, and "alive" state, $z(i, j, t)$; and two observed variables, "predetermined" residency state, $r(i, j, t)$, and the observed alive (i.e., encountered) state, $y(i, j, t)$, which are conditional on $R(i, j, t)$ and $z(i, j, t)$, respectively.

We let $R(i, j, t) = 1$ for individuals that are resident in the sampled population and $R(i, j, t) = 0$ for nonresidents (i.e., transients). We modeled $R(i, j, t)$ as a Bernoulli random variable:

$$R(i,j,t) \sim \text{Bern}(\pi_{ijf_i})$$

where π_{ijf_i} is the probability that individual i at location j and newly captured at time f_i is a resident. Although we typically cannot observe $R(i, j, t)$ directly, we can often "predetermine" some individuals as residents based on supplementary data. For example, whenever multiple subsamples are collected within primary sampling occasions (as in "robust design" studies; Pollock et al. 1990), individuals captured in multiple subsamples might be considered a priori to be residents (Nott and DeSante 2002, Hines et al. 2003). We can denote these predetermined residents with an indicator variable, $r(i, j, t)$, such that $r(i, j, t) = 1$ for predetermined residents, and $r(i, j, t) = 0$ otherwise. We can express the relationship between $r(i, j, t)$ and true residency, $R(i, j, t)$, as

$$r(i,j,t) \,|\, R(i,j,t) \sim \text{Bern}[R(i,j,t)\rho_{ijf_i}]$$

where ρ_{ijf_i} is the probability of predetermining an individual to be a resident. This model admits the assumption that the probability of identifying a nonresident [$R(i, j, t) = 0$] as a predetermined resident [$r(i, j, t) = 1$] is 0. Conversely, the probability of assigning a resident [$R(i, j, t) = 1$] to be a predetermined resident [$r(i, j, t) = 1$] is ρ_{ijf_i}. While ρ_{ijf_i} is a nuisance parameter, it is needed to express the relationship between observations $r(i, j, t)$ and parameters that are directly relevant (see below), which is done by use of the latent variables $R(i, j, t)$.

We describe the survival process in terms of an individual's "alive state," $z(i, j, t)$, where $z(i, j, t) = 1$ for individuals, i, that are alive and available to be encountered at site j and time t, and $z(i, j, t) = 0$

otherwise. We define the model for $z(i, j, t)$ as

$$z(i,j,t) \,|\, z(i,j,t-1) \sim \text{Bern}[R(i,j,t)z(i,j,t-1)\phi_{ijt-1}].$$

That is, the alive state of a resident [$R(i, j, t) = 1$] that was alive and in the population on the previous sampling occasion [$z(i, j, t-1) = 1$] is a Bernoulli random variable with success (i.e., survival) probability ϕ_{ijt-1}. An individual that was not alive and in the population on the previous sampling occasion [$z(i, j, t-1) = 0$] or that is not a resident [$R(i, j, t) = 0$] has alive state $z(i, j, t) = 0$ with probability 1. Note that the model is conditional on time of first capture, f_i, such that $z(i, j, f_i) = 1$ with probability 1.

The observations, $y(i, j, t)$, describe whether individual i at location j is encountered on sampling occasion t; $y(i, j, t) = 1$ if individual i is encountered and $y(i, j, t) = 0$ if it is not. We modeled $y(i, j, t)$ conditional on $z(i, j, t)$, such that:

$$y(i,j,t) \,|\, z(i,j,t) \sim \text{Bern}[z(i,j,t)p_{ijt}]$$

where p_{ijt} represents recapture probability. Thus, if $z(i, j, t) = 0$ then $y(i, j, t) = 0$ with probability 1; otherwise $y(i, j, t)$ is a Bernoulli trial with success probability p_{ijt}.

Based on this individual-level formulation of the CJS model, we used logit-linear models to model the two population parameters ϕ_{ijt} and π_{ijt}. For survival we assume that survival of individual i captured at location j during year t only depends on location and year according to

$$\text{logit}(\phi_{ijt}) = \mu_t + u_j$$

and, for residency probability,

$$\text{logit}(\pi_{ijt}) = \alpha_t + v_j$$

where ϕ_{ijt} is survival probability for individual i at location j between occasion t and $t + 1$, and π_{ijt} is residency probability for individual i at location j on occasion t; μ_t and α_t are their respective year-specific means; and u_j and v_j are zero-mean random effects assumed to be spatially autocorrelated.

