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Recovering small Cape Sable seaside sparrow subpopulations: the breeding and dispersal of sparrows in the eastern Everglades

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EXECUTIVE SUMMARY
The fate of the Cape Sable seaside sparrow is of central concern to the restoration of the Everglades. It, and other endangered species, are the primary focus of restoration activities in the sense that ‘getting the water right’ is likely to lead to recovery of a suite of threatened species. Over the last 5 years we have provided critical information both in a statistically rigorous way and as real-time feedback to managers charged with making seasonal water flow decisions. We have addressed several outstanding questions about how to attain the recovery goals for the Cape Sable seaside sparrow. Among these were the usefulness of conspecific attraction in speeding occupation of restored habitat, the influence of various environmental factors (principally water flow) on sparrow demography, the effectiveness of predator exclosures for increasing sparrow breeding success, and the breeding success of sparrows occupying small populations.

This report consists of six manuscripts, three of which have already been published and the other three are in final revision for publication. We have included these either as reprints below, or as drafts that are nearing their final composition before publication. An abstract of each follows.


When to commence breeding is a fundamental decision made by individuals that inhabit seasonal environments. Although photoperiod determines the timing of breeding in most temperate zones, other abiotic conditions can also play a significant role by influencing food availability and, consequently, reproductive performance throughout a breeding cycle. This study used the multibrooded endangered Cape Sable Seaside Sparrow to test whether water conditions (rainfall and groundwater levels) influenced breeding variables in a subtropical environment, the Florida Everglades. Timing of breeding was related to rainfall preceding the breeding season, with females initiating nesting up to 1 month earlier in years with greater rainfall. Clutch size averaged 3.4 eggs, and females showed an increase in clutch size as the breeding season progressed and in response to higher groundwater levels during the laying period. This effect was more apparent for first nesting attempts, with drier conditions limiting clutch size. Although wetter conditions favored earlier breeding and larger clutch sizes, annual nest survival (range: 12–36%) was negatively associated with high average rainfall late in the breeding season. Clutch-size variation and high nest survival in Cape Sable Seaside Sparrows’ first nesting attempts suggests that food-mediated processes affect their reproductive decisions early in the breeding season, whereas predator-mediated processes drove overall reproductive output, possibly through increased activity of major nest predators during wetter conditions.
RESPONSE OF ENDANGERED CAPE SABLE SEASIDE SPARROWS (AMMODRAMUS MARITIMUS MIRABILIS) TO NEST EXCLOSURES. Rebecca Boulton and Julie Lockwood. Florida Field Naturalist 38: 8-11.

The federally Endangered Cape Sable Seaside Sparrow suffers high nest predation, especially late in the breeding season when nests rarely succeed. These late-season nests are important for population recovery, so investigating management practices that may assist sparrow nest survival seem critical in helping conserve this species. We found Cape Sable Seaside Sparrows unwilling to accept predator exclosure fences positioned around nest sites. Throughout our experiment, we changed fence positioning in a number of ways, attempting to understand which aspects of the structure the female disliked. However, because only one female accepted the fence, it was difficult to evaluate what these were. We suggest that acceptance was more likely dependent on an individual female’s willingness to tolerate the structure. We do not recommend that nest exclosures be pursued further in the management of this species due to extremely low acceptance rates, and the amount of time and labor involved in deploying the structures. Finally, we do not know if the fences are capable of protecting a nest from predators because the single nest that fledged was during a period of high nest survival regardless of being fenced.


We investigated survival for male, female, and first-year Cape Sable seaside sparrows. Accurate estimates of survival are critical to improve management decisions and population estimates for this and other threatened species. We used Program MARK to evaluate effects of age, sex, population membership, temporal variation, and ground-water levels on annual survival from mark–recapture data collected across 3 sparrow populations from 1997 to 2007. We found little evidence that annual survival rates differed between the populations or across ground-water levels, but we found high variability between years for both adult and juvenile survival. Our results revealed female sparrows experienced 14–19% lower survival than males. Sparrows experienced much lower survival during their first year of life and were short-lived (2–3 yr). Our results highlight the sparrows’ susceptibility to population declines and suggest that management actions aimed at increasing survival may be effective for this species’ management.


Survival estimates generated from live capture-mark-recapture studies may be negatively biased due to the permanent emigration of marked individuals from the study area. In the absence of a robust analytical solution, researchers typically sidestep this problem by simply reporting estimates using the term “apparent survival”. Here, we present a
A hierarchical Bayesian multistate model designed to estimate true survival by accounting for predicted rates of permanent emigration. Initially, we use dispersal kernels to generate spatial projections of dispersal probability around each capture location. From these projections, we estimate emigration probability for each marked individual, and use the resulting values to generate bias-adjusted survival estimates from individual capture histories. When tested using simulated datasets featuring variable detection probabilities, survival rates and dispersal patterns, the model consistently eliminated negative biases shown by apparent survival estimates from standard models. When applied to a case study concerning juvenile survival in the endangered Cape Sable seaside sparrow, bias-adjusted survival estimates increased more than twofold above apparent survival estimates. Our approach is applicable to any capture-mark-recapture study design, and should be particularly valuable for organisms with dispersive juvenile life stages.


Social information in the form of songs, calls, or other overt behaviors may assist birds in assessing the quality of potential breeding habitat by providing direct public information about site quality or by providing indirect cues (e.g., the presence of conspecifics) that may be used to infer site quality. Artificial song playback has been used to demonstrate the influence of conspecific cues on the settlement decisions of migratory passerines, however, there is currently a dearth of information regarding resident species. We tested the influence of conspecific attraction and the effectiveness of artificial song playback on an endangered resident grassland species, the Cape Sable Seaside Sparrow (*Ammodramus maritimus mirabilis*). We implemented a song playback system designed specifically to broadcast artificial song over large areas of suitable breeding habitat in the Florida Everglades in an attempt to influence the settlement decisions of male sparrows during territory establishment. Our analyses included the creation of a qualitative sound map that formed a basis for measuring the species’ response to artificial song playback. Our results suggested that territory establishment by Cape Sable Seaside Sparrows was influenced by artificial conspecific cues provided by our playback system. Our findings have important conservation implications for the species in light of ongoing large-scale habitat restoration efforts in the Everglades ecosystem.


The detection of Allee effects is critical in assessing extinction risk, but is extremely difficult when sampling small, low-density populations. Failure to detect true Allee effects could lead to over-optimistic assessments of threat status, as well as the development of inappropriate species recovery plans. We outline a broadly-applicable approach for evaluating Allee effect likelihood in analyses of sparse demographic data,
explicitly acknowledging the uncertainties associated with detecting subtle Allee effects amongst the suite of factors that can influence demographic variability. Detailed information on the probability of Allee effects will empower conservation decision-makers to balance extinction risks against the political and economic costs associated with management action. We use an illustrative case study involving demographic analyses of the endangered Cape Sable seaside sparrow, highlighting the value of information on Allee effect likelihood for the development of restoration measures within species recovery plans.

ACKNOWLEDGEMENTS

There are a lot of people to thank for their help spanning the duration of this project. We owe a special debt to the many field technicians that have collected this data over the years. We thank Everglades Air Safety, Fire Cache and Dispatch for their willingness to help us build and stock our camps and ensure our safety every time we go into the field. There are folks in nearly every department at Everglades National Park that have lent us a hand at some point or provided safe haven when life got too hectic. We thank them all and promise to buy them each a beer. We thank David Lockwood for contributing his time and money to help us build and maintain the camps, and for ensuring that we always kept up a healthy sense of humor. We very much appreciate the expertise of Casey Kittel in designing our conspecific playback system. Our mentors within the sponsor agencies, Sonny Bass and Tylan Dean, have been extraordinarily helpful and encouraging. We thank Phillip Cassey, Chris Elphick, Doug Armstrong, Olaf Jensen, and Michael Reed for statistical advice on the various parts of this report. Finally we thank the administrative staff at Rutgers University and the Grant F. Walton Center for Remote Sensing and Spatial Analysis for their expert guidance through the red-tape, especially Kathy Peirano.
VARIATION IN LAYING DATE AND CLUTCH SIZE: THE EVERGLADES ENVIRONMENT AND THE ENDANGERED CAPE SABLE SEASIDE SPARROW

(AMMODRamus Maritimus Mirabilis)

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Abstract.—When to commence breeding is a fundamental decision made by individuals that inhabit seasonal environments. Although photoperiod determines the timing of breeding in most temperate zones, other abiotic conditions can also play a significant role by influencing food availability and, consequently, reproductive performance throughout a breeding cycle. This study used the multibrooded endangered Cape Sable Seaside Sparrow (Ammodramus maritimus mirabilis) to test whether water conditions (rainfall and groundwater levels) influenced breeding variables in a subtropical environment, the Florida Everglades. Timing of breeding was related to rainfall preceding the breeding season, with females initiating nesting up to 1 month earlier in years with greater rainfall. Clutch size averaged 3.4 eggs, and females showed an increase in clutch size as the breeding season progressed and in response to higher groundwater levels during the laying period. This effect was more apparent for first nesting attempts, with drier conditions limiting clutch size. Although wetter conditions favored earlier breeding and larger clutch sizes, annual nest survival (range: 12–36%) was negatively associated with high average rainfall late in the breeding season. Clutch-size variation and high nest survival in Cape Sable Seaside Sparrows’ first nesting attempts suggests that food-mediated processes affect their reproductive decisions early in the breeding season, whereas predator-mediated processes drove overall reproductive output, possibly through increased activity of major nest predators during wetter conditions. Received 23 August 2010, accepted 22 February 2011.

Key words: Ammodramus, clutch size, Florida Everglades, rainfall, subtropical environment, timing of breeding.

Variación en la Fecha de Puesta y Tamaño de la Nidada: El Ambiente de los Everglades el Ave en Peligro Ammodramus maritimus mirabilis

Resumen.—La fecha de inicio de la reproducción es una decisión fundamental que toman los individuos que habitan los ambientes estacionales. Aunque el fotoperíodo determina la fecha de reproducción en la mayoría de las zonas templadas, otras condiciones abióticas pueden también jugar un papel importante al influenciar la disponibilidad de alimentos y, consecuentemente, el desempeño reproductivo a lo largo del ciclo de cría. Este estudio usó al ave en peligro con crías múltiples Ammodramus maritimus mirabilis para evaluar si las condiciones del agua (lluvia y niveles freáticos) influenciaron las variables reproductivas en un ambiente subtropical, los Everglades de Florida. La fecha de cría estuvo relacionada con la lluvia que precedió la estación reproductiva: las hembras iniciaron la anidación hasta un mes antes en los años con mayores lluvias. El tamaño de la nidad promedió 3.4 huevos y las hembras mostraron un incremento en el tamaño de la nidad a medida que la estación reproductiva avanzó y en respuesta a niveles freáticos más altos durante el período de puesta. Este efecto fue más marcado durante los primeros intentos de anidación, cuando las condiciones más secas limitaban el tamaño de la nidad. Aunque condiciones más húmedas favorecieron la anidación más temprana y tamaños de nidad mayores, la supervivencia anual de los nidos (rango: 12–36%) se asoció negativamente con un promedio elevado de lluvias a fines de la estación reproductiva. La variación en el tamaño de la nidad y la alta supervivencia de los nidos del primer intento de anidación de A. m. mirabilis sugieren que los procesos mediados por los alimentos afectan las decisiones reproductivas a inicios de la estación reproductiva. Mientras tanto, los procesos mediados por depredadores condujeron el resultado reproductivo general, posiblemente a través de un incremento en la actividad de los depredadores de nidos más grandes bajo condiciones más húmedas.
In seasonal environments, deciding when to breed is a fundamental aspect of a species’ annual cycle. Shifting photoperiod lengths generally stimulate physiological changes in reproductive hormones and organs in species that breed in temperate and high-altitude environments (Farner and Lewis 1971, Dawson et al. 2001). These physiological changes are usually correlated with seasonal fluctuation in temperature and, importantly, food availability (Hau 2001). To date, most studies of avian phenology have focused on these temperate-zone species, but some studies have shown reproductive seasonality and response to photoperiod length in tropical and subtropical bird species (Tewary and Dixit 1986, Wikelski et al. 2003), despite less-pronounced photoperiod variability.

It is also apparent that other abiotic factors, such as rainfall, can influence important components of a species’ reproductive performance besides the timing of breeding, through food-mediated and predator-mediated processes (Morrison and Bolger 2002). Food-mediated processes are particularly apparent in arid-zone species, in which rain events and warm conditions are associated with increased food availability and, consequently, increased breeding activity, clutch size, and reproductive success (Lloyd 1999, Morrison and Bolger 2002, Illera and Díaz 2006, Barrientos et al. 2007). Similar food-mediated climatic effects are also evident for species breeding in subtropical environments (Morrison et al. 2007, 2009; Monadjem and Bamford 2009).

The subtropical climate of the Florida Everglades is dominated by an annual wet and dry season that varies locally with the timing and magnitude of rainfall. Reliance on these rains is evident in the large breeding colonies of wading birds, in which water levels govern both food density and availability, and, ultimately, the birds’ overall breeding success (Frederick and Ogden 2001, Gawlik 2002, Lorenz et al. 2009). However, the Everglades now suffer major hydrological alterations resulting from the construction of levees, canals, and pumping stations that modify the natural water flow (Light and Dineen 1994). Such anthropogenic alterations can dramatically influence avian phenology and other aspects of breeding. For example, if colonial wading birds mis-time their breeding attempts because of the loss of short-hydroperiod wetlands, summer rains can disperse prey across the aquatic landscape of the Everglades, resulting in chicks starving in large numbers (Frederick et al. 2009).

Here, we investigate the effect of rainfall and groundwater levels on the phenology and other aspects of the breeding biology of a small, multibrooded passerine that inhabits the Everglades marl prairies. Unlike the extremely mobile wading birds that are capable of long-distance flights to new foraging or nesting areas, the endangered Cape Sable Seaside Sparrow (Ammodramus maritimus mirabilis; hereafter “sparrow”) is relatively sedentary and remains within the marl prairie year-round (Pimm et al. 2002, Van Houtan et al. 2010). Accordingly, we might expect them to time their onset of breeding in accordance with favorable water conditions. We might also expect that water conditions will dictate clutch size and overall breeding success in a species, such as the sparrow, that relies on aquatic food resources.

We used 8 years of sparrow breeding-biology data to test whether (1) timing of breeding was associated with water conditions (both rainfall and groundwater levels) during the preceding months; (2) clutch size varied with nesting attempt or water conditions during the laying period; and (3) variation in water conditions during or late in the breeding season were related to annual nest survival. We predicted that sparrows would show some patterns similar to resident multibrooded species—that is, commence breeding when they had acquired enough resources to form a clutch (Crick et al. 1993). With much of the literature originating from temperate species, it was unclear whether sparrows would show a marked midseason peak or a seasonal decline in clutch size (Klomp 1970, Perrins 1970, Crick et al. 1993, Davis 2003), because we would expect enduring resource abundance throughout a subtropical breeding season, compared with temperate environments. However, the risk of nest predation may also affect seasonal clutch-size variation (Slagsvold 1982). We already knew that nest survival of sparrows substantially declined across the breeding season (Baiser et al. 2008); therefore, we predicted that females would lay smaller clutches as the breeding season progressed.

**Methods**

*Study species and area.—*The study species is restricted to the freshwater ecosystem of the Florida Everglades. This subspecies is closely allied to the Atlantic matrilineal clade of seaside sparrows (Nelson et al. 2000), and thus has sister taxa that span both temperate and more northerly subtropical climates (e.g., the now extinct Dusky Seaside Sparrow [*A. m. nigrescens*]). The Cape Sable Seaside Sparrow is nonmigratory and remains relatively faithful to breeding locations (Van Houtan et al. 2010). Although pairs generally remain together and defend a breeding territory (~2 ha; Pimm et al. 2002) throughout the breeding season, pair bonds are not always maintained to the next year. Within the marl prairies, the sparrow constructs a small, cup-shaped nest of dead grass and sedge ~16 cm above the ground. Females re-nest after both successful and failed nesting attempts, with up to 3 or 4 attempts per breeding season (March–July), laying an average of 2–4 eggs per attempt (Lockwood et al. 1997). Although some nests fail because they are flooded (Lockwood et al. 1997), this is relatively uncommon, and most sparrow nests fail because of predation (97% of failures; Baiser et al. 2008).

We studied the sparrow during eight breeding seasons (March–July, 2002–2009) in eastern Everglades National Park, Florida (25°30′N, 80°40′W). We established a single study plot (2 km²) at this site (referred to as “subpopulation E” in Baiser et al. 2008) in 1998, but intensive monitoring did not occur until 2002. Vegetation on the plot is dominated by Gulfhairawn Muhly (*Muhlenbergia filipes*), Jamaica Swamp Sawgrass (*Cladium mariscus jamaicensis*), beaksedges (*Rynchospora spp.*), and Florida Little Bluestem (*Schizachyrium rhizomatum*).

*Field methods.—*During the start of each breeding season (late March), we searched weekly for sparrow nests on breeding territories by observing the behavior of both male and female sparrows. Generally, either the male or the female was individually color-banded for identification. All nest sites were marked with a surveyor flag situated 2 m on either side of the nest and checked every 2–3 days until they successfully fledged or failed. We defined nest survival as the probability that a nest survived from the first egg laid to fledging at least one young (a 25-day period for this species; Lockwood et al. 1997).
The 2008–2009 dry season ranked as the second driest on record for most of south Florida according to the National Oceanic and Atmospheric Administration, with the eastern half of south Florida receiving rainfall totals 25–40% below average. These severe drought conditions gave way to an early and very abrupt start to the wet season. Unfortunately, because of these extreme thunderstorms late in May 2009 (>30 cm of rain in a week), we suspended field work early, which resulted in only first nesting attempts being monitored (Virzi et al. 2009). For this reason, we include only 2009 data in the timing of breeding analysis because of strong seasonal changes in nest survival (Lockwood et al. 1997, Baiser et al. 2008) and changes in clutch size between nesting attempts (see results below).

Typically, we discovered nests during the incubation or nesting period and extrapolated laying dates from known hatch dates (Lockwood et al. 1997). When nests failed during incubation, we extrapolated laying date by subtracting the incubation midpoint (5 days) and number of eggs (assuming 1 egg laid each day) from when the nest was first located. When determining timing of breeding we only used the first nesting attempt from each pair, excluding pairs whose earliest nests we discovered after the years’ first renesting pair. This is a conservative measure to avoid including renesting attempts in our sample, because we likely underrepresented late first-time breeders. We calculated for each year the first egg-laying date (earliest nest found during each breeding season) and the median first egg-laying date. Clutch size was calculated from nesting attempts found during the incubation or laying periods only (after the female initiated incubation) because partial predation or mortality of nestlings can occur in this species. We calculated hatching success (the proportion of original eggs in the clutch that successfully hatched) from clutches of known clutch size only.

