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RESEARCH ARTICLE

Using local dispersal data to reduce bias in annual apparent survival and mate fidelity

Caz M. Taylor,[1]* David B. Lank,[2] and Brett K. Sandercock[3]

[1] Department of Ecology and Evolutionary Biology, Tulane University, New Orleans, Louisiana, USA
[2] Centre for Wildlife Ecology, Department of Biological Sciences, Simon Fraser University, Burnaby, British Columbia, Canada
[3] Division of Biology, Kansas State University, Manhattan, Kansas, USA
* Corresponding author: caz@tulane.edu

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ABSTRACT

In mark–recapture studies conducted on fixed-area study sites, apparent (or "local") survival (ϕ) is the product of the probabilities of true survival (S) and site fidelity to the sampling area (F). If marked individuals permanently emigrate from the study site, apparent survival will be biased low relative to true survival. Similarly, estimates of mate fidelity will be biased high because site fidelity is typically higher for individuals that reunite with their previous mates than among pairs that divorce. Here, we develop a method for calculating site fidelity that takes plot boundaries into account, based on a dispersal model estimated from local movements within a fixed study site. We use dispersal estimates to adjust apparent survival and mate fidelity for the effects of short-distance movements out of a fixed area. We demonstrate our method with a retrospective analysis of a published study of 2 species of sandpipers breeding sympatrically at a field site in western Alaska. Estimates of survival probability increased by 0.01–0.03 for males and 0.07–0.08 for females in both species. The larger adjustments for females were expected based on their longer local dispersal movements. Adjusted mate fidelity estimates were lower than the original estimates by 0.04–0.07. Use of local movement data to estimate site fidelity cannot account for permanent emigration due to long-distance movements and, if such movements occur, our adjusted estimates of ϕ remain a function of true survival and site fidelity. Nevertheless, our method can reduce bias in demographic parameters resulting from local dispersal movements, improving estimates of annual survival and mate fidelity for use in demographic models.

Keywords: apparent survival, breeding dispersal, demography, live-encounter data, site fidelity

Uso de datos de dispersión local para reducir el sesgo en la estimación de la supervivencia aparente anual y la fidelidad a la pareja

RESUMEN

En los estudios de marcado-recaptura que se hacen en sitios de estudio de área fija, la supervivencia aparente o local (ϕ) es el producto de las probabilidades de supervivencia verdadera (S) y de fidelidad al área muestreada (F). Si los individuos marcados emigran permanentemente del sitio de estudio, la supervivencia aparente estará sesgada hacia valores bajos en comparación con la supervivencia verdadera. De forma similar, los estimados de fidelidad a la pareja estarán sesgados hacia valores altos porque la fidelidad al sitio es típicamente mayor para los individuos que se reúnen con sus parejas previas que entre parejas que se divorcian. En este trabajo desarrollamos un método para calcular la fidelidad al sitio que tiene en cuenta los límites del área de estudio y que se basa en un modelo de dispersión estimado a partir de movimientos locales en un sitio de estudio determinado. Usamos estimados de dispersión para ajustar la supervivencia aparente y la fidelidad a la pareja a los efectos de los movimientos de corta distancia por fuera de un área fija. Demostramos el uso de nuestro método con un análisis retrospectivo de un estudio publicado sobre dos especies de playeros que se reproducen simpátricamente en un sitio de campo en Alaska occidental. Los estimados de la probabilidad de supervivencia se incrementaron 0.01–0.03 para machos y 0.07–0.08 para hembras en ambas especies. Los mayores valores ajustados para las hembras se esperaban debido a sus mayores movimientos de dispersión local. Los estimados ajustados de fidelidad a la pareja fueron 0.04–0.07 más bajos que los estimados originales. El uso de datos de movimiento local para estimar la fidelidad al sitio no puede tener en cuenta la emigración permanente debido a movimientos de larga distancia. Si tales movimientos ocurren, nuestros estimados ajustados de ϕ aún son una función de la supervivencia verdadera y de la fidelidad al sitio. Sin embargo, el método que proponemos puede reducir el sesgo en los parámetros demográficos que resultan de los movimientos locales de dispersión, mejorando los estimados de supervivencia anual y de fidelidad a la pareja para su uso en modelos demográficos.

Palabras clave: datos en tiempo real, demografía, dispersión reproductiva, fidelidad al sitio, supervivencia aparente

INTRODUCTION

Sound management and conservation decisions for bird populations require accurate estimates of demographic parameters (Sillett and Holmes 2002, Sandercock 2006). Robust estimates of annual survival are particularly important because rates of population change in birds are often sensitive to the mean and variance of juvenile or adult survival (Oli and Dobson 2003, Stahl and Oli 2006). Adult survival of nongame birds is often estimated from encounter histories of marked individuals at fixed-area breeding study sites, using mark–recapture techniques. The Cormack–Jolly–Seber (CJS) statistical model provides estimates of apparent survival (ϕ) adjusted for the probability of encounter (p; Lebreton et al. 1992, Sandercock 2006). Estimation of apparent annual survival from recaptures and resightings at a single study site is only possible if some proportion of a population exhibits site fidelity, which we define as the probability that a marked individual returns to, or remains on, a fixed-area study site in consecutive years. However, it is impossible to estimate mortality separately from permanent emigration with models based solely on live-encounter data, and the estimated parameter ϕ is thus considered "apparent" or "local" survival. Expressed symbolically, apparent survival (ϕ) is the product of 2 probabilities, true survival (S) and site fidelity (F), and the CJS model cannot separate the 2 parameters without auxiliary data (Powell et al. 2000, Sandercock 2006, Schaub and Royle 2013). Apparent survival provides a lower bound on the estimate of true survival, but true survival cannot be calculated without a separate estimate of site fidelity. In a review of methods and models to estimate demographic parameters, Sandercock (2006) described the inability to separate S from F as one of the greatest drawbacks to estimating survival rates from live-encounter data.

