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Estimating dispersal among numerous sites using capture–recapture data

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Abstract. Dispersal affects processes as diverse as habitat selection, population growth, and gene flow. Inference about dispersal and its variation is thus crucial for assessing population and evolutionary dynamics. Two approaches are generally used to estimate dispersal in free-ranging animals. First, multisite capture–recapture models estimate movement rates among sites while accounting for survival and detection probabilities. This approach, however, is limited in the number of sites that can be considered. Second, diffusion models estimate movements within discrete habitat using a diffusion coefficient, resulting in a continuous processing of space. However, this approach has been rarely used because of its mathematical and implementation complexity. Here, we develop a multi-event capture–recapture approach that circumvents the issue of too many sites while being relatively simple to be implemented in existing software. Moreover, this new approach allows the quantifying of memory effects, whereby the decision of dispersing or not on a given year impacts the survival or dispersal likelihood of the following year. We illustrate our approach using a long-term data set on the breeding ecology of a declining passerine in southern Québec, Canada, the Tree Swallow (*Tachycineta bicolor*).

Key words: capture–recapture; dispersal; memory model; multi-event model; multisite model; site fidelity; southern Quebec, Canada; Tachycineta bicolor; *Tree Swallow.*

Introduction

Dispersal is a fundamental mechanism in ecology and evolution as well as a demographic process that affects the growth rate of populations and determines their spatial structure, particularly in fragmented habitats (Clobert et al. 2009). At the individual level, it reduces competition and provides opportunities to find new sites and ultimately to benefit from the best available habitats or mates while tracking favorable environmental conditions in a changing world (Ronce 2007). Regarding evolutionary dynamics, dispersal of individuals and the gene flow that it can cause interact to constrain or facilitate adaptation (Garant et al. 2007). Assessing dispersal is thus a key step in conservation biology to understand extinction–colonization processes and population dynamics (Hanski 1999).

Fine-scale abiotic and biotic features, such as habitat loss and fragmentation, individual productivity, or conspecific and predator densities, can affect dispersal behavior and therefore genetic and demographic patterns of animal populations (Holderegger and Wagner 2008, Shanahan et al. 2011). Estimating dispersal within highly heterogeneous landscapes thus requires setting up a design with numerous monitoring sites to capture the influence of potentially important local features (Fernández et al. 2003).

Both indirect and direct methods exist to estimate dispersal in free-ranging populations. Indirect methods including techniques such as the measurement of isotope ratios incorporated in living tissues allow one to determine the chronological suite of areas visited by an individual (Kendall and Nichols 2004). Analogously, the analysis of allele frequencies at different loci allows one to assess the (relative) likelihood that an individual originates from a given population composed within a set of putative sources (Rousset 2001). However, because these indirect methods make it possible to infer movements only among coarse regions or populations, they cannot be used to quantify the influence of fine-scale landscape heterogeneity on dispersal. Direct methods circumvent this drawback by marking individuals and "resighting" or recapturing them at known locations. These methods include the use of modern tracking devices, such as Argos-GPS platform transmitters, which can track individual movements with a high spatial resolution in real time, but are financially expensive and generally too big or heavy to be fitted on small animals (Patterson et al. 2008). Another set of direct methods, usually referred to as capture–recapture approaches (CR; see Lebreton et al. 1992), includes the simple marking of individuals using bands or tags. Although the latter conveys much less information than

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the former, its cost affordability makes it the most widely used approach of both past and current animal population monitoring programs (Kendall and Nichols 2004). Here, we focus on CR methods that rely on banding programs to estimate dispersal while explicitly accounting for imperfect detection of individuals (Lebreton et al. 1992).

Two CR approaches are available to investigate dispersal in wild populations. In multisite CR models, individuals can die, or survive and be recaptured as in standard CR models, but they can also move among sites according to probabilities of transition among geographical sites (Arnason 1973, Schwarz et al. 1993). However, this approach is computationally limited by the number of sites that can be considered because the number of transition parameters quickly increases with the number of sites (Lebreton and Pradel 2002). For example, with two sites, one would need to estimate two transition probabilities, 20 for five sites, 90 for 10 sites, and so forth. Alternatively, a CR approach based on a diffusion model can be used to infer dispersal movements (Ovaskainen et al. 2008*a*, *b*). However, biologists have rarely used this approach because it is mathematically complex (including the manipulation of differential equations) and requires a solid understanding of algorithmic tools for their practical implementation.