**Water variables.**—Within the Everglades, rain falls mainly during the hot, humid wet season (June–September) as intense thunderstorms and severe tropical storms. By contrast, weather during the mild dry season (October–May) is generally dry, with low humidity. At the beginning of the sparrows’ breeding season, toward the end of the dry season, groundwater levels tend to be low, with very little or no permanent water in solution holes across the marl prairie. Solution holes are eroded depressions within the limestone and, unlike sinkholes, they do not meet the water table but fill via rainwater. It is around these solution holes that sparrows before and during pair formation. We used four additional water variables in our analysis of annual nest survival: rainfall and groundwater levels during the entire breeding season (Lockwood et al. 2008, Cade and Dong 2008, Elderd and Nott 2008, Boulton et al. 2009), we used groundwater levels from the nearby water-monitoring station CR3, situated ~1.5 km south of the study site (25°29′N, 80°39′W). The precision for the gauge-adjusted radar is considered the same as standard rain-gauge precision, which is typically reported to the nearest 0.25 mm. Rainfall data from 16 to 31 December 2001 were obtained directly from the weather station NP-RPL, 15 km south of the study site (25°23′N, 80°35′W). We extracted daily groundwater depths (m) from the Everglades Depth Estimation Network (EDEN; Palaszyn and Pearlstine 2008), a hydrological module using ground-elevation measurements and continuous water-level data from 253 real-time gauge stations across the greater Everglades. Validation of the EDEN model shows that the data presented on a 400-m² grid is a reliable estimation (±5 cm) of field-observed water levels (Liu et al. 2009). Using the EDEN xLocater Tool, version 1.4, we extracted water depths across the study plot, resulting in 23 EDEN cells (400 × 400 m cells). We averaged the water depth across these cells to obtain daily average groundwater levels.

In our analysis of timing of breeding, we created four water variables: average rainfall (R) and groundwater levels (WL) 3 months prior to breeding (mid-December to mid-March; 3monthR and 3monthWL) and 2 months prior to breeding (mid-January to mid-March; 2monthR and 2monthWL). We regard these variables as potentially important periods throughout the sparrows’ annual cycle because they represent abiotic conditions experienced by sparrows before and during pair formation. We used four additional water variables in our analysis of annual nest survival: rainfall and groundwater levels during the complete breeding season (mid-March to mid-July; BreedingR and BreedingWL) and during the late breeding season (mid-May to mid-July; LateR and LateWL). For the clutch-size analysis, we calculated water variables for each clutch as the average daily rainfall and groundwater level for a 7-day period, running 5 days before and 1 day after laying of the first egg (7dayR and 7dayWL). We regard this 7-day window as the average egg-formation period, given that follicle growth in small passerines lasts 3–5 days before oviposition (King 1973, Ojane 1983). Thus, these water variables represent the environmental conditions that females experience during egg formation, a period when food availability is critical for egg production (Ardia et al. 2006). For the hatching success analysis, we calculated water variables for each clutch as the average daily rainfall and groundwater level for a 20-day period running from 5 days before laying until hatch day (20dayR and 20dayWL). Analyses.—We used the nest-survival module in Program MARK, version 5.1, to produce annual nest-survival estimates (White and Burnham 1999, Dinsmore et al. 2002). Although MARK is a powerful program capable of assessing the influence of a wide range of independent variables on daily survival probabilities, we use only a single yearly estimate here, because Baiser et al. (2008) previously analyzed daily survival rates and their relationship to groundwater levels at this plot. Although Baiser et al. (2008) used groundwater levels from the nearby water-monitoring station, comparison with simulated EDEN data shows a difference of <0.01 m between our plot averages and their data. For nests with known clutch size, we used MARK to calculate average nest survival for first, second, and third nesting attempts.

We tested the relationship between timing of breeding (first and median egg laying dates) and annual nest survival against our water variables using generalized linear models with a normal link function, PROC GLM, in SAS, version 9.2 (SAS Institute, Cary, North Carolina). Before carrying out these analyses, we assessed the level of collinearity among the water variables by calculating variance inflation factors (VIF) for each variable (PROC REG).
Large VIF scores indicated potential collinearity, and although dropping the variable with the highest VIF value reduced VIFs to 2–3, collinearity can still be a problem with weak ecological signals (Zuur et al. 2010). Adopting the more conservative approach, we constructed models with only one of a pair of collinear water variables at a time. Models were ranked using Akaike’s information criterion corrected for small sample size (AICc), and models with ΔAICc values ≤2 were considered equivalent (Burnham and Anderson 2002). We present effect sizes as linear model estimates ± SE for the top models.

We analyzed the response variable “clutch size” using generalized linear mixed models with a normal link function fitted with the SAS GLIMMIX macro (Littell et al. 1996). To control for the non-independence of multiple nests per individual female, within and between breeding seasons, we included female identity as a random effect. We also included year as a random effect to control for annual variation in clutch size due to unexplained seasonal differences. We examined the relationship between the response variable and the following predictor variables: nesting attempt (consecutive female nesting attempt per breeding season; first, second, third, date (laying date for each clutch); Julian day index standardized from 20 March), dateQ (quadratic date effect), and 7dayWL. There was evidence of collinearity between the variables nesting attempt and date (VIF > 3); therefore, they were not considered in models simultaneously. Models were ranked using AICc. Because of the extremely small number of fourth nesting attempts (n = 5), we combined third and fourth nesting attempts in the analysis. We analyzed the proportional response variable “hatching success” fitted with a binomial link function.

**RESULTS**

**Timing of breeding.**—The earliest date on which an egg was observed in a sparrow nest varied from 20 March (2004 and 2007) to 21 April (2009). The earliest median first egg-laying date was 25 March (2004) and the latest was 30 April (2009). The best model indicated that there was a significant negative relationship between median first egg-laying date and average rainfall 2 months prior to breeding (Table 1A and Fig. 1), which indicated that sparrows initiated breeding earlier in years of higher rainfall. Although the best model explaining first egg-laying date indicated a negative relationship with rainfall 3 months prior to breeding (Table 1B), the standard error around this estimate was very large (i.e., the 95% confidence interval includes zero) and thus provided no confidence in the effect size.

**Annual nest survival.**—We monitored 315 sparrow nests from 2002 to 2008, with daily nest-survival probabilities ranging from 0.919 to 0.960. When extrapolated to a 25–day nesting period, these daily nest-survival probabilities gave an annual nest survival range of 12–36% across the study period. Only one model received substantial support (Table 1C), with sparrows experiencing reduced nest survival in years of high average rainfall late in the breeding season. Nest survival was not related to changes in groundwater levels (Table 1C).

**Table 1.** The best generalized linear models explaining variation in (A) median first egg date, (B) first egg date, and (C) nest survival in relation to water conditions for Cape Sable Seaside Sparrows in the Everglades National Park, Florida, 2002–2009. All models within five AICc units of the top model are included. The variables are average rainfall 2 months (2monthR) and 3 months (3monthR) prior to breeding, throughout the breeding season (BreedingR) and late in the breeding season (LateR).

<table>
<thead>
<tr>
<th>Model</th>
<th>k*</th>
<th>AICc</th>
<th>ΔAICc</th>
<th>wICc</th>
<th>Estimate ± SE</th>
</tr>
</thead>
<tbody>
<tr>
<td>(A) Median first egg date</td>
<td>2</td>
<td>35.0</td>
<td>0.0</td>
<td>0.93</td>
<td>–146.28 ± 21.55</td>
</tr>
<tr>
<td>(B) First egg date</td>
<td>2</td>
<td>42.8</td>
<td>0.0</td>
<td>0.71</td>
<td>–54.48 ± 76.09</td>
</tr>
<tr>
<td>(C) Nest survival</td>
<td>2</td>
<td>44.9</td>
<td>2.1</td>
<td>0.25</td>
<td>–39.52 ± 43.26</td>
</tr>
</tbody>
</table>

n*Number of parameters in model.

ΔAICc Difference in AIC value from that of the best model.

wICc Akaike’s weight, indicating the relative support for the models.

Nest survival data do not include the year 2009.

**Clutch size.**—Over the 2002–2008 study period, females laid an average (± SE) of 3.4 ± 0.05 eggs nest–1 (range: 2–5, n = 175). The largest clutch size was recorded in 2007, when females laid no 2-egg clutches and the overall average clutch size was 3.7 ± 0.11 eggs (range: 3–5, n = 26). In 2004, we recorded the smallest average clutch size (3.1 ± 0.16 eggs; range: 2–4, n = 16). Only one model in our candidate set received substantial support (Table 2A), including the variable nesting attempt and its interaction with groundwater levels during egg formation and laying. Clutch size differed among nesting attempts (Fig. 2A), with first nesting attempts
having significantly smaller clutches than both second and third attempts. As shown in Figure 2B, clutch size declined as ground-water levels dropped only in the females’ first nesting attempts. Daily nest-survival probabilities for these first nesting attempts was 0.964 (overall success 40%; 95% confidence interval [CI]: 28–52%), which is considerably higher than for both second (0.935; overall success 19%; 95% CI: 10–28%) and third nesting attempts (0.905; overall success 8%; 95% CI: 2–19%).

Only one candidate model substantially supported the 2002–2008 hatching-success data for sparrows (Table 2B), and it showed that hatching success declined when rainfall was high prior to hatching. However, the standard error around this estimate was very large (20dayR linear estimate $\pm$ SE = 0.196 ± 0.604), and the interval included zero, thus providing no confidence in the effect size for our final model.

**Discussion**

We found that water, as either rainfall or groundwater, helped explain both within-nest and within-season variation in reproductive measurements for the Cape Sable Seaside Sparrow. Whereas wetter conditions were associated with earlier breeding and larger clutch sizes for first nesting attempts, wetter conditions were also linked to reduced annual nest survival. We hypothesize that this variation may indicate both food-mediated and predator-mediated processes influencing sparrows’ reproductive decisions during different stages of the breeding cycle.

Rainfall levels appeared to influence the timing of breeding in the sparrow prior to the onset of breeding, with females initiating laying earlier with increased rain during the 2 months before breeding. Although rain late in the dry season is not as episodic or widespread as wet-season rainfalls, its absence appears to delay breeding by up to a month (most evident in 2009). This relationship may be driven by the response of sparrows to their dominant prey items; we would expect a multibrooded species to commence breeding as soon as sufficient resources become available to form a clutch (Crick et al. 1993). The mechanism behind the seasonal patterns in tropical insect abundance is poorly understood and may or may not be related to rainfall (Wolda 1978b, 1989), although environments with pronounced dry seasons often experience lower insect abundance during this period (Wolda 1978a, 1988). In the Everglades, before the sparrow’s breeding season, water levels are often below ground level throughout the marl prairie, with no freely available water. The significance of rainfall, not groundwater levels, during this period may suggest rapid invertebrate response to localized rainfall or that sparrows are capable of using rainfall as a cue for future food availability (Zann et al. 1995). Although we did not measure arthropod abundance in the present study, we know from previous work that during the breeding season sparrows feed largely on the insect orders Orthoptera, Lepidoptera, and Odonata and are capable of shifting their diets in response to the changing availability of these insects (Lockwood et al. 1997).
Drier conditions during first nesting attempts were associated with smaller clutches, providing support for the view that food resources are limited at the start of the breeding season. With predation pressure in this system being lowest at the beginning of the breeding season (Baiser et al. 2008), we expect females to lay larger first clutches, because clutch size is strongly related to predation rates in the closely related tidal-marsh sparrows (Greenberg et al. 2006). It appears that Cape Sable Seaside Sparrows lay their first clutch in suboptimal conditions (Crick et al. 1993), perhaps to allow additional time for raising multiple broods throughout the season or to avoid increasingly higher nest-predation rates later in the season.

In our study, the clutch sizes of sparrows increased midseason during the onset of the wet season, when groundwater levels began to rise and solution holes started to contain standing water. Although this increase in clutch size is in accord with a multibrooded-species model (Crick et al. 1993), it is somewhat surprising given the increase in nest predation (Greenberg et al. 2006, Olsen et al. 2008). However, females experience relatively high nest success during their first nesting attempt, and with increasingly favorable conditions lay larger second clutches. After experiencing higher predation rates, females have the opportunity to assess future offspring value and reduce their reproductive investment (Doligez and Clobert 2003, Eggers et al. 2006). Unfortunately, because of extremely high nest predation, our sample of third nesting attempts was small and we observed only a slight decline in clutch size. With a larger sample, it is possible that we would have observed a significant decline in clutch size toward the end of the breeding season.

Despite finding that lower annual nest survival in breeding seasons is clearly associated with high average rainfall, we recognize that the overall relationship between rainfall and nest survival is undoubtedly more complex. Directly linking these variables has proved difficult in this system because of the strong seasonal decline in nest survival, which is synchronized with wetter conditions late in the breeding season (Lockwood et al. 1997, Baiser et al. 2008). Although actual flooding of nests is rare, predation levels steadily increase as the breeding season advances and conditions get progressively wetter, which implies that predator-mediated processes affect breeding success (Rotenberry and Wiens 1991, Morrison and Bolger 2002, Baiser et al. 2008). We propose that late-season rainfall interacts with the sparrow’s major nest predators, possibly through increased search efficiency. Two known sparrow predators are the Marsh Rice Rat (Oryzomys palustris) and Water Moccasin (Agkistrodon piscivorus) (Dean and Morrison 1998). How water levels influence their behavior is currently unknown. However, we assume that their activity in the sparrow’s nesting area is controlled by the amount of standing water. Although this increase in clutch size is in accord with a multibrooded-species model (Crick et al. 1993), it is somewhat surprising given the increase in nest predation (Doligez and Clobert 2003, Eggers et al. 2006). Unfortunately, because of extremely high nest predation, our sample of third nesting attempts was small and we observed only a slight decline in clutch size. With a larger sample, it is possible that we would have observed a significant decline in clutch size toward the end of the breeding season.

We are exceedingly grateful to the many field technicians who located and monitored the sparrow nests used in these analyses. We thank P. Cassey for statistical advice, and the manuscript was improved by comments from B. Olsen, C. Elphick, and an anonymous reviewer. We owe a great debt of gratitude to the many employees of Everglades National Park Fire Cache and Dispatch who have aided us over the years, especially S. Sass, B. Panko, and G. Carnell. This research was funded by grants from the U.S. Fish and Wildlife Service (USFWS) and Everglades National Park Critical Ecosystem Studies Initiative (to J.L.L.). All monitoring and protocols complied with our USFWS permit and Everglades National Park permit restrictions. Daily rainfall data were obtained from sofia.usgs.gov/eden/ston.php?ston_name=CR3 and sofia.usgs.gov/eden/index.php.

Evidence concerning the importance of water levels for food resources, predators, and subsequent breeding success in south Florida birds varies (Frederick and Ogden 2001; Beissinger and Snyder 2002; Morrison et al. 2007, 2009; Lorenz et al. 2009). Contrasting results among raptors, wading birds, and small passerines likely reflect the different foraging substrates and prey items consumed by each species and differing predation pressure. Clearly, the relationships we have reported here between water and breeding by sparrows is complex. We have demonstrated that wetter conditions early in the breeding season may favor reproduction through food-mediated processes, while wetter conditions late in the breeding season may have negative effects on nest survival via predator-mediated processes. We know that successful second and third nesting attempts are critical for positive population growth in this species (Lockwood et al. 2001). Therefore, wetter conditions early in the season could benefit the species, in that females could nest earlier, lay slightly larger clutches, and initiate second attempts before water level and predation rates dramatically increase. Water management for this endangered species has been and will continue to be controversial (Walters et al. 2000). Our results help highlight the potential consequences that water-management decisions can have on the sparrow’s breeding biology within this subtropical environment.

**Acknowledgments**

We are exceedingly grateful to the many field technicians who located and passionately monitored the sparrow nests used in these analyses. We thank P. Cassey for statistical advice, and the manuscript was improved by comments from B. Olsen, C. Elphick, and an anonymous reviewer. We owe a great debt of gratitude to the many employees of Everglades National Park Fire Cache and Dispatch who have aided us over the years, especially S. Sass, B. Panko, and G. Carnell. This research was funded by grants from the U.S. Fish and Wildlife Service (USFWS) and Everglades National Park Critical Ecosystem Studies Initiative (to J.L.L.). All monitoring and protocols complied with our USFWS permit and Everglades National Park permit restrictions. Daily rainfall data were obtained from sofia.usgs.gov/eden/ston.php?ston_name=CR3 and sofia.usgs.gov/eden/index.php.

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Habitat protection and restoration are often the first step in endangered species management. While habitat preservation may prevent short-term extinction risk, in many circumstances, further conservation action is required. Avian conservation routinely implements the use of lethal predator control and nest protection as management tools owing to high nest predation rates suffered by many species. Lethal control practices, although effective in some situations (e.g., Innes et al. 1999, Powlesland et al. 1999, Moorhouse et al. 2003), can evoke a negative public response, particularly when the predator itself is native or threatened (e.g., Roemer and Wayne 2003). A common, non-lethal method employed to reduce nest predation is the protection of the nest site via cages, barriers, or electric fences (Post and Greenlaw 1989, Johnson and Oring 2002, Murphy et al. 2003, Isaksson et al. 2007).

The federally Endangered Cape Sable Seaside Sparrow (*Ammodramus maritimus mirabilis*) suffers high nest predation, especially late in the breeding season when nests rarely succeed (Baiser et al. 2008). These late-season nests are important for population recovery (Lockwood et al. 2001), so investigating management practices that may assist sparrow nest survival seem critical in helping conserve this species. Here, we examine the willingness of Cape Sable Seaside Sparrows to accept predator exclosure fences positioned around nest sites and their effectiveness as a management tool to increase sparrow nest survival.

**Methods and Results.**—During April and May 2008, we searched for sparrow nests in the 0.5 km$^2$ Dog Leg and Alligator Hammock plots within sparrow subpopulation B, Everglades National Park, Florida (for a further description of the sites see Pimm et al. 2002). We attempted to assign fences to nests randomly; however, a nest’s distance from the road (placing the exclosure required carrying heavy equipment in the prairie) and nesting stage sometimes determined assignment. We monitored control nests on adjoining territories to test the effectiveness of the fences at increasing nest survival.

We modified a fence design originally described by Post and Greenlaw (1989) for use with another race of the seaside sparrow, *A. m. peninsulae*, in Florida salt marshes. We constructed fences from 0.6 m × 15 m rolls of White & Brown Aluminum Trim Coil (Amerimax Home Products, Lancaster PA), which we cut in half, resulting in a fence with a diameter of approximately 2.4 m (~7.6 m circumference) and 0.6 m height. We drove the fences 5-6 cm into the ground and further stabilized them with 5-6 wooden stakes (2.5 cm diameter) on their inner sides. An L-bracket was screwed to the top of
each stake to help hold down the aluminum flashing. We used duct tape to seal the joint where the ends of the fence material met, and flattened any vegetation that could serve as a predator bridge on the outside of the fence.