Spatial dependence in u_j and v_j could be parameterized a number of ways. An efficient class of spatial models that has seen recent widespread use in ecology are conditional autoregressive (CAR) models (e.g., He and Sun 2000, Lichstein et al. 2002, Thogmartin et al. 2004, Webster et al. 2008). The general CAR model relates elements of a vector of random effects [e.g., for ϕ the spatial effects are $\mathbf{u} = (u_1, \ldots, u_M)$] to nearby values in the conditional mean. Here we consider the intrinsic version of the CAR model (Besag et al. 1991) for u_j and v_j:

$$u_j \,|\, \mathbf{u}_{-j} = \text{Norm}\left(\frac{1}{n_j}\sum_{k \in \mathbf{N}_j} u_k, \sigma_\phi^2/n_j\right)$$

and

PLATE 1. Wood Thrush (*Hylocichla mustelina*) banded as part of broad-scale bird monitoring efforts. Photo credit: J. F. Saracco.

$$v_j \mid \mathbf{v}_{-j} = \text{Norm}\left(\frac{1}{n_j}\sum_{k \in \mathbf{N}_j} v_k, \sigma_\pi^2/n_j\right)$$

where $\mathbf{N}_j$ denotes the neighborhood of spatial location j, which is the collection of identities of neighboring locations, and n_j is the number of neighbors of location j; i.e., $n_j = \dim(\mathbf{N}_j)$. CAR models are ideally suited to situations in which space is inherently discrete (e.g., geopolitical units). However, a continuous geographic region can also be discretized into contiguous "strata" by overlaying a regular grid. In such cases, neighborhoods are typically defined as "rook's" (four neighbors in cardinal directions) or "queen's" (cardinal directions plus diagonals) neighborhoods.

Because ϕ_{ijt} and π_{ijt} cannot be completely observed, we had to also define models for the two nuisance parameters, ρ_{ijt}, the probability of predetermining an individual to be a resident, and p_{ijt}, the encounter probability. As for ϕ_{ijt} and π_{ijt}, we modeled these parameters using logit-linear links. We did not include spatial effects, however, in the models for ρ_{ijt} and p_{ijt}.

EXAMPLE: WOOD THRUSH

We applied the model to data for Wood Thrush (*Hylocichla mustelina*) collected as part of the Monitoring Avian Productivity and Survivorship (MAPS) program (see Plate 1). Although Wood Thrush is a common breeding forest bird of eastern and central North America, it has declined over the past 40 years and is of high conservation concern (Rich et al. 2004, Sauer et al. 2007). The MAPS program is a cooperative network of nearly 500 constant-effort mist-netting stations operated across North America each summer; it provides demographic data for >180 landbird species (DeSante and Kaschube 2007). Similar programs exist

in Europe, where they are central components of national and international bird-monitoring efforts (Peach et al. 2004, Robinson et al. 2009).

Details of MAPS data collection are described in DeSante and Kaschube (2007) and references therein. Briefly, a mist net array (typically ten 12×2.5 m nets) is operated at each station (approximately 20 ha) on six to nine days per year. Although stations drop out and enter the program each year, many are operated for long time spans (e.g., 227 stations [nearly 25%] have operated for ≥ 10 yr). Unbanded birds captured during mist-netting operations are identified to species, age, and (if possible) sex (Pyle 1997); and are banded with uniquely numbered metal bands issued by the USGS Bird Banding Laboratory. Band numbers of recaptures are recorded.
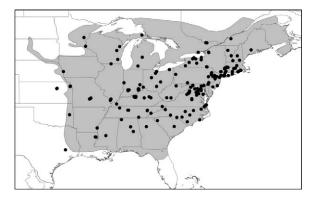

FIG. 1. Locations of 179 Monitoring Avian Productivity and Survivorship (MAPS) stations operated between 1992 and 2003 included in the analysis of Wood Thrush (*Hylocichla mustelina*) capture–recapture data. Breeding range (based on Ridgely et al. [2007]) is indicated by shaded area; note that several MAPS stations where the species regularly bred fell outside of that range and were also included in the analysis.
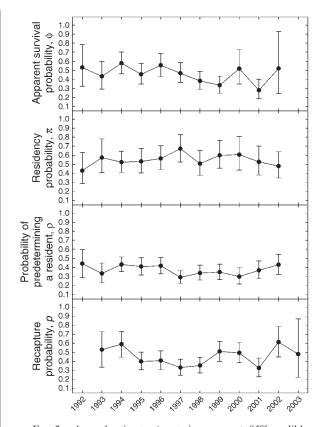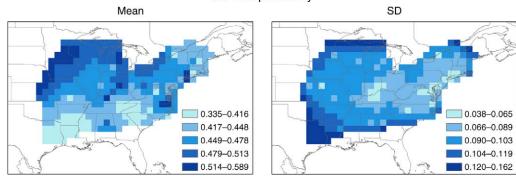
Reports

FIG. 2. Annual estimates (posterior means ± 95% credible intervals) of apparent survival probability, residency probability, probability of predetermining a resident, and recapture probability for Wood Thrush (*Hylocichla mustelina*) capture–recapture data collected between 1992 and 2003 as part of the Monitoring Avian Productivity and Survivorship (MAPS) program.