Here, we propose a new alternative to estimate breeding dispersal rate and site fidelity within a study area comprising many recapture sites. We develop a multi-event CR approach (Pradel 2005) to circumvent the issue of too many transition probabilities in multisite CR models when the number of sites is large. More precisely, we categorize the state of an individual in a given year as being (1) in the same location as the year before or (2) in a different location. In contrast with standard multisite CR models, a state here can correspond to several events, depending on whether an individual was seen in two consecutive years (or breeding events), in which case its state is known with certainty, or in only one year, in which case its state is uncertain. By doing so, we can estimate dispersal and site fidelity while accounting for mortality and imperfect detection as in multisite CR models, and coping with possibly numerous sites as in CR diffusion models. Moreover, the potential effect of behavior in a given year (i.e., staying vs. leaving a site) on survival or dispersal in the following year—a so-called memory effect—can also be investigated as with multisite CR models (Hestbeck et al. 1991, Brownie et al. 1993). Overall, our method relies on well-adapted CR models and is relatively simple to implement in existing software.

To illustrate our approach, we use a long-term data set on a migrating North American passerine, the Tree Swallow (*Tachycineta bicolor*). This secondary-cavity nester is an aerial insectivore that typically occurs in open habitats near water (Winkler et al. 2011). As for most aerial insectivores, its population has been declining over a large part of its breeding range (Nebel et al. 2010, Shutler et al. 2012), and at alarming rates averaging 4.2% per year between 1989 and 2009 in Québec, Canada (Shutler et al. 2012). Putative causes of this decline include a decrease in nesting site availability as well as the diminution of food resources and intoxication linked to agricultural intensification and widespread pesticide use. However, the exact mechanisms underlying the population decline of Tree Swallows and other aerial insectivores are still unknown (Nebel et al. 2010). Estimating dispersal among a large number of sites differing in habitat quality may help to better understand this trend.

A Multi-event CR Model to Estimate Dispersal among Numerous Sites

Setting the scene with events and states

In multi-event CR models, a distinction is made between events and states (Pradel 2005). An event is defined as the presence or absence of an observable character or symptom at each occasion in the encounter history of the individual. It is distinguished from the underlying, not necessarily observable, state to which it is related by a probabilistic relationship (Pradel 2005, Gimenez et al. 2012).

Here, we consider seven states (Fig. 1) defined by combining the feature of interest, namely whether an individual occupies the same site as on the previous occasion (H for here) or not (E for elsewhere), with the information about whether it was captured or not on the previous and current occasions. The previous capture status is important because it partly determines the kind of events that are observable. Indeed, we are able to recognize if an individual moved or not only if it was observed on the previous occasion. The current capture also determines our ability to recognize whether the individual moved. Because in multi-event models (and more generally in hidden Markov processes) only the information embedded in the state is carried over to the next occasion, the capture status at $t - 1$ must be incorporated in the state to remain available at t, where it is needed. For a similar problem and solution, see the treatment of trap dependence by Pradel and Sanz-Aguilar (2012). We denote the composite states that we are using by prefixing to the dispersal status (H or E) the previous capture status (+ if detected or o if not detected) and suffixing to it the current capture status (same notation). For instance, oH+ is for an individual in the same site at t and $t - 1$ (dispersal status H) that was not captured at $t - 1$ (prefix o) and captured at t (suffix +). When an individual is not captured at t, it does not matter whether it was captured at $t - 1$; in this case, we do not specify its capture status at $t - 1$. Thus, we retain the six composite states: Ho, oH+, +H+, Eo, oE+, +E+, to which we add the state dead (D). Only four events appear in the capture histories. For individuals