Before we put fences around active sparrow nests, we tested whether the aluminum flashing significantly increased the temperature at the nest site, possibly due to the obstruction of wind or heating of the aluminum. We recorded ambient temperature inside and outside the fence using Thermochron iButtons (Maxim Integrated Products, Sunnyvale CA). The average temperatures recorded from iButtons within the fence were similar to those from outside, confirming that the aluminum flashing would not adversely affect nest temperatures.

We attempted to establish predator exclosure fences around six sparrow nests, one containing day-old nestlings and five with eggs. To allow females to habituate to the structure we positioned the fence within 2-50 m of their active nest for one day. All females tolerated this initial attempt at habituation. The next day we positioned the fence around the nest, but left a gap (0.3 m) and the vegetation undisturbed, to allow the birds to enter the nest by walking on the ground, which is a common behavior for this species. At this stage only one female entered the structure; she returned to the vicinity of the fence within 5 min of construction, and 25 min later dropped inside it from a nearby grass stem, without using the gap. The following day we closed the gap in the fence around her nest. The other five females (and the male in two cases) generally reappeared within 15 min of the initial enclosure of their nests (with the gap left open), but did not enter the fence, though they sat relatively close to it and sometimes flew over it. After one hour the parental birds had still not returned to the nest and continued to show signs of stress (alarm calling, panting), so we removed the fence as quickly as possible and immediately left the area. Four of the females returned to their nests after we removed the fence. We were unable to confirm if one female returned to her nest because the nest had failed when we checked its contents the following day. Of the other four nests, three successfully fledged and one failed six days after the fence experiment ended. The fully fenced nest fledged 14 days later whereby we removed the fence to allow the fledglings’ easier mobility.

Conclusion.—The unwillingness of females to accept exclosures around their nests hampered our ability to examine the success of this method. Throughout the experiment, we changed fence positioning in a number of ways, attempting to understand

Figure 1. (a) Small-ground predator exclosure fences made from aluminum flashing to protect Cape Sable Seaside Sparrow nests in the Florida Everglades 2008, and (b) L-bracket attached to wooden stake to hold down aluminum flashing during high winds.
which aspects of the structure the female disliked. However, because only one female accepted the fence, it is difficult to evaluate what these were. We suggest that acceptance was more likely dependent on an individual female’s willingness to tolerate the structure. We do not recommend that nest exclosures be pursued further in the management of this species due to extremely low acceptance rates, and the amount of time and labor involved in deploying the structures. Finally, we do not know if the fences are capable of protecting a nest from predators because the single nest that fledged was during a period of high nest survival regardless of being fenced.

Considering the documented acceptance of similar fences by *A. m. peninsulae*, we had not anticipated such an adverse reaction by *A. m. mirabilis*. Our experiment highlights the need for stringent contingency plans when working with endangered species and the need to test thoroughly any management action that has the potential to modify individual behavior.

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**LITERATURE CITED**


Endangered Cape Sable Seaside Sparrow Survival

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ABSTRACT We investigated survival for male, female, and first-year Cape Sable seaside sparrows (Ammodramus maritimus mirabilis, hereafter sparrows), a federally endangered bird restricted to the Florida Everglades, USA. Accurate estimates of survival are critical to improve management decisions and population estimates for this and other threatened species. We used Program MARK to evaluate effects of age, sex, population membership, temporal variation, and ground-water levels on annual survival from mark–recapture data collected across 3 sparrow populations from 1997 to 2007. We found little evidence that annual survival rates differed between the populations or across ground-water levels, but we found high variability between years for both adult and juvenile survival. Our results revealed female sparrows experienced 14–19% lower survival than males. Sparrows experienced much lower survival during their first year of life and were short-lived (2–3 yr). Our results highlight sparrows' susceptibility to population declines and suggest that management actions aimed at increasing survival may be effective for this species’ management. (JOURNAL OF WILDLIFE MANAGEMENT 73(4):530–537; 2009)

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Florida's Everglades (USA), a freshwater marsh stretching from Lake Okeechobee south toward Florida Bay and the Gulf of Mexico, is a wetland of global importance (Davis and Ogden 1994). Historically, seasonal floods would cause the area to be inundated by shallow, slow-moving water stretching up to 90 km wide. Seasonal flooding creates a spectrum of hydroperiods (annual period of water inundation) responsible for the diverse vegetation communities of the Everglades. The construction of levees, canals, and pumping stations have altered Everglades' water flows leading the United States government to list nearly 40 species native to the ecosystem as endangered or threatened (Nott et al. 1998, Armentano et al. 2006). Restoration of water flows to predrainage conditions, while maintaining ecological processes and viable populations of all native species, has become a major focus of Everglades' management (South Florida Ecosystem Restoration Task Force 2000).

Bordering Shark River Slough, the main drainage system for the southern Everglades, is a complex mosaic of wet prairie, sawgrass (Cladium mariscus jamaicensis), tree islands, and tropical hammock communities. Water management practices have directly influenced southern freshwater prairies surrounding Shark River Slough and, consequently, available habitat for the federally endangered Cape Sable seaside sparrow (Ammodramus maritimus mirabilis, hereafter sparrow), which is restricted to these prairies. Reduced water flows through the eastern Slough have shortened hydroperiods, increasing drought and fire severity in the eastern sparrow habitat, while unseasonable pulses of water to the west extended hydroperiods and reversed natural drying patterns in the western sparrow habitat (Pimm et al. 2002, Davis et al. 2005). One measure of Everglades restoration success is a viable population of Cape Sable seaside sparrows, and thus the fate of this subspecies has become an indicator to evaluate success of alternative restoration options (DeAngelis et al. 1998, Curnutt et al. 2000, Fuller et al. 2008).

During restoration implementation, it is important for managers to understand which of the sparrow’s demographic parameters are more likely to respond to restoration efforts and contribute significantly to the populations’ growth. Simple demographic models in the past have considered nest success and duration of the sparrow's breeding season as two of the most important demographic parameters (Lockwood et al. 2001). Recent modeling suggests factors increasing mortality of both adult and juvenile sparrows may also pose an extinction risk (Elderd and Nott 2007). However, reliability of this and any related model (e.g., Fuller et al. 2008) is largely determined by the accuracy and variance estimate of the demographic parameters they utilize (Ludwig 1999). Until now, there has been insufficient data to permit robust analyses of sparrow survival estimates, particularly with respect to the possible impact of water levels, sex, and age. Our research objectives were to 1) determine whether survival varied between populations, varied by age or sex class, 2) examine annual variation in adult and juvenile survival, 3) examine the degree to which nonbreeding and breeding-season water levels influence annual survival rates, and 4) demonstrate the value of long-
term research to understand survival of Cape Sable seaside sparrows.

**STUDY AREA**

We conducted our research within the boundaries of Everglades National Park and Big Cypress National Preserve (USA), the places that hold almost all the Cape Sable seaside sparrows (Pimm et al. 2002). We established study plots in 3 of the 6 extant sparrow populations: 6 0.5-km² plots within population B, 1 0.5-km² plot in population A, and 1 2-km² plot within population E (Fig. 1). Cape Sable seaside sparrow populations are restricted to the short-hydroperiod (<7 months standing water) freshwater marl prairies, dominated by muhly grass (*Muhlenbergia capillaris filipes*), sawgrass, beak rushes (*Rhynchospora spp.*), and Florida little bluestem (*Schizachyrium rhizomatum*) in the southern Everglades ecosystem (Pimm et al. 2002). The region was semitropical, with a hot, humid wet season (Jun–Oct) and a mild dry season (Nov–May). Average rainfall ranged from 160 cm to 185 cm and fell mainly during the wet season as intense thunderstorms and severe tropical storms (Miamiap weather station 2000–2006; Everglades National Park Everdata 2007).

We established 6 plots from 1993 to 1994 in the central population B, east of southeastern Shark River Slough. This population was relatively stable, holding the largest distribution and highest sparrow density (Cassey et al. 2007). We also situated plots outside population B in 2 smaller, peripheral populations that experienced different hydrologic flows. In 1997, we established one plot in population A, which was the only sparrow population west of Shark River Slough. This plot was by far the wettest due to the diversion of water into this area that once flowed eastward into northeastern Shark River Slough (Davis et al. 2005). We also established a plot in population E during 1998, east of mid-Shark River Slough, in an area that experienced shorter hydroperiods than population A. Intensive monitoring of this plot did not occur until 2002, when a fire burned the southern section of the plot and it became part of a long-term demography study (La Puma et al. 2007). Both populations A and E were isolated and required helicopter access. For further detail of the plots see Pimm et al. (2002).

**METHODS**

**Capture, Marking, and Monitoring**

We searched for Cape Sable seaside sparrows across the study plots during each breeding season (Apr–Jun). Throughout the breeding season, a team of 2–4 people searched within each study plot, using playback calls of male territory song to catch sparrows opportunistically in mist nets (single 6–12 m). We marked each sparrow with a unique color band combination plus an individually numbered United States Fish and Wildlife Service aluminum band. We determined sex of each breeding adult either by presence of a brood patch for females, a large cloacal protuberance for males, or the bird’s behavior prior to capture (only M sing). It is not possible to reliably age adult sparrows based on plumage; thus, we aged sparrows as adults (after hatch yr, >1 yr old) or juveniles. Although we refer to juveniles in the analyses below, we banded most of these individuals as nestlings (96% nestlings, 4% fledglings). At each plot, we resighted color-marked individuals during visits to capture unbanded sparrows. We also systematically resighted sparrows throughout the breeding season using a spotting-scope.

Although we made every effort to capture females, we captured no females until the 1996 breeding season. We supplemented the above procedure by capturing females in close proximity to their active nests. Implementation of this capture method began in 1997 when intensive nest searching commenced in population B. Using sparrow behavioral cues (i.e., nestling feeding, aggressive chipping), 2–4 people systematically searched all territories across the plots every 2–4 weeks from April to early July to locate nests. Nest-searching activity occurred from 1997 to 2001 in the 6 plots within population B and from 2002 to 2007 in population E. We visited nests every 2–3 days (and on the day of fledging) to confirm whether the nest successfully fledged or failed (Baiser et al. 2008). We individually color-banded all nestlings surviving until 4–6 days after hatching. We removed from the data set all individuals banded in nests known to have failed.

**Survival Analysis**

We estimated apparent survival (θ) and recapture probabilities (φ) using the standard Cormack–Jolly–Seber (CJS) model in Program MARK 5.1 (White and Burnham 1999). We constructed all models using a logit-link function. Data for each analysis consisted of capture histories obtained from the 3-month breeding season of each year, pooled into one.
capture occasion per individual. We examined effects of population membership, sex, and age on annual survival and recapture estimates, in which we modeled each covariate as a group effect and year as the time-dependent variation in the data.

Many environmental variables can cause temporal variation in survival estimates and only long-term data sets allow examination of this variation. Attempting to understand the cause of temporal variation in survival estimates is essential, particularly for endangered species when trying to mediate species recovery. We evaluated the effect of ground-water levels, the central component of the Everglades ecosystem, on annual sparrow survival. We obtained water-level data from United States Geological Survey water-monitoring station NP46 situated close to population B study plots (Fig. 1). We used water-level data from NP46 for 3 reasons: 1) we marked no sparrows in E early in the sampling period, 2) >73% of marked sparrows were located within B, and 3) water levels at NP46 reflected variation at CR3 the closest water station to population E (Pearson’s correlation r = 0.863, P = 0.001; breeding season r = 0.863, P = 0.001). We divided each year into 2 periods, the nonbreeding season (1 Aug–14 Mar; WaterRH) and breeding season (15 Mar–31 Jul; WaterBH). We calculated water levels across these periods using the daily average water level (m) above and below ground level (ground level set to zero). We chose these 2 water covariates because they represent 2 behavioral periods in the sparrow’s life-cycle and biologically we anticipated that stress associated with variation in water levels at either time could affect adult survival. Although our recapture period took place throughout the breeding season we used water levels from this period because stressful conditions (e.g., flooding or drought) incurred during breeding may influence future survival (Visser and Lessells 2001, Hanssen et al. 2005). We only considered the effect of these water-level covariates on survival parameters, because we had no reason to expect water levels would affect recapture rates.

We assessed goodness-of-fit of global models using the bootstrap procedure in Program MARK (n = 500 replicates). The global model was the most parameterized, not necessarily the fully saturated model. Simulated results provided an estimate of the over-dispersion parameter (c), which we calculated as the observed model c of the original data divided by the mean simulated c.

We used this variance inflation factor to correct for over-dispersion, if detected. We fit a time-since-marking model to our most general model (ad data only) to test for the presence of transient individuals, that is, birds who are marked and released and then who permanently emigrate from the population and, thus, cannot be resighted (Pradel et al. 1997). Based on these analyses, we found no evidence of transience in our data and do not present these results here. Our annual samples were not instantaneous, because our sampling periods extended over several months. O’Brien et al. (2005) illustrated that violating this assumption by increasing recapture periods actually increased precision in survival estimates and that bias is minimal if survival is relatively constant throughout the recapture period and if recapture rates are >0.2. Based on detailed nest monitoring, we have no evidence that within-breeding-season survival of sparrows is low and our recapture rate was >0.4 (see below). However, we present an analysis using both 1-month and 3-month recapture duration to test whether survival estimates were biased by recapture duration.

We based model selection on a quasi Akaike’s Information Criterion (QAICc), corrected for small sample sizes and over-dispersion using the c adjustment from our bootstrap simulations (Burnham and Anderson 2002). We used Akaikie weights and the difference (AQAICc) between QAICc for each model and that for the model with the smallest QAICc, from the set of candidate models when examining the relative support for each model. By definition, the best-fit model has a AQAICc, value of zero, but we considered other models if AQAICc ≤ 2.

### Data Sets and Candidate Models

The overall Cape Sable seaside sparrow project had research objectives and study sites that changed somewhat across the years. Therefore, to adequately examine the effect of sex, population membership, age, and annual variation on survival we used different subsets of our mark–recapture data. To achieve a standardized capture effort we used data from 1997, because throughout the earlier years of the project (1994–1996) we were still establishing methodologies and study sites.

To establish if it was reasonable to pool across the 2 larger populations (B and E) we examined population-specific survival for adult males from 2002 to 2007, resulting in 6 sampling occasions. Using the design matrix tool in MARK, we investigated whether survival varied with population or year (time; t) and recapture probability with population membership. We estimated overall survival for population A to allow comparison between small and large sparrow populations. We had few data from population A, which only allowed us to run a constant survival and recapture model. For estimating survival in population A, we used all available data (i.e., both ad M and F from 1997 to 2007) resulting in 11 sampling occasions.

There was no evidence that sparrow survival rates differed between populations B and E (see below). Therefore, we pooled all adult sparrows of known sex from these populations to examine sex and annual variation in survival and recapture probabilities, using data from 1997 to 2007 (11 sampling occasions). To evaluate whether water levels explained any observed variation in temporal survival probabilities we fit linear water-level covariates to survival parameters.

We estimated survival probability for all sparrows captured and marked for the first time as nestlings or fledglings. Juvenile survival included probability that a banded sparrow nestling survived the remaining 4–6 days in the nest, that fledged individuals survived the 8–20-day period when they were still dependant on adults for food and predator protection, and that independent juveniles survived to their
first breeding season. We used banding and resight information from populations B and E 1998–2007, thus resulting in 10 sampling occasions. We built 2 age-class models that allowed a juvenile age-class to span one sampling occasion after capture (first-yr survival) and one adult age-class. We compared these age models with the standard CJS models with no age effects.

RESULTS

Using adult sparrows from population E (2002–2007), we found that bias in survival estimates did not increase with recapture period duration. Between 67% and 82% of all individual resights occurred in the first 1-month recapture period. With a 1-month recapture period, overall survival estimates were 0.60 (95% CI = 0.52–0.68). Using a 3-month recapture period, we estimated overall survival to be 0.59 (95% CI = 0.52–0.66). As predicted, recapture estimates were lower with a 1-month recapture period (0.67, 95% CI = 0.54–0.78) compared with the 3-month recapture period (0.90, 95% CI = 0.79–0.96).

Populations and Survival

We obtained 421 captures and resights, representing 239 individuals within populations B and E (146 from population B and 93 from E; resight individuals = 60 from population B and 56 from E). The global model Φ (group × t) p (group) fit the data well (goodness-of-fit: P = 0.39). We found little evidence of over-dispersion but used the ț adjustment of 1.08 in our analysis to make parameter estimates as robust and valid as possible. The best model was one that included time-dependence in survival and a difference in recapture rates between the 2 populations (Table 1). Apparent survival estimates (95% CI) using this model varied across years: 2002 = 0.75 (0.58–0.87); 2003 = 0.60 (0.45–0.74); 2004 = 0.69 (0.55–0.81); 2005 = 0.44 (0.33–0.56); and 2006 = 0.66 (0.49–0.79). Probability of recapture was 0.91 (95% CI = 0.78–0.97) for population E and 0.60 (95% CI = 0.48–0.72) for population B. The higher recapture probability for population E during this period may be explained by a greater investment in nest monitoring extending the recapture period in this population.

We obtained 81 captures and resights, representing 52 individuals in population A. The constant model Φ (c) p (c) fit the data well (goodness-of-fit: P = 0.66) and we found no evidence of over-dispersion (ț = 0.99). Population A experienced an overall survival rate of 0.56 (95% CI = 0.41–0.70) and recapture rate of 0.54 (95% CI = 0.32–0.74).

Sex and Survival

We obtained 947 captures and resights, representing 550 adults (389 M and 161 F; resight individuals = 200 M and 51 F) across populations E and B. The global model Φ (sex × t) p (sex) fit the data well (goodness-of-fit: P = 0.41) and over-dispersion of the data was minimal (ț adjustment = 1.09). The best model from our candidate set for survival included the covariate nonbreeding-season water levels and the interaction of nonbreeding-season water levels with sparrow sex (Table 2). However, we interpret these results with caution because the 95% confidence interval for WaterNBS overlapped zero (−3.80–13.26) and the 2 models without the nonbreeding-season water covariate were within approximately 2 QAIC, units of the best model (Table 2). In other words, models that included a water covariate failed to improve fit to the data any more than a model including annual variation in survival. In addition, nonbreeding-season water levels had a positive effect on female survival but a negative effect for males (intercept β = −0.89, WaterNBS β = 4.73, sex β = 2.38, WaterNBS × sex β = −12.68). Male (range Φ = 0.47–0.83) and female (range Φ = 0.29–0.69) survival estimates varied considerably across the sampling period, with females recording 14–19% lower survival than males (Fig. 2A). There were negligible differences in recaptures rates between males (p = 0.65,
The worst survival for juveniles was in 2000, with a survival estimate of just 0.09 (95% CI = 0.03–0.22), whereas the best survival was in 2002, with a survival of 0.47 (95% CI = 0.21–0.76; see Fig. 2B). Models 1 and 2 indicate equivocal support for age-structuring in the recapture estimates. Model 1 does not include age-structure (φ = 0.47, 95% CI = 0.35–0.58), whereas Model 2 supports slightly higher recapture rates for juveniles (φ juveniles = 0.54, 95% CI = 0.38–0.70) compared to adults (φ adults = 0.40, 95% CI = 0.27–0.54). Although we had few resights for this data set we attempted to model the water covariate WaterNBR for the 2 best models; however, these models provided little support for explaining annual variation in survival estimates (ΔQAICc > 3.5). We did not include the covariate WaterNBR because we banded most juveniles late in the breeding season.

