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Journal of Ornithology

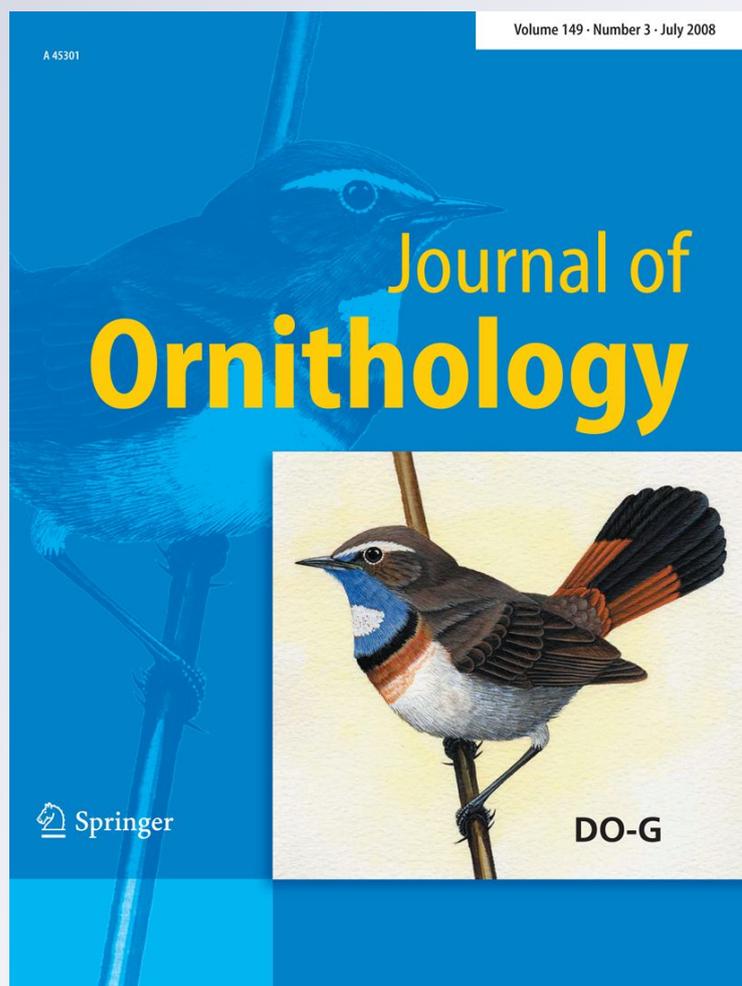
ISSN 2193-7192

Volume 152

Supplement 2

J Ornithol (2012) 152:469-476

DOI 10.1007/s10336-010-0565-1



 Springer

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Spatial modeling of survival and residency and application to the Monitoring Avian Productivity and Survivorship program

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Received: 13 September 2009/Revised: 14 July 2010/Accepted: 20 July 2010/Published online: 10 August 2010
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Abstract Broad-scale bird-ringing programs are a core component of national and international avian monitoring and research efforts. Despite rich spatial structure in data from these programs, little attention has been paid to spatial modeling of demographic rates. Here we implemented a Bayesian analysis of a hierarchical capture–recapture model to provide spatially explicit (2° blocks) and year-specific estimates of adult apparent survival (hereafter survival) and residency probabilities for Common Yellowthroat *Geothlypis trichas*, a bird species commonly captured as part of the Monitoring Avian Productivity and Survivorship (MAPS) program in North America. The model was based on a transient Cormack–Jolly–Seber model. We modeled spatial dependence in survival and residency with an intrinsic conditional autoregressive model and modeled capture probability with a random block-level effect. We modeled sex-effects on survival and residency probability, as well as on two nuisance parameters, capture probability and the probability of predetermining a bird to be a resident (based on multiple within-season captures). Inclusion of sex effects in the model illustrated how missing data are easily accommodated within the modeling framework. We found little evidence of temporal variation in survival or residency.