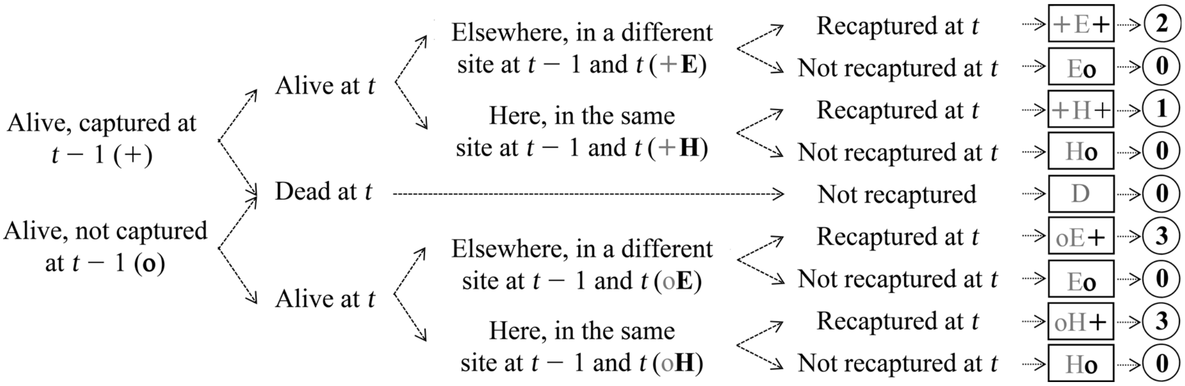

FIG. 1. Transition steps of an individual from $t-1$ to t and explanation of states associated with events. The diagram shows the steps leading to the observation (at $t-1$ and t) of an individual: survival (alive or dead, D), fidelity (Here, H; Elsewhere, E) and recapture (recaptured, +; or not, letter o). Each updated information appears in bold while the old one is grayed out. We end up in the last step with seven states (in boxes; note that E**o** and H**o** are repeated) that can generate four events (rings numbered 0, 1, 2, 3). States are: Elsewhere and captured at $t-1$ and t; Elsewhere and not captured at t (whatever the capture at $t-1$); Here and captured at $t-1$ and t; Here and not captured at t (whatever the capture at $t-1$); Dead; Elsewhere and captured at t but not at $t-1$; Here and captured at t but not at $t-1$. Events are: not recaptured at t, recaptured at t and not recaptured at $t-1$, recaptured at t in the same site as at $t-1$, recaptured at t in another site as at $t-1$.

captured on both occasions, we encode (1) if they occupied the same site on the two occasions and (2) if they occupied different sites; otherwise, we encode (0) for individuals not captured at t and (3) for individuals captured at t but not at $t-1$ (Fig. 1). Fig. 2 provides an example of a capture history for an individual captured at several sites and the corresponding encoding of events and states.

Parameterization

We distinguish three successive transitions, which update in a stepwise fashion the information carried by the state taking place between times $t-1$ and t: survival, fidelity, and recapture. Survival comes first; then, site fidelity conditional on survival, and eventually, the recapture process at time t. For other examples of decomposition of transitions into several steps, see Sanz-Aguilar et al. (2011) for skipping behavior and Pradel and Sanz-Aguilar (2012) for trap dependence.

When an individual is captured for the first time, its previous location, and thus its dispersal status, is unknown, but its previous and current capture statuses are known. Its state is either oE+ or oH+. With $1-\pi$ denoting the probability of being a disperser for a newly encountered individual, the probabilities of the initial states are as follows:

Initial states

$$= \begin{array}{ccccccc} \text{Ho} & \text{oH+} & \text{+H+} & \text{Eo} & \text{oE+} & \text{+E+} & \text{D} \\ \Big(\; 0 & \pi & 0 & 0 & 1-\pi & 0 & 0 \; \Big) \end{array}.$$

Later on, individuals will survive with a probability S (possibly dependent on their dispersal status). In the following matrix and afterward, rows correspond to time $t-1$, columns to time t, and the probabilities on the same row add up to 1. The departure state (in row) describes the situation at $t-1$. Each time a status element is updated to its situation at time t, it becomes bold. At the end of the survival step, only the dead state is updated.

Survival

$$= \begin{array}{c} \\ \text{Ho} \\ \text{oH+} \\ \text{+H+} \\ \text{Eo} \\ \text{oE+} \\ \text{+E+} \\ \mathbf{D} \end{array} \begin{array}{c} \begin{array}{ccccccc} \text{Ho} & \text{oH+} & \text{+H+} & \text{Eo} & \text{oE+} & \text{+E+} & \mathbf{D} \end{array} \\ \begin{pmatrix} S & 0 & 0 & 0 & 0 & 0 & 1-S \\ 0 & S & 0 & 0 & 0 & 0 & 1-S \\ 0 & 0 & S & 0 & 0 & 0 & 1-S \\ 0 & 0 & 0 & S & 0 & 0 & 1-S \\ 0 & 0 & 0 & 0 & S & 0 & 1-S \\ 0 & 0 & 0 & 0 & 0 & S & 1-S \\ 0 & 0 & 0 & 0 & 0 & 0 & 1 \end{pmatrix} \end{array}.$$