### Table 3. Models used in Program MARK to determine age-specific effects on apparent survival and recapture probabilities of Cape Sable seaside sparrows marked as juveniles from populations B and E (1998–2007), Everglades National Park, Florida, USA. Only the top 5 mark-recapture models are shown with the global model.

<table>
<thead>
<tr>
<th>Model no.</th>
<th>Model structureb</th>
<th>Qlev</th>
<th>K</th>
<th>QAICi</th>
<th>ΔQAICi</th>
<th>wj</th>
</tr>
</thead>
<tbody>
<tr>
<td>1</td>
<td>φ(a2 – t / c) p (c)</td>
<td>106.78</td>
<td>11</td>
<td>620.13</td>
<td>0.00</td>
<td>0.42</td>
</tr>
<tr>
<td>2</td>
<td>φ(a2 – t / c) p (a2)</td>
<td>104.74</td>
<td>12</td>
<td>620.18</td>
<td>0.04</td>
<td>0.41</td>
</tr>
<tr>
<td>3</td>
<td>φ(a2 – c / c) p (c)</td>
<td>126.28</td>
<td>3</td>
<td>623.21</td>
<td>3.08</td>
<td>0.09</td>
</tr>
<tr>
<td>4</td>
<td>φ(a2 – c / c) p (a2)</td>
<td>124.87</td>
<td>4</td>
<td>623.83</td>
<td>3.70</td>
<td>0.07</td>
</tr>
<tr>
<td>5</td>
<td>φ(a2 – t / c) p (c)</td>
<td>100.90</td>
<td>18</td>
<td>628.99</td>
<td>8.86</td>
<td>0.01</td>
</tr>
<tr>
<td>Global</td>
<td>φ(a2 – t / c) p (a2)</td>
<td>99.79</td>
<td>19</td>
<td>630.01</td>
<td>9.88</td>
<td>0.01</td>
</tr>
</tbody>
</table>

a Model statistics: deviance (Qdev), no. of parameters (K), quasi Akaike's Information Criterion (QAICi), difference in QAICi (ΔQAICi), and QAICi, wt (wj).

b Model structure: φ = probability of apparent survival; t = time; c = constant; p = probability of recapture; a2 = indicates a 2 age-class model structure, with one juv age-class spanning 1 yr and one ad age-class (i.e., φ a2 – t / c specifies time-varying φ for a juv age-class and constant φ for ad age-class).
DISCUSSION

Compared to other demographic parameters, survival is often difficult to estimate due to cryptic behavior and difficulties in marking and monitoring individuals (Murray and Patterson 2006). Inaccessibility and the secretive nature of Cape Sable seaside sparrows previously produced survival estimates based on small sample sizes and largely anecdotal interpretation of data (88% survival, Werner 1975; 90% survival, Kushlan et al. 1982). Our long-term data set and robust analysis expands on the simple male survival analysis presented by Lockwood et al. (2001; 1994–1998 Φ 0.66 ± SE 0.06). We accurately estimated annual adult survival and increased knowledge concerning sex, age, and population survival; all are important components of the sparrow’s life-history.

Our estimate of annual adult survival rates fall within the range recorded for other Emberizid sparrows (Karr et al. 1990, Perkins and Vickery 2001, Sandercock and Jaramillo 2002, Morrison et al. 2004). Indeed, Sandercock and Jaramillo (2002) found moderate annual survival rates (0.35–0.56) within Emberizidae species regardless of their ecology. Because many sparrow species are monomorphic during winter capture periods, both sexes are often lumped during analyses (Sandercock and Jaramillo 2002, Thatcher et al. 2006). By capturing our sparrows in the breeding season we could reliably sex adults and ascertain lower survival rates for female sparrows. Although authors allude to the possibility of lower survival for female sparrows and its possible implication for population growth, all models to date have used one adult survival parameter (Lockwood et al. 2001, Pimm et al. 2002, Elder and Nott 2007). Differential mortality between sexes can cause skewed adult sex ratios, a pattern more prevalent in globally threatened species and small, isolated populations (Dale 2001, Donald 2007). Highly skewed adult sex ratios increases a species’ risk of extinction, a process observed during the extinction of the dusky seaside sparrow (Ammodramus maritimus nigrescens; Delany et al. 1981). Nonbreeding male sparrows occur in larger populations during the breeding season but not in large numbers (Dean and Morrison 1998); however, recent evidence suggests lower female survival may have greater impacts in smaller sparrow populations, because we frequently observe a large proportion of unmated males (R. L. Boulton, Rutgers University, personal communication).

High recapture rates, for both male and female sparrows, reflect high site fidelity and nonmigratory behavior of Cape Sable seaside sparrows (Dean and Morrison 1998, Lockwood et al. 2001). Males during the breeding season sing from sawgrass tops, making males easier to resight than females, which are more elusive. The sparrows’ cryptic behavior during the nonbreeding season makes them impossible to detect, restricting our resight period to a few months during breeding.

Juvenile survival is typically hard to measure in the field, and the Cape Sable seaside sparrow is no exception. We banded young sparrows while they were still in the nest and we rarely observed them during their fledgling period or even as independent juveniles within their banding year. We provided our best estimate for survival of young sparrows but acknowledge that this survival rate is likely to be an underestimate of true juvenile survival. Moderate levels of natal dispersal will lower apparent juvenile survival if young birds permanently emigrate from the study area. We have limited data on sparrow dispersal but radiotagged juveniles moved on average 577 m from natal territories (Dean and Morrison 1998). In addition, examination of the resighting data set reveals 8 between-population movements of which only 3 involved juvenile birds. Our apparent juvenile survival was variable (range = 0.09–0.47) but overlapped with the estimate of 11.4% recorded for the closely related saltmarsh sharp-tailed sparrow (Ammodramus caudacutus, hatching to second yr; DiQuinzio et al. 2001), and Ricklefs (1973) estimated that average juvenile survival for resident temperate passerines is approximately 25% of adult survival. Our analysis is the first to attempt survival estimates for juvenile Cape Sable seaside sparrows and provides managers with a more appropriate estimate instead of using surrogate studies or arbitrary estimates when constructing management decisions.

Water levels can quickly rise in the Everglades, particularly in the wet season when one thunderstorm can produce 10–30 cm of rain in a 24-hour period. Water flows and levels throughout the Everglades are somewhat mediated by management actions that divert water through the extensive canal systems, but we still observed >20-cm increases in water levels within 24-hour periods across all of our study plots. Extremely variable water levels and the complexity of the Everglades water flow make it difficult to assign water-level parameters to annual sparrow survival and potentially limited our inability to detect strong influences on survival. In addition, we monitored most sparrows in our study in populations that are somewhat protected from extreme water fluctuations. Unfortunately, low sparrow densities in all small peripheral populations, which all experience more extreme ends of Everglades water fluctuations relative to the larger populations we monitored (A, C, D, and F; Fig. 1), means we cannot conduct rigorous survival analysis for these populations. Although we provide an overall survival estimate for population A, we were unable to examine water-level covariates with so few individuals detected each year. However, there is no clear evidence that sparrow survival in the wetter population A was any lower than sparrow survival in drier populations B and E.

Long-term sparrow surveys show the species’ decline between 1981 and 1996, after 1996 sparrow numbers and occupancy remained relatively constant (Cassey et al. 2007). During the last 11 years, while occupancy remained constant, we observed highly variable survival, which possibly helps explain the lack of recovery during this period. Post et al. (1983) regarded Cape Sable seaside sparrow population declines as paradoxical in light of their high reproductive potential and high survival rate. Our results help resolve this paradox, demonstrating why the sparrows’ variable survival and short lifespan make it
susceptible to population declines but not quick to recover. For example, high breeding-season water levels like those experienced in population A from 1993 to 1996 would have allowed little annual recruitment (Nott et al. 1998). Water levels recorded in this habitat were high enough to have likely drowned most active nests or prohibited sparrows from nesting altogether. Our estimates of low juvenile and female survival and an average life span of only 2–3 years provide support that extreme environmental factors (natural or otherwise; e.g., high water levels, fire, or severe hurricanes) that cause sharp declines in sparrow numbers will be slow to reverse.

**MANAGEMENT IMPLICATIONS**

High variability in annual survival of both adult and juvenile Cape Sable seaside sparrows we observed suggests that this vital rate may respond positively (or negatively) to management activities. With the expected construction of Comprehensive Everglades Restoration Projects (1999) set to commence within the next 5 years there is an enormous opportunity to closely monitor the sparrow’s survival response to these adaptive management actions. Although we did not reveal strong relationships between water levels and survival we recommend that water managers attempt to mediate unnaturally high water levels in sparrow habitat due to the species’ susceptibility to extended unsuitable conditions. We suggest that future research focus on identifying probable causes of high juvenile and female mortality and attempt to better identify sources of variation in survival to help guide management recommendations.

**ACKNOWLEDGMENTS**

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**LITERATURE CITED**


A Bayesian approach to the ‘apparent survival’ problem: estimating true survival rates from mark-recapture studies in finite plots

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ABSTRACT
Survival estimates generated from live capture-mark-recapture studies may be negatively biased due to the permanent emigration of marked individuals from the study area. In the absence of a robust analytical solution, researchers typically sidestep this problem by simply reporting estimates using the term “apparent survival”. Here, we present a hierarchical Bayesian multistate model designed to estimate true survival by accounting for predicted rates of permanent emigration. Initially, we use dispersal kernels to generate spatial projections of dispersal probability around each capture location. From these projections, we estimate emigration probability for each marked individual, and use the resulting values to generate bias-adjusted survival estimates from individual capture histories. When tested using simulated datasets featuring variable detection probabilities, survival rates and dispersal patterns, the model consistently eliminated negative biases shown by apparent survival estimates from standard models. When applied to a case study concerning juvenile survival in the endangered Cape Sable seaside sparrow, bias-adjusted survival estimates increased more than twofold above apparent survival estimates. Our approach is applicable to any capture-mark-recapture study design, and should be particularly valuable for organisms with dispersive juvenile life stages.

KEY WORDS: Demography, natal dispersal, juvenile survival, hierarchical multistate models.

INTRODUCTION
Accurate estimates of survival are essential in almost all branches of ecology. Researchers typically estimate survival rates using capture-mark-recapture sampling protocols (CMR), applying analytical techniques derived from the Cormack-Jolly-Seber (CJS) modelling framework (Cormack 1964; Jolly 1965; Seber 1965). Over many years, CMR methodology
has been refined to resolve various confounding issues including variation in detection probability and temporary emigration (Pollock et al. 1990; Lebreton et al. 1992). However, one confounding factor remains something of an ‘elephant in the living room’ for survival analysis from live-recapture CMR data: permanent emigration from the study area (Marshall et al. 2004; Zimmerman et al. 2007; Cooper et al. 2008; Horton & Letcher 2008). Whilst temporary emigration can be accounted for using the ‘robust approach’ to data sampling and analysis (Pollock et al. 1990), few widely-applicable methods are available to differentiate permanent emigration from mortality under live-recapture CMR sampling (Marshall et al. 2004). In lieu of a working solution to this problem, it has become customary to report CJS-based estimates using the term ‘apparent survival’, offering a simple acknowledgment of the uncertainty associated with permanent emigration (Lebreton et al. 1992).

If the geographical limits of a finite study area correspond perfectly with those of the population of interest (e.g. an island population), the conflation of mortality and permanent emigration may be sensible; permanent emigrants genuinely represent functional losses to the focal population. If the study area is nested within a wider population of interest, however, emigrants surviving outside the study area may continue to contribute to population processes. In these circumstances, mortality and emigration have diametrically opposite implications for population dynamics. Evidently, lumping these opposing components within the same parameter will give a misleading impression of true survival within the target population. If these ‘apparent’ survival estimates are used to make further inferences about population dynamics (e.g. in population viability analysis), resultant conclusions may be flawed and misleading.

This issue draws together two allied but disparate avenues of inquiry associated with CMR sampling: survival estimation and dispersal modelling. Despite their close inter-relation, the analytical methods used within these two fields have evolved largely in isolation;
researchers interested in survival have focussed largely on developing the CJS framework (Lebreton et al. 1992), whilst those studying dispersal have focussed on applying kernel-based distributional models (Kot et al. 1996; Fujiwara et al. 2006). Few attempts have been made to combine these fields in order to draw inferences about survival and permanent emigration (but see Baker et al. 1995; Cooper et al. 2008). Here, we present a Bayesian approach in which information on survival and dispersal is combined in order to account for permanent emigration probability within finite-plot CMR data. We test the model using simulated datasets representative of typical finite-plot studies, and present a case study concerning juvenile survival in the endangered Cape Sable seaside sparrow (Ammodramus maritimus mirabilis).

**METHODS**

*Using dispersal kernels to estimate emigration probability*

In finite-plot CMR studies, recaptures provide information on dispersive movements up to a theoretical limit corresponding with the maximum distance between two points in the sampled area (Baker et al. 1995). By fitting a distributional model (kernel) to these data, it is possible to generate spatially-explicit predictions of dispersal probability around a given capture location (Kot et al. 1996; Van Houtan et al. 2010). Our approach is to apply these predictions as supplementary information in the process of estimating survival from capture histories.

To illustrate, we consider a scenario in which CMR sampling occurs in a single finite study plot within the range of a dispersive species. For simplicity, we assume that dispersal occurs in discrete periods between sampling events, and that emigration from the study plot is always permanent (e.g. in the case of species with high natal dispersal). In this scenario, the probability of recapture $P(x)$ at time $t$ of an individual marked within the plot at time $t-1$ is composed of the survival probability $S$, the detection probability $p$ (for an individual within
the plot) and the probability that a surviving individual will remain in the plot at time $t$, which we term the residence probability $r$, thus:

$$P(x)_t = S_{t-1} \cdot r \cdot p_t$$  \hspace{1cm} \text{Eqn. 1}$$

We cannot estimate $r$ directly from CMR data as it is completely confounded with mortality. Hence, in a classical CJS model the probability of recapture collapses to the product of $p$ and the apparent survival rate $\phi$ (i.e. the probability of surviving and remaining within the study area; Lebreton et al. 1992). However, if we assume dispersal is random in direction (and survival probability is similar inside and outside the plot), we can simply use a one-dimensional dispersal kernel to estimate $r$ by generating a probability density surface (PDS) around the capture location (Figure 1). The kernel is estimated by estimating the parameters of a distribution function (e.g. Gaussian, Cauchy, log-normal etc.) that best fits the distribution of observed dispersal events (Kot et al. 1996; Fujiwara et al. 2002). If dispersal direction is non-random, two-dimensional kernels may be used to model directional bias. We estimate $r$ using the cumulative density function (CDF) of the kernel, calculating the proportion of the total cumulative probability density falling within the study plot. For kernels with unbounded support, an appropriate cut-off distance must be used in order to estimate $r$ as a proportion of the CDF (e.g. 99.99% of the cumulative probability density).

The probability of emigration is simply $1 - r$.

The validity of this approach hinges on how well the dispersal kernel predicts the true distribution of dispersal events in space. Dispersal probability is likely to vary in both space and time, and may be strongly influenced by factors such as habitat quality, patchiness, and barriers to movement (Schneider 2003; Schooley and Wiens 2004). If this heterogeneity is adequately represented within the study plot, a plot-specific kernel may be valid across the wider landscape (e.g. Fig. 1b). However, if environmental conditions outside the study plot differ widely from those within, settlement patterns outside the plot may be difficult to
predict using models derived from within-plot data (e.g. Fig. 1c). The modelling approach
described in the next section assumes that meaningful kernel-based predictions of spatial
dispersal probability can be generated for the system in question.

The emigration model
Our model is an extension of the Bayesian CJS model developed by Calvert et al. (2009),
adopting a hierarchical structure to model heterogeneity across discrete random variables
(e.g. sites, years). We describe parameter notation for hierarchical structuring around years
(index y), although the model can easily be generalised to other structures. In this
parameterisation, we assume that dispersal occurs between sampling periods, and that
emigration is always permanent. The model can be readily extended to account for temporary
emigration (provided that data can be partitioned into secondary sampling periods, i.e. days
or weeks within years) by including an additional level of parameter indexing, estimating
detection probabilities in a manner analogous to the robust approach (see Appendix 1;
Pollock et al. 1990; Calvert et al. 2009).

