

Annual survival estimation of migratory songbirds confounded by incomplete breeding site-fidelity: study designs that may help

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Abstract

Annual survival estimation of migratory songbirds confounded by incomplete breeding site-fidelity: study designs that may help.— Many species of bird exhibit varying degrees of site-fidelity to the previous year's territory or breeding area, a phenomenon we refer to as incomplete breeding site-fidelity. If the territory they occupy is located beyond the bounds of the study area or search area (i.e., they have emigrated from the study area), the bird will go undetected and is therefore indistinguishable from dead individuals in capture-mark-recapture studies. Differential emigration rates confound inferences regarding differences in survival between sexes and among species if apparent survival rates are used as estimates of true survival. Moreover, the bias introduced by using apparent survival rates for true survival rates can have profound effects on the predictions of population persistence through time, source/sink dynamics, and other aspects of life-history theory. We investigated four study design and analysis approaches that result in apparent survival estimates that are closer to true survival estimates. Our motivation for this research stemmed from a multi-year capture-recapture study of Prothonotary Warblers (*Protonotaria citrea*) on multiple study plots within a larger landscape of suitable breeding habitat where substantial inter-annual movements of marked individuals among neighboring study plots was documented. We wished to quantify the effects of this type of movement on annual survival estimation. The first two study designs we investigated involved marking birds in a core area and resighting them in the core as well as an area surrounding the core. For the first of these two designs, we demonstrated that as the resighting area surrounding the core gets progressively larger, and more "emigrants" are resighted, apparent survival estimates begin to approximate true survival rates (bias < 0.01). However, given observed inter-annual movements of birds, it is likely to be logistically impractical to resight birds on sufficiently large surrounding areas to minimize bias. Therefore, as an alternative protocol, we analyzed the data with subsets of three progressively larger areas surrounding the core. The data subsets provided four estimates of apparent survival that asymptotically approached true survival. This study design and analytical approach is likely to be logistically feasible in field settings and yields estimates of true survival unbiased (bias < 0.03) by incomplete breeding site-fidelity over a range of inter-annual territory movement patterns. The third approach we investigated used a robust design data collection and analysis approach. This approach resulted in estimates of survival that were unbiased (bias < 0.02), but were very imprecise and likely would not yield reliable estimates in field situations. The fourth approach utilized a fixed study area size, but modeled detection probability as a function of bird proximity to the study plot boundary (e.g., those birds closest to the edge are more likely to emigrate). This approach also resulted in estimates of survival that were unbiased (bias < 0.02), but because the individual covariates were normalized, the average capture probability was 0.50, and thus did not provide an accurate estimate of the true capture probability. Our results show that the core-area with surrounding resight-only can provide estimates of survival that are not biased by the effects of incomplete breeding site-fidelity.

Key words: Apparent survival, Site-fidelity, Dispersal, Emigration, Cormack-Jolly-Seber model, Migratory birds.

Resumen

Estimación de la supervivencia anual de aves canoras migratorias bajo el efecto de una fidelidad incompleta al área de reproducción: diseños de estudios que pueden resultar de utilidad.— Numerosas especies de aves presentan distintos grados de fidelidad al territorio o área de reproducción del año anterior, fenómeno que denominamos fidelidad incompleta al lugar de reproducción. Si el territorio que ocupan las aves está situado más allá del área de estudio o investigación (es decir, si las aves han emigrado del área de estudio), el ave no podrá ser detectada y, por consiguiente, en los estudios de captura–marcaje–recaptura, no podrá distinguirse de los individuos muertos. Si se emplean las tasas de supervivencia aparente como estimaciones de la supervivencia real, las tasas de emigración diferencial sesgan las distintas inferencias sobre variaciones en supervivencia entre sexos y entre especies. Además, el sesgo introducido por el empleo de tasas de supervivencia aparente en lugar de tasas de supervivencia real puede repercutir significativamente en las predicciones de la persistencia poblacional a través del tiempo, la dinámica de fuente/sumidero, y otros aspectos de la teoría sobre historias vitales. Investigamos cuatro enfoques de diseños de estudios y análisis que proporcionan estimaciones de supervivencia aparente más próximas a las estimaciones de supervivencia real. Esta investigación es fruto de un estudio multianual de captura–recaptura de reinitas cabecidoradas (*Protonotaria citrea*) en múltiples parcelas de estudio incluidas en un paisaje más amplio de hábitats de reproducción adecuados, en los que se documentaron los movimientos interanuales más importantes entre distintas parcelas de estudio adyacentes por parte de individuos marcados. Nuestro objetivo era cuantificar los efectos de este tipo de movimiento en la estimación de la supervivencia anual. Los dos primeros diseños de estudio que investigamos consistían en el marcaje de aves en un área central, para posteriormente volverlas a avistar, tanto en dicha área como en un área adyacente a la misma. Por lo que respecta al primero de estos dos diseños, demostramos que cuando el área de reavistaje que rodea al área central se va ampliando y el número de "emigrantes" reavistados aumenta, las estimaciones de supervivencia aparente empiezan a aproximarse a las tasas de supervivencia real (sesgo < 0,01). Sin embargo, teniendo en cuenta los movimientos interanuales de las aves observados, lo más probable es que, desde un punto de vista logístico, no resulte práctico reavistar aves en áreas adyacentes que sean lo suficientemente amplias como para minimizar el sesgo. Por consiguiente, como protocolo alternativo, analizamos los datos con subconjuntos de tres áreas adyacentes al área principal, que se iban ampliando de forma progresiva. Los subconjuntos de datos proporcionaron cuatro estimaciones de supervivencia aparente que abordaban asintóticamente la supervivencia real. Lo más probable es que, desde un punto de vista logístico, este diseño de estudio y enfoque analítico resulte viable en estudios de campo, además de producir estimaciones de supervivencia real no sesgadas (sesgo < 0,03) por fidelidad incompleta al área de reproducción en un rango de patrones de movimiento territorial interanual. El tercer enfoque que investigamos empleaba una serie de datos de un diseño robusto de toma de datos y un enfoque analítico. Este enfoque proporcionó estimaciones de supervivencia que, si bien no eran sesgadas (sesgo < 0,02), resultaban muy imprecisas, por lo que probablemente no proporcionarían estimaciones fiables en situaciones de campo. El cuarto enfoque utilizaba un tamaño de área de estudio fijo, pero modelaba la probabilidad de detección como una función de la proximidad de las aves al límite de la parcela de estudio (es decir, las aves situadas más cerca del borde presentan más probabilidades de emigrar). Este enfoque también produjo estimaciones de supervivencia no sesgadas (sesgo < 0,02), pero debido a que las covarianzas individuales se normalizaron, la probabilidad de captura media era de 0,50, por lo que no proporcionaba una estimación precisa de la probabilidad de captura real. Nuestros resultados demuestran que el hecho de combinar el área principal con áreas adyacentes dedicadas exclusivamente al reavistaje puede proporcionar estimaciones de supervivencia que no resulten sesgadas por los efectos de una fidelidad incompleta al área de reproducción.