Males tended to have higher and less variable survival and residency probabilities than females. Capture probability and probability of predetermining residency were higher for males than for females. We found broad-scale spatial patterns in survival and residency. Spatial variation was higher for residency than for survival. Although the residency parameter in our model applies to the subset of the population that are newly ringed birds, clear spatial pattern and high spatial variation suggests that this parameter has important ecological relevance. Further development and application of hierarchical capture–recapture models to data from bird-ringing programs provides the opportunity to more thoroughly investigate spatial and temporal pattern in population processes and inform conservation.

Keywords Capture–recapture model · Common Yellowthroat · Conditional autoregressive model · *Geothlypis trichas* · Hierarchical spatial model · MAPS program

Introduction

Standardized broad-scale bird-ringing programs (or “bird-banding” programs, as they are known in North America) are a core component of national and international avian monitoring and research efforts (DeSante and Kaschube 2007; Robinson et al. 2009). Despite the rich spatial structure of the data collected by these programs (e.g., arrays of mist nets, clusters of monitoring stations, regional collections of stations) and widespread interest in understanding spatial patterns in population dynamics (e.g., Jones et al. 2007), little attention has been paid to spatial modeling of capture–recapture (or capture–recovery/resighting) data. Some level of spatial aggregation of capture–recapture data from

Communicated by M. Schaub.

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bird-ringing programs is necessary because data are too sparse at very fine scales (e.g., individual mist net locations) to provide meaningful information about population parameters of interest. However, stratification across broad regions (e.g., Saracco et al. 2008) is undesirable because it may obscure spatial pattern at scales most relevant to population dynamics. Explicit modeling of spatial structure allows aggregation of data at finer scales than would be possible if data were assumed to be spatially independent and enables relatively high-resolution inferences about population parameters. In addition, modeling spatial structure can also improve inference about covariate effects (e.g., weather, habitat) on population parameters (Lichstein et al. 2002, Webster et al. 2008).

Conditional autoregressive (CAR) models provide an efficient means of modeling spatial structure in a variety of data, and these models have seen widespread application to avian point count studies (e.g., Lichstein et al. 2002; Thogmartin et al. 2004; Webster et al. 2008). Recently, CAR models have been extended to capture–recapture data under a Bayesian hierarchical framework, and have been applied to bird-ringing data collected as part of the Monitoring Avian Productivity and Survivorship (MAPS) program in North America (Royle and Dorazio 2008, Ch. 11; Saracco et al. 2010). The Bayesian hierarchical approach, with Markov chain Monte Carlo (MCMC) implementation, affords several advantages over classical approaches, including (1) flexibility in modeling heterogeneity in responses at a variety of levels from individuals to groups using fixed or random effects and (2) ease of handling and modeling missing data (both response and predictor variables). Such advantages make these models especially well-suited to application to data from large-scale cooperative studies where missed sampling visits are common and where primary interest is often in understanding spatial pattern and heterogeneity in population parameters.

Here, we implement the hierarchical CAR model described in Saracco et al. (2010) to provide spatially and temporally specific estimates of adult apparent survival (hereafter ‘survival’) and residency probabilities for a bird species commonly captured as part of the MAPS program, Common Yellowthroat *Geothlypis trichas*. We interpret ‘residents’ here to be (at least attempted) local breeders, distinguishing them from ‘floaters’, dispersing birds, or passage migrants. We acknowledge that the residency parameter in our model is conditioned on first capture (it is based on the ‘transient’ Cormack–Jolly–Seber, CJS, model; Pradel et al. 1997) and thus applies to a subset of the larger population of interest; however, we believe that spatial modeling of this parameter can lend insight into demographic processes. We adapt the model of Saracco et al. (2010) to highlight how the basic modeling approach can accommodate simple random effects (here heterogeneity in

capture probability, p) and missing covariate data (here an indicator variable for ‘sex’).

Methods

MAPS data

We applied our analysis to capture–recapture data collected as part of the MAPS program between 1992 and 2003. The MAPS program is a cooperative network of constant-effort mist-netting stations operated across North America each summer; it provides demographic data for >180 landbird species (DeSante and Kaschube 2007). MAPS stations are broadly distributed across the continent (Fig. 1). Station densities are greatest near human population centers along coasts and south of Canada; more than half are located within natural protected areas.