Survivors can go back to the same site (**H**, Here) or move to another one (**E**, Elsewhere). Although in

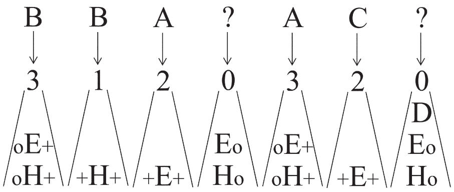

FIG. 2. Example of a capture history. The top level lists the sites (letters) where individuals were captured; a question mark codes for "unknown" as the individual was not captured at this time step. The intermediate level provides the encoding of the capture history in terms of events. The bottom level displays the corresponding sequence of states as identified in Fig. 1.

standard multisite CR we would have as many transitions as pairs of sites, we opted for a more economical approach that considers the alternative: the individual did or did not change site, and we expressed the probabilities of transition in terms of the probability of site fidelity, F:

Fidelity

$$= \begin{array}{c} \\ \text{Ho} \\ \text{oH+} \\ \text{+H+} \\ \text{Eo} \\ \text{oE+} \\ \text{+E+} \\ \text{D} \end{array} \begin{array}{c} \begin{array}{ccccccc} \mathbf{H}\text{o} & \text{o}\mathbf{H}\text{+} & \text{+}\mathbf{H}\text{+} & \mathbf{E}\text{o} & \text{o}\mathbf{E}\text{+} & \text{+}\mathbf{E}\text{+} & \text{D} \end{array} \\ \left(\begin{array}{ccccccc} F & 0 & 0 & 1-F & 0 & 0 & 0 \\ 0 & F & 0 & 0 & 1-F & 0 & 0 \\ 0 & 0 & F & 0 & 0 & 1-F & 0 \\ F & 0 & 0 & 1-F & 0 & 0 & 0 \\ 0 & F & 0 & 0 & 1-F & 0 & 0 \\ 0 & 0 & F & 0 & 0 & 1-F & 0 \\ 0 & 0 & 0 & 0 & 0 & 0 & 1 \end{array} \right) \end{array} .$$

For instance, a previously unobserved faithful individual at time $t - 1$ (state Ho, row 1) may remain faithful to its breeding site at time t (its dispersal status is then confirmed in bold in the first column **H**o), or may change site (its dispersal status becomes **E**o, column 4). Note that the fidelity probability can be made dependent on the dispersal status at time t, thus allowing testing for a "memory" effect in dispersal behavior (F on the first three rows with dispersal status H distinct from F on the following three rows with dispersal status E).

Eventually, survivors can be captured with a probability R at time t. In this last transition matrix, we introduce the capture status at time t as a suffix to the dispersal status and the capture status at time $t - 1$ (the suffix in the row state), if relevant, is now prefixed to the dispersal status:

Recapture

$$= \begin{array}{c} \\ \mathbf{H}\text{o} \\ \text{o}\mathbf{H}\text{+} \\ \text{+}\mathbf{H}\text{+} \\ \mathbf{E}\text{o} \\ \text{o}\mathbf{E}\text{+} \\ \text{+}\mathbf{E}\text{+} \\ \text{D} \end{array} \begin{array}{c} \begin{array}{ccccccc} \text{Ho} & \text{oH+} & \text{+H+} & \text{Eo} & \text{oE+} & \text{+E+} & \text{D} \end{array} \\ \left(\begin{array}{ccccccc} 1-R & R & 0 & 0 & 0 & 0 & 0 \\ 1-R & 0 & R & 0 & 0 & 0 & 0 \\ 1-R & 0 & R & 0 & 0 & 0 & 0 \\ 0 & 0 & 0 & 1-R & R & 0 & 0 \\ 0 & 0 & 0 & 1-R & 0 & R & 0 \\ 0 & 0 & 0 & 1-R & 0 & R & 0 \\ 0 & 0 & 0 & 0 & 0 & 0 & 1 \end{array} \right) \end{array} .$$

For instance, the individual that has remained faithful to its site but was not captured at time $t - 1$ (first row **H**o) receives the state **oH+** if it is captured at t (second column) because it was not captured at $t - 1$ (hence the prefix **o**), remained faithful at t to the site occupied at $t - 1$ (dispersal status **H**), and was just captured (suffix +). On the other hand, if the same individual is not captured at t, it is uninformative whether it was captured at $t - 1$. It receives the state **Ho** (first column), meaning that it remained faithful (dispersal status **H**) and was not captured at t (suffix **o**).