Palabras clave: Supervivencia aparente, Fidelidad al área de reproducción, Dispersión, Emigración, Modelo de Cormack–Jolly–Seber, Aves migratorias.

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Introduction

Biologists are able to estimate annual survival rates for many species of migratory songbirds via traditional capture–mark–recapture methodology largely because many surviving individuals are faithful to the breeding (or wintering) area of the previous year. Birds are captured and marked during one breeding season and recaptured (typically, color-banded individuals are resighted) during subsequent breeding seasons. However, not all surviving individuals return to precisely the same breeding territory the following year, a phenomenon we refer to as incomplete breeding site–fidelity. If the territory they occupy in a subsequent year is located beyond the bounds of the study area, the bird will go undetected. Researchers usually cannot determine how many of these non–returning birds are dead and how many are alive somewhere outside the study area. This inability to distinguish between death and dispersal poses a problem for obtaining accurate survival rate estimates with potentially profound effects on the predictions of population persistence through time, source/sink dynamics, and other aspects of life–history theory and conservation ecology.

The effect of incomplete breeding site–fidelity on annual survival estimation using a Cormack–Jolly–Seber (CJS) model (Cormack, 1964; Jolly, 1965; Seber, 1965) has long been recognized; the survival parameter, ϕ , represents those birds that survive and remain on the study area (Lebreton et al., 1992). Hence, terms such as "apparent survival" and "local survival" are used to describe the survival parameter. The use of apparent survival estimates are clearly superior to simple return rates because a detection probability is incorporated (Lebreton et al., 1992; Martin et al., 1995). Furthermore, if the objective of a study is to compare demographic rates among different treatments, management options, habitats, or other factors, apparent survival is a meaningful parameter because it reflects the multiple ways in which the population may be affected by the factor in question (e.g., birds may have lower survival or abandon a treated area). Hypotheses regarding the effects of a particular treatment can still be tested as long as it is recognized that the response variable includes both mortality and permanent emigration from the study area (Marshall et al., 2000). However, if the study questions involve aspects of life–history theory, such as sex–specific survival or the costs of reproduction, then it is required that survival be estimated. If apparent survival estimates are used in these cases (i.e., as estimates of true survival) it must be assumed or demonstrated that permanent emigration does not occur. If permanent emigration does occur, then, by definition, apparent survival will underestimate true survival by some unknown amount and may vary among groups (among age/sex classes and/or species).

Recent studies of migratory songbirds have examined the degree to which apparent survival rate

estimates potentially underestimate true survival rates because of emigration from the study area (Cilimburg et al., 2002; M. R. Marshall, unpublished data), whereas others have begun to elucidate the ecological mechanisms explaining why individuals exhibit varying degrees of site–fidelity (Haas, 1998; Hoover, 2003). For example, Cilimburg et al. (2002) found that permanent emigration of Yellow Warblers (*Dendroica petechia*) from their study sites was common (30% of resighted birds were found outside their original study site in one year of the study), and survival probabilities increased by 0.07–0.23 with the inclusion of these capture events.

Our motivation for this study stemmed from a multi–year capture–recapture study of Prothonotary Warblers (*Protonotaria citrea*) on multiple study plots within a larger, homogenous, landscape of suitable breeding habitat (Wood, 1999). We (L. A. Wood, unpublished data) detected substantial inter–annual movements of marked individuals among neighboring study plots and found that these movements could have resulted in underestimates of true survival of 0.17 for males and 0.19 for females had these movements not been detected (M. R. Marshall, unpublished data). Underestimates of survival were greater for females than males because of more frequent and longer movements of females, a pattern expected given a female bias in between–year breeding site–fidelity (Clark et al., 1997), especially among females with lower reproductive success (Hoover, 2003).

These studies (Cilimburg et al., 2002; M. R. Marshall, unpublished data) serve as cautionary notes on the interpretation of apparent survival rate estimates (i.e., the bias introduced by emigration if apparent survival estimates were used as true survival rate estimates), but also highlight the fact that true survival rate estimation (often the parameter of interest when addressing predictions of population persistence through time, source/sink dynamics, and other aspects of life–history theory) will remain problematic until sampling designs and analytic approaches are developed that account for incomplete site–fidelity. The objectives of this study were to investigate, via simulations parameterized with empirical data, several study area designs and analytical approaches intended to reduce or eliminate the effect of incomplete site–fidelity on estimates of survival using a CJS model. Our goal was to identify study designs and methods of estimating annual survival for migratory songbirds that would provide estimates of true survival in the presence of incomplete breeding site–fidelity.

Study designs

Core with resight–only area I

The first study design we investigated consisted of a study site with a core area where birds were both marked and resighted in following years and a

surrounding resight-only area where marked individuals were resighted but no new individuals were marked (fig. 1). The motivation behind this study design was to centralize the area where birds were marked relative to study area edges to increase the chances that birds that switch territory location between years would be detected in the resight-only area. We investigated increasingly larger resight-only areas to evaluate what size area would be required to minimize or eliminate bias in apparent survival rates because of emigration when true survival rates are desired. We investigated bias in survival estimates using two different core area sizes (16 and 36 territories) and two different movement patterns ("males" and "females") and progressively increased the larger resight-only areas until the complete habitat patch simulated (2,500 territories; see Simulations below) was considered part of the resight-only study area.

We used capture histories for all birds marked and resighted on both the core and resight-only areas in a traditional CJS model in software MARK 3.1 (White & Burnham, 1999) to estimate apparent survival (ϕ). All assumptions of traditional CJS models apply (e.g. Lebreton et al., 1992) and we also assume that (1) capture probability in the resight-only area equals that of the core area, (2) survival of birds that leave the core area is the same for birds that remain on the core area, and (3) the habitat is homogenous such that progressively larger resight-only areas will increase the proportion of individuals resighted. CJS survival estimates that include capture history information from the resight-only areas will have less bias because birds that move off the core study area can be resighted in the resight-only area.