Following initial capture, marking and release, individuals (i) belong either to one of K
observable states representing living individuals within the study area, or an unobservable
state K+1 representing individuals that are dead or have permanently emigrated. All model
parameters and variables are defined in Table 1. The model is separated into two elements: 1)
a standard CJS-based hierarchical model that concerns individual capture histories; and 2) a
hidden Markov process that concerns residence probabilities estimated through dispersal
kernel analysis. The CJS-based model adopts a state-space parameterisation, separating the
likelihood of observed individual capture histories (x_{i,y}) into process and observation
components. The process component estimates apparent survival and transitions between true
underlying states (z_{i,y}), whilst the observation component estimates detection probabilities for
individuals in observable states (denoted by the binary indicator $w_{i,y}$). The likelihood for the CJS-based model takes the following general form:

$$P\{x|\phi, \Psi, p\} = P\{z, w|\phi, \Psi, p\} = \sum_{i=1}^{N} \sum_{y=c_i+1}^{Y} P\{z_{i,y}|z_{i,y-1} \phi_y^{a,b} \Psi_y^{a,b}\} \times P\{w_{i,y}|z_{i,y} p_y^b\}$$

Eqn. 2

where $a = z_{i,y-1}$ and $b = z_{i,y}$. Note that the model conditions on time at first capture for each individual. The process component of the CJS-based model is defined by a categorical distribution with probabilities given thus:

$$P(z_{i,y} = b|z_{i,y-1} = a) = \begin{cases} 
\phi_y^{a,b} & a = 1, \ldots, K, b = 1, \ldots, K \\
1 - \phi_y^a & a = 1, \ldots, K, b = K + 1 \\
1 & a = K + 1, b = K + 1 \\
0 & a = K + 1, b = 1, \ldots, K 
\end{cases}$$

Eqn. 3

where the top row represents probabilities associated with transitions between the $K$ observable states (e.g. study areas), whilst the second row represents the probability of transition to the unobservable state (mortality plus permanent emigration). The remaining rows ensure that individuals in the unobservable state remain there permanently. The observation component is a Bernoulli process determined by the probability of detection of an individual (indicated by the data structure containing $w_{i,y}$ values), conditional on its true state $z_{i,y}$. Probabilities are defined thus:

$$P(w_{i,y}|z_{i,y} = a) = \begin{cases} 
p_y^a & a = 1, \ldots, K \\
0 & a = K + 1 
\end{cases}$$

Eqn. 4

where the top row represents detection probabilities for each observable state and the bottom row dictates that detection is impossible for individuals in the unobservable state (apparent mortality). The hidden Markov process is computed simultaneously with the CJS-based model, decomposing apparent mortality (i.e. transitions to state $K+1$) into true mortality and
permanent emigration. The process is based on the notion that the true survival probability \( S_y \) for a marked sample of individuals in a finite study area is related to the apparent survival rate \( \phi_y \) and the residence probability \( r_y \) thus:

\[
S_y = \frac{\phi_y}{r_y} \quad \text{Eqn. 5}
\]

Using a set of kernel-derived estimates of \( r \) for each individual and capture occasion, we re-arrange Eqn. 5 into a likelihood function where true survival \( S^* \) can be estimated using the apparent survival estimate \( \phi_y \) taken from the CJS-based model, with values of \( r \) modelled as a normal distribution with mean estimated thus:

\[
P(r_{i,y} | x_{i,y} = a) = \begin{cases} 
\frac{\phi_y^a}{S_y^a} & a = 1, ..., K \\
0 & a = K + 1
\end{cases} \quad \text{Eqn. 6}
\]

The function is conditional on the observed state of the individual \( x_{i,y} \), reflecting the limitation that \( r \) values can only be generated when the state and location of the individual were observed in the preceding time period.

Parameter values at each hierarchical level (e.g. years) are assumed to form a random sample drawn from a ‘hyperprior’ distribution (Carlin and Louis 1996). In order to ensure that parameter values are bounded between 0 and 1, we specify hyperprior distributions on the logit scale. Following Calvert et al. (2009), we use diffuse conjugate normal distributions for parameter means and gamma distributions for parameter precisions \( \tau \) (used in WinBUGS, rather than variance \( 1/\tau \)). For observable state transition probabilities \( \Psi \), parameter values must sum to unity for each observable state. As such, in a model with \( K \) possible state transitions, hyperpriors are specified for \( K-1 \) transitions, with the \( K^{th} \) transition being defined as one minus the sum of all other transitions. As our focus is on unbiased parameter estimation, we do not directly address the issues of model goodness of fit or model selection directly in this study, although both are discussed in Appendix 1.
Testing model performance with simulated data

We used a stochastic simulation process to generate realistic datasets with six years of mark-recapture sampling in a single study plot (full details in Appendix 2). We incorporated two age classes (juvenile and adult), and restricted dispersal to juveniles such that all dispersive movements occurred in the first year of life. Dispersal was simulated as a one-dimensional process where individuals were assigned random capture locations relative to the plot boundary, moving out to a distance sampled from a lognormal distribution with fixed or time-varying parameters. We generated 25 datasets for each of eight scenarios combining variation in recapture probability, true juvenile survival rate and dispersal distribution (see Appendix 2 for details). Sample sizes were fixed at N=100 juveniles captured and released per year.

To analyse each dataset we estimated individual-specific residence probabilities $r_{i,y}$ from spatial projections of a lognormal dispersal kernel CDF with parameters corresponding with the mean underlying dispersal distribution ($\mu = 5, \sigma = 2$). The resulting $r_{i,y}$ values and sampled capture histories were then used to fit the emigration model in WinBUGS version 1.4 (Lunn et al. 2000) using the code given in Appendix 3. We used the Gelman-Rubin diagnostic (Gelman & Rubin 1992) to assess convergence based on three chains for each scenario, setting a precautionary burn-in run of 10,000 iterations and estimating parameters based on 50,000 subsequent iterations.

We also examined model performance when residence probability was estimated using a dispersal kernel derived from right-censored data, as expected in typical finite plot studies where long-distance movements are detected infrequently. We compared three scenarios of varying study plot size, capturing the shortest 25%, 50% and 75% of dispersal events respectively. We generated 25 datasets for each scenario and estimated kernel parameters for each dataset (including only within-plot recaptures) using maximum-likelihood routines in
the \textit{fitdistr} function in R version 2.9.2 (\url{http://www.r-project.org}). We used $r_{ij}$ values estimated from each kernel to fit the emigration model. We then repeated each simulation allowing some recaptures to occur within a narrow range of distances corresponding to the 90\% and 95\% limits of the true kernel CDF. This scenario was therefore akin to a study design with two plots located within the dispersal range of a target species, allowing the detection of a small proportion of long-distance dispersal events (i.e. those occurring between disparate plots).

\textit{Field-based case study: Cape Sable seaside sparrow}

Between 1998 and 2007, intensive CMR monitoring was conducted in eight finite plots (5.5km$^2$ in total) across the sparrow’s range in southern Florida (Van Houtan et al. 2010). Robust-approach apparent survival estimates for these data were presented by Boulton et al. (2009); we revisit their dataset to evaluate the potential effect of permanent emigration on juvenile survival estimates. We estimated residence probabilities using a published juvenile dispersal kernel generated from the same dataset (Van Houtan et al. 2010). We mapped habitat suitability (treated as a dichotomous variable) using occupancy data from annual breeding season point counts conducted at 1km intervals throughout the known range (Van Houtan et al. 2010) and generated kernel projections representing two dispersal hypotheses: 1) dispersal probability independent of habitat suitability and 2) dispersal constrained to suitable habitat (see Appendix 4). We used both sets of residence probability estimates to fit the Bayesian emigration model with age-specific survival parameters (juvenile or adult, $K=2$), using the uninformative priors and convergence diagnostics described for simulated datasets.

\textbf{RESULTS}

Survival estimates from the emigration model closely approximated true values across all simulated scenarios, whilst the equivalent standard CJS model consistently produced
negatively biased estimates (Figure 2a & b). Year-specific estimates showed little evidence of
parameter ‘shrinkage’ towards the mean (Calvert et al. 2009; Appendix 5), suggesting that
inter-annual variation was captured effectively by the emigration model given the sample
sizes we simulated (n=100 individuals marked per year). The model was robust to temporal
variation in emigration probability, with little change in mean squared error rates relative to
time-constant dispersal scenarios (Appendix 6). Negative bias increased significantly when
kernels derived from right-censored data were used to estimate residence probability,
particularly when only short distance dispersal events were captured within the study plot
(Fig. 2c). However, bias was reduced for all plot sizes when recaptures were allowed to occur
within a small proportion of the true kernel tail (i.e. long distance events), analogous to a
multi-plot study design (Fig. 2d).

For the sparrow dataset, spatial kernel projection yielded individual residence
probability estimates ranging from 0.276 to 0.725 (mean 0.528, 95% LCI 0.305, UCI 0.699)
under an assumption that dispersal probability was independent of habitat suitability. When
dispersal probability was constrained to suitable habitats, estimates ranged from 0.264 to
0.690 (mean 0.518, 95% LCI 0.290, UCI 0.649), indicating that these assumptions had
negligible impact on the estimation of emigration probability. The mean juvenile survival
estimate from the emigration model assuming habitat independence (0.339 ± 0.078 s.d.) was
more than double that of the standard CJS model (0.151 ± 0.055 s.d.), and showed a
significantly wider 95% credible interval (0.191 – 0.585 for the emigration model, 0.094 –
0.240 for CJS), reflecting increased uncertainty once permanent emigration was taken into
account. Results changed little when the model was fitted using kernel projections with
habitat-dependent dispersal, producing a slightly higher mean juvenile survival rate of 0.342
(± 0.082 s.d.). Annual survival estimates and 95% credible intervals are given in Appendix 7.

DISCUSSION
Since the inception of analytical methods for survival estimation from live-recapture data, researchers have struggled to develop widely-applicable methods to deal with the confounding issue of permanent emigration (Marshall et al. 2004; Zimmerman et al. 2007; Cooper et al. 2008). By combining information on survival and dispersal within a Bayesian framework, we were able to generate unbiased estimates of survival despite high rates of permanent emigration. Our model performed consistently across simulated scenarios of varying detection probability, survival rate and dispersal probability. Fundamentally, the model is similar to other hierarchical applications of the CJS family (Gimenenz et al. 2007; Calvert et al. 2009), and is relatively simple to implement. It generates standard apparent survival estimates (from the CJS-based model component) alongside true survival estimates accounting for emigration probability, so no information is lost relative to traditional survival models. Rather, valuable information is gained on the likely impact of permanent emigration on survival estimates within a given study system.

In real-world CMR studies, we anticipate that application of our model may be hindered by inadequate sampling of the true dispersal distribution (Schneider 2003; Cooper et al. 2008). Our simulations suggested that the inclusion of even small numbers of long-distance dispersal events can dramatically improve kernel fit, reducing bias in subsequent survival estimates. This result was unsurprising given that the distribution we used to simulate dispersal (lognormal) exhibits an inverse power law tail, and therefore shows self-similarity across spatial scales, allowing adequate modelling from restricted samples (Halley and Inchausti 2002). Inverse power law distributions are thought to occur frequently amongst dispersive organisms (Brown et al. 2002), and have been detected in numerous birds (Van Houtan et al. 2007) and butterflies (Fric and Konvicka 2007). Study designs involving multiple plots are likely to be highly beneficial in these cases, as the detection of even small numbers of long-distance movements between plots should facilitate accurate kernel fitting.
(Halley and Inchausti 2002; Cooper et al. 2008). Direct modelling of spatial variation in
detection probability within the kernel likelihood function will also act to reduce bias
associated with right censorship (Van Houtan et al. 2010), whilst non-parametric kernels
might be more appropriate in sampling designs with severe right censorship. Whichever
approach is taken, extreme care should be exercised when selecting models used to represent
dispersal; gross errors such as the selection of an inappropriate model family for the dispersal
kernel might lead to highly misleading estimates of emigration probability. In cases where
there is considerable uncertainty in selecting the best model to represent dispersal, increased
spatial sampling effort may be the most sensible approach to generating robust survival
estimates.

Whilst the problem of sampling the full distribution of dispersal distances can be
addressed through appropriate study design and analysis, environmental heterogeneity
presents a greater challenge to robust estimation of survival and dispersal (Ovaskainen et al.
2008). As dispersal is an emergent phenomenon reflecting interactions between an organism
and its environment, a kernel generated from CMR data may only be truly meaningful within
the conditions occurring in the sampled area (Schneider 2003). Owing to the lack of data
beyond plot boundaries, predictions of emigration probability must ultimately rely on
uninformed assumptions about dispersal behaviour with respect to environmental variation.
One way to account for this uncertainty is by constructing models representing different
plausible hypotheses about off-plot dispersal. In the sparrow analysis, we compared scenarios
where dispersal was assumed to be dependent or independent of habitat variation. In fact,
survival and emigration estimates for the sparrow varied little between these divergent
scenarios, reflecting the low relative impact of long-distance dispersal events (i.e. those
reaching unsuitable habitats) on the overall probability of emigration for any given
individual. Rather, emigration probability was largely dependent on the likelihood of short-
distance movements carrying individuals to areas of suitable habitat just outside the study plot bounds.

In the absence of data on permanent emigration, we have no means of testing hypotheses relating to emigration rates. As such, probability density surfaces generated under our approach are more akin to best-guesses than data-based inferences. Whilst relatively crude, we believe our approach represents a step in the right direction towards a better integration of survival and dispersal within empirical demographic models. We anticipate that further advances will be made via extensions to our approach, particularly if dispersal kernel estimation can be directly incorporated within a spatially-explicit CJS model (e.g. Saracco et al. 2010). We encourage researchers to make maximum use of the information at hand within capture history data, and take advantage of the highly flexible range of tools available for demographic modelling within the Bayesian framework. We hope our model will provide a basis for further advances in the field of survival estimation in study systems where permanent emigration is likely to occur.

ACKNOWLEDGEMENTS
Funding was provided by the US Fish and Wildlife Service and Everglades National Park. We thank Michelle Davis, Tabby Fenn, Sonny Bass, Gary Carnell and many others for their hard work collecting and curating data on the sparrow.

REFERENCES


Table 1. Descriptions of model parameters and data structures used in the Bayesian multistate model incorporating information on emigration probability

<table>
<thead>
<tr>
<th>Parameter or data structure</th>
<th>Definition</th>
</tr>
</thead>
<tbody>
<tr>
<td>$S_t^a$</td>
<td>Probability that an individual in state $a$ at time $t$ survives to time $t+1$</td>
</tr>
<tr>
<td>$\phi_t^a$</td>
<td>Probability that an individual in state $a$ at time $t$ survives to time $t+1$ and does not permanently emigrate from the study area</td>
</tr>
<tr>
<td>$\Psi_t^{a,b}$</td>
<td>Probability that an individual in state $a$ at time $t$ will be in state $b$ at time $t+1$ given that it survives to $t+1$</td>
</tr>
<tr>
<td>$p_t^a$</td>
<td>Probability that an individual in state $a$ at time $t$ will be detected at time $t$</td>
</tr>
<tr>
<td>$x_{i,t}$</td>
<td>Observed state of individual $i$ at time $t$</td>
</tr>
<tr>
<td>$z_{i,t}$</td>
<td>True state of individual $i$ at time $t$</td>
</tr>
<tr>
<td>$w_{i,t}$</td>
<td>Binary indicator of whether individual $i$ was observed at time $t$</td>
</tr>
<tr>
<td>$r_{i,t}$</td>
<td>Estimated probability that individual $i$ observed at time $t$ will remain within the study area at time $t+1$, given that it survives to $t+1$</td>
</tr>
<tr>
<td>$c_i$</td>
<td>Time of first capture for individual $i$</td>
</tr>
<tr>
<td>$K$</td>
<td>Total number of observable states</td>
</tr>
</tbody>
</table>
Figure 1. Hypothetical examples of probability density surfaces describing dispersal probability around a single capture location within a study plot (delimited by broken red line), generated from a lognormal distribution. Surfaces reflect environments of varying heterogeneity: a) homogeneous environment in which dispersal probability is independent of environmental conditions; b) heterogeneous environment comprising suitable and unsuitable habitats (zero dispersal probability in the latter), where heterogeneity is adequately sampled within the study plot; c) heterogeneous environment where the plot is poorly representative of heterogeneity within the wider landscape, such that a dispersal kernel modelled from plot-specific data may be a poor predictor of movements outside the plot.

Figure 2. Performance of the Bayesian emigration model against simulated capture history datasets. Upper panels show correlations between true survival rates and model estimates (posterior means and 95% credible intervals) for a dispersive age class, showing a) estimates from the standard Cormack-Jolly-Seber survival model (filled circles) and b) estimates from the emigration model (open squares). Solid lines indicate perfect correlation. Lower panels show biases calculated from emigration model survival estimates (posterior median – true value) when ill-fitting dispersal kernels were used to estimate residence probability. Kernels were modelled for each simulated dataset using recaptures from plots with a maximum dimension equating to the 25th, 50th and 75th percentiles of the cumulative distribution function (CDF) of the true dispersal distribution. In c), sampling occurred only within the study plot; in d), recaptures were allowed within a small proportion of the tail of the true dispersal distribution (between the 90th and 95th percentiles), analogous to a second study plot. All datasets shown were simulated with low recapture probability (p=0.5) and fixed dispersal distributions.
Fig. 1

(a) Graph showing dispersal probability.

(b) Graph showing dispersal probability with different distribution.

(c) Graph showing dispersal probability with another scenario.
Fig. 2
EFFECTIVENESS OF ARTIFICIAL SONG PLAYBACK ON INFLUENCING THE SETTLEMENT DECISIONS OF AN ENDANGERED RESIDENT GRASSLAND PASSERINE

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Abstract: Social information in the form of songs, calls, or other overt behaviors may assist birds in assessing the quality of potential breeding habitat by providing direct public information about site quality or by providing indirect cues (e.g., the presence of conspecifics) that may be used to infer site quality. Artificial song playback has been used to demonstrate the influence of conspecific cues on the settlement decisions of migratory passerines, however, there is currently a dearth of information regarding resident species. We tested the influence of conspecific attraction and the effectiveness of artificial song playback on an endangered resident grassland species, the Cape Sable Seaside Sparrow (*Ammodramus maritimus mirabilis*). We implemented a song playback system designed specifically to broadcast artificial song over large areas of suitable breeding habitat in the Florida Everglades in an attempt to influence the settlement decisions of male sparrows during territory establishment. Our analyses included the creation of a qualitative sound map that formed a basis for measuring the species’ response to artificial song playback. Our results suggested that territory establishment by Cape Sable Seaside Sparrows was influenced by artificial conspecific cues provided by our playback system. Our findings have important conservation implications for the species in light of ongoing large-scale habitat restoration efforts in the Everglades ecosystem.

Key words: Cape Sable Seaside Sparrow, conspecific attraction, grassland birds, habitat selection, resident species, song playback
INTRODUCTION

The selection of suitable breeding habitat is a critical choice for birds because it directly affects reproduction and survival and thus influences population dynamics. Social information in the form of songs, calls, or other overt behaviors may assist birds in assessing the quality of potential breeding habitat. Social cues provide direct public information about site quality and indirect cues (e.g., the presence of conspecifics) that may be used to infer site quality (Stamps 1988; Danchin et al. 2004). In the context of bird conservation, failure by managers to recognize the importance of social cues in habitat selection can lead to large inefficiencies in the use of scarce political and monetary resources. Managers may restore or protect highly suitable habitat for a threatened species, however, the benefits of this action in terms of population increases may never materialize if the target species does not settle in these areas due to lack of social cues (Ahlering and Faaborg 2006). One proven solution to this issue is to erect playback audio systems within unused but suitable habitat, and broadcast calls and songs of the target species during appropriate times of the year (e.g. early in the breeding season). These artificial song playback systems then provide the necessary social cues to attract individuals to settle and breed in the restored or protected habitat (Ahlering et al. 2010). Here we test the effectiveness of artificial song playback systems, and thus the role of social cues in making settlement decisions, in the Cape Sable Seaside Sparrow (Ammodramus maritimus mirabilis), a highly threatened passerine endemic to the Florida Everglades.