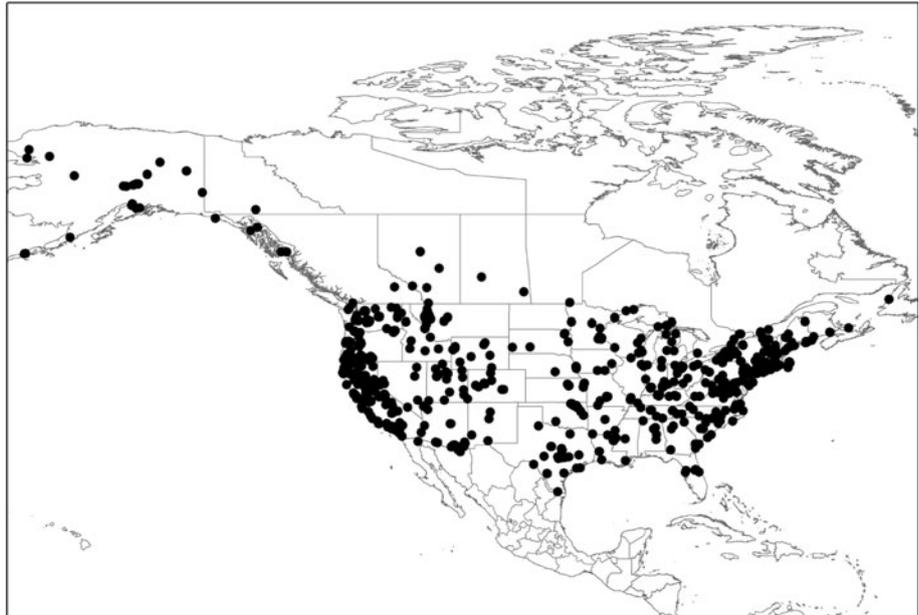
MAPS field protocol consists of operating an array of mist nets (typically ten 12 m × 2.5 m nets) at each station (approx. 20 ha) on 6–9 days each breeding season (May–August). Days of mist net operation are generally spaced at equal intervals, such that a given station is operated about once every 10 days. Unringed birds captured during mist-netting operations are identified to species, age, and (if possible) sex (Pyle 1997), and are ringed with uniquely numbered metal rings issued by the United States Geological Survey Bird Banding Laboratory. Ring numbers of recaptures are carefully recorded. DeSante and Kaschube (2007) provide additional details of data collection methods. The MAPS protocol was standardized in 1992, and 531 stations were operated between 1992 and 2003 for ≥ 4 years with sufficient effort to be useful for survival analyses. Most stations were operated for at least half of the 12 years.

We selected Common Yellowthroat as our target species for analysis. It is a migratory species typical of shrub land and wetland habitats (Guzy and Ritchison 1999). It breeds across most of the United States and Canada, and in parts of Mexico; and winters from the southern United States to northern South America. North American Breeding Bird Survey data suggest that this species is experiencing a small (about 0.5%/year) but significant long-term (40+ years) population decline. It is one of the most commonly captured species in the MAPS program with 12,110 adult birds ringed between 1992 and 2002 at 295 stations (multiple stations <1 km apart considered single stations) where it is a regular breeder. It is common in both eastern and western North America and shows large spatial variation in population trend (Sauer et al. 2008).

Data analysis

We aggregated MAPS capture–recapture data at the spatial scale of 2° blocks (hereafter ‘grid cells’). This scale

Fig. 1 Distribution of 760 Monitoring Avian Productivity and Survivorship (MAPS) stations operated between 1992 and 2003 (multiple stations <1 km apart considered one station)



allowed for relative computational efficiency and prevented inclusion of large numbers of grid cells without data when examining patterns across the program-wide (i.e., continental) scale. Encounter histories were summarized for each individual bird at the scale of the MAPS station (or multiple stations if <1 km apart) within these grid cells. Although multiple capture–recapture sessions were conducted at a MAPS station each year (described above), we collapsed capture histories to provide a single encounter indicator for each year. Following the ad hoc robust design transient model (Hines et al. 2003), we used multiple within-season encounters only to ‘predetermine’ some individuals as local breeding residents (see below).