Core with resight-only area II—subsets analysis

The second study design we investigated used the same core area and resight-only area design for collecting data, but the estimation of survival was performed differently. The motivation behind this study design arose from the recognition that in most situations it is logistically impractical for researchers to resight marked birds in the very large resight-only areas described heretofore. Here again we used the traditional CJS model, but instead estimated ϕ on subsets of the data. The smallest subset was the capture histories of birds marked and resighted on the core area only. The next subset included the capture histories of birds on the core area as well as resightings that occurred in a resight-only area surrounding the core area. The resight-only area was one territory width surrounding the core area. For example, a 16 territory core area (simulated by a 4 × 4 territory area) with a one territory larger resighting area would result in a 6 × 6 territory area (36 territories total; 16 territories in the core area with a ring of 20 territories surrounding the core that make up the resight-only area). The next two subsets increased the size of resight-only area by one additional territory width,

respectively. We investigated this study design starting with core areas of 16, 36, and 64 territories each with progressively larger resight-only areas up to three territories in width. This resulted in study area sizes of 100, 144, and 196 territories, respectively. Thus, we were able to obtain four estimates of ϕ for each area based on capture histories that resulted from progressively larger subsets (i.e., larger resight-only areas) that were inclusive of the preceding subsets.

The four estimates of ϕ obtained from these subsets of the data had diminishing bias (see Results) because each subset had an increasingly larger area to resight birds. Thus, we used these four estimates of ϕ in an asymptotic nonlinear model to obtain an unbiased estimate of survival (S). We used the following model to estimate S :

$$\phi = S \left(\frac{A}{K + A} \right)$$

where A is the size of the study area (number of territories or hectares) and k is a nuisance parameter. We used SAS (PROC NLIN; SAS Institute, Cary, North Carolina, U.S.A.) to estimate the parameters of the nonlinear model (S , k) and a bootstrap procedure to estimate the 90% CI. In the bootstrap procedure we used the estimates of $SE(\hat{\phi})$ to generate 1,000 random-normal deviates for each of the four estimates of ϕ . We used these randomly-generated values in PROC NLIN to obtain 1,000 estimates of S . We used the 5th and 95th percentiles of the bootstrapped S estimates as the 90% CI limits.

Robust design

The third study design we investigated was based on the robust design approach (Pollock, 1989; Kendall & Nichols, 1995; Kendall et al., 1995, 1997). The motivation behind this study area design and analysis approach was the recognition that the between year movements of territory locations did not necessarily result in permanent emigration (L. A. Wood, unpublished data) and, thus, constituted a form of temporary emigration. Here, we used a single study area of 100 territories in which we captured and resighted birds during primary (between year) and secondary (within year) sampling occasions. We simulated three secondary sampling occasions within each primary sampling period, in which the probability of capturing a bird ≥ 1 time during a secondary sampling period was equivalent to the annual capture probabilities of other CJS simulations. Data were analyzed in software MARK 3.1 using the robust design with Huggins' estimator (Huggins, 1989, 1990; Alho, 1990) to estimate S . All assumptions of traditional robust design models applied (e.g., Kendall et al., 1997).

Individual covariates

In the fourth study design we used a fixed-size study area but modeled capture probabilities as a

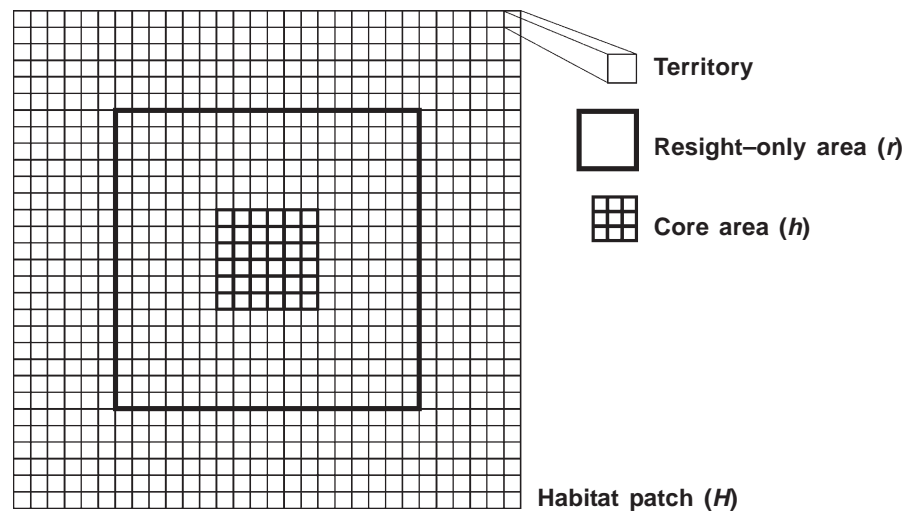


Fig. 1. Illustration of the habitat patch (H) composed of $H \times H$ individual bird territories, with a core area ($h \times h$ territories) for marking and resighting and a surrounding resight-only area ($r \times r$ territories) used in the simulations (see Methods).

Fig. 1. Ilustración de la parcela de hábitat (H), compuesta por territorios de aves individuales $H \times H$, con un área central (territorios $h \times h$) para marcaje y reavistaje, y un área adyacente dedicada exclusivamente al reavistaje (territorios $r \times r$), empleada en las simulaciones (véase Methods).

function of distance from the boundary of the study area. During the simulation we recorded the distance from the nearest study area boundary where each bird was first captured. We used the same input parameters for males and females as used in the other study designs, but specified a fixed study area size of 196 territories for females and 100 territories for males. We analyzed the data as a CJS model with the capture probabilities modeled as a function of distance from the study area boundary as an individual covariate with a logit link function. We did not include an intercept term and normalized the individual covariates.