Understanding the way species use social information in habitat selection decisions is critically important for the conservation of endangered species (Podolsky and Kress 1992; Jeffries and Brunton 2001; Ward and Schlossberg 2004). A primary conservation goal is to
increase population size, and creating or improving habitat for breeding often accomplishes this. However, it may not be as simple as ‘if you build it they will come’ if the use of social cues strongly influences the habitat selection process (Ahlering and Faaborg 2006). In recognition of this issue, several researchers have successfully used artificial song playback as a way to encourage settlement of migratory passerines including Black-capped Vireo (*Vireo atricapilla*), Baird’s Sparrow (*A. bairdii*), American Redstart (*Setophaga ruticilla*) and Black-throated Blue Warbler (*Dendroica caerulescens*) into protected or restored habitat (Ward and Schlossberg 2004; Ahlering et al. 2006; Hahn and Silverman 2006, 2007). The use of song playback may be most beneficial for species that are philopatric, tend to naturally occur at low densities, and have fast life histories. Philopatry tends to slow population response to habitat changes as it tends to ‘pin’ the distribution of breeding individuals to only previously occupied sites (Hahn and Silverman 2006, 2007). Species at low densities have reduced chances for encounters with conspecifics, thus providing artificial conspecific cues may encourage settlement in managed habitat that might otherwise be ignored by dispersers. The use of song playback to encourage settlement may be particularly beneficial when managing species with fast life histories since these species have fewer lifetime opportunities to reproduce. Grassland bird species, as a group, tend to show many of these traits, and accordingly, several grassland species have been shown to use social cues to select breeding territories (Ahlering et al. 2006; Nocera et al. 2006, 2009). Since grassland birds in North America have seen precipitous declines over the last decades (Brennan and Kuvlesky 2005), this group is a prime target for using artificial song playback as a conservation tool.
Here we describe an experiment designed to test the effectiveness of artificial song playback on the settlement decisions of the Cape Sable Seaside Sparrow, a critically endangered year-round resident of the Florida Everglades. The species is restricted to short hydroperiod marl prairies, occurs at very low densities in most subpopulations, is short-lived, and is strongly philopatric (Boulton et al. 2009a, Pimm et al. 2002). The species has experienced recent population declines due in large part to degradation of the Everglades ecosystem (Pimm et al. 2002; Cassey et al. 2007). However, the sparrow may benefit from unprecedented large-scale habitat restoration efforts currently underway. If Cape Sable Seaside Sparrows respond to artificial song playback, the colonization process into newly restored habitats in the Everglades may be sped up. These early settlers into restored habitat should initiate establishment of philopatric resident individuals that will later serve as natural attractants to maintain a new, or expanded, a subpopulation (Ahlering and Faaborg 2006). Increasing the number of Cape Sable Seaside Sparrow subpopulations, and increasing the number of individual sparrows occupying existing subpopulations, would greatly increase the probability of long-term persistence in the species by spreading out stochastic extinction risks across space.

METHODS

STUDY AREA

The Cape Sable Seaside Sparrow is presently distributed among two large (B and E) and four small subpopulations (A, C, D and F; Fig. 1). Sparrow adults stay within 2 km of breeding territories during winter, and they are strongly philopatric. Our study site, which covered 900 ha,
was located in sparrow subpopulation C (25°43′N, 80°61′W) in the eastern portion of Everglades National Park (ENP). Since 2006 we had conducted an intensive demographic study of breeding sparrows in this subpopulation (Virzi et al. 2009), which provided us with detailed knowledge about the distribution of sparrows prior to our artificial song playback experiment. This study site was selected because we had these prior distributional data, and because there was unoccupied habitat that was apparently suitable for sparrow breeding.

PLAYBACK SYSTEM DESIGN

We designed a playback system to broadcast sparrow song over large areas (> 1 km radius) of sparrow habitat. The playback units consisted of an Apple iPod Nano connected to a JBL marine amplifier (model MA-6002) wired with a programmable timer (Flexcharge 8 Event Timer) to turn the units on and off daily. All electronic components were housed in a waterproof Pelican Case (model 1520) modified for the electronics and necessary wiring. Each unit broadcasted song using two 16-inch uni-directional speakers (Dayton RPH16) powered by 75-watt speaker drivers (Dayton D1075T) mounted to tripods approximately 2 m above the ground, which was high enough to mimic the height at which sparrows perch to sing but low enough to be unobtrusive in the environment. The playback units were powered with 12-volt marine batteries (Battery Werker WKDC12-33J) charged with solar power generated by a single BP solar panel (model SX320M) mounted on the tripod next to the speakers. The design allowed song to be broadcast daily throughout the playback period without the need for regular visitations, which is necessary due to difficulties in accessing remote areas in the Everglades where sparrows breed.
The playback units were deployed on 02 February 2009; male sparrows typically begin to establish territories in early-February (Pimm et al. 2002). The playback units were placed in the eastern portion of our study area where there was unoccupied suitable breeding habitat. Units were placed 700 m apart to ensure adequate coverage of song playback across this area. Timers were initially set to broadcast sparrow song beginning at sunrise for a period of three hours, which is the approximate time of peak singing by sparrows. The start time was adjusted earlier as the breeding season progressed to account for change in sunrise. We used a medley of sparrow song recorded from several individuals breeding within ENP in previous years as our song broadcast from the playback units. The units were turned off on 13 April 2009 at the time when we first observed nesting behavior by sparrows in the subpopulation to reduce the risk of the song playback interfering with breeding activity.

STATISTICAL ANALYSES

SOUND FIELD

Prior experiments testing the response of birds to artificial song playback systems either never defined the reach of the sound through available habitat, or made simplifying assumptions about where song could be reasonably heard (e.g., within a certain radius around the playback unit). However, sound does not diffuse through air in a regular pattern but instead follows established and predictable physical laws. We modeled the sound field generated by our playback units using these laws, and tested for sound quality in the field.
Sound waves from a uni-directional source carry across space in a conical shape following the inverse square law where the decibel level decreases as distance from the source increases, while at the same time expanding wider with distance at a scale dependent on the shape of the speakers (Celik and Guremen 2008). We used data on sound quality collected in the field to seed a sound model based on these equations in order to generate a qualitative map of sound generated from our playback units across our study area. We walked line transects at 45 degree angles away from each playback unit stopping every 50 m to record the level of sound being broadcast by the speakers. Observers recorded the sound level placing it in one of four categories: (1) song heard faintly – sounds natural, (2) song heard well – sounds natural, (3) song loud – sounds unnatural, and (4) song very loud – sound quality degraded by distortion. Data used in our sound model was collected under consistent ambient conditions (e.g. low wind speed). These data were entered into a geographic information system (GIS, ESRI® ArcMap version 10.0) and were used to interpolate a sound field where artificial song could be heard around each playback unit using the kriging function in ArcMap. The mapped area of the sound field was categorized based on the sound values indicated above providing a map of sound ‘quality’. Mapped areas with sound values below three were considered to have the most natural sounding artificial sparrow song from our playback units. Thus, these areas were where we expected to observe the strongest response by settling male sparrows to our song playback units. From these maps, we estimate that 35% of our study area was regularly inundated with artificial sparrow song, while the remaining 65% was not. We thus expected that if artificial song is used by sparrows to decide where to place their breeding territories, sparrows will be more likely to place their territories within this sound field. We expect there to be no pattern of territory
placement relative to the sound field if sparrows effectively ignore the artificial song playback units, and for territories to be preferentially placed outside the sound field if they are responding negatively to the presence of artificial song.

VEGETATION SURVEYS

A central assumption in our analysis is that all habitat within our study area was suitable for sparrow breeding, and thus plays no appreciable role in determining territory placement. To test this assumption we analyzed vegetation data collected along eight 100 m line transects located at eight sampling sites spaced 1 km apart within the boundary of our study site (Sah et al. 2009). Vegetation composition (percent cover) was estimated in 10 subplots (5 x 5 m) spaced at 6 m intervals along each of the eight transects. The vegetation data were collected at sites on a three-year rotation; therefore, data used in our analyses were from multiple years (2006 – 2009).

Following La Puma et al. (2007), we analyzed species composition with the multivariate software Primer-E® to examine the similarity of sampling sites across our entire study area. We calculated the full Bray-Curtis species similarity matrix for all samples and then used this matrix as the basis for analyzing compositional similarity using non-metric multidimensional scaling (NMDS) (Clark and Warwick 1994). Relative similarities of sampling sites across our study area were compared using analysis of similarity (ANOSIM), which is similar to a standard univariate analysis of variance. ANOSIM calculates a test statistic ($R$) that is used to compare compositional similarity, where values range between +1 and -1, taking the value of +1 when samples at one site are more similar to each other than samples at other sites and -1 in the
opposite situation. In the event of any observed dissimilarity between plots, we used the Primer-
E® SIMPER routine to disaggregate the Bray-Curtis similarity matrix and computed the average
dissimilarity between all pairs of inter-group samples to identify which species were driving the
dissimilarity (Clark and Warwick 1994). This allowed us to assess whether vegetative
dissimilarities were likely to influence habitat suitability for sparrows within the study area,
based on previous analyses of sparrow breeding habitat requirements (Lockwood et al. 2003).

**MEASURING SPARROW RESPONSE**

We surveyed the entire study area on multiple occasions each week from 24 March to 29 July in
an attempt to locate all sparrows occupying territories during the 2009 breeding season.
Systematic surveys were conducted by 2-4 researchers at least once per week (usually twice)
over the period, with equal effort in areas where playback was audible or not. Territory
occupancy was determined based on the observation of individual adult males singing on
multiple occasions, observation of aggression towards neighbors, and/or pairing with females.
Most male sparrows in the study area were color-marked making the accurate identification of
individuals possible. During surveys the location of all sparrows and nests encountered were
recorded with a handheld global positioning system (GPS) device that allowed us to map
territory boundaries for later GIS analysis.

We imported the GPS data collected during our sparrow surveys into ArcMap and used these
point data to generate territory polygons for all adult male sparrows observed in our study area
with the minimum convex polygon tool in Hawth’s Analysis Tools for GIS version 3.27 (Beyer
We then located the central position of each polygon, and considered this to represent the center of each male sparrow’s territory. Next, we buffered each observed territory point by 80 m in ArcMap to create a hypothetical 2 ha territory for each male sparrow, which is the approximate size of actual sparrow territories (Pimm et al. 2002).

To evaluate the influence of song playback on territory distribution in our study area, we compared the locations of ‘real’ sparrow territories to a set of simulated territory distributions that we created based on competing hypotheses (described below; Fig. 2). The first step in the simulation process was to create vector files to constrain the placement of random territory centroids within spatial bounds expected based on each competing hypothesis (grey-shaded areas in Fig. 2). Once these vector files were created, we used ArcMap to generate randomized territory distributions under each competing hypothesis. In each simulation we generated 14 random points, matching the number of ‘real’ sparrow territories found in our study area (see Results), to create a set of expected territory locations that we could overlay onto observed territory locations. We simulated territories by buffering the random points by 80 m to create 2 ha sparrow territories, similar to the process described above for observed data. For each hypothesis we ran 1000 simulations generating 14 points per simulation to obtain a frequency distribution of resultant territory locations.

Settlement decisions of male sparrows may be influenced by factors including habitat quality, philopatry, conspecific attraction, or a combination of these factors. Therefore, we developed six competing hypotheses (shown in Fig. 2) to explain the settlement decisions made by male sparrows. The first three hypotheses (A-C) assume no influence of our song playback system and the remaining three hypotheses (D-F) assume some influence as described below.
Since Cape Sable seaside sparrows are known to cluster breeding territories (Pimm et al. 2002), for our first hypothesis (Hypothesis A\textsubscript{Clustered}) we assumed that sparrows clustered during settlement whether due to the influence of natural conspecific cues or some other mechanism. This hypothesis assumed that there was no effect of artificially generated song cues created by our playback system. Thus, when we generated random points for this hypothesis we allowed the first point in each simulation to occur anywhere in the study area, but forced clustering of all remaining points based on randomly selected nearest neighbor distances (NND) within the range observed in sparrow subpopulation C in 2006 (the year of maximum observed density in the plot; NND\textsubscript{Minimum} = 160 m; NND\textsubscript{Maximum} = 1400 m).

For Hypothesis B\textsubscript{Habitat} we assumed that sparrows based settlement decisions on habitat quality alone. Given the degree of uncertainty inherent in using analyses of vegetation data to infer habitat quality, we based our assessment of habitat quality on the prior distribution of sparrow territories with the study area rather than on habitat measures. For this hypothesis we therefore constrained random points to the area where sparrows were observed breeding in the years 2006-2008, making the assumption that the presence of breeding sparrows in previous years indicates consistent habitat quality in this area. This constraint takes into consideration how micro-site habitat characteristics not measured in our vegetation analysis might have influenced settlement decisions.

Since adult Cape Sable Seaside Sparrows are known to exhibit strong breeding site fidelity between years (Pimm et al. 2002), we developed a hypothesis that takes into consideration philopatry. Thus, Hypothesis C\textsubscript{Philopatry} assumed that settlement decisions were influenced most strongly by philopatry of sparrows to areas where they nested in the previous year. Therefore,
we constrained the selection of random points to the area where sparrows were observed breeding in 2008, forcing a high level of philopatry to previous breeding sites.

The remaining three hypotheses take into consideration the effect on settlement decisions of the sound field generated by our artificial song playback units. For Hypothesis D_{Playback} we assumed that settlement decisions by male sparrows were influenced most strongly by the artificial song cues we provided. For this hypothesis we constrained the selection of random points to areas within the sound field generated by our playback units (see Results, Fig. 3 below). We further allowed points to be generated only in the areas where artificial song broadcast from our playback units was expected to sound most natural. Thus, we did not allow points to be generated in areas in close proximity to the playback units, where we thought sound was too loud to mimic natural cues based on our sound modeling.

The final two hypotheses consider that settlement decisions by male sparrows may be influenced by artificial song cues working in conjunction with other cues such as philopatry and habitat suitability. For Hypothesis E_{Playback/Philopatry} we assumed that settlement decisions were influenced to some degree by the presence of artificial conspecific song and adult philopatry. Thus, for this hypothesis we combined the constraints placed on the generation of random points from Hypothesis D_{Playback} and Hypothesis C_{Philopatry} taking into consideration the potential effect of both artificial song cues and adult philopatry. Finally, for Hypothesis F_{Playback/Habitat} we assumed that settlement decisions were influenced by both the presence of artificial conspecific song and habitat suitability. Thus, for this hypothesis we combined the constraints placed on the generation of random points from Hypothesis D_{Playback} and Hypothesis B_{Habitat} into a single model.
We analyzed differences in the location of simulated and real sparrow territories using a one-way ANOVA (Program R version 2.11.1). The response variable in our ANOVA was the mean number of overlapping territories ($\Omega_{\text{Overlap}}$) detected when overlaying simulated territory locations to observed territory locations. We used $\Omega_{\text{Overlap}}$ as our response variable since we considered any overlap an indication that we could not differentiate between the location of the simulated and observed (real) territories. We also ran our ANOVA comparing $\Omega_{\text{Overlap}}$ at larger territory sizes (3-, 4-, and 5 ha) to account for uncertainty in the size of sparrow territories since previous research had shown that sparrow territories may be larger in small subpopulations (Boulton et al. 2009b). We compared Hypothesis A_{Clustered} to all other competing hypotheses, all of which were set as factors in the ANOVA, to determine if there were significant differences from a simple clustered distribution. We used the Tukey honest significant difference method (Tukey HSD) to examine multiple comparisons to evaluate the significance of competing hypotheses. Values reported in the Results section are means ± SE (or SD as indicated) and significant P-values were based on $\alpha = 0.05$.

RESULTS

VEGETATION COMPOSITION

The ANOSIM comparing vegetation composition across our study plot indicated that there was some difference in species composition ($R = 0.258, P = 0.001$). The SIMPER results indicated that the relative abundances of two species, *Muhlenbergia capillaries* and *Cladium jamaicense*, were driving the between-plot dissimilarity. Comparing the within-plot similarity for all samples
revealed that these were the most abundant species in all plots; however, their rank order differed between plots (Table 1). Thus, the vegetation community across our entire study area may be classified as *Muhlenbergia-Cladium*, which is known to be suitable breeding habitat for the Cape Sable Seaside Sparrow (Lockwood et al. 2003).

**SPARROW RESPONSE**

We observed 14 territory settlement events (n = 13 individuals; one male sparrow changed its territory location after a failed nesting attempt) during our surveys and used these data to map territories (mean number of GPS points per bird = 13). Two adult males were color-marked in previous years on their breeding territories within our study plot. We captured and marked 10 of the remaining 11 adult male sparrows bringing the total 2009 marked population of males to 12. Since most of the male sparrows breeding in subpopulation C in 2008 were color-marked individuals (9 out of 10), the unmarked individuals found during our study were likely individuals that either recruited into the population as first year juveniles or dispersed into our study area in 2009.

Ten of the male sparrows that settled in our study plot in 2009 established territories within the sound field generated by our playback systems (Fig. 3). All were in areas of the sound field where sound values were below three, which is where we expected artificial song broadcast from our playback units to sound most natural. Further, no sparrows established territories in areas where sound values were greater than three (one male’s territory bordered this area). One of the four male sparrows that settled in the area outside the sound field had been previously marked as
an adult, and settled in close proximity to its territory from the previous year (distance = 128 m). A second male that established its territory outside the sound field had been previously marked as a nestling, and settled relatively close to its natal site (distance = 984 m). Thus, all sparrows that established territories in our study plot either settled in areas where artificial conspecific song cues could be heard or in areas where sparrows nested in the previous year despite the availability of suitable breeding habitat across the entire study plot.

The frequency distributions of territory overlap between simulated and observed (real) territories were normally distributed for all competing hypotheses (Fig. 4). We only report the results based on simulated territory sizes of 2 ha since the results were identical when we increased the size of territories to 3-, 4- and 5 ha (except that $\Omega_{\text{Overlap}}$ increased under all hypotheses). Our simulations resulted in little overlap between simulated and real territories for the first three hypotheses (Hypothesis $A_{\text{Clustered}}$, Hypothesis $B_{\text{Habitat}}$, and Hypothesis $C_{\text{Philopatry}}$). Two of the simulations that considered the effect of artificial song playback on territory location (Hypothesis $D_{\text{Playback}}$ and Hypothesis $E_{\text{Playback/Philopatry}}$) showed more overlap between simulated and real territories. The $\Omega_{\text{Overlap}}$ was highest for Hypothesis $D_{\text{Playback}}$ (mean = 3.5, ± 0.05) indicating that this hypothesis may explain the observed distribution of sparrow territories best (Fig. 5). Hypothesis $E_{\text{Playback/Philopatry}}$ also had a substantially higher number of simulated territories overlapping real ones than any of the first three competing hypotheses (mean = 2.8, ± 0.05). The final hypothesis that considered the interactive effect of song playback and habitat suitability (Hypothesis $F_{\text{Playback/Habitat}}$) showed less overlap between simulated and observed territories than Hypotheses D and E (mean = 2.2, ± 0.04). Our ANOVA rejected the null hypothesis that $\Omega_{\text{Overlap}}$ from competing hypotheses were the same as Hypothesis $A_{\text{Clustered}}$.
(F_{5,594} = 183.1, P < 0.001). Tukey HSD pairwise comparisons of ANOVA results from the six competing hypotheses showed non-significant differences for Hypothesis B_{Habitat}, Hypothesis C_{Philopatry}, and Hypothesis F_{Playback/Habitat}, which thus formed one group indistinguishable from each other (Table 2). Hypothesis D_{Playback} and Hypothesis E_{Playback/Philopatry} were not significantly different from each other, but were significantly different from all other hypotheses. This result suggests that both artificial song playback and philopatry explained the distribution of sparrow territories to some degree.