The last step of multi-event CR models links events to states. In our case, each state corresponds to only one possible event (but one event can correspond to several states), making the event probabilities trivial:

$$\text{Event} = \begin{array}{c} \\ \text{Ho} \\ \text{oH+} \\ \text{+H+} \\ \text{Eo} \\ \text{oE+} \\ \text{+E+} \\ \text{D} \end{array} \begin{array}{c} \begin{array}{cccc} \mathbf{0} & \mathbf{1} & \mathbf{2} & \mathbf{3} \end{array} \\ \left(\begin{array}{cccc} 1 & 0 & 0 & 0 \\ 0 & 0 & 0 & 1 \\ 0 & 1 & 0 & 0 \\ 1 & 0 & 0 & 0 \\ 0 & 0 & 0 & 1 \\ 0 & 0 & 1 & 0 \\ 1 & 0 & 0 & 0 \end{array} \right) \end{array} .$$

Calculating the probability Pr of a capture history is straightforward. For instance, let us consider the first four occasions of the capture history illustrated in Fig. 2 and composed of the following four events (i.e., 3120). For simplicity, let us also assume that all parameters are constant and that the animal did not die at the fourth occasion. As events 3 and 0 can be associated with different states, we have four scenarios to estimate Pr(3120): (oE+, +H+, +E+, Eo) or (oE+, +H+, +E+, Ho) or (oH+, +H+, +E+, Eo), or (oH+, +H+, +E+, Ho). The addition of these four probabilities gives: $\Pr(3120) = [(1 - \pi)R^2S^3F(1 - F)^2\,(1 - R)] + [(1 - \pi)R^2S^3F^2\,(1 - F)\,(1 - R)] + [\pi\, R^2S^3F(1 - F)^2\,(1 - R)] + [\pi\, R^2S^3F^2(1 - F)\,(1 - R)]$, which gives: $\Pr(3120) = R^2S^3F(1 - F)\,(1 - R)$.

Goodness of fit (GOF) and model selection

GOF tests are not yet developed for multi-event models (Pradel et al. 2005). We therefore resorted to GOF tests for standard CR one-site models (Pradel et al. 2005) as implemented in program U-CARE (Choquet et al. 2009*a*). To do so, we simplified our data set by using only recaptures (coded 1) or non-recaptures (coded 0) of individuals (Sanz-Aguilar et al. 2011). This approach is conservative because in doing so we test a coarser model than the one we will be able to fit. If some lack of fit occurs, inference tools (standard errors, confidence intervals, and AIC values) can be adjusted by using a coefficient of overdispersion, $\hat{c}$.

Models were built and fitted using maximum-likelihood methods in program E-SURGE (Choquet et al. 2009*b*). Details can be found in the Appendix. Model selection was based on the Akaike information criterion corrected for small samples and overdispersion (QAIC_c; Burnham and Anderson 2002).

APPLICATION

Species and study sites

Breeding Tree Swallows are easily captured and manipulated, and tolerate high levels of nest disturbance, making them an exemplary model for studies in natura (Winkler et al. 2011). CR data were collected as part of a long-term study assessing the influence of spatiotemporal environmental heterogeneity on the breeding ecology of Tree Swallows in southern Québec, Canada (Ghilain and Bélisle 2008). The study was

TABLE 1. Model selection examining the effect of sex, memory and time on demographic parameters of Tree Swallows (*Tachycineta bicolor*) breeding in southern Québec, Canada.

Model	k	Deviance	QAIC$_c$	ΔQAIC$_c$	w_i
S(sex + time) F(memory + sex) R(time)	19	4306.18	2871.28	0.00	0.37
S(sex + time) F(memory × sex) R(time)	20	4304.23	2871.73	0.45	0.30
S(sex × time) F(memory × sex) R(time)	24	4293.92	2873.36	2.08	0.13
S(sex × time) F(memory × sex) R(sex + time)	25	4292.10	2874.20	2.92	0.09
S(sex) F(memory × sex) R(time)	14	4328.10	2875.58	4.30	0.04
S(time) F(memory × sex) R(time)	18	4316.63	2876.12	4.84	0.03
S(sex × time) F(memory × sex) R(.)	19	4315.27	2877.25	5.97	0.02
S(sex × time) F(memory × sex) R(sex)	20	4314.86	2879.01	7.73	0.01
S(.) F(memory × sex) R(time)	13	4339.33	2880.95	9.67	0.00
S(sex × time) F(memory × sex) R(sex × time)	29	4339.33	2880.95	9.67	0.00
S(sex + time) F(sex) R(time)	17	4329.32	2882.45	11.17	0.00
S(sex + time) F(memory) R(time)	18	4344.97	2894.77	23.49	0.00
S(sex + time) F(.) R(time)	16	4374.83	2910.36	39.08	0.00