Simulations

We wrote a simulation program in FORTRAN (Digital Visual Fortran 6.0, Digital Equipment Corporation, Maynard, Massachusetts, U.S.A.) to generate capture histories under the study designs described heretofore. User-specified parameter values generated capture histories under a specified study design. The following user-specified input parameters were required: H . Habitat patch width (H), where $H \times H$ = number of possible territories in habitat patch; each cell representing one territory (fig. 1); h . Core study area width (h), where $h \times h$ = area where birds can be marked and resighted, $h \leq H$ (fig. 1); r . Distance surrounding the core study area where birds only can be resighted, (i.e., resight-only area) $0 \leq r \leq H - h$

(fig. 1); L . Number of capture intervals (i.e., years; primary sampling intervals in robust design), $L = 1, 2, 3, \dots$; l . Number of independent capture events within a primary sampling occasion (i.e., secondary sampling intervals in robust design), $l = 1, 2, \dots, 5$; S_i . Survival rate between primary sampling intervals (i.e., annual survival), $0 \leq S_i \leq 1$; p_i . Capture probability each year (under the robust design the capture probability for each secondary sampling event was defined as $l\sqrt[p_i]{p_i}$), $0 < p_i < 1$; D . Maximum distance a bird could move its territory between years, $D < H$; ϕ . Mean distance moved according to a negative exponential distribution, $\phi \ll D$; m . Proportion of individuals who do not move their territory according to a negative exponential distribution between primary sampling intervals, $0 \leq m \leq 1$; N_0 . Initial number of birds occupying territories, $0 < N_0 < H \times H$

The simulation performed the following sequence of events: 1. Randomly assigned N_0 individuals to territories within the habitat patch; 2. For each individual within the study area ($h \times h$) if a random number $U(0,1) \leq p_i$ then the bird was captured. If $l > 1$ (i.e., robust design) then the bird was captured if a random number $U(0,1) \leq l\sqrt[p_i]{p_i}$ for each of l occasions; 3. Birds that were captured (or resighted in later capture occasions) were assigned a "1" to their capture history and "0" if not captured (or resighted); 4. A bird died if a random number $U(0,1) > S_i$; 5. A bird did not move if a random number $U(0,1) \leq m$; 6. Of those birds that could potentially move ($1 - m$), they moved terri-

tory locations according to a negative exponential distribution ($\bar{x} = \theta$) in a random direction, $U(0,1)$ (although the movements were modeled from continuous distributions for distance and direction, the coordinate of the new territory location was the truncated integer x - y values; if the new territory location was already occupied, or the movement would take the bird outside the habitat patch, then the process was repeated); 7. $(1 - S_i) \times N_o$ new birds were randomly placed in the habitat patch in unoccupied territories; 8. For each individual within the study area ($h \times h$), and the r territories surrounding the study area, if a random number $U(0,1) < p_i$ then the bird was captured or resighted. If $l > 1$ (i.e., robust design) then the bird was captured or resighted if a random number $U(0,1) < \sqrt[l]{p_i}$; 9. The process was repeated beginning with Step #3 for each of the remaining $L \times l$ capture occasions.

For each simulation scenario, we conducted 100 simulations (200 simulations for females in study designs 2 and 3) in which survival and capture probabilities were constant over time and no heterogeneity existed among birds. The output from the FORTRAN program was formatted for input into software MARK to estimate ϕ under the CJS model and S under the Huggins estimator robust design model. The CJS model specified a constant ϕ and p , and the robust design model specified a constant survival rate (S), immigration and emigration rate (γ' and γ''), p , recapture probability (c), and $p = c$.

We based our simulations on empirical data from a 5-year capture-mark-resight study of 423 Prothonotary Warblers (*Protonotaria citrea*) at the White River National Wildlife Refuge, Arkansas, U.S.A., 1994–1999 that provided estimates of the distribution of movement distances, survival and capture probabilities, density of individuals in the landscape, and territory size (Wood, 1999; L. A. Wood & R. J. Cooper, unpublished data; M. R. Marshall, unpublished data). The White River National Wildlife Refuge is a 60,000-ha tract of bottomland hardwood forest, one of the largest contiguous bottomland hardwood forests remaining in the United States (Harris & Gosselink, 1990), much of it suitable breeding habitat for Prothonotary Warblers. From 1994–1999 we recorded the territory locations of all marked birds and calculated the distance between territory centers for all birds that were resighted in subsequent years. Due to the spatial arrangement of six 50-ha study plots, we were able to detect between-year movements up to 3 km. Not all movements had an equal probability of detections (Koenig et al., 1996), thus, we utilized the method of Baker et al. (1995) to eliminate the bias in movement distributions inherent in studies conducted within a finite area. The corrected movement distributions indicated that inter-annual movements of territories differed between males and females with females moving more frequently between years and longer distances, but both could be described with a negative exponential distribution (fig. 2). For males, the shape of the negative exponential distribution that

reflected the empirical, corrected movement distributions was accurately described with a maximum distance moved (D) of 12 territories, an average movement (θ) of 3.87 territories, and 35% of males not moving between years (m , in addition to the movements of zero territories under the negative exponential model). For females, we described movements with a maximum distance moved (D) of 22 territories, an average movement (θ) of 3.87 territories, and 8% of females not moving between years (m , in addition to the movements of zero territories under the negative exponential model). In our simulations, we used an annual survival rate of 0.69 for males and 0.57 for females and capture probability of 0.95 for males and 0.68 for females. All simulations began with $H = 50$, $N_o = 1,875$ (75% of all possible territories occupied), and an average territory size of 125 m in diameter (L. A. Wood & M. R. Marshall, unpublished data).

Our model was spatially-explicit in terms of the location of birds on the landscape (i.e., the habitat patch, H ; fig. 1), but we expressed distances in terms of territories in which each unit of distance represented 1 territory. Thus, our simulation results should be comparable across species if scaled to an average breeding territory size. In our simulations we assumed a homogeneous habitat (i.e., contiguous patches of habitat suitable for the species of interest) large enough to contain the study area designs of interest. Each set of simulations for each of the four study area designs represented a 5-year capture-mark-recapture scenario and was conducted separately for males and females. Consequently, we were able to evaluate each design with one group (males) that was less likely to move territory locations between years and moved shorter distances and another group (females) that moved territory locations more often and moved greater distances when movement occurred (M. R. Marshall, unpublished data). We evaluated the accuracy and precision of each study design by comparing estimated parameters ($\hat{\phi}$ and $\hat{\beta}$) to the true value used to simulate the data, estimating the SD of estimated parameters, and calculating the average square root of mean square error ($RMSE$).