DISCUSSION

Our results suggest that Cape Sable Seaside Sparrows use social cues, in the form of song, produced by conspecific individuals as one criterion for selecting breeding habitat. Ours is one of the few studies to show that resident avian species use social cues from conspecifics to make settlement decisions (see Parejo et al. 2007 for an example showing the use of public information by resident Blue Tits *Cyanistes caeruleus*). Our results indicate that Cape Sable Seaside Sparrows use a mixed-strategy to make settlement decisions based on philopatry and conspecific cues, a strategy that is expected to be the theoretical stable solution for many settlement problems (Doligez et al. 2003). Sparrows responded to artificial song playback broadcast over a large area of suitable breeding habitat, with the strongest response in areas where sound quality was predicted to be closest to the sound of natural song based on sound modeling. Our findings have important conservation implications for the species in light of the ongoing large-scale habitat restoration in the Florida Everglades.
Our results suggest managers may profitably use song playback systems to increase the number of subpopulations or promote settlement of sparrows in newly restored habitats in the Everglades. While our results show that settlement decisions can be influenced on a local scale, the true benefit of this management tool would be its efficacy in influencing the settlement decisions of individuals that disperse long distances. Long-distance dispersal events between sparrow subpopulations do occur, and although rare, such events are likely to influence population dynamics (Nathan et al. 2003; Van Houtan et al. 2010). Once restored habitat becomes suitable for breeding it may be possible to encourage faster recruitment and settlement of long-distance dispersers into restored areas by strategically placing several playback systems there. Since Cape Sable Seaside Sparrows winter near their breeding territories, are philopatric, and have a higher probability of dispersing short distances, placing song playback systems near existing breeding populations may also encourage residents to expand into any neighboring newly restored habitat. The location of playback systems should take into consideration the properties of the artificial cues being broadcast to ensure that the best-quality sound is broadcast into target areas, rather than trying to attract sparrows directly to the playback systems themselves. The systems we designed can be used to create appropriate cues over a large area (250 ha) and are relatively inexpensive to build, and implement, making them a viable conservation tool for this species.

Care should be taken to avoid creating ecological traps in any attempts to redistribute Cape Sable Seaside Sparrows across the Everglades landscape, given that careless placement could encourage settlement of species into poor quality habitats (Betts et al. 2008). We did not test whether sparrows that nested within the sound field generated by the artificial playback units had
higher, or lower, nesting success than individuals that nested outside the field because of low sample sizes. This aspect of the use of artificial song playback in conservation of Cape Sable Seaside Sparrows, or any other endangered species, is a critical question to be answered. At a minimum, managers should use the most accurate habitat models available to assess the quality of restored habitat for sparrows before encouraging recruitment into these areas. Additionally, effects on the avian community as a whole should be taken into consideration since broadcasting conspecific song of one species may cause other species to abandon suitable sites (Betts et al. 2008; Ahlering et al. 2010; Betts et al. 2010).

While our results suggest that the Cape Sable Seaside Sparrow uses early-season song as a cue for habitat selection during the current year, it is possible late-season song might also be used as a cue for selecting territories in the following year, particularly amongst failed breeders and/or the year’s fledglings (Doligez et al. 2002; Danchin et al. 2004). Older, more experienced individuals tend to use previous experience to select high-quality breeding sites while younger, more inexperienced birds settle near older birds (Nocera et al. 2009). It is these inexperienced settlers that are most likely to collect information on habitat quality by observing settlement decisions of others (Serrano et al. 2004; Nocera et al. 2006; Nocera and Forbes 2010). Since the sparrow is a resident species with strong site fidelity and sequential breeding, dispersers are likely using early-season song as an important cue for selecting habitat each year. However, we have observed adult and juvenile sparrows searching areas near our playback units after breeding (M. Davis personal observation) indicating that sparrows may indeed be using late-season song as a social cue. Future conspecific attraction experiments for this species should measure
sparrow response to both early- and late-season song playback to more efficiently target attempts to manipulate sparrows to settle in new areas.

Finally, we address an important aspect of playback studies that has received little attention in the literature: the effect of sound quality and amplitude on a species’ response to social cues in making settlement decisions (Ahlering et al. 2010). If song amplitude is too low it could provide stimulation too weak to affect a response. If song amplitude is too high, the intense stimulation or sound distortion could disrupt or deter settlement. Deciding how to measure a species’ response in playback studies is a difficult task, especially for rare species with small population sizes; therefore, understanding how sound quality affects the response can vastly improve such studies. In our study, sparrows did not establish territories in areas in close proximity to speakers where high amplitude resulted in sound degradation based on our qualitative measurements. It is possible that the high amplitude deterred sparrows from settling in the areas near our speakers; however, sparrows may also have simply avoided these areas thinking that another territorial male had already settled there (territoriality hypothesis). While we cannot rule out the equally parsimonious territoriality hypothesis, our study does highlight the importance of taking into consideration the properties of artificial cues when implementing song playback studies. By modeling sound quality across our study area, our study provides a more realistic measure of the response to song playback than studies that assume species will approach playback units directly.

ACKNOWLEDGEMENTS
We would like to thank Casey Kittle (planetinnovation@yahoo.com) for his help in designing and constructing the song playback systems used in this study. We thank David La Puma for his sparrow recordings and valuable input into the early design of the playback systems. We thank Jay Sah and Mike Ross from Florida International University for providing the vegetation data used in our analyses. We are very grateful towards those in the Grant F. Walton Center for Remote Sensing and Spatial Analysis for GIS assistance including John Bognar, Scott Haag and Jim Trimble. We would also like to thank everyone at ENP, Fire Cache and Dispatch who have aided us over the years, especially Sonny Bass. This research was funded by grants from the United States Fish and Wildlife Service and ENP Critical Ecosystem Studies Initiative. All monitoring and protocols complied with our Federal Fish and Wildlife Service permit and ENP permit restrictions.
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FIGURE LEGENDS

FIGURE 1. Map showing boundary of Everglades National Park in South Florida and approximate extent of Cape Sable Seaside Sparrow habitat (cross-hatched areas) with subpopulations labeled (A – F). Inset (lower right): Conspecific playback experiment study plot in sparrow subpopulation C showing location of sparrow territories observed over previous three years (2006-2008).

FIGURE 2. Competing hypotheses explaining Cape Sable Seaside Sparrow territory distribution across subpopulation C study plot in 2009 relative to location of song playback units (black triangles). Each panel of the figure shows one example simulation of 14 random points (black circles) generated under each hypothesis (A – F) buffered to create 2 ha sparrow territories (grey circles). For each hypothesis, the placement of random points was constrained to areas in grey as follows: Hypothesis A\text{Clustered} – points could occur anywhere in study area, however, clustering of points was forced at level observed in natural sparrow population; Hypothesis B\text{Habitat} – points constrained to area where breeding occurred between 2006 and 2008; Hypothesis C\text{Philopatry} – points constrained to area where breeding occurred during 2008 only; Hypothesis D\text{Playback} – points constrained to area where artificial song playback could be heard at natural-sounding levels based on sound model; Hypothesis E\text{Playback/Philopatry} – points allowed to occur in both song playback area and 2008 breeding area; and Hypothesis F\text{Playback/Habitat} – points allowed to occur in both song playback area and 2006-2008 breeding areas.
FIGURE 3. Distribution of Cape Sable Seaside Sparrow territories observed in subpopulation C study plot in 2009 (grey circles – 2 ha territory boundaries) relative to location of playback units (black triangles), sound field (shaded area), and location of 2008 breeding population (solid line – unshaded area). Each playback unit broadcast song from two speakers; north unit speakers faced NE and NW; south unit speakers faced N and SW. Sound field shows relative decibel levels of playback units across space; lighter grey tones indicate areas where song sounded most natural (sound values < 3) and darker grey tone surrounding playback units indicates area where high decibel levels degraded sound quality (sound values > 3).

FIGURE 4. Frequency distributions of overlap levels between observed Cape Sable Seaside Sparrow territory locations in subpopulation C in 2009 (n = 14) and simulated territory locations (n = 1000) under six competing hypotheses: Hypothesis A_{Clustered}, Hypothesis B_{Habitat}, Hypothesis C_{Philopatry}, Hypothesis D_{Playback}, Hypothesis E_{Playback/Philopatry}, and Hypothesis F_{Playback/Habitat}. Results in this figure were based on 2 ha territory sizes.

FIGURE 5. Mean number of overlapping Cape Sable Seaside Sparrow territories (+/- SE) between observed and simulated data under six competing hypotheses: Hypothesis A_{Clustered}, Hypothesis B_{Habitat}, Hypothesis C_{Philopatry}, Hypothesis D_{Playback}, Hypothesis E_{Playback/Philopatry}, and Hypothesis F_{Playback/Habitat}. Results in this figure were based on 2 ha territory sizes.
FIGURES

FIGURE 1
FIGURE 3
FIGURE 4

Hypothesis A

Hypothesis B

Hypothesis C

Hypothesis D

Hypothesis E

Hypothesis F

Frequency

Frequency

Frequency

0  2  4  6  8  10

0  2  4  6  10

0  2  4  6  10

Number of Overlapping Territories
FIGURE 5

![Bar chart showing mean count for different hypotheses]

- **Hypothesis A**: Mean Count = 2.1
- **Hypothesis B**: Mean Count = 2.1
- **Hypothesis C**: Mean Count = 1.9
- **Hypothesis D**: Mean Count = 3.5
- **Hypothesis E**: Mean Count = 2.8
- **Hypothesis F**: Mean Count = 2.2

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TABLES

TABLE 1. Average similarity (Sim, SD) of vegetation cover (Cover) within vegetation plots broken down into contributions (%Con) from each species. Includes only species whose cumulate contribution accounts for 90% of similarity.

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Rhynchospora tracyi

Vernonia blodgettii

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Cladium jamaicense

Muhlenbergia capillaris

Vernonia blodgettii
TABLE 2. Pairwise comparisons of mean number of overlapping territories between observed data and simulated data under six competing hypotheses (A - F) based on Tukey HSD method. All competing hypotheses are significantly different from Hypothesis $A_{\text{Clustered}}$. Hypothesis $D_{\text{Playback}}$ and Hypothesis $E_{\text{Playback/Philopatry}}$ are significantly different from all other competing hypotheses.

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Too few data and not enough time: the importance of detecting Allee effects in threatened species

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Running title: Detecting Allee effects in threatened taxa

Keywords: Demographic analysis, positive density dependence, extinction risk, prediction bootstrap, survival modelling, Cape Sable seaside sparrow

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References: 36

Tables: 3. Figures: 5.

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Abstract:

The detection of Allee effects is critical in assessing extinction risk, but is extremely difficult when sampling small, low-density populations. Failure to detect true Allee effects could lead to over-optimistic assessments of threat status, as well as the development of inappropriate species recovery plans. We outline a broadly-applicable approach for evaluating Allee effect likelihood in analyses of sparse demographic data, explicitly acknowledging the uncertainties associated with detecting subtle Allee effects amongst the suite of factors that can influence demographic variability. Detailed information on the probability of Allee effects will empower conservation decision-makers to balance extinction risks against the political and economic costs associated with management action. We use an illustrative case study involving demographic analyses of the endangered Cape Sable seaside sparrow, highlighting the value of information on Allee effect likelihood for the development of restoration measures within species recovery plans.
Introduction

Factors that cause declines in individual fitness with decreasing population density, termed Allee effects, are important determinants of extinction risk (Allee et al. 1949; Stephens & Sutherland 1999; Courchamp et al. 1999). Various lines of evidence hint that they may be widespread in nature (Leung et al. 2004; Lockwood et al. 2005), and they have played deciding roles in the extinctions of various once-abundant species such as the passenger pigeon *Ectopistes migratorius* and Carolina parakeet *Conuropsis carolinensis* (Bucher 1992). However, they are difficult to detect and are seldom documented even amongst well-studied species (Courchamp et al. 2008; Kramer et al. 2009). The uncertainty surrounding Allee effects inhibits conservation prioritization, as it clouds our ability to accurately assess the immediacy of threats. In order to improve extinction forecasting and conservation prioritization, there is an urgent need for more concerted efforts amongst conservation biologists to assess Allee effects in threatened taxa. We address this issue, presenting a general framework for Allee effect assessment in the conditions of data paucity typically associated with rare or threatened species.

The principal reason Allee effects are seldom measured directly is a practical one: the difficulty of gathering data from small or low density populations (Courchamp et al. 2008). Sample size limitation is often seen as an insurmountable barrier, leaving conservationists with little choice but to make uninformed assumptions about extinction risk (Foin et al. 1998). For example, the IUCN criteria for assessing species’ conservation status do not directly consider Allee effects (unless incorporated within a bespoke population viability analysis), but adopt blanket rules of thumb relating to population and range sizes, and rates of decline (IUCN 2001).
This approach is sensible in the absence of detailed information on Allee effects, but inevitably runs the risk of underestimating extinction risk in some taxa (Sanderson 2006; Mace et al. 2008). Uncertainty over Allee effects can inhibit the design of species recovery plans, as commonplace interventions such as habitat restoration may be ineffective for small populations exhibiting positive density dependence (Shirley & Lambertini 2009).

Positive relationships between population density and fitness can arise through a wide variety of mechanisms, including the inhibition of mate-finding, offspring-protection and successful foraging (Courchamp et al. 2008). Mechanisms operating on a single fitness parameter are typically referred to as component Allee effects (Stephens et al. 1999). In the absence of compensatory negative density dependence in other fitness parameters, these component effects can cause negative population growth rates, resulting in a demographic Allee effect (Stephens et al. 1999). Although demographic effects are of greatest significance for conservation, the difficulty of measuring population growth rate means that field studies typically focus on evaluating component Allee effects individually (Kramer et al. 2009). In this paper, we consider an approach that involves demographic comparisons between spatially-isolated subpopulations of varying size. Such fragmented populations are commonplace amongst threatened taxa, and effectively represent ‘natural experiments’ on the effects of population density. We provide a set of analytical tools that can maximize the information extracted from sparse demographic samples, demonstrating their use via a case study involving the endangered Cape Sable seaside sparrow (Ammodramus maritimus mirabilis), a taxon subject to ongoing conservation recovery initiatives (Lockwood et al. 2003; Cassey et al. 2007). In addition, we use simulations to illustrate the key challenges associated with the detection of component Allee effects from imperfect field data. We demonstrate that sample size limitation does not necessarily preclude
meaningful analysis of demographic patterns at low densities, and that the information gained from analysis of sparse data on threatened taxa may be of high value for conservation practice.

**Materials and methods**

*Motivating example: management of the Cape Sable seaside sparrow*

The sparrow occurs in just six spatially isolated subpopulations within freshwater marl prairies in southern Florida (Fig. 1; Lockwood et al. 2003). These subpopulations vary considerably in size and population density, and the smallest low-density subpopulations (particularly subpopulation A) have shown limited recovery following significant declines in the 1990s, despite the imposition of direct management actions (Walters et al. 2000, Cassey et al. 2007). Possible reasons for the failure of sparrow populations to recover post-management include: (1) management actions were insufficient to ameliorate threats, (2) other unmanaged environmental factors have prevented population recovery, or (3) the biology of the species itself dictates limited population increases despite the alleviation of threats, i.e. via Allee effects. We examine the likelihood that breeding productivity in small sparrow populations is subject to a component Allee effect, evaluating the weight of evidence for (or against) the latter factor as the responsible agent for the failure to recover. Plausible mechanisms by which decreased population density might influence nest survival include weakened nest defense (Soutullo et al. 2006) and decreasing parental investment (Møller & Legendre 2001). We analyze nest survival data collected between 2002 and 2009 in a 1x2 km intensive-survey plot within the large and relatively stable subpopulation E, together with plots covering two small subpopulations: A (6 km², 2009-2010) and C (9 km², 2006-2009). Territory mapping indicated that densities were an order of magnitude lower in the small subpopulations (1-4 males km⁻² year⁻¹) than in the large
subpopulation E (13-26 males km$^{-2}$ year$^{-1}$; Supporting Information Table S1). Nests were found via exhaustive searches and monitored at 2–4 day intervals until fledging or failure.

**Framework for measuring Allee effects**

Detecting a relationship between population density and fitness is challenging in any circumstance (Freckleton et al. 2006), but is particularly difficult when data collection is impaired at very low densities. Data sampled across a population density gradient will often display ‘availability bias’, as there are inevitably more individuals to sample at the high-density end of the spectrum. With such unbalanced data, the signal of an Allee effect can easily be drowned out by ‘noise’ associated with sampling error, environmental stochasticity or other influential factors that drive variation in the parameter in question (Dinsmore et al. 2002). Most statistical procedures isolate the dominant relationships within any given dataset (Burnham & Anderson 2002), and consequently perform poorly in resolving patterns associated with such unbalanced samples.

We use a two-tier approach to test for Allee effects within datasets of the kind exemplified by the sparrow case study. As a first step, we assess the strength of evidence for a subpopulation-level effect on the parameter in question using information-theoretic model selection (Burnham & Anderson 2002), a procedure that can be readily accomplished for a broad range of demographic parameters in the widely-used Program MARK (White & Burnham 1999). In order to detect patterns consistent with Allee effects, it is essential that the effects of ‘nuisance’ parameters (i.e. influential factors that are not of immediate interest in analysis) are controlled by modeling variation in the parameter in question as a function of covariates (e.g. habitat quality,
seasonal variability). The effect of population size on the response variable can then be tested by assessing the magnitude of change in Akaike’s Information Criterion (AIC) upon addition of an appropriate variable (e.g. a categorical term indicating membership of a small or large subpopulation) to the model. AIC differences exceeding -2 are typically taken to indicate strong support for a given model (Burnham & Anderson 2002). As model selection can be sensitive to sample size and data imbalance across covariate levels (Burnham & Anderson 2002), we also use a bootstrap prediction interval method (Stine 1985) to examine for the influence of sample size on effect detection. This method assesses whether a) there are differences in the demographic parameter in question with respect to population size (i.e. patterns consistent with an Allee effect), and b) whether these differences exceed the range of variation that is expected to arise for a given sample size in the absence of an Allee effect.