Notes: Each model is defined by three parameters: survival probability (S), site fidelity probability (F), and recapture probability (R). The effects were tested alone, in addition (+), or in interaction (×) including the main effects. A constant parameter is represented by a dot. The number of parameters (k) and deviance were used to calculate the QAIC$_c$ (with $\hat{c} = 1.52$) and weight (w_i) of each model. ΔQAIC$_c$ gives the difference between the QAIC$_c$ value of the model and that of the best model (i.e., with the lowest QAIC$_c$).

initiated in 2004 and the CR data include recaptures until 2011, which represents 1999 individuals banded and captured at least once as breeders, of which 33% were males. The study area covers $\sim$10 200 km^2 and includes 40 farms (sites) separated by a distance to the nearest farm of 7.28 ± 0.57 km (mean ± SD) and a pairwise distance of 42.21 ± 21.09 km within a gradient of agricultural intensification. Each farm bears a transect composed of 10 nest boxes spaced by 50 m for a total of 400 nest boxes. Aside from these nest boxes, there are very few alternative nesting sites (i.e., natural cavities or nest boxes) in the study area. Although Tree Swallows defend a territory of a few meters around the nest, foraging during the chick-rearing period extends over a radius of a few hundred meters (Dunn and Hannon 1992, Dunn and Whittingham 2005). We thus used a 500 m radius to define the spatial scale of "nest box colonies" located on the farms of the study area (Ghilain and Bélisle 2008). The farm thus determines the basic unit for defining site fidelity ("Here" means captured on the same farm as the previous year), or otherwise dispersing to another site ("Elsewhere" means captured on a farm different from that of the previous year).

Effects on demographic parameters

We investigated the effect of time and sex on recapture (R) and survival (S) probabilities as well as that of memory on fidelity (F) probability through a sequential model selection procedure. We assessed R, S, and F in turn, while holding the most general structure on the two other parameters. At each step, the best parameterization of the focal parameter expressed through the model with the lowest QAIC$_c$ was selected to proceed with the next parameter. Regarding R, capture effort was relatively constant between years for females, but may have varied for males between years. Moreover, males were targeted and captured mostly during the chick-rearing period, whereas females were captured throughout the breeding season according to our protocol. Similarly, we tested the effect of time and sex on S because males are expected to survive better than females in passerines (Siriwardena et al. 1998), but the opposite in swallows (Siriwardena et al. 1998, Hallinger et al. 2011). Lastly, we focused on F, for which we investigated a sex effect to verify empirical evidence of a higher dispersal propensity for females in passerines (Greenwood and Harvey 1982, Winkler et al. 2011). In addition, we considered a memory effect to assess the potential dependence of dispersal on the previous biological state (H or E). Additive effects and interactions were considered, resulting in a total of 13 candidate models (Table 1). To accommodate model selection uncertainty, we resorted to model averaging to calculate parameter estimates and their associated unconditional standard errors (SE) based on QAIC$_c$ weights (w_i) using models for which $w_i \geq 0.01$ (Burnham and Anderson 2002). Except where noted otherwise, estimates are presented with their standard error.

RESULTS

We detected a lack of fit of the most complex model that we fitted to the data (global test: $\chi^2 = 47.06$, df = 31, $P = 0.03$). A closer inspection showed that this was due to a transience effect in females (component 3SR in Choquet et al. 2009*a*: $\chi^2 = 27.81$, df = 6, $P < 0.001$), which was accounted for by using a coefficient of overdispersion ($\hat{c}$) of 1.52. Models with $w_i > 0.01$ suggested an effect of time on recapture probability, of memory and sex on fidelity, and of time and sex on survival, with some uncertainty about the type of effect (interaction or additive effect) on fidelity and survival (Table 1). As expected, males showed a stronger site fidelity than females. Indeed, fidelity was estimated at 0.94 ± 0.04 for males and 0.70 ± 0.10 for females when a dispersal event occurred the year before, and at 0.99 ± 0.01 for males and 0.94 ± 0.02 for females otherwise.