Results of simulations

Core with resight-only area I

Simulation results from the first study area design indicate that the negative bias in apparent survival rate estimates relative to true values decreases for both males and females as the resight-only area increases in size (fig. 3). With progressively larger resight-only area size, an increasing number of marked birds that move territory locations between years are resighted in the resight-only area and bias approaches zero. Females, which move more frequently and far-

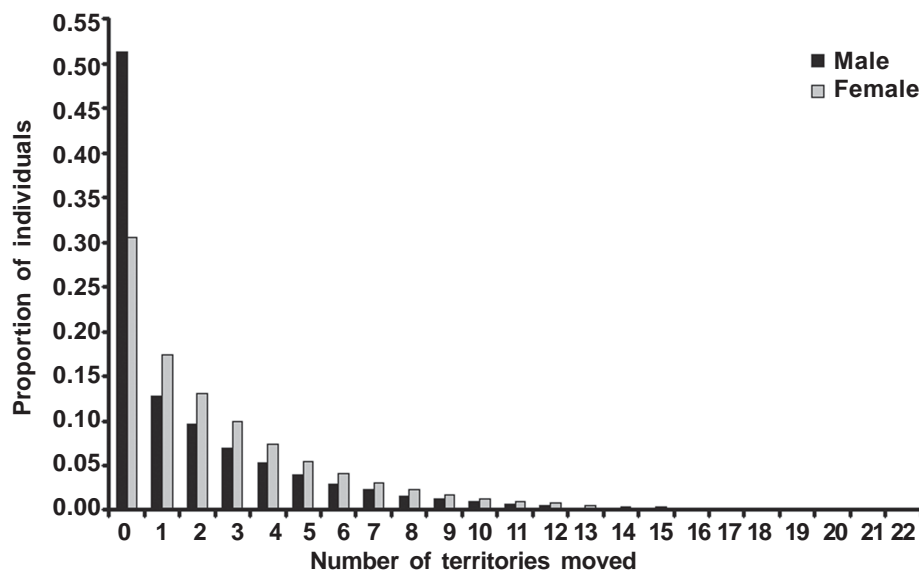


Fig. 2. Distribution of movements used in simulations (distance between inter-annual placement of breeding territories) for male and female Prothonotary Warblers expressed as the number of territories moved between years.

Fig. 2. Distribución de los movimientos utilizados en las simulaciones (distancia entre la ubicación interanual de los territorios de reproducción) para reinitas cabecidoradas macho y hembra, expresados como el número de territorios recorridos entre un año y otro.

ther distances than males, and were, therefore, more likely to move beyond the bounds of the resight-only areas, exhibited a greater bias in both the 16 and 36 territory core area design at smaller resight-only areas. Bias for both sexes began to converge at the 20 × 20 resight-only size and bias was negligible at the 30 × 30 resight-only area size.

Core with resight-only area II-subsets analysis

Study areas containing 196 territories (64 territory core area) exhibited little bias in estimates of survival (\hat{O}) for both males and females (table 1) and estimates had reasonable precision. Study areas of 144 territories (36 territory core area) in size exhibited a slight negative bias, and study areas of 100 territories (16 territory core area) provided estimates of survival with poor precision. If capture probabilities were high (e.g., males, table 1), the smallest study area size provided reasonable survival estimates, but when capture probabilities were low (e.g., females, table 1) the survival estimates were extremely variable. Using a bootstrap approach to incorporate variability from both the CJS model and the asymptotic model of nested survival estimates provided confidence intervals close to the nominal value; 93.5–95.0% of 90% CIs encompassed the true value.

Robust design

Results from the robust design analysis indicated that the average survival and capture probability estimate from simulations, for both males and females, exhibited little bias (table 2). However, the precision of survival estimates was poor (males, range 0.51–1.00; females, range 0.35–1.00).

Individual covariates

The survival estimates when capture probability was modeled as a function of distance from the study area boundary were precise and unbiased ($S_{\text{males}} = 0.69$, $\hat{O}_{\text{males}} = 0.69$, $SE_{\text{males}} = 0.027$; $S_{\text{females}} = 0.55$, $\hat{O}_{\text{females}} = 0.53$, $SE_{\text{females}} = 0.028$). Because the individual covariates were normalized and the logit of capture probability was modeled without an intercept parameter, the average estimated capture probability was 0.50, and thus did not provide an accurate estimate of the true capture probability if birds were available to be captured on the study area. Although these models provided unbiased survival estimates, they were always inferior (AIC weight < 0.01) to standard CJS models. Consequently, when analyzing data in which true survival is not known, it is unlikely AIC would indicate selection of the model with unbiased survival estimates, thus limiting the utility of this approach.

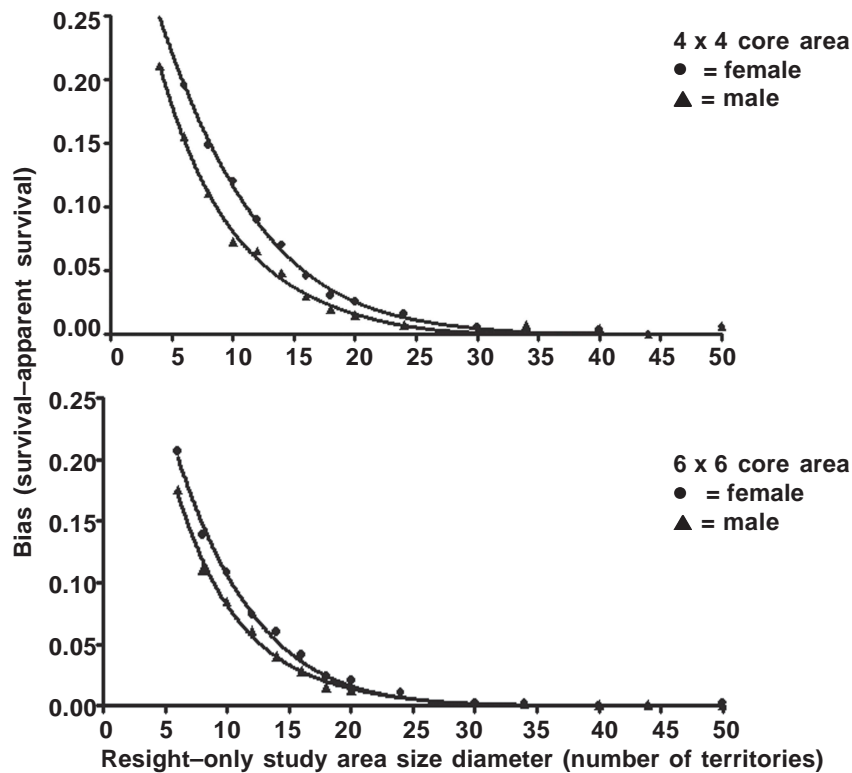


Fig. 3. Results of simulations of the "Core with resight-only area I" design for a 16 territory core area (top) and a 36 territory core area (bottom). Bias approaches zero as the resight-only area size increases.

Fig. 3. Resultados de las simulaciones en las que se utilizó el diseño de combinación del área central con el área I dedicada exclusivamente al reavistaje, para un área central compuesta por 16 territorios (arriba) y un área central compuesta por 36 territorios (abajo). El sesgo se aproxima a cero a medida que el tamaño del área dedicada exclusivamente al reavistaje aumenta.