Site fidelity, apparent survival, and local dispersal movements often differ among demographic classes in a population. For migratory birds, return rates to a study site ($rr = \phi\ p$) and estimates of apparent survival (ϕ) are often different between males and females (Clarke et al. 1997, Arlt and Pärt 2008). From mark–recapture studies of socially monogamous, migratory birds conducted at breeding sites, apparent survival and return rates are typically lower for females than for males (Holmes 1971, Oring and Lank 1984, Sandercock and Gratto-Trevor 1997, Flynn et al. 1999, Sandercock et al. 2000, 2005). Sexual differences in ϕ have frequently been attributed to variation in site fidelity rather than differences in true survival (Sillett and Holmes 2002). Sexual differences arise because breeding dispersal distances between nests in consecutive years are often greater for females than males, at least in male-territorial species (Greenwood 1980, Jackson 1994). Longer breeding dispersal movements should lead to more females than males moving outside of a fixed-area study site, producing lower local site fidelity among adult females than males ($F_f < F_m$), which potentially accounts for sexual differences in apparent survival ($\phi_f < \phi_m$; Sandercock et al. 2000). Longer female movements may be caused by usurpation of territories or mates by early returning females (Soikkeli 1970, Holmes 1971; but see Arlt and Pärt 2008). Hence, females that change mates often have longer breeding dispersal distances than females that reunite with the same mate from the previous year (Ens et al. 1993, Flynn et al. 1999, Sandercock et al. 2000).

Differences in local site fidelity between sexes and among individuals of different pairing status might also bias estimates of mate fidelity. Mate fidelity is often calculated from live-encounter data as the proportion of returning pairs that reunite (Ens et al. 1993, Black 1996). In contrast to annual survival, mate fidelity may be overestimated relative to its true value because the probability of detecting a reuniting pair is greater than the probability of detecting two individuals that have changed mates. This occurs since (1) two nests rather than one must be located within a study site, and (2) widowed or divorced individuals tend to disperse farther and are more likely to leave the study area than individuals of reuniting pairs (Sandercock et al. 2000).

The goal of this paper is to present a general approach that first estimates local site fidelity taking local dispersal into account, and then uses the estimate to reduce negative bias in estimates of apparent survival and positive bias in mate fidelity relative to true values. For context, we categorize previous attempts to address this issue into 4 basic approaches that use information at different spatial scales: multiple sites, buffer zones, balanced dispersal and immigration, and local dispersal distributions.

The most powerful approach is to include other types of encounter data from multiple sampling sites or large geographic areas (Lebreton et al. 1992, Sandercock 2006). If recoveries of markers are available from dead individuals or resightings are available from multiple sampling areas in a larger geographic region, joint models for live encounter, dead recovery, and resighting data can be used to obtain separate estimates of true survival and site fidelity (Barker et al. 2004, Horton and Letcher 2008). Joint models using dead recovery data have been useful for game species and inclusion of auxiliary resighting data and technologies can make this approach practical for nongame species as well. Powell et al. (2000) combined recapture and relocation with radio-telemetry to estimate short-term survival and site fidelity of songbirds, whereas LeDee et al. (2010) estimated true survival and breeding-site fidelity by combining capture data with extensive resighting data for individually marked and highly visible plovers.

A second approach is to increase the size of a study area or add a buffer zone to detect longer dispersal events (Jackson 1994, Cilimburg et al. 2002, Zimmerman et al. 2007, Cooper et al. 2008). Increasing the study area by adding buffer zones can be effective in reducing biases in survival, but it is often not feasible to search expanded areas with sufficient intensity. A third approach, which has been used to improve juvenile survival estimates, sets local emigration rates ($1 - F$) as equal to observed rates of local immigration (Baker et al. 1995, Cooper et al. 2008). Constraints on movement rates make the assumption that population numbers are stable, which may not always be reasonable (Hitchcock and Gratto-Trevor 1997). The model also requires estimates of immigration, which are not always straightforward to obtain, especially if reliable methods for aging individuals are not available (Cooch et al. 2001).

The final approach involves estimating the probability that an individual will disperse outside a study area based on a generalized or simulated function, which may be derived from local movements within a study area and used to adjust apparent survival. Marshall et al. (2004) included distance of a resighted individual from the boundary of the study plot as covariate for the recapture probability p in a CJS model. However, the authors found that even in applications to simulated data, the models that gave the most accurate estimates of survival were greatly affected by model selection techniques. Three recent papers have integrated spatial data directly into CJS models by using a normal or other distributions to model the probability of moving a particular distance (dispersal kernel), and using the dispersal kernel to estimate emigration probabilities from the study area. The likelihood of observations of recapture histories and dispersal distances depends on survival, emigration, and probability of recapture (Gilroy et al. 2012, Ergon and Gardner 2013, Schaub and Royle 2013). Joint models of mark–recapture data and locations can bring estimates of apparent survival closer to true survival, and will be useful in many future studies. However, spatially explicit models cannot be applied retrospectively if location data are not available for each detection record. Estimates of apparent survival and mate fidelity will also remain biased if imperfect detection of long-distance dispersers remains an issue (Schaub and Royle 2013).