We implemented the hierarchical model described in Saracco et al. (2010). Here we provide a brief description and modifications specific to the analysis presented here. We based models on $i = 1, \dots, N$ individuals, $j = 1, \dots, M$ grid cells, and $t = 1, \dots, T$ years. We modeled observations on the ‘residency’ and ‘alive’ states of individual birds, as well as for latent (unobserved) variables representing the true alive and residency states. We modeled observations of residency as a Bernoulli random variable, $r(i)$, conditional on the true (unobserved) residency state $R(i)$:

$$r(i)|R(i) \sim \text{Bern}(R(i)\rho_{iff_i}),$$

where ρ_{iff_i} is the probability of predetermining individual i being a resident at its MAPS station of capture in grid cell j in the year of its initial capture, denoted here by the subscript f_i . We assessed predetermined residency status based on within-season recapture data of individuals in their initial year of capture (i.e., the year they were ringed). We set $r(i) = 1$ (predetermined residents) for individuals captured on multiple days >6 days apart in their initial

year of capture and $r(i) = 0$ otherwise (Hines et al. 2003, Nott and DeSante 2002). In our analysis of Common Yellowthroats, the number of predetermined residents was 2,289 out of 12,110 individuals in the dataset (19%). We modeled the true residency state as:

$$R(i) \sim \text{Bern}(\pi_{iff_i}),$$

where π_{iff_i} is the probability that individual i at location j and time f_i is a resident. We let $R(i, j, t) = 1$ for individuals that are resident in the sampled population and $R(i, j, t) = 0$ for non-residents (i.e., transients).

We modeled annual observations of the alive state of individuals, $y(i, j, t)$, conditional on the true ‘alive state’ $z(i, j, t)$:

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

where p_{ijt} is the capture probability of individual i at its station of capture in grid cell j at time t . The alive state is defined such that $z(i, j, t) = 1$ denotes a marked individual that is alive and at its station of capture in grid cell j at time t , and $z(i, j, t) = 0$ indicates a marked individual not alive or available for sampling. Similarly, $y(i, j, t) = 1$ for individuals encountered at their station of capture in grid cell j in year t and $y(i, j, t) = 0$ for those not encountered. Thus, if $z(i, j, t) = 0$ then $y(i, j, t)$ is a Bernoulli trial with probability 0, while if $z(i, j, t) = 1$ then $y(i, j, t)$ is a Bernoulli trial with probability p_{ijt} . We modeled $z(i, j, t)$ conditional on $z(i, j, t - 1)$ as:

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

That is, an individual i that was a resident and present at its station of capture in grid cell j in the previous time period ($t - 1$) will be alive and available for sampling at its

station of capture in that grid cell in the current time period with probability ϕ_{ijt-1} , the survival probability. Note that because CJS models are conditional on first capture, we set $z(i, j, f_i) = 1$ with probability 1.

We developed the spatial model in terms of the two population parameters of interest, survival probability, ϕ_{ijt} , and residency probability, π_{ijt} . We modeled survival and residency probabilities of individual i in grid cell j during year t as dependent on location, sex, and year according to:

$$\text{logit}(\phi_{ijt}) = \mu_t + a_t \times \text{sex}_i + u_j$$

and

$$\text{logit}(\pi_{ijt}) = \alpha_t + b_t \times \text{sex}_i + v_j,$$

where ϕ_{ijt} is survival probability for individual i at its station of capture in grid cell j between occasion t and $t + 1$, and π_{ijt} is residency probability for individual i at its station of capture in grid cell j on occasion t . The parameters μ_t and α_t represent the year-specific means on the logit scale for female survival (ϕ_t) and female residency (π_t), respectively; a_t and b_t are year-specific effects of an indicator variable sex_i , where $\text{sex} = 1$ for males and 0 for females; and u_j and v_j are spatially autocorrelated random effects parameterized according to an intrinsic CAR model (Besag et al. 1991; Saracco et al. 2010). The intrinsic CAR model estimates j grid-cell random effects conditional on neighboring grid cells according to:

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

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

where \mathcal{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., $n_j = \text{dim}(\mathcal{N}_j)$. We defined neighbors of individual grid cells based on a ‘queen’s’ neighborhood (cardinal directions plus diagonals). The intrinsic CAR model requires estimation of spatial heterogeneity for both u_j and v_j ; in the Bayesian framework, we estimate these as precision parameters, τ_ϕ and τ_π , which can be transformed to standard deviations according to $\sigma_\phi = 1/\sqrt{\tau_\phi}$ and $\sigma_\pi = 1/\sqrt{\tau_\pi}$.