Discussion

We investigated four study design and analysis approaches that resulted in estimates of survival that were not biased by the effects of incomplete breeding site-fidelity (some proportion of marked individuals moving beyond the bounds of the study area and going undetected). The first two involved a smaller core area where all marking of birds takes place and progressively larger resight-only areas surrounding the core where researchers search for marked birds. For the first of these two designs, we demonstrated that as the resighting areas get progressively larger, and therefore incorporates more "emigrants", apparent survival estimates begin to approximate true survival rates. Given observed inter-annual movements of birds, however, it is likely to be logistically impractical to resight birds on a sufficiently large resight-only area to minimize bias. For example, a resight-only area of at least 400 territories (20 × 20 terri-

tory study area; fig. 3) would be needed to eliminate the relative difference in bias between males and females because of greater movements of females, whereas a resight-only area of approximately 900 territories (30 × 30 territory study area) would be needed to eliminate the bias for both sexes completely.

Whether study areas of 400–900 territories are logistically feasible depends on the average territory size of a species. We believe any study area larger than 196 territories (14 × 14 territory study area) would be logistically impractical in a field setting for Prothonotary Warblers (L. A. Wood & M. R. Marshall, personal observation). A 196 territory study area for Prothonotary Warblers would be > 300 ha where marked birds would have to be resighted (table 3), whereas a 900 territory area would be approximately 1,400 ha. Therefore, we conclude that increasing the resighting area to an area large enough to eliminate bias from inter-annual territory relocations is logistically impractical for most species.

Table 1. Mean estimated parameters from simulations using the "Core with resight-only area II-subsets analysis" design to estimate S : N . Number of simulations; SAS . Study area size (units are number of territories, size of core area —no. territories— where unmarked birds can be captured); n . Mean number of birds marked over 5 year period.

Tabla 1. Parámetros promedio estimados, obtenidos a través de simulaciones en las que para estimar S se empleó el diseño de análisis de subconjuntos—combinación del área central con el área II dedicada exclusivamente al reavistaje: N . Número de simulaciones; SAS . Tamaño del área de estudio, (las unidades son el número de territorios, tamaño del área central —número de territorios— donde se pueden capturar aves no marcadas); n . Promedio de número de aves marcadas en un periodo de 5 años.

Sex	SAS	N	n	S	\hat{S}	$\hat{SD}(\hat{S})$	\overline{RMSE}	p	\hat{p}	$\hat{SD}(\hat{p})$
Male	100(16)	100	38	0.69	0.64	0.0769	0.0917	0.95	0.93	0.0796
Male	144(36)	100	62	0.69	0.67	0.0520	0.0557	0.95	0.94	0.0641
Male	196(64)	100	126	0.69	0.69	0.0391	0.0391	0.95	0.95	0.0381
Female	100(16)	200	32	0.57	0.55	0.2214	0.2223	0.68	0.75	0.3449
Female	144(36)	200	47	0.57	0.56	0.1287	0.1291	0.68	0.71	0.2442
Female	196(64)	200	130	0.57	0.57	0.0848	0.0848	0.68	0.70	0.1170

Table 2. Mean estimated parameters from simulations for a robust design model for a study area of 100 territories in size, 5 primary sampling periods (e.g., years), and 3 secondary sampling periods (e.g., within-year sampling). For males $S = 0.69$ and $p = 0.95$ and for females $S = 0.57$ and $p = 0.68$: N . Number of simulations; Probability. Probability captured ≥ 1 time within a primary sampling period.

Tabla 2. Parámetros promedio estimados, obtenidos a través de simulaciones para un modelo de diseño sólido para un área de estudio compuesta por 100 territorios, cinco periodos de muestreo primario (años, por ejemplo) y tres periodos de muestreo secundario (muestreo interanual, por ejemplo). Para los machos, $S = 0,69$ y $p = 0,95$, y para las hembras $S = 0,57$ y $p = 0,68$: N . Número de simulaciones; Probabilidad. Probabilidad de ser capturado ≥ 1 durante el primer periodo de muestreo.

Sex	N	Survival		Immigration		Emigration		Probability	
		\hat{S}	$\hat{SD}(\hat{S})$	$\bar{\gamma}'$	$\hat{SD}(\bar{\gamma}')$	$\bar{\gamma}''$	$\hat{SD}(\bar{\gamma}'')$	\bar{p}	$\hat{SD}(\bar{p})$
Male	100	0.71	0.176	0.49	0.469	0.18	0.177	0.95	0.011
Female	200	0.55	0.178	0.43	0.438	0.21	0.188	0.68	0.022

The second approach utilized the same study area design, but estimated ϕ for three progressively larger resight-only areas and modeled the ϕ 's as asymptotically approaching true survival. This study design and analytical method provided estimates of S with little bias and reasonable precision. This approach is likely to be logistically feasible in field settings because of the smaller study area sizes required (100–200 territories in size). Furthermore, the number of marked birds used in the simulations is comparable to what could realistically be marked in most field situations.

The choice of study area size using this core area and resight-only area study design and subset analysis approach depends on several factors: capture probabilities, territory sizes, and the distribution of the distances between inter-annual territory locations. For example, compared to females, male Prothonotary Warblers had high capture probabilities ($p = 0.95$), fewer birds moved their territories between years, and they moved shorter distances when they did move. This resulted in survival estimates with reasonable \overline{RMSE} (table 1) even when study areas were 156 ha (100 territories) in

Table 3. Approximate study area size in hectares for two species of migratory songbird given average territory size. Territory size used in conversion equals: A. Prothonotary Warblers, 1.45 ha (125 m diameter) (L. A. Wood, unpublished data); B. Red-eyed Vireos, 0.50 ha (71 m diameter) (*Vireo olivaceus*; Marshall & Cooper, 2004).

Tabla 3. Tamaño aproximado del área de estudio, expresado en hectáreas, para dos especies de aves cantoras migratorias dado el tamaño territorial medio. El tamaño territorial empleado en la conversión equivale: A. Reinitas cabecidoradasa, 1,45 ha (125 m diámetro) (datos no publicados de L. A. Wood); B. Vireos ojirrojos, 0,50 ha (71 m diámetro) (*Vireo olivaceus*; Marshall & Cooper, 2004).