Here, we present a new method that uses local dispersal data to adjust estimates of apparent survival and mate fidelity that have been derived from standard CJS models. We do not use a spatial CJS model because our method is intended to be applied retrospectively to cases where individual location data may not be available. Our method also differs from previous approaches by providing the flexibility to address situations where site fidelity is heterogeneous among different social classes of individuals. Specifically, we consider cases where site fidelity differs between sexes and we take mate fidelity into account. To reduce bias in apparent survival estimates we do not just simply divide ϕ by estimated F. Instead, we estimate F separately for 3 classes of mating status: pairs that reunited, males that changed mates, and females that changed mates. We then adjust estimates of survival and mate fidelity for all females and for all males. Another difference in our method is that we do not use the "raw" dispersal data directly as observations in a spatial CJS model. Instead, we make corrections using the dispersal distance distribution to reduce bias. Dispersal distances from fixed-area sites are expected to be biased low since short distance events are detected with higher probability than long-distance movements (Barrowclough 1978, Koenig et al. 1996).

We demonstrate the utility of our method with a retrospective analysis of a published study of Western (*Calidris mauri*) and Semipalmated sandpipers (*C. pusilla*; Sandercock et al. 2000) breeding sympatrically. These 2 species of arctic-breeding shorebird have a male-territorial system and show high levels of adult site fidelity and mate fidelity. Dispersal distances between nest sites in consecutive years showed that females of both species move longer distances than males, and that individuals not paired with their mate from the previous year moved longer distances than reuniting pairs (Sandercock et al. 2000). Our example illustrates that adjustments have substantial but different effects on estimates of apparent survival and mate fidelity in males compared to females.

METHODS

Example Study System

Mate fidelity, apparent survival, and dispersal distances were previously published for Western Sandpipers and Semipalmated Sandpipers at Nome, Alaska (Sandercock et al. 2000). The 2 species of sandpipers were studied at a 4-km^2 study site 21 km east of Nome, Alaska (64°20′N, 164°56′W), during a 4-year period from 1993 to 1996. Sandercock et al. (1999) described the study protocols in detail. The study area consisted of low tundra ridges, mud flats, and shallow freshwater ponds, and was searched daily for nesting birds by 3 or 4 observers for a 6–8 week period each summer. The study area was part of a much larger contiguous region of suitable habitat. For this analysis, we made the simplifying assumptions that the study area was circular, homogeneous, and surrounded on all sides by suitable nesting habitat. The encounter data used are detection records for marked birds recaptured at nest sites.

Modeling Breeding Dispersal

Dispersal data based on mark–recapture studies in a fixed study area are known to underestimate the frequency of long-distance movements because the probability of observing a dispersal event is inversely proportional to dispersal distance (Koenig et al. 1996). Analytical methods for correcting dispersal distributions are based on the premise that the expected number of dispersal events within a range of distances is the observed number of events divided by the probability of detecting a dispersal event in that range. In a homogeneous landscape with equal detection effort throughout the site, the probability that a dispersal event of a given distance will remain within the study areas (and therefore be detected) can be calculated by drawing a circle with a radius of that distance centered on each point in the sampling area and then summing the area of overlap between all circles and the study area. Barrowclough (1978) made the simplifying assumption that a sampling area is homogeneous and circular, and derived a general formula for the probability of detection of dispersal events. In the case of a heterogeneous landscape, Baker et al. (1995) showed that it is possible to estimate the probability of a dispersal event based on a spatially explicit map of the landscape, including and surrounding the sampling area, in which grid cells are classified as either suitable or unsuitable habitat. We used Barrowclough's approach to demonstrate corrections for bias in a retrospective analysis of published work, but a spatially explicit approach could be used for heterogeneous study sites if additional information were available.

We modeled the 4-km^2 study site at Nome as a circle with a radius of 1,128 m. Breeding dispersal is defined here as the Euclidean distance between nests of an individual in consecutive years. In the original study, breeding dispersal data were presented as the proportion of individual sandpipers that dispersed in 6 distance categories (0 m or reuse of the same nest cup, 1–100 m, 101–200 m, 201–300 m, 301–400 m, and 401–2,256 m) and were presented separately for 3 social classes of birds: reunited pairs, females that changed mates, and males that changed mates (Figure 1; Sandercock et al. 2000). We computed correction factors for each of these distance intervals for a circle of radius 1,128 m (Barrowclough 1978). The probabilities that a dispersing individual remained on the study area were 1.00, 0.97, 0.92, 0.86, 0.80, and 0.53 for the 6 distance intervals, respectively. We divided the fraction of observations in each interval by the probability of detection of dispersal, and re-normalized the frequencies to produce a "Barrowclough-corrected" distribution of dispersal events (Figure 1). The Barrowclough-corrected distribution assumes a uniform search effort throughout the study area, which was the case in the original field study.