We also defined linear models for the nuisance parameters, p and ρ . Although capture probability, p , can be modeled as a function of covariates (e.g., Julliard 2004; Saracco et al. 2008, 2010), it is generally difficult to quantify factors that affect capture probability independently from population parameters. Here we modeled p as varying by sex and grid cell:

$$\text{logit}(p_{ij}) = \eta + c \times \text{sex}_i + \varepsilon_j,$$

where η is the overall mean, c is the linear parameter for the sex effect, and ε_j is a grid-cell level random effect assumed to be drawn from a normal distribution with mean zero and precision τ_p . We expected capture probability to vary by sex because captures (of sexed individuals; see below) were skewed toward males (60% of individual adults) and because males may be more active during the breeding season (when females on nests). We modeled p as time-constant, as previous analyses of these data showed little support for time dependence in p and relatively consistent year-specific estimates of p (DeSante and Kaschube 2007; Saracco, unpublished data). These results are expected because effort among years at a given MAPS station is typically very consistent (as dictated by the field protocol). Because the probability of predetermining a resident (i.e., catching an individual multiple times in a season) also likely reflects sex-specific differences in behavior, we also included a time-constant sex effect on ρ :

$$\text{logit}(\rho_i) = \beta + d \times \text{sex}_i$$

As described above, we included linear (on logit scale) ‘sex’ effects in the models for both the population parameters (ϕ and π) and the nuisance parameters (p and ρ). Although sex is easily determined for yellowthroats because of strong sexual plumage dimorphism (and to a lesser degree breeding condition and size dimorphism), sex data were not recorded for a small number of individuals (75 or 0.6% of all individuals in the analysis). In order to include all individuals in analyses (not just those sexed), we treated sex as a random, rather than fixed, variable. Specifically, we modeled sex as:

$$\text{sex}_i \sim \text{Bern}(\psi),$$

where ψ is the probability of an individual being a male.

We implemented a Bayesian analysis of the model. We used proper uniform prior distributions, $U(0, 1)$, for the inverse-logit transformed intercepts from the logit-linear models and for ψ ; $\text{Gamma}(0.001, 0.001)$ priors for precision parameters τ_ϕ , τ_π , and τ_p ; and $\text{Norm}(0, 0.1)$ as priors for the coefficients for sex effects, a_t , b_t , c , and d . 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) via the R2WinBUGS package (Sturtz et al. 2005) in R (R Development Core Team 2007). Posteriors were based on 20,000 iterations of two chains after discarding the first 4,000 iterations and thinning by two. We assessed convergence by examining trace and density plots of posterior distributions of the two chains and from values of the potential scale reduction factor, \hat{R} , which were <1.1 for all model parameters (Gelman et al. 2003).

Results

Apparent survival probability, ϕ , for adult Common Yellowthroats tended to be higher for males than for females [posterior mean across years (95% credible interval) = 0.494 (0.406–0.625) for males; 0.463 (0.295–0.639) for females] and was also more consistent among years for males than for females (range in annual means: 0.460–0.573 for males; 0.344–0.557 for females; Fig. 2). Residency probability showed a similar pattern (i.e., males tending to have higher and more consistent estimates) with mean (95% credible interval) of 0.515 (0.395–0.657) for males compared to 0.486 (0.333–0.727) for females. The range of annual posterior means for π was 0.459–0.587 for males compared to 0.400–0.666 for females (Fig. 2). For both ϕ