Territories	Study Area Size (ha)	
	A	B
16 (4 x 4)	25	8
25 (5 x 5)	39	12
36 (6 x 6)	56	18
49 (7 x 7)	76	24
64 (8 x 8)	100	32
81 (9 x 9)	126	40
100 (10 x 10)	156	50
121 (11 x 11)	189	60
144 (12 x 12)	225	72
169 (13 x 13)	264	85
196 (14 x 14)	306	99

size. Comparable precision of survival estimates for females required study areas 306 ha (196 territories) in size. In general, greater capture probabilities and shorter inter-annual movements of breeding territories result in greater precision of survival estimates.

Study area sizes also will be greater for species with larger territories possibly affecting the precision of survival estimates because of the logistical difficulties of capturing and resighting birds over these larger areas. We present study area sizes for two species of migratory songbird that translate the territory units of the simulations into actual field dimensions (table 3). The Red-eyed Vireo was arbitrarily chosen to represent those songbirds with territory sizes smaller than a Prothonotary Warbler. This example assumes that both species have the same distribution of movements even though male Red-eyed Vireos tend to be more site-faithful and move shorter distances than Prothonotary Warblers (Marshall et al., 2002). Decisions as to the feasibility of resighting birds over these areas will be dependent on multiple factors, but we believe data collection on study areas of the presented size is possible. Moreover, an example analysis was provided (table 4) with a 64 territory core area (8 x 8 territory study area) and three progressively larger resight-only areas resulting in the largest resight area of 196 territories (14 x 14 territory study area). Assuming researchers can feasibly mark a similar number of birds on the core area as were marked in the simulations as well as resight birds in a study area with these dimension, the results of this example (table 4) demonstrate that the survival estimates generated with this approach were unbiased and had reasonable precision.

Lastly, table 5 presents analyses investigating the effects of different distributions of the distances between inter-annual territory locations (fig. 5) on the utility of a 64 territory core area and three progressively

Table 4. Results of an example analysis using the "Core with resight-only area II-subsets analysis" design with a 64 territory (8 x 8) core area and three progressively larger (one territory width each) resight-only areas (196 territories for largest resight-only area): n. Number of birds marked over 5 year period.

Tabla 4. Resultados de ejemplo de análisis en el que se utilizó el diseño de análisis de subconjuntos-combinación del área central con el área II dedicada exclusivamente al reavistaje, en un área central (8 x 8) compuesta por 64 territorios y tres áreas dedicadas exclusivamente al reavistaje (cada una de ellas con una anchura equivalente a un territorio), progresivamente más grandes (196 territorios para el área más grande dedicada exclusivamente al reavistaje): n. Número de aves marcadas a lo largo de un periodo de 5 años.

Sex	n	S	\hat{S}	$\hat{SE}(\hat{S})$	90%CI (\hat{S})	p	\hat{p}	$\hat{SE}(\hat{p})$	90% CI(\hat{p})
Males	140	0.69	0.73	0.074	0.62–0.87	0.95	0.90	0.035	0.84–0.96
Females	128	0.57	0.50	0.097	0.37–0.68	0.68	0.83	0.331	0.54–1.27

Table 5. Results of analyses using the "Core with resight-only area II-subsets analysis" design with a 64 territory (8 x 8) core area and three progressively larger (one territory width each) resight-only areas (196 territories for largest resight-only area) over a range of between-year territory movement distributions as shown in figure 5: θ . The value of the mean from a negative exponential distribution describing bird movement patterns; 90% CI cov. Proportion of 90% CI coverage that encompass the true value.

Tabla 5. Resultados de los análisis en los que se utilizó el diseño de análisis de subconjuntos-combinación del área central con el área II dedicada exclusivamente al reavistaje, en un área central (8 x 8) compuesta por 64 territorios y tres áreas dedicadas exclusivamente al reavistaje (cada una de ellas con una anchura equivalente a un territorio) (196 territorios para el área más grande dedicada exclusivamente al reavistaje), en un rango de distribuciones de movimientos territoriales interanuales, según se indica en la figura 5: θ . El valor de la media a partir de una distribución exponencial que describe los patrones de movimiento de las aves; 90% CI cov. Proporción del 90% CI que incluye el valor real.

θ	S	Core-area only		Core-area with resight-only areas			
		$\hat{\phi}$	RMSE	\hat{S}	$\hat{S}D(\hat{S})$	90% CI cov	RMSE
1.0	0.70	0.64	0.07	0.72	0.05	0.91	0.08
2.0	0.70	0.58	0.12	0.71	0.05	0.92	0.09
3.0	0.70	0.53	0.17	0.71	0.06	0.97	0.10
6.0	0.70	0.43	0.27	0.66	0.09	0.94	0.17

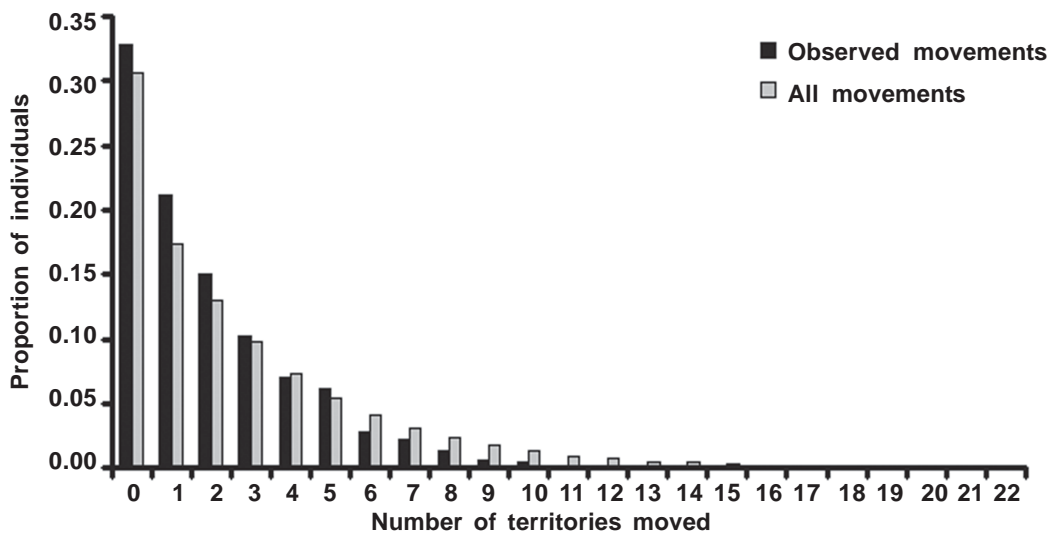


Fig. 4. Distribution of observed movements of marked birds (i.e., resighted individuals) closely matched the distribution of movements for all birds in the habitat patch. Values are based on females and a 64 territory core area with a 196 territory resight-only area.