After dispersal data have been corrected for the probability of detection, estimates of dispersal distance are still biased toward shorter distances because the probability of detection for dispersing individuals that move farther than the diameter of the study area is zero and unobserved dispersal events cannot be "corrected." We addressed this source of bias by assuming that the dispersal data were generated from a continuous infinite dispersal kernel. Thus, the tail of the dispersal kernel provides an estimate for the probability of long-distance but unobserved dispersal events. Mechanistic competition models usually assume that dispersal kernels are geometrically distributed (Waser 1985). We modeled the probability of dispersal of distance x as an exponential distribution, which is the continuous-space analog to the discrete geometric distribution. The dispersal kernel $K(x)$ or the cumulative distribution of dispersal distances X with a mean dispersal distance μ is given by:

$$\Pr(X \leq x) = K(x) = 1 - e^{\frac{-x}{\mu}} \tag{1}$$

The probability of dispersal for an interval of distances between x_1 and x_2 is then:

$$\Pr(x_1 < X < x_2) = K(x_2) - K(x_1) = e^{\frac{-x_1}{\mu}} - e^{\frac{-x_2}{\mu}} \tag{2}$$

From the empirical dispersal data, we calculated a mean dispersal distance (μ) for each social class of sandpipers (females that had changed mates, μ_{cf}, males that had changed mates, μ_{cm}, and reunited pairs, μ_{pair}) by finding the best fit of the exponential kernel to the Barrowclough-corrected distribution. We calculated the value of μ that gave the minimum sum of squared differences between the distribution predicted by the dispersal kernel and the Barrowclough-corrected distributions. We used parametric bootstrapping to calculate standard errors for site-fidelity estimates. We first generated 1,000 bootstrapped datasets of the same size as the original dispersal data from an exponential distribution with the mean dispersal distance estimated from the data. For each bootstrapped dataset, we re-fit an exponential distribution to obtain 1,000 new estimates of mean dispersal (μ_{cf}, μ_{cm}, μ_{pair}; Table 1). All statistics are reported as means ± 1 SE.

For both species of sandpipers, females that changed mates dispersed farther than males that changed mates or reuniting pairs. The best-fit mean dispersal distance among females that changed mates was 310 ± 66 m for Western Sandpipers and 431 ± 226 m for Semipalmated Sandpipers. Among males that changed mates, mean dispersal distance was 82 ± 18 m for Western Sandpipers and 56 ± 17 m for Semipalmated Sandpipers. For reunited pairs of both species, mean dispersal distance was similar at 48 ± 18 m for Western Sandpipers and 47 ± 14 m for Semipalmated Sandpipers (Table 1, Figure 1). The errors on mean dispersal distances were large because of small sample sizes, but females that changed mates were clearly dispersing farther than males that changed mates or reunited pairs (Table 1, Figure 1).