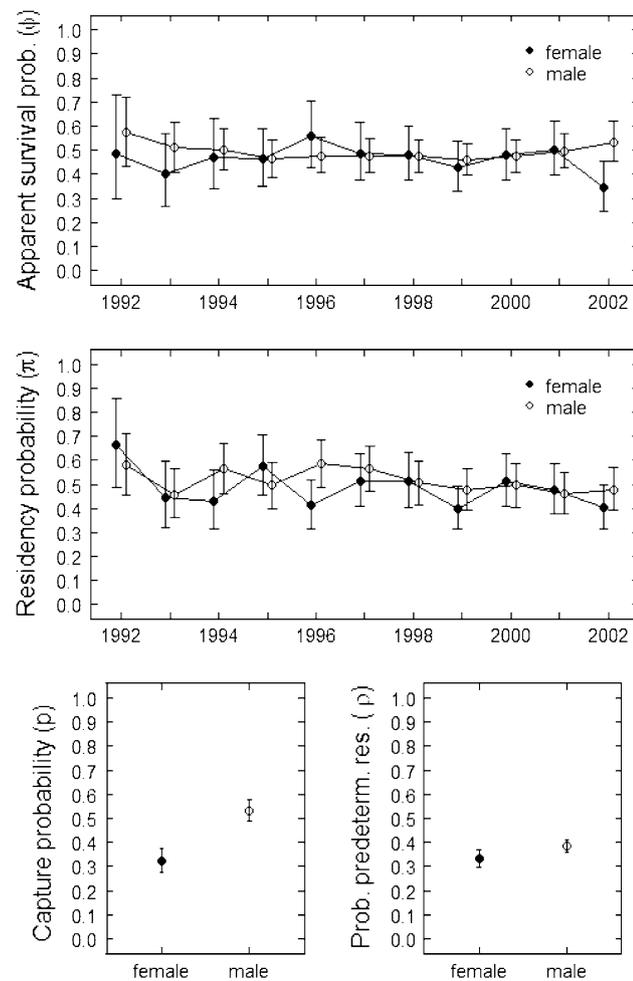


Fig. 2 Posterior means and 95% credible intervals for parameters from the hierarchical spatial model applied to 12-year (1992–2003) capture histories of 12,110 adult Common Yellowthroats (*Geothlypis trichas*) from 295 Monitoring Avian Productivity and Survivorship (MAPS) stations (multiple stations <1 km apart considered one station). Parameters are summarized by sex and include: annual apparent survival probability (ϕ ; top), annual residency probability (π ; middle), capture probability (p ; bottom left), and probability of predetermining a resident (ρ ; bottom right)

and π , 95% credible intervals overlapped broadly among years. The greatest year-specific difference in ϕ between sexes was in 2002 (i.e., 2002–2003 survival), with the mean male survival 54% higher than female survival in that year [mean (95% credible interval) = 0.532 (0.452–0.619) for males; 0.344 (0.248–0.455) for females]. For π , the greatest year-specific difference was in 1996, when residency probability averaged 42% higher for males than for females [mean (95% credible interval) = 0.587 (0.489–0.686) for males; 0.412 (0.317–0.520) for females].

Mean capture probability, p , was 65% higher for males than for females [mean (95% credible interval) = 0.533 (0.488–0.578) for males; 0.323 (0.275–0.376) for females; Fig. 2]. The probability of predetermining a resident, ρ , was just slightly (15%) higher for males than for females [mean (95% credible interval) = 0.384 (0.359–0.409) for males; 0.332 (0.297–0.368) for females; Fig. 2].

Common Yellowthroats showed broad-scale spatial pattern in both ϕ and π (Fig. 3). The mean predicted ϕ tended to be highest in the west and northeast and lowest in the southeastern coastal plain. In contrast, π tended to be highest in the southeast and northwest and lowest in the southwest and northeast. Spatial variation was much higher for residency (mean $\sigma_\pi = 1.728$; 95% credible interval: 1.322–2.240) than for survival (mean $\sigma_\phi = 0.552$; 95% credible interval: 0.356–0.802) probability. Spatial variation in capture probability was relatively low (mean $\sigma_p = 0.409$; 95% credible interval: 0.232–0.609).