Fig. 4. La distribución de los movimientos observados realizados por aves marcadas (es decir, individuos reavistados) concordó estrechamente con la distribución de los movimientos de todas las aves en la parcela de hábitat. Los valores se basan en hembras y en un área central compuesta por 64 territorios, con un área dedicada exclusivamente al reavistaje compuesta por 196 territorios.

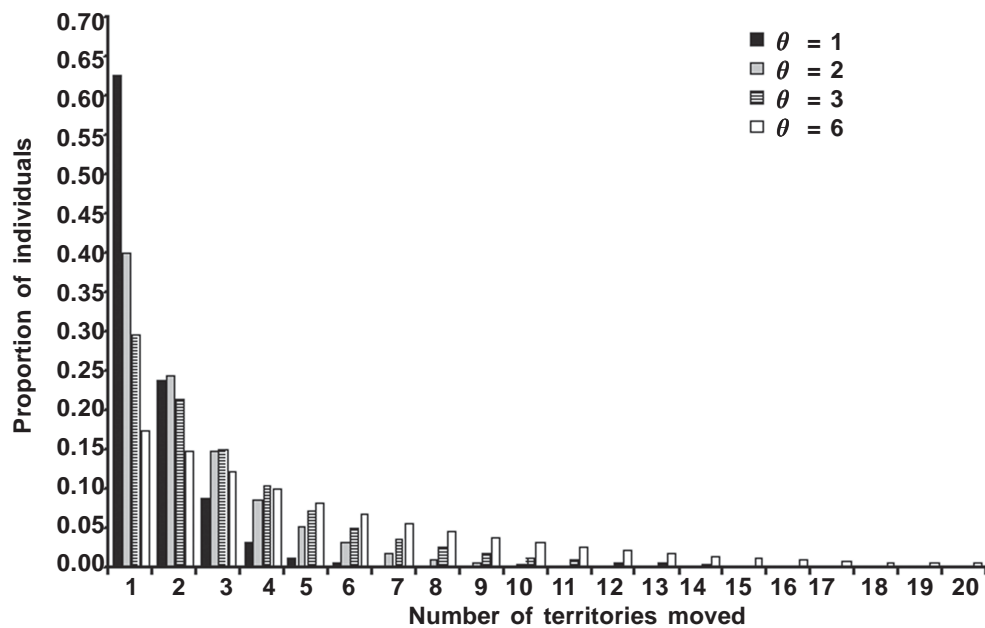


Fig. 5. Range of between-year territory movement distributions used to evaluate the "Core with resight-only area II-subsets analysis" design with a 64 territory (8 x 8) core area and three progressively larger (one territory width each) resight-only areas (196 territories for largest resight-only area). Results of analyses presented in table 5.

Fig. 5. Rango de distribuciones de movimientos territoriales interanuales utilizado para evaluar el diseño del análisis de subconjuntos-combinación del área central con el área II dedicada exclusivamente al reavistaje, con un área central (8 x 8) compuesta por 64 territorios y tres áreas dedicadas exclusivamente al reavistaje (cada una de ellas con una anchura equivalente a un territorio) progresivamente mayores, (196 territorios para el área más grande dedicada exclusivamente al reavistaje). Resultados de los análisis presentados en la tabla 5.

larger resight-only areas approach. These results indicate that the approach would yield unbiased estimates of survival with reasonable precision that would allow comparisons in survival estimates between sexes of a species (or among multiple species) with different fidelity/movement distributions. This is in contrast to the erroneous conclusions that would be drawn from evaluating apparent survival estimates from the core area only (i.e., a typical fixed study area approach; table 5). Furthermore, the error (as defined by $RMSE$) associated with \hat{S} from the core-resight area approach is equal to or less than that associated with $\hat{\phi}$ from the core-area only because of the reduction in bias. It appears that this study area design and analysis approach can yield reliable results over a range of capture probabilities, territory sizes, and movement patterns. Data on these basic biological parameters is required to effectively design a study area for a given species or suite of species that may vary in patterns of site-fidelity and between-year movements.

The third approach we investigated was a robust design (Kendall et al., 1995). We investigated the robust design because even though the majority of movements that resulted in emigration observed for Prothonotary Warblers were permanent, not all were (L. A. Wood, unpublished data). That is, some individuals moved off the study area in one year, only to return to the study area in a subsequent year. This constitutes a form of temporary emigration that could be estimated with the robust design. However, so little temporary emigration was observed that parameter estimation was unreliable. This may not be true for other species where inter-annual movements may more typically resemble temporary emigration. Another problem with the robust design simulations is that the model investigated did not consider the heterogeneity that existed in the probability of immigrating or emigrating; birds closer to the border of the study area had a greater probability of leaving (entering) the study area. However, we believe further research on the use of the robust design is warranted.

The fourth analysis modeled capture probabilities as a function of distance from the study area boundary. Although this approach (unlike the robust design approach) does incorporate some of the heterogeneity in capture probabilities due to the proximity of birds to the study area edges, it cannot account for birds, for example, that are first captured in the center of the study area in one year and in a subsequent year move to a territory near the study area boundary. Although birds with these types of movements have a high probability of staying on the study area in the first year, they have a much lower probability in subsequent years. Furthermore, the individual covariate value is unknown for years in which a bird is not recaptured. Finally, the greatest problem with this approach is that use of the AIC criterion failed to select the model with the most accurate survival estimate because of the biased estimates of capture probability.

An additional avenue of future research could involve constructing a model that explicitly incorporates the probability that a bird present on the study area in one year will remain within the study area in subsequent years. For example, the simulations indicated that the distribution of observed movements of marked birds (i.e., individuals resighted on the study area) closely matched the distribution of movements for all birds in the habitat patch (fig. 4; values were based on females and a 64 territory core area with a 196 territory resight-only area). If one could model the probability of movement of all individuals based only on the observed data (e.g., Rodriguez, 2002), and had spatially explicit data on territory locations, one could estimate the probability that a bird at location x, y in year i will be within the study area in year $i + 1$. If so, one could potentially construct a model that estimates ϕ , p , and the probability of remaining on the study plot, where ϕ approximates S .

The study designs and analysis approaches presented here need to be field-tested and may be limited by the logistical difficulties of data collection. However, we believe a core area with surrounding resight-only areas (subsets analysis) has the potential to provide estimates of survival rates that can be used to evaluate aspects of life-history theory, population viability and other aspects of conservation ecology that apparent survival estimates confounded with incomplete breeding site-fidelity cannot.

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