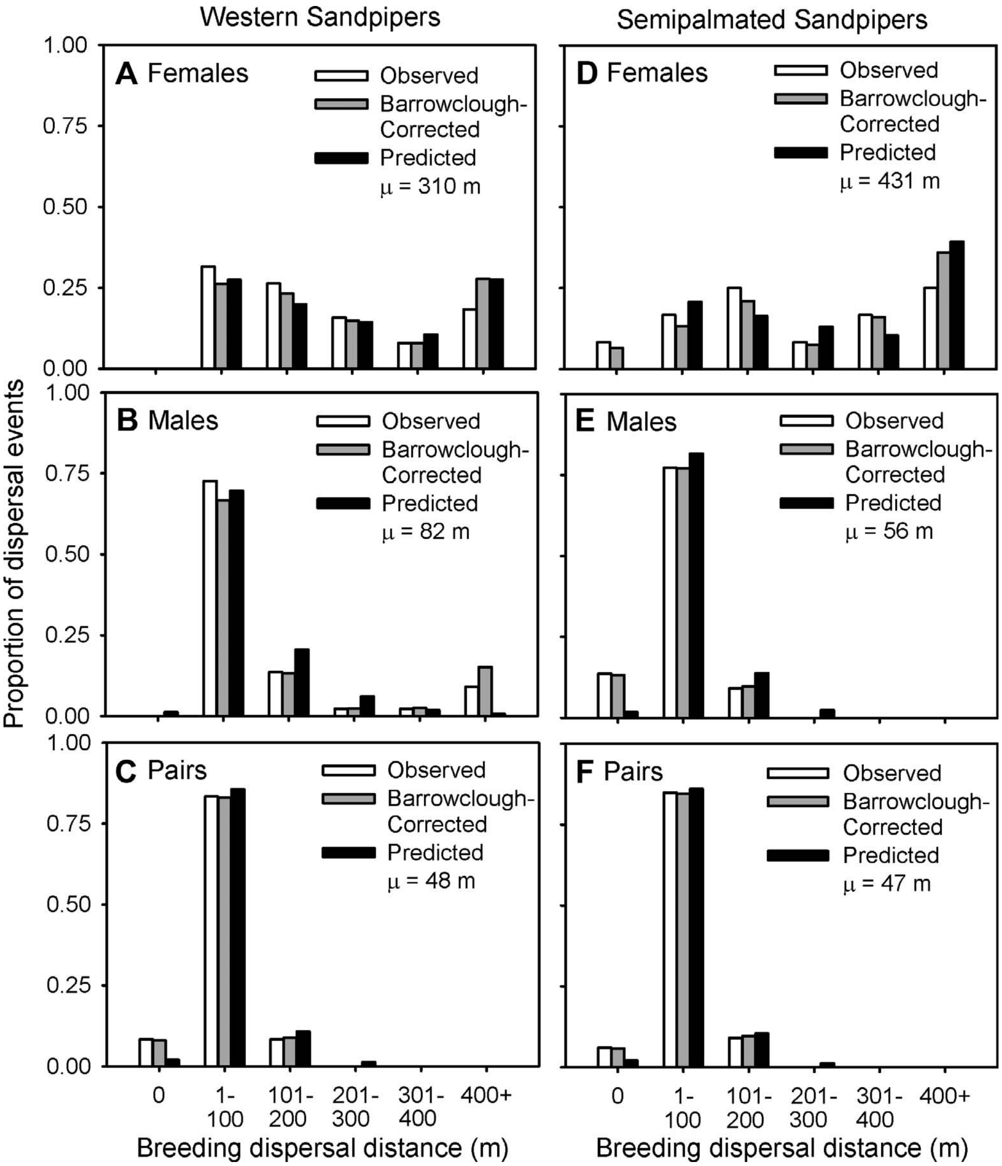

FIGURE 1. Proportion of breeding dispersal events among 3 social classes (females that changed mates, males that changed mates, and reuniting pairs) of Western Sandpipers (**A**, **B**, **C**) and Semipalmated Sandpipers (**D**, **E**, **F**). White bars are the original dispersal data presented by Sandercock (2000: figure 1). Gray bars are the dispersal data corrected using the method of Barrowclough (1978). Black bars are the proportion of dispersal events in each range as predicted by the exponential distribution with mean μ that best fit the corrected data.

Calculation of Site Fidelity Based on Dispersal Model

A breeding adult with a nest located at distance r from the center of a study area with radius R will disperse the following year in a random direction θ if habitat quality is homogeneous (Figure 2). The distance x from the nest to the edge of a circular study area is given by:

$$x(\theta, r) = -r\cos\theta + \sqrt{R^2 - r^2\sin^2\theta} \tag{3}$$

The probability of a dispersal event taking the individual outside the study area is:

$$P(X > x(\theta, r)) = 1 - K(x(\theta, r)) \tag{4}$$

where $K(x)$ is the probability of short-distance dispersal less than distance x (Equation 1). If nests are evenly distributed over the study area, the probability of a dispersal event moving outside the study area is obtained

TABLE 1. Original estimates of median breeding dispersal distances, mean dispersal distance estimated by fitting an exponential dispersal distribution (μ), and mean site fidelity for each social class (*F*). Standard errors were derived from bootstrapping (see text).

Species	Median dispersal distance (m)	Dispersal distance (m) (mean ± SE)	Site fidelity (mean ± SE)	Least sum of squares (fit of dispersal kernel to data)
Western Sandpipers				
Females that changed mates	157	310 ± 66	0.829 ± 0.034	0.00196
Males that changed mates	48	82 ± 18	0.954 ± 0.010	0.0280
Reunited pairs	38	48 ± 18	0.973 ± 0.001	0.00469
Semipalmated Sandpipers				
Females that changed mates	203	431 ± 226	0.767 ± 0.095	0.0185
Males that changed mates	41	56 ± 17	0.968 ± 0.010	0.0171
Reunited pairs	38	47 ± 14	0.973 ± 0.008	0.00181

by summing $P(X > x)$ for every possible point in the circle and every possible dispersal direction at each point. Site fidelity (F), or the probability of a dispersal event resulting in a nest remaining inside the study area, is the complement of the probability of leaving the study area, such that:

$$F = 1 - \frac{1}{\pi R^2}\int_0^{2\pi}\int_0^R 2\pi r(1 - K(\theta, r))drdy \qquad (5)$$

We used numerical integration to calculate separate estimates of site fidelity for males that changed mates (F_{cm}), females that changed mates (F_{cf}), and reuniting pairs (F_{pair}; Table 1). In both species, estimated site fidelity was high for males that changed mates and reuniting pairs, but lower for females that changed mates (Western Sandpipers: $F_{\mathrm{cm}} = 0.95 \pm 0.010$, $F_{\mathrm{pair}} = 0.97 \pm 0.010$, $F_{\mathrm{cf}} = 0.83 \pm 0.034$; Semipalmated Sandpipers: $F_{\mathrm{cm}} = 0.97 \pm 0.010$, $F_{\mathrm{pair}} = 0.97 \pm 0.008$, $F_{\mathrm{cf}} = 0.77 \pm 0.095$; Table 1). Standard errors were estimated by generating an estimate of site fidelity for each social class (F_{cf}, F_{cm}, F_{pair}) from each of the 1,000 bootstrapped mean dispersal distances (μ_{cf}, μ_{cm}, μ_{pair}; see above; Table 1).

Adjustment of Mate Fidelity and Apparent Survival Estimates

The probability of divorce in socially monogamous birds is likely to be underestimated for 2 reasons. First, detection of a reunited pair requires detection of a single nest instead of 2 nests for a pair of divorced individuals. Second, both individuals that changed mates, but especially females, disperse farther and have lower site fidelity than reuniting pairs (Sandercock et al. 2000).

The probability of detecting a reuniting pair is given by pF_{pair}, and the probability of detecting 2 nests for both members of a divorced pair is $p^2F_{\mathrm{cf}}\,F_{\mathrm{cm}}$ where p = probability of detection of the nest for a returning marked bird, F_{pair} is the site fidelity of a reuniting pair, and F_{cf}, F_{cm} are the site fidelities of females that changed mates and males that changed mates, respectively. In our example, for the value of p, we used the individual probability of encounter calculated from the CJS analysis and pooled for the sexes (Western Sandpiper: 0.801 ± 0.060; Semipalmated Sandpiper: 0.668 ± 0.056; table 5 in Sandercock et al. 2000). The individual probabilities of detection may be biased estimates of nest detection for reuniting pairs since the CJS model that was used to generate the estimate included an assumption that detection probabilities of individuals were independent. Although individuals in this study were generally detected at nests, we do not believe this bias is substantial in this study system.