Survival probability for females was lower than male survival and varied over time from 0.31 ± 0.03 to 0.53 ± 0.06 for females and from 0.40 ± 0.04 to 0.57 ± 0.09 for males (Fig. 3).

Recapture probabilities varied between 0.58 ± 0.07 and 0.86 ± 0.09 over time, for males and females pooled.

Finally, initial probabilities (probability of being in a particular state at first capture) were estimated at 0.51 ± 0.23 in state "Here," suggesting an equal proportion of individuals in each state at first capture. The high level of imprecision associated to this estimate is caused by the memory integrated in the state: when an individual enters in the population for the first time, it is impossible to define its state because the location of the previous year is unknown. This does not distort the other estimates as fidelity rates.

Discussion

We developed a multi-event CR model to estimate site fidelity and dispersal within and among numerous recapture sites, thereby allowing us to further quantify the influence of fine-scale spatiotemporal heterogeneity on these behaviors within landscapes of large extents. The widely used multisite CR modeling approach to estimating dispersal is limited in the number of sites that can be considered because it explicitly considers all possible transitions among all sites. As a consequence, these CR models are highly demanding in terms of data to accurately estimate the parameters (Lebreton and Pradel 2002), and even impossible to implement in practice if the number of sites is too high. For instance, our case study would have implied >1500 transitions among the 40 farms. By considering only two states (Here and Elsewhere) depending on the site occupied at $t-1$ and t, this issue was circumvented, therefore allowing the reliable and accurate estimation of site fidelity and dispersal among sites. Compared to the complex CR diffusion approach developed by Ovaskainen et al. (2008*a*, *b*), our proposal is a convenient and relatively easy method to implement in order to quantify dispersal in a large study area with numerous recapture sites.

Our case study with Tree Swallows illustrates well the benefits of using multi-event CR methods to estimate survival and breeding dispersal rates among numerous sites. In our study area, adult males showed a much higher mean survival rate than adult females in most years (0.40–0.57 vs. 0.31–0.53), a result that contrasts with apparent survival rate estimates reported in Saskatchewan (0.51 for both sexes; Shutler and Clark 2003), Massachusetts (0.40–0.48 for females; Custer et al. 2007), and Virginia (0.45–0.46 vs. 0.46–0.49; Hallinger et al. 2011), where no sex difference or a slightly higher survival rate for adult females was found. This result warrants more attention, as adult females in our study system have shown a significant decrease in body mass between 2005 and 2011, which may be indicative of the presence of an ecological stress that impacts females more strongly than males (Rioux-Paquette et al. *in press*). Despite also showing a greater interannual variability, which may result from a greater number of years, most of our yearly estimates fall within the 0.40–0.50 range reported elsewhere, at least for males. Regarding breeding dispersal, we found dispersal rates that were higher for females than for males, as in previous studies on Tree Swallows (Shutler and Clark 2003, Winkler et al. 2004) and other species (Greenwood and Harvey 1982). If we ignore the memory effect, we obtain dispersal rates similar to those found in New York State (females vs. males: 0.15 vs. 0.02 and 0.14 vs. 0.04 in Québec and New York, respectively). Yet, the spatial configuration of nest box networks varies considerably among studies, and such comparisons should be made cautiously.

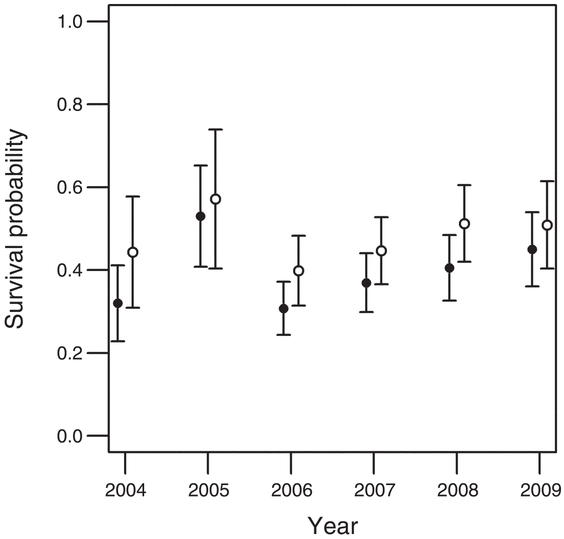

FIG. 3. Model-averaged annual survival probability (± 1.96 × unconditional SE) for female (solid circles) and male (open circles) Tree Swallows (*Tachycineta bicolor*) breeding in southern Québec, Canada, from 2004 to 2009. Note that survival over the last time interval of the study (2010 to 2011) was not estimable because there was not enough recapture at the end of the data set.