We included capture–recapture data from 1992–2003 on 6241 adult Wood Thrush banded at 179 MAPS stations where the species was considered to be a regular breeder (Fig. 1). We identified 1282 individuals as predetermined residents [i.e., $r(i, j, t) = 1$] based on multiple captures >6 days apart in the year that they were banded. We stratified the study region at the scale of 1° (latitude and longitude) grid cells; i.e., data were pooled across stations at the scale of 1° blocks for spatial models of ϕ and π. This scale of resolution represented a compromise between excessive computation (too many grid cells) and poor characterization of spatial structure. Exploratory studies of spatial pattern in count data suggested that this resolution would be adequate to detect broad-scale spatial pattern for this species (e.g., Jones et al. (2007) report a characteristic scale of autocorrelation in abundance of approximately 400 km). Spatial random effects were assigned intrinsic CAR priors (as defined in *The Model*). We defined N_j as a queen's neighborhood, such that each 1° cell had a maximum of eight neighbors. Building on the general model described above, we included a "time-constant" covariate for the model for p at the scale of stations that

represented the mean number of times per year that individual adult Wood Thrushes were captured (Julliard 2004). This parameterization represents the hypothesis that recapture probability increases as individuals are captured more frequently at a station within a season. Alternative parameterizations of p not reported here (e.g., constant across stations or random grid effects) yielded similar results.
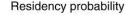
We used proper uniform prior distributions, $U(0,1)$, for ϕ, π, ρ, and p; Gamma(0.1, 0.1) priors for the conditional precision parameters, τ_ϕ, and τ_π (where $\tau = 1/\sigma^2$); and $\mathcal{N}(0, 0.001)$ as a prior for β, the slope parameter of the covariate on p. We obtained posterior distributions by sampling full conditional distributions using Markov chain Monte Carlo (MCMC) methods (Gilks et al. 1996), as implemented in WinBUGS (Spiegelhalter et al. 2003). Posteriors were based on 20 000 iterations of two chains after discarding the first 10 000 iterations and thinning by two. We provide model implementation detail, R (R Development Core Team 2007) and WinBUGS code, and data in the Supplement.

Posterior means for all model parameters were somewhat variable among years (Fig. 2). Annual point estimates of residency probability, π, ranged from 0.429 to 0.673, while estimates of survival probability, ϕ, ranged from 0.279 to 0.579. Spatial variation in π was particularly high compared to spatial variation in ϕ (Fig. 3). The relatively high spatial heterogeneity in π was reflected in high estimated standard deviation for this parameter (posterior mean $\sigma_\pi = 1.464$, 95% credible interval = 0.990, 2.058) compared to estimated standard deviation for survival probability (posterior mean $\sigma_\phi = 0.813$, 95% credible interval = 0.446, 1.263). Precision of estimates of ϕ and π was highest in regions with the highest density of MAPS stations that capture breeding Wood Thrushes and lowest along the periphery of the study region where stations were fewer and fewer neighboring grid cells were available to contribute information to predictions (Fig. 3). The slope parameter for the covariate in the model for p was positive, supporting the hypothesis that p is higher at stations where individual Wood Thrushes are caught more frequently within a season (mean $\beta = 2.235$, 95% credible interval = 1.689, 2.818).

Both ϕ and π showed broad-scale spatial pattern (Fig. 3). Survival probability was high along the Mid-Atlantic coast and in the Midwest and low in the Southeast and along an axis extending from the southwest to northeast extents of the breeding range. Residency probability was also high along the Mid-Atlantic coast, and in the Southeast and central Midwestern states; it was low along a southwest-northeast axis (also similar to survival) and near the western and northern periphery of the Wood Thrush breeding range. Although grid cells of high or low ϕ and π coincided in some cases, there was little evidence of spatial correlation between the two parameters (mean correlation of the MCMC chains for

Survival probability

Mean   SD

Residency probability

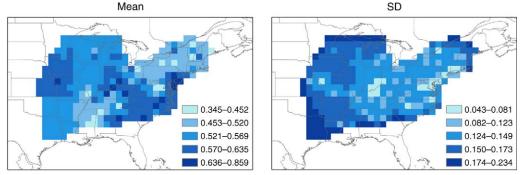Mean   SD

FIG. 3.   Mean and standard deviation (SD) of predicted apparent survival and residency probabilities, across all years, for adult Wood Thrush at the scale of 1° blocks. Estimates are based on the spatial model applied to capture histories of 6241 birds from 179 Monitoring Avian Productivity and Survivorship (MAPS) stations operated between 1992 and 2003.

time-averaged values of ϕ and $\pi = 0.007$; 95% credible interval $= -0.214, 0.234$).