If mate fidelity (m) is defined as the proportion of pairs that reunite when both mates return and ($1 - m$) is the proportion of pairs that change mates, then an adjusted estimate of mate fidelity (m_{adj}) can be calculated as:

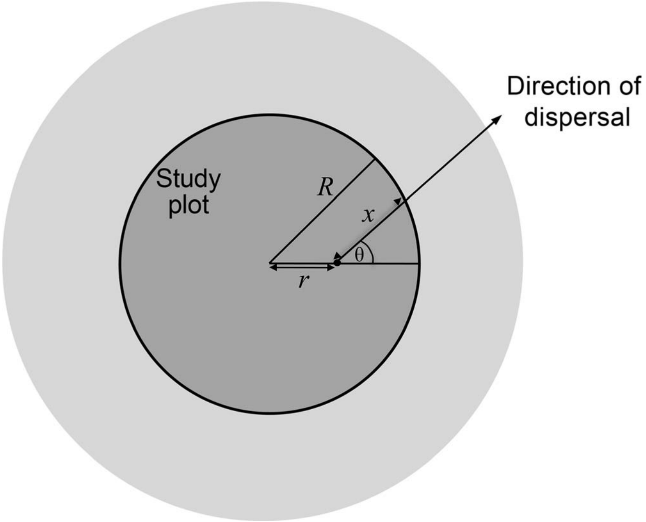

FIGURE 2. A dispersal event in direction θ from a nest site at distance *r* from the center of a circular study area with radius *R*. The probability that a dispersal event will take the individual outside the study area is the probability that the dispersal distance is greater than distance *x*, where *x* is given by Equation 3. The dark gray area represents the study area and the surrounding light gray area represents suitable nesting habitat outside the study area.

TABLE 2. Original estimates of apparent survival ϕ from Sandercock et al. (2000), adjusted survival (S), and sex-specific site fidelity (F).

Sex	Annual interval	$\phi \pm 1$ SE	$S \pm 1$ SE	$F \pm 1$ SE
Western Sandpipers				
Females	1993–1994	0.592 ± 0.067	0.672 ± 0.078	0.881 ± 0.026
	1994–1995	0.548 ± 0.070	0.624 ± 0.080	0.878 ± 0.025
Males	1993–1994	0.616 ± 0.064	0.641 ± 0.065	0.961 ± 0.008
	1994–1995	0.574 ± 0.067	0.596 ± 0.089	0.961 ± 0.008
Semipalmated Sandpipers				
Females	1993–1994	0.558 ± 0.079	0.620 ± 0.096	0.900 ± 0.042
	1994–1995	0.631 ± 0.096	0.691 ± 0.108	0.913 ± 0.040
Males	1993–1994	0.702 ± 0.067	0.723 ± 0.066	0.971 ± 0.006
	1994–1995	0.767 ± 0.077	0.790 ± 0.078	0.971 ± 0.006

$$m_{\mathrm{adj}} = \frac{m/pF_{\mathrm{pair}}}{m/pF_{\mathrm{pair}} + (1-m)p^2F_{\mathrm{cf}}F_{cm}} \quad (6)$$

Our adjustment accounts for the differences in site fidelity among birds of different social class, as well as the higher probability of detecting one joint nest of a reunited pair (p) versus the probability of detecting 2 separate nests of a divorced male and female pair (p^2).

We calculated overall sex-specific site fidelity for all social classes combined. If the mate survives, the site fidelity of females will be F_{pair} with probability m_{adj} and F_{cf} with probability $(1 - m_{\mathrm{adj}})$. The site fidelity of all females combined is given by:

$$F_{\mathrm{f}} = S_{\mathrm{m}}m_{\mathrm{adj}}F_{\mathrm{pair}} + S_{\mathrm{m}}(1 - m_{\mathrm{adj}})F_{\mathrm{cf}} + (1 - S_{\mathrm{m}})F_{\mathrm{cf}} \quad (7)$$

and the site fidelity of all males is given by:

$$F_{\mathrm{m}} = S_{\mathrm{f}}m_{\mathrm{adj}}F_{\mathrm{pair}} + S_{\mathrm{f}}(1 - m_{\mathrm{adj}})F_{\mathrm{cm}} + (1 - S_{\mathrm{f}})F_{\mathrm{cm}} \quad (8)$$

where S_{f} and S_{m} are the adjusted survival probabilities of females and males, and the 3 terms correspond to reuniting pairs, divorced individuals with surviving mates, and widowed individuals with dead mates. The available estimates of apparent survival from CJS models are a product of both adjusted survival and site fidelity due to local movements:

$$\phi_{\mathrm{f}} = S_{\mathrm{f}}F_{\mathrm{f}} \quad (9)$$

$$\phi_{\mathrm{m}} = S_{\mathrm{m}}F_{\mathrm{m}} \quad (10)$$

We solved the system of equations (6 to 10) to calculate mate fidelity (m_{adj}), site fidelity of females and males (F_{f} and F_{m}), and adjusted survival probabilities for females and males (S_{f} and S_{m}). We used parametric bootstrapping to calculate standard errors for m_{adj}, F_{m}, F_{m}, S_{f}, and S_{m}. We generated 1,000 random values for F_{cm}, F_{cf}, and F_{pair}, m, p, ϕ_{m}, and ϕ_{f} and re-solved Equations 6–10 for each set of values. F_{cm}, F_{cf}, and F_{pair} were sampled with replacement from our bootstrap distributions, whereas m was sampled from a beta distribution. Mean mate fidelity was the total proportion of pairs (where both members returned) that reunited over the 4 years of the original study (table 1 in Sandercock et al. 2000). The standard error was calculated as the square root of $m(1 - m)/N$, where N is the total number of pairs and m is the mean, and assumes that the number of reuniting pairs is a binomially distributed random number. p, ϕ_{m}, and ϕ_{f} were also sampled from beta distributions with means and standard errors as reported in the original study. Means and SE of ϕ_{m} and ϕ_{f} for each year are shown in Table 2 along with the resulting estimates of F_{m}, F_{m}, S_{f}, and S_{m} for each time interval.

