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

A second approach is to increase the size of a study area or add a buffer zone to detect longer dispersal events 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

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(θ

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:

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

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 $(1 - m_{adj})$. The site fidelity of all females combined is given by:

$$F_f = S_m m_{adj} F_{pair} + S_m (1 - m_{adj}) F_{cf} + (1 - S_m) F_{cf} \tag{7}$$

and the site fidelity of all males is given by:

$$F_m = S_f m_{adj} F_{pair} + S_f (1 - m_{adj}) F_{cm} + (1 - S_f) F_{cm} \tag{8}$$

[redacted] 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:

$$\phi_f = S_f F_f \tag{9}$$

ϕ_m S

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. ±±

in several ways. Following Barrowclough (1978), we made

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