DISCUSSION

Despite widespread recognition of the importance of spatial variation in the processes that drive animal population dynamics (Ozugal et al. 2006, Ciannelli et al. 2007), little attention has been paid to developing spatial capture–recapture models. A practical motivation for developing such models is that capture–recapture data are often sparse at local scales (e.g., at the scale of an individual MAPS station), preventing fine-scale parameter estimation (Royle et al. 2007). This is the motivation underlying classical "small-area estimation" (Ghosh and Rao 1994). With the spatial model described and implemented here, we achieve model-based aggregation of the data that allows spatially-explicit estimation of survival and residency probabilities at relatively fine spatial scales. By essentially "borrowing" information across space, the model also improves precision of estimates at the nominal scale of prediction (e.g., as compared to simple stratification approaches; Saracco et al. 2008).

The hierarchical model described here is parameterized to provide not just spatially-explicit, but also time-specific estimates of population parameters. Time-specific estimates of survival and residency probabilities

could also be achieved by applying maximum likelihood estimation techniques (e.g., as implemented in the software program TMSURVIV; Hines et al. 2003) to the classical formulation of the transient CJS model described by Pradel et al. (1997). However, as for the spatial problem, data sparseness can make estimation of large numbers of time-specific parameters using classical methods difficult. Under the hierarchical modeling framework, we can obtain year-specific estimates, and improve precision on these estimates, by combining all of the data within a single model that links data across years (and space) via explicit model structure. Random effects (e.g., to account for "heterogeneity") and covariates could be included in models to further improve the precision of parameter estimates (Royle 2007). It would even be possible to introduce time-varying site-specific or individual covariates with missing data (e.g., for missed sampling occasions or whenever an individual is not encountered), although this would require specification of prior distributions for covariates (Gimenez et al. 2009).

Most studies that have applied transient CJS models to capture–recapture data have been largely concerned with reducing negative bias in estimates of survival probability (Sandercock 2006). Little attention has been paid to modeling residency probability itself (Sasso et al. 2006, Whitaker et al. 2008), despite the clear links

between this parameter and other important population attributes such as abundance, dispersal, and population dynamics. The striking variation in residency probability revealed by our Wood Thrush analysis emphasizes the need for greater understanding of residency and transience patterns and the factors driving them. The model presented here, because it is parameterized explicitly in terms of residency probability, should facilitate such investigation. Nevertheless, we emphasize that the residency probability parameterized here is based on a model conditioned on first capture; as such, it is confounded with encounter probability in a complex fashion, rendering the parameter a mixture of both ecological and sampling processes. We can resolve this by exploiting an individual-based formulation of the Jolly-Seber model (Royle and Dorazio 2008: Chapter 10), in which residency status applies to the population of individuals alive in each year. This is ongoing research.

The Wood Thrush analysis revealed broad-scale spatial pattern in both survival and residency probabilities. These patterns lend insight into population dynamics and can direct conservation and research. For example, regions with low Wood Thrush apparent survival coincide with regions experiencing severe population declines (Sauer et al. 2007). Because mortality in long-distance migratory birds, such as Wood Thrush, may be largely effected via processes acting during the nonbreeding season (Sillett and Holmes 2002), conservation efforts for this species may be most effective if aimed at improving quality and quantity of stopover and winter habitat. The spatial pattern of residency probability draws attention to regions of potentially low quality habitat or limited habitat availability. Low residency probability in the Northeast and Appalachian Mountains could be caused by diminished habitat quality near latitudinal and elevational limits of the species' range (Roth et al. 1996). In the Midwest, where forest fragmentation has been severe (Riitters et al. 2002), low residency probability in some areas could reflect limited habitat availability or low habitat quality due to high nest predation or parasitism levels (Robinson et al. 1995). The introduction of environmental covariates into the model could test these hypotheses.

In addition to providing spatially explicit estimates of vital rates to inform conservation and management, further development and application of spatial capture–recapture models offers the opportunity to better investigate scales of autocorrelation in processes driving population changes. Historical approaches to investigating spatial and temporal pattern in vital rates are limited in their ability to provide such information. In the extreme, data sparseness can limit the resolution of investigations to such an extent that little or no information on spatial or temporal pattern is obtained, and the scales of parameter estimates may have little biological relevance. A modern approach to statistical

modeling and inference based on hierarchical models makes much more efficient use of sparse monitoring data and can provide a solid foundation for investigations of spatial and temporal variation in vital rates. Such an approach is applicable to a variety of existing broad-scale avian monitoring programs (e.g., Royle and Dubovsky 2001, Robinson et al. 2009), and we hope it will stimulate similar efforts for other taxa.

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Reports

SUPPLEMENT

Model implementation detail, R, and WinBUGS code, and data for the Wood Thrush example presented in the paper (*Ecological Archives* E091-126-S1).