RESULTS

For Western Sandpipers, the original estimate of mate fidelity pooled over the 3 years of the study was 0.667 ± 0.078 (24 of 36 pairs; Sandercock et al. 2000) and our adjusted estimate was reduced to 0.566 ± 0.089. For Semipalmated Sandpipers, mate fidelity was originally estimated as 0.943 ± 0.039 (33 of 35 pairs) and our adjusted estimate was similar at 0.89 ± 0.072. The magnitude of the adjustments of survival, or the difference between apparent and adjusted survival, were larger for females than males because females disperse farther and therefore had lower site fidelity than males. For Western Sandpipers, adjusted survival was 0.02–0.03 higher for males and 0.08 higher for females than the original estimates of apparent survival. Estimated site fidelity was higher for males (~0.96) than for females (~0.88) in Western Sandpipers (Table 2). For Semipalmated Sandpipers, adjusted survival of males was 0.02 higher and for females 0.06 higher than the original apparent survival, and estimates for site fidelity were ~0.97 for males and 0.90–0.91 for females (Table 2).

DISCUSSION

We present a new quantitative approach for estimating and adjusting mark–recapture estimates of annual apparent survival (ϕ) and mate fidelity (m) for variation in site fidelity (F). Using distributions of within-study site dispersal distances and estimates of mate fidelity for different social classes of birds, we estimated the magnitude of local dispersal beyond fixed site boundaries and adjusted our estimates of apparent survival accordingly. Our method reduces bias in apparent survival such that adjusted estimates for different sexes are less biased relative to one another and all estimates more closely approach true survival, an important parameter for demographic models.

Our approach still faces one fundamental limitation with respect to estimating true survival. Use of a dispersal kernel accounts for some movements beyond the boundaries of a fixed-area study plot but may still fail to account for long-distance permanent emigration (Schaub and Royle 2013). Our approach will thus be most useful when most breeding dispersal distances are short relative to the dimensions of a fixed-area study plot and larger-scale movements are rare. Local movements are common in field studies of territorial birds, as shown when effective study area has been expanded by increased search effort, or by use of genetic or radio-telemetry methods (Cilimburg et al. 2002, Hansson et al. 2002, Hosner and Winkler 2007). The limitation could also be addressed if long-distance dispersal data were available from dead recoveries, radio telemetry, or other sources. If the probabilities or mechanisms of long-distance movements and permanent emigration were known, simulation models could be developed to estimate the degree of bias remaining in estimates from our model or others. Unfortunately, such mechanisms are not currently known, but could follow with development of new tracking technologies. Another limitation of our approach is that it does not include adjustments for temporary emigration, when an individual disperses outside the study site for one or more years but then moves back inside in a future year. In a 4-year study of short-lived birds, we expected that the probability of temporary emigration events to be negligible, but they might be important to the calculation of site fidelity in long-term studies of vertebrates with intermittent breeding. With a large number of temporary emigrants in a sample, our method would underestimate site fidelity and should be extended by adjusting for the probability of temporary emigration, a parameter that can be estimated with robust design models (Kendall et al. 1997, Ergon and Gardner 2013).

One advantage of our approach is that it can be applied to previously published studies if movement data are available, or if a dispersal distribution can be estimated from independent sources. Our method thus does not require that spatial information be associated with specific encounter records, as do spatially explicit CJS models (Gilroy et al. 2012, Ergon and Gardner 2013, Schaub and Royle 2013). In our retrospective analysis of a published study of 2 species of sandpipers, apparent annual survival increased by 0.06 to 0.08 for female sandpipers, and 0.01 to 0.03 for males (Table 2). A greater increase in estimates of female survival was expected from their longer local dispersal distances. For Semipalmated Sandpipers, males retained higher estimated annual survival, but the sex difference was smaller than the estimates in the original study. For Western Sandpipers, our adjusted female annual survival was higher than our adjusted male survival, and opposite to the pattern of the original apparent survival estimates.