Discussion

Data from standardized bird-ringing programs offer an ideal opportunity for developing spatial models that can lend insight into the scales of population processes and resulting patterns in distribution, abundance, and trends. Here we describe a hierarchical version of the ad hoc robust design transient model (Pradel et al. 1997; Hines et al. 2003) that allows spatial dependence in survival and residency parameters through inclusion of conditional autoregressive terms (Royle and Dorazio 2008, Ch. 11; Saracco et al. 2010). We illustrate the model with an application to data on Common Yellowthroat collected as part of the Monitoring Avian Productivity and Survivorship (MAPS) program in North America, but the basic approach could be applied to constant effort schemes across Europe (Robinson et al. 2009) and elsewhere as standardized mist-netting programs expand to other regions and continents (e.g., DeSante et al. 2005).

Our general modeling approach affords several advantages over historical approaches to analyzing spatial capture–recapture data, such as those derived from ringing programs (e.g., DeSante and Kaschube 2007; Saracco et al.

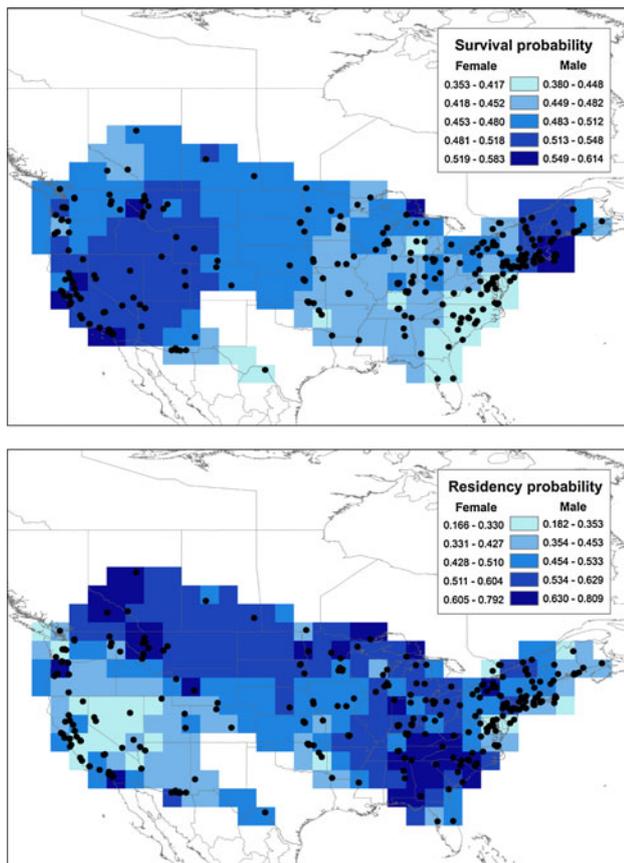


Fig. 3 Mean predicted apparent survival and residency probabilities for adult male and female Common Yellowthroats (*Geothlypis trichas*) derived from the hierarchical spatial model applied to data from the Monitoring Avian Productivity and Survivorship program (1992–2003). Data for 12,110 individuals from 295 MAPS stations (black dots; multiple stations <1 km apart considered one station) were included in the analysis. Predicted values represent posterior means averaged across all years plus spatial effects at the scale of 2° blocks

2008). capture–recapture data are often sparse at local scales, preventing fine-scale parameter estimation (Royle et al. 2007). By modeling spatial dependence using the CAR model, we are able to stratify data at relatively fine scales and improve precision of parameter estimates at those scales. Our choice of spatial resolution for the present analysis (2° blocks) was motivated in part by computational efficiency, but also by a desire to avoid including large numbers of grid cells without MAPS stations. However, some spatial gaps in data were unavoidable given the distribution of stations, which was not design-based (at least at the program-wide scale; Fig. 1). Finer scale stratification would be possible in cases where interest is in patterns across smaller regions, provided station densities are high.

By estimating population parameters at relatively fine scales, scales of population processes can be better

understood, and appropriate regions for conservation more easily identified. For example, patterns in survival and residency revealed by our analysis of the yellowthroat data were not always consistent with boundaries of existing conservation units (e.g., Bird Conservation Regions). In some areas there appeared to be spatial gradients across individual regions [e.g., survival from north (high) to south (low) along the Appalachian Mountains]; in others, patterns were broad, encompassing several regions (e.g., survival high across much of the western United States). At the broadest scales, spatial structure of survival and residency might reflect regional variation in major terrestrial ecosystem types, climate, migratory strategies, or overwintering areas (Awise and Ball 1992; Guzy and Ritchison 1999; Lovette et al. 2003; Pagenkopp et al. 2008). For example, southern populations may be relatively sedentary, while migratory populations from eastern and western portions of the breeding range may overwinter in different areas. Eastern migrants may overwinter largely in eastern and southern parts of the winter range, while western migrants may overwinter in the north and west (Lovette et al. 2003). At finer scales, spatial variation in population parameters may reflect effects of spatially explicit (e.g., landscape scale) environmental variables. Inclusion of such variables in models as covariates could further improve parameter estimates and understanding of factors driving demographic rates.