Our method also revealed individual heterogeneity, suggesting that some phenotypes may be more predisposed to disperse than others. Although some evidence of phenotype-dependent dispersal propensity is starting to accumulate (Clobert et al. 2009), memory effects on dispersal have been reported mostly in long-lived bird species (Hestbeck et al. 1991). Our case study provides the first evidence that such a phenomenon may occur in short-lived bird species. Being able to assess such individual heterogeneity in dispersal behavior is important, given that it has the potential to strongly influence the dynamics of spatially structured populations (Leimar and Norberg 1997, Clobert et al. 2009, Cote et al. 2010).

Our model can be extended to study dispersal into more detail. For example, the decision to disperse between breeding seasons is often associated with breeding success (Greenwood and Harvey 1982). Such an influence of individual annual breeding success on the decision to stay or leave a breeding site could be assessed by, for instance, considering the following states: "Here" after successful reproduction, "Here" after failed reproduction, "Elsewhere" after successful reproduction, and "Elsewhere" after failed reproduction. Analogously, our model could be modified to assess if dispersal propensity is constrained by the structure of the landscape in which sites are embedded ("Here" to illustrate after breeding in a highly connected landscape, otherwise "Elsewhere"; Bélisle 2005). Although this would imply amending the coding of events, these new models would allow easy and precise estimates of dispersal.

Although the case study dealt with birds, our approach can be used to investigate dispersal of any organisms amenable to CR monitoring protocols. For example, Casula (2006) addressed the determinants of fine-scale dispersal behavior of butterflies within a multisite CR framework, but had to restrict his analyses to a subset of four sites, a constraint that could have been avoided with our approach. Another instance in which our approach would be particularly relevant is the study of rodent movement behavior, which is usually conducted within trapping grids containing a large number (in the hundreds) of traps (sites), such as when addressing the infestation dynamics of a pathogen (Begon et al. 2003).

Despite the potential of our approach, it comes with some limitations. The first lies in the coding of the data that can be tedious, because one needs to consider the previous capture to determine each event. This step can nevertheless be made less cumbersome via some programming (see the R script provided in the Supplement). Second, in contrast with the approach of Ovaskainen et al. (2008*a*, *b*), it cannot explicitly make use of the distance (Euclidean, intervening landscape structure, or functional connectivity) between recapture sites to improve dispersal estimates. As a consequence, the fact that dispersal between two close or connected sites is more likely to happen than between two distant or "disconnected" sites is informative in estimating dispersal (Bélisle 2005), but cannot be used in our approach. It remains that dispersal distance is constrained by the position of recapture sites. Indeed, dispersal rates are likely to be overestimated when recapture sites are too close, and underestimated if too distant, as individuals are forced to remain on their site. For this reason, we emphasize that our model should be used only when the extent of the study area is greater, and the distance among recapture sites is less, than the mean dispersal distance of the species of interest. Moreover, the spatial scale defining sites, and thus dispersal events, must be clearly specified and taken into account when comparing dispersal rates among studies in order to avoid biases resulting from mismatched spatial scales. Third, the way in which we have defined the states puts an emphasis on behavior (staying vs. leaving) rather than explicitly using the site of departure or arrival. This is particularly problematic for models incorporating a memory effect in which we cannot discriminate whether an individual dispersed between the two same sites from $t-1$ to $t+1$ or moved to a new site at each time step (i.e., visited three different sites). Biologically, the former behavior would suggest fidelity with occasional movements caused by unavailable breeding sites, whereas the latter would characterize the phenotype of a disperser likely to play a role in extinction–colonization processes among local populations. The solution would be to build a model distinguishing sites already visited from first capture to t from those new at $t+1$.

In conclusion, we developed a CR model to estimate fidelity and dispersal in a finely spatially described landscape. The main feature of our method relies on well-adopted CR models and is relatively simple to implement in existing software. We hope that this new approach will provide new insights into the mechanisms underlying dispersal in free-ranging populations.

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SUPPLEMENTAL MATERIAL

Appendix

Implementation of the new dispersal model in E-SURGE (*Ecological Archives* E095-205-A1).

Supplement

R code to build the data set for analyses in E-SURGE (*Ecological Archives* E095-205-S1).