We can gain perspective on the utility of our adjusted survival estimates by comparing the values with apparent survival reported elsewhere. For Western Sandpipers, another breeding study, in the Yukon-Kuskokwim Delta, also reported higher male than female apparent survival ($\phi = 0.78 \pm 0.04$ for males and 0.65 ± 0.05 for females; Johnson et al. 2010), consistent with the pattern at Nome. A more informative comparison is with survival estimates from nonbreeding sites. If site fidelity to nonbreeding sites is lower than that to breeding sites, these estimates will have a larger negative bias relative to true survival than those from a breeding site. However, if we can assume that site fidelity to the nonbreeding site does not differ between sexes, then the sex-specific nonbreeding estimates should be less biased relative to one another. For Western Sandpipers, estimates of apparent survival (ϕ) are available from 2 nonbreeding sites, calculated from data for both juveniles and adults (Fernández et al. 2004). At Chitré, Panama, sex differences in apparent survival are small ($\phi = 0.54 \pm 0.1$ for males and $\phi = 0.62 \pm 0.13$ for females), a pattern more similar to our adjusted estimates than to the original values (Table 2). At Punta Banda, Mexico, the best-fitting CJS model reported $\phi = 0.48 \pm 0.04$ for males and females, with no improvement of fit from adding a sex term, also consistent with no sex difference. For Semipalmated Sandpipers, CJS estimates of apparent survival from a breeding site at La Pérouse Bay, Manitoba, were $\phi = 0.61$, 95% CI = 0.56–0.66 for males and 0.56, 95% CI = 0.51–0.61 for females (Sandercock and Gratto-Trevor 1997), paralleling our male sex bias at Nome in both original and adjusted estimates, but with lower mean values. The true site fidelity of female Semipalmated Sandpipers may be lower than the 3 other classes of birds. A study at a nonbreeding site estimated $\phi = 0.62 \pm 0.04$ for adults of unassigned sexes (Rice et al. 2007); sex-specific estimates of apparent survival for Semipalmated Sandpipers are not yet available from any nonbreeding site.

The general approach that we have implemented for sandpipers could be adapted for other situations and refined in several ways. Following Barrowclough (1978), we made the simplifying assumptions that our study site was circular and surrounded by suitable breeding habitat. The assumptions allowed use of geometry to estimate correction factors and the probability of dispersing outside the study area, and are especially suitable for retrospective analyses of published data. If additional data were available and a heterogeneous study area was well mapped, another approach would be to use a spatially explicit map of the study area and surrounding territory to estimate site-specific correction factors for dispersal data and the probability of dispersal within a study area. Baker et al. (1995) used a spatially explicit model to estimate natal recruitment and yearling survival of Wrentits (*Chamaea fasciata*). Their method avoids extrapolating from a dispersal function, as we have done, but the authors assumed that no dispersal events greater than the maximum observed distance occurred. The approach of Baker et al. (1995) could also be extended with use of a dispersal kernel, but would require simulating a large number of dispersal events drawn from the dispersal kernel from random starting points on the particular map. The estimate of F would be calculated as the proportion of points that fell into suitable territory inside the study area. The spatially explicit approach would be preferable in situations where study sites are irregularly shaped or if suitable habitat is not available in all directions. On the other hand, the method we present here may be the only option in situations where explicit mapping of study areas is not possible, such as retrospective analyses of previously published data.

We chose the exponential distribution to model dispersal as a continuous analog to the geometric distribution, the distribution predicted by competition models (Waser 1985, Buechner 1987). Other probability distributions could be considered. Use of a geometric distribution, which predicts the probability of moving a discrete number of territories, would be appropriate in cases where dispersal data are reported in terms of number of territories moved or when the size of the territory is well known and not highly variable. Other dispersal kernels might be more appropriate for different biological situations, including normal, lognormal, Weibull, or gamma distributions (Cunningham 1986, Gilroy et al. 2012, Schaub and Royle 2013). A bimodal dispersal kernel in which some fraction of individuals does not disperse could be used to explicitly account for the high nest-site fidelity shown by many bird species (Hansson et al. 2002, Marshall et al. 2004). For example, Winkler et al. (2004) found that short-distance movements were more common and long-distance movements less common than predicted by either an exponential or a uniform model for cavity-nesting Tree Swallows (*Tachycineta bicolor*). Choice of an appropriate distribution will vary with species' requirements such as the distribution of suitable nesting habitat.

Our example with 2 species of sandpipers considered heterogeneity due to sex and pair status in a monogamous mating system with biparental care. Applying our approach to other species could require adjustments to the model. For example, among shorebirds and other species that provide uniparental care, detection probabilities of males and females in reuniting pairs are independent. If sufficient data are available, similar procedures could be used for adjusting survival and mate fidelity for different categories of age class, local experience, or past breeding success (Johnson and Walters 2008). Birds breeding for the first time might be treated as a separate group (Greenwood and Harvey 1982). We incorporated steps to take the potential effects of mate fidelity on dispersal distances into consideration. As predicted by Sandercock et al. (2000), we show that adjusted mate fidelity was substantially lower than original estimates from observations within the study site. However, dispersal distances categorized by pairing status may be unknown. In this case, our method could be applied by simply dividing estimates of ϕ by estimates of F to obtain adjusted estimates of mean apparent survival and using the delta method or bootstrapping to estimate standard errors (Powell 2007).

In summary, our method provides estimates of local site fidelity using spatial data that are readily available in many field projects and survival estimates. Our adjusted apparent survival estimates may still be biased low relative to true survival, but nevertheless are an improvement as estimates of a lower bound for true survival. Our approach has several key assumptions and must be applied with appropriate caveats. Nevertheless, it can be adapted to other systems and will give demographers a new set of tools for bounding realistic parameter values of true annual survival. The information required is threefold: estimates of apparent survival, auxiliary data on dispersal distances, and the size of local study sites, which should be readily available for many population studies of migratory birds. Currently, comparisons of estimates of apparent survival and mate fidelity among independent studies, even of the same study species, are hampered by a lack of standards for describing the attributes of sites. In the future, empirical applications and further development of our quantitative method will help to generate improved estimates for conservation and management, and will assist direct comparisons of key demographic parameters.

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