The spatial pattern of Common Yellowthroat survival (with the possible exception to the New England–mid-Atlantic coast) is remarkably consistent with spatially explicit estimates of long-term (1966–2003) population trend for this species (Sauer et al. 2008), highlighting the utility of analyses such as these for identifying proximate demographic causes of spatial variation in population trends (see also Saracco et al. 2010). The scale of spatial pattern for survival was smaller and more heterogeneous in the east compared to the west (in part possibly due to differences in station coverage) and populations tended to have lower survival in the east where populations tend to be declining (especially southeast) than in the west where they seem to be mostly increasing.

The spatial pattern in yellowthroat residency contrasted somewhat with the pattern of survival. Regions where survival probability was high and residency probability was low (e.g., due to large numbers of ‘floaters’; Brown 1969) could suggest some combination of good non-breeding season conditions and breeding habitat limitation. In contrast, areas with low survival and high residency could suggest areas where individuals experienced low survival due to poor non-breeding season conditions, with subsequent ample opportunity for new territory establishment (and thus few floaters).

In addition to contrasting spatial patterns, yellowthroat residency probability showed greater spatial heterogeneity

than did yellowthroat survival probability. This relatively high spatial variance in residency probability is in accord with results for other species (Saracco et al. 2010, and unpublished data), and suggests an important ecological role for this parameter. Although we highlight the potential role of residency based on our results, we acknowledge that residency probability, as parameterized here, is based on a CJS model, and as such is conditioned on first capture, confounding its interpretation to some degree because of its representation of a mixture of both ecological and sampling processes. We are currently investigating the use of an alternative model based on an individual-based formulation of the Jolly–Seber (JS) model (Royle and Dorazio 2008, Ch. 10) to address this problem.

Additional advantages of the hierarchical Bayesian approach taken here include the ability to easily handle missing data with prior distributions, improved ability to provide year-specific (as well as spatially explicit) estimates of population parameters, and the easy accommodation of covariates and random effects (Gimenez et al. 2009; Saracco et al. 2010). Our model for Common Yellowthroat suggested relatively weak annual variation and sex differences in survival and residency probabilities. However, both residency and survival probabilities tended to be higher and more consistent for males, a pattern that could result from sex-specific differences in non-breeding season habitat use (Ornat and Greenberg 1990) if males exclude females from higher quality and less variable habitats (e.g., Marra 2000). Higher male survival could also reflect higher between-year fidelity to breeding territories. Sex-specific differences in capture probability and the probability of predetermining a bird to be a resident were much stronger, with males more likely to be recaptured within (necessary to predetermine a bird as a resident) and between years. This is likely due to females being less active and more closely tied to the nest site for incubation and brooding (Guzy and Ritchison 1999).

Our application of the hierarchical model described here illustrates some of the advantages of hierarchical models for analyzing broad-scale capture–recapture data. Further development of these models will enable more thorough investigation of the spatial and temporal scales at which population processes operate, providing important insights into population dynamics to direct future research and guide conservation efforts.

Acknowledgments This work was supported by the National Fish and Wildlife Foundation, The Institute for Bird Populations (IBP), and the United States Geological Survey. C. Francis and two anonymous reviewers provided comments that improved an earlier version of the manuscript. IBP staff biologists carefully vetted the MAPS data and D. Kaschube helped prepare data for analyses. We are indebted to the hundreds of MAPS station operators, field assistants, and interns that have contributed to the MAPS program. Any use of trade,

product, or firm names in this publication is for descriptive purposes only and does not imply endorsement by the U.S. Government. This is IBP Contribution No. 390.

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