Initially, we partition the dataset into separate samples from large and small subpopulations. We use the large subpopulation sample to generate a statistical model describing variation in the parameter in question as a function of relevant covariate effects (e.g. habitat features or other ‘nuisance’ variables) in Program Mark. We use this model to generate predicted values for the small subpopulation samples, based on equivalent covariate data. These predictions are effectively ‘null’ estimates of expected survival rates in small subpopulations if we assume Allee effects are absent. We use the difference between predicted and observed survival rates (prediction errors) as a proxy measure of the magnitude of Allee effect. We calculate these errors thus:

\[
\text{Prediction error} = \frac{(\lambda - \phi)}{\lambda} \quad \text{Eq. 1}
\]
where $\lambda$ is the mean predicted survival rate for the low-density sample, and $\phi$ is the observed mean survival rate.

In order to determine whether resultant prediction errors represent meaningful differences, we generate a null distribution of errors by applying the same model to equivalently-sized samples of data drawn at random from the large subpopulation data. These ‘null’ errors reflect the differences that can arise between small and large populations in the absence of a true Allee effect, due to unexplained residual variation in the data. We calculate prediction errors for 1,000 bootstrap resamples (without replacement), each being of the same size as the low-density sample in question, and use them to generate a 95% interval of null errors. Observed values from small subpopulations that fall outside this interval are taken to indicate statistically meaningful effects (at an $\alpha=0.05$ level) after controlling for covariates.

For the sparrow case study, we tested for Allee effects by controlling for a suite of environmental variables that are likely to influence nest survival. Previous studies have shown that sparrow nest survival is closely linked to hydrologic variability (Lockwood et al., 2001; Pimm & Bass, 2002; Baiser et al. 2008), so we used model selection to evaluate the influence of six hydrological variables (Table 1) drawn from the Everglades Depth Estimation Network database (Liu et al. 2009). Using MARK, we selected the best model from a candidate set including all combinations of these hydrological variables, together with a categorical term indicating membership to large high-density (E) or small low-density (A and C) subpopulations (“subpopulation”). We then applied the bootstrap prediction method using the best model fitted to data exclusively from the high-density subpopulation (E), calculating errors between model-
predicted nest survival rates and actual maximum likelihood (ML) nest survival estimates for each small subpopulation dataset (A and C).

Simulating the challenges associated with Allee effect detection

To provide a broader illustration of the sampling issues arising in field studies of threatened taxa, we also used simulations to generate dummy datasets incorporating a range of widely-encountered data limitations (sample imbalance, nuisance parameter effects and sampling error). We use these datasets to evaluate the utility and limitations of the analytical methods presented above. Again, we use nest survival as a representative parameter, although the same principals apply to data on any demographic variable. We simulate nest survival in subpopulations of varying size, where survival probability is influenced by an Allee effect together with two ‘nuisance’ parameters: seasonal variation (doubling the probability of nest failure in the second half of the breeding season) and variation associated with nest placement (25% lower failure probability for nests in a “high survival” group throughout the season). Sampling error is incorporated by directly simulating the observation process, whereby ‘observed’ nest encounter histories are extracted from ‘true’ nest survival histories in a manner analogous to standard field protocols (see Supporting Information, Figure S1).

We examine a range of sample size and dataset imbalance scenarios (100 datasets in each scenario) by combining sets of nest histories from large and small subpopulations of varying size (large = 200 or 400 nests; small = 10 to 50 nests in increments of 10). To simulate an Allee effect, we increased nest failure probability by 30% in small subpopulations, resulting in datasets with survival rates ranging from 0.09 to 0.63 (mean 0.35) in the small subpopulation and 0.49 to
0.63 (mean 0.55) in the large subpopulation. To demonstrate the risk of Type I error (i.e. detecting a spurious effect) under each scenario, we also simulate datasets with no underlying Allee effect, where data heterogeneity arises purely from sampling error and ‘nuisance’ parameters. In these datasets, realized nest survival rates ranged from 0.29 to 0.82 (mean 0.55) in small subpopulation samples, and from 0.49 to 0.63 (mean 0.55) in large subpopulation samples.

Results

Sparrow nest survival

In the sparrow example, we observed lower nest survival probability in small subpopulations (mean 0.18, LCI 0.11, UCI 0.28) than in the large high-density subpopulation (mean 0.23, LCI 0.18, UCI 0.28). However, following model selection we found no support for an effect of subpopulation membership ($\sum AIC_w = 0.28$), and hence no evidence for a component Allee effect (Table 2). Rather, variation in nest survival across all subpopulations was best explained by environmental variables (Table 3), principally seasonal water table depth ($\sum AIC_w = 0.98$) and timing of nest activity relative to onset of flooding ($\sum AIC_w = 0.99$), with weaker support for a positive effect of the number of days of flooding during the nest period ($\sum AIC_w = 0.82$). Prediction bootstrapping confirmed the underlying similarity of survival rates between high- and low-density subpopulations, as the best model for data from the large high-density subpopulation ($AIC_w = 0.13$) generated broadly accurate predictions when applied to the small subpopulations (Fig. 2). The observed mean survival rate in small subpopulations (pooled across years, $n=72$) was very close to the model prediction based on high-density data (prediction error 0.02), strongly suggesting that factors influencing nest survival were
fundamentally similar across both large and small subpopulations (Fig. 3). Annual nest survival rates in small subpopulations consistently fell within the 95% null interval generated by bootstrapping (Fig. 3), indicating that observed rates of nest survival in low density subpopulations were within the range of equivalently-sized samples from the high density subpopulation. The only exception was the sample from subpopulation C in 2007, where the observed rate exceeded the upper limit of the 95% null interval (Fig. 3). It is notable that observed nest survival rates in subpopulation A were consistently low (prediction error 0.43 for the pooled sample, n=24; Fig. 3). Differences of this magnitude arose in only 10% of equivalent bootstrap resamples of high-density subpopulation data, suggesting that survival may have been genuinely lower than the null expectation in this small subpopulation.

Inferential error rates with simulated data

Our simulated datasets displayed a high degree of variation in the magnitude of difference in nest survival rates between small and large subpopulation samples (Fig. 4a & b), despite the simulated Allee effect being constant (30% increased failure rate). This variation arose due to process stochasticity, nuisance parameter effects and sampling error, all of which are to be expected in any field-sampled dataset. Testing our framework against these simulated datasets indicated that the risk of overlooking a true Allee effect was highly sensitive to sample size (Fig. 5), as expected given the inevitable reduction in statistical power when dealing with small samples. At the smallest sample size considered (n=10), model selection techniques correctly detected Allee effects in 51% of simulated datasets, rising to 93% at the largest sample size considered (n=50, Fig. 5a). Prediction bootstrapping provided more conservative inferences, detecting true Allee effects in 86% of datasets at n=50 and 33% at n=10 (Fig. 5c). This
conservatism was reflected in the reduced rate of false positive error (i.e. the detection of
spurious Allee effects in datasets where none were present) with prediction bootstrapping (Fig.
5b & d). Doubling the sample size in the large subpopulation dataset (n=400 nests) had little
effect on inferential error rates, and did not change the relative performance of either model
selection or bootstrap prediction techniques in detecting Allee effects (Supporting Information,
Fig. S2).

Discussion

The difficulty of analyzing demographic variability within low-density populations presents a
major barrier for the study of Allee effects in threatened species (Doak et al. 2005; Courchamp et
al. 2008; Kramer et al. 2009). The perceived gravity of this barrier has likely deterred researchers
from attempting to address the issue in many cases. We suggest that with appropriate analysis,
limited samples can indeed provide useful information on Allee effect likelihood. Our
simulations highlight the complementary value of model selection and bootstrap prediction in
balancing the risk of inferential errors in these analyses, with bootstrapping providing a direct
measure of the uncertainty associated with data limitation. Our framework can be applied to any
fitness component that is expected to vary in relation to population density, and could equally be
used to evaluate demographic Allee effects directly in systems where measurements of
population growth rate are feasible. The method is easy to implement within freely available
software packages, requiring only basic randomization routines (example Excel files are
available on request from the authors).

In the sparrow case study, we hypothesized that diminished nest productivity at low
densities might be inhibiting population growth. However, we found no clear evidence of an
Allee effect on this fitness component after controlling for habitat and seasonal effects. Using prediction bootstrapping, we were able to estimate the magnitude of variation that might be expected between subpopulation samples in the absence of an Allee effect; at the maximum pooled sample size available for small sparrow subpopulations (n=72), this variation extended to values 23% below the null model prediction based on large-subpopulation data (95% null interval limit 0.23 at n=72; Fig. 5). We therefore cannot exclude the possibility of a weak component Allee effect (<23%) being masked as a result of unexplained variation within the dataset. Nevertheless, the close similarity between the mean nest survival rate in the small subpopulations and the null model prediction suggests that a pervasive Allee effect on this parameter is unlikely. We note that without further analyses on other fitness components that contribute to intrinsic population growth rate, we cannot discount the possibility of a demographic Allee effect (Stephens et al. 1999).

Even allowing for the uncertainties associated with small samples, the information provided under our approach is of significant value in determining the likely efficacy of different conservation interventions (Foin et al. 1998; Boersma et al. 2001). For the sparrow, actions targeted at increasing breeding productivity in small subpopulations (e.g. sympathetic water flow management) should be effective in the absence of a strong Allee effect on nest survival. If population growth is driven primarily by other fitness components (e.g. adult survival), such interventions might still be insufficient to reverse declines, particularly if other Allee effects are involved. Under a strong Allee effect, direct actions such as translocation might be required in order to reverse negative trends in low-density areas (Courchamp et al. 2008; Shirley & Lamberti 2009). Whilst further analyses are clearly needed, our analysis provides a valuable demonstration of the methodological approaches required in order to evaluate component Allee effects. In
future, improved probabilistic information on Allee effects should facilitate the application of risk analysis, allowing a more rigorous analytical evaluation of threats to the population relative to economic and political costs of management (Harwood 2000).

Although our methods can be applied to a wide variety of study systems, we recognize several limitations to our approach. Principally, we rely on the availability of data from small and large subpopulations (or low- and high-density conditions), which in some cases may be difficult to acquire. For example, ‘ecologically rare’ taxa are unlikely to be found at high densities even in unperturbed environments (Gaston 1994), precluding such comparisons. Furthermore, whilst our method is designed to improve inferences about small samples from low-density populations, its success may be dependent on the availability of relatively large datasets from high-density conditions. Consequently, despite being designed specifically to deal with sparse data, our method still carries a relatively high requirement for sampling effort. Finally, the efficacy of our approach will be highly sensitive to other influential factors such as habitat quality, particularly if these vary across subpopulations (Lebreton et al. 1992; Rotella et al. 2007). Unless other influential factors are adequately controlled statistically via the inclusion of model covariates, the presence of unexplained heterogeneity in the data will substantially inhibit power to detect true Allee effects. Whilst this problem is inevitably difficult to resolve, the use of prediction bootstrapping at least allows a direct assessment of the uncertainty arising from unexplained variation, which should be of significant value in systems where covariate effects are poorly understood.

Although biodiversity conservation increasingly targets community or landscape-level actions (Brooks et al. 2006), species-orientated approaches remain critical for endangered
species recovery (Shirley & Lambertini 2009). These actions rely heavily on detailed knowledge of the biology of the species in question. For endangered taxa, information on demographic variability at low population density remains a major data gap (Kramer et al. 2009). Often, attempts to estimate minimum viable population sizes in threatened species must rely on untested assumptions about demographic variability and Allee effects (Sanderson 2006). We suggest that researchers make maximum use of the data available, acknowledging uncertainties associated with sample size and data heterogeneity, in order to estimate the probability of Allee effects in taxa targeted by conservation action. Information of the kind provided under our framework will extremely valuable in developing precautionary assessments of species vulnerability on a case by case basis.

Acknowledgements

Funding was provided to JLL by Everglades National Park and the US Fish and Wildlife Service. We thank the numerous field technicians that collected data for the sparrow, particularly Michelle Davis. We also thank Tabby Fenn for careful curation of this data. Finally, we thank Sonny Bass, Gary Carnell, and other staff at Everglades National Park for their assistance and for looking after our safety in the field.

References


Table 1 Hydrologic variables used to model Cape Sable seaside sparrow nest survival, derived from the EDEN database (Liu et al. 2009).

<table>
<thead>
<tr>
<th>Variable name</th>
<th>Scale of measurement (spatial*, temporal†)</th>
<th>Description</th>
</tr>
</thead>
<tbody>
<tr>
<td>depth</td>
<td>Nest, nest monitoring period</td>
<td>Maximum water depth above ground</td>
</tr>
<tr>
<td>water cover</td>
<td>Region, nest monitoring period</td>
<td>Proportion of region with standing water</td>
</tr>
<tr>
<td>water days</td>
<td>Region, nest monitoring period</td>
<td>Number of days with standing water during nest period</td>
</tr>
<tr>
<td>flood</td>
<td>Region, nest monitoring period</td>
<td>Nest found before/after the onset of flooding (&gt;90% standing water cover)</td>
</tr>
<tr>
<td>watertable</td>
<td>Region, season</td>
<td>Mean depth of regional water table</td>
</tr>
<tr>
<td>season flood</td>
<td>Regional, season</td>
<td>Proportion of days with &gt;50% standing water cover</td>
</tr>
</tbody>
</table>

* Nest – 0.5km² grid square containing nest site; regional scale = 4km² grid square containing nest site. † Nest monitoring period = period from date found to assumed date of fledging or failure; season = maximum period of breeding activity, 31st March to 10th August.
Table 2 Results of model selection for nest survival models including data from two small subpopulations (A and C) and one large subpopulation (E), showing the ten best-performing models in explaining variability in daily survival rate.

<table>
<thead>
<tr>
<th>Model</th>
<th>K</th>
<th>AICc</th>
<th>ΔAICc</th>
<th>AICw</th>
<th>Deviance</th>
</tr>
</thead>
<tbody>
<tr>
<td>1. season + flood + water days + watertable</td>
<td>5</td>
<td>1142.0</td>
<td>0.000</td>
<td>0.172</td>
<td>1132.0</td>
</tr>
<tr>
<td>2. season + flood + water days + watertable + water cover</td>
<td>6</td>
<td>1142.7</td>
<td>0.626</td>
<td>0.126</td>
<td>1130.6</td>
</tr>
<tr>
<td>3. season + flood + water days + watertable + depth</td>
<td>6</td>
<td>1143.7</td>
<td>1.665</td>
<td>0.075</td>
<td>1131.7</td>
</tr>
<tr>
<td>4. season + flood + water days + watertable + subpop</td>
<td>6</td>
<td>1143.9</td>
<td>1.855</td>
<td>0.068</td>
<td>1131.9</td>
</tr>
<tr>
<td>5. season + flood + water days + watertable + season flood</td>
<td>6</td>
<td>1144.0</td>
<td>1.964</td>
<td>0.064</td>
<td>1132.0</td>
</tr>
<tr>
<td>6. season + flood + watertable + water cover</td>
<td>5</td>
<td>1144.2</td>
<td>2.170</td>
<td>0.058</td>
<td>1134.2</td>
</tr>
<tr>
<td>7. season + flood + water days + watertable + water cover + subpop</td>
<td>7</td>
<td>1144.6</td>
<td>2.506</td>
<td>0.049</td>
<td>1130.5</td>
</tr>
<tr>
<td>8. season + flood + water days + watertable + water cover + season flood</td>
<td>7</td>
<td>1144.6</td>
<td>2.595</td>
<td>0.047</td>
<td>1130.6</td>
</tr>
<tr>
<td>9. season + flood + water days + watertable + water cover + depth</td>
<td>7</td>
<td>1144.7</td>
<td>2.606</td>
<td>0.047</td>
<td>1130.6</td>
</tr>
<tr>
<td>10. season + flood + water days + watertable + depth + season flood</td>
<td>7</td>
<td>1145.5</td>
<td>3.472</td>
<td>0.030</td>
<td>1131.5</td>
</tr>
<tr>
<td>Null model (season)</td>
<td>2</td>
<td>1155.8</td>
<td>13.744</td>
<td>0.001</td>
<td>1151.8</td>
</tr>
<tr>
<td>---------------------</td>
<td>---</td>
<td>--------</td>
<td>--------</td>
<td>-------</td>
<td>--------</td>
</tr>
</tbody>
</table>

* Number of model parameters
Table 3 Variable selection probabilities and parameter estimates (with standard errors and 95% CI) for each predictor variable included in model selection analyses for Cape Sable seaside sparrow nest survival data from two small subpopulations (A and C) and one large subpopulation (E). Parameter estimates are averaged across all models in the candidate set (Burnham & Anderson 2002).

<table>
<thead>
<tr>
<th>Variable name</th>
<th>$\Sigma AIC_w$</th>
<th>Estimate</th>
<th>s.e.</th>
<th>Lower</th>
<th>Upper</th>
</tr>
</thead>
<tbody>
<tr>
<td>intercept</td>
<td>-</td>
<td>4.592</td>
<td>0.342</td>
<td>4.025</td>
<td>5.367</td>
</tr>
<tr>
<td>season</td>
<td>1.000</td>
<td>-0.023</td>
<td>0.004</td>
<td>-0.032</td>
<td>-0.017</td>
</tr>
<tr>
<td>depth</td>
<td>0.290</td>
<td>0.010</td>
<td>0.047</td>
<td>-0.075</td>
<td>0.109</td>
</tr>
<tr>
<td>water cover</td>
<td>0.492</td>
<td>0.192</td>
<td>0.546</td>
<td>-0.670</td>
<td>1.469</td>
</tr>
<tr>
<td>water days</td>
<td>0.823</td>
<td>0.049</td>
<td>0.030</td>
<td>-0.012</td>
<td>0.105</td>
</tr>
<tr>
<td>flood</td>
<td>0.992</td>
<td>-0.882</td>
<td>0.365</td>
<td>-1.702</td>
<td>-0.274</td>
</tr>
<tr>
<td>watertable</td>
<td>0.981</td>
<td>-0.016</td>
<td>0.007</td>
<td>-0.029</td>
<td>-0.002</td>
</tr>
<tr>
<td>season flood</td>
<td>0.314</td>
<td>-0.039</td>
<td>0.748</td>
<td>-1.803</td>
<td>1.129</td>
</tr>
<tr>
<td>subpopulation</td>
<td>0.278</td>
<td>0.008</td>
<td>0.189</td>
<td>-0.323</td>
<td>0.418</td>
</tr>
</tbody>
</table>

$\Sigma AIC_w$ are selection probabilities derived by summing $AIC_w$ from all models including that variable (Whittingham et al. 2005).
Figure captions

Figure 1 Map showing approximate extent of Cape Sable seaside sparrow subpopulations (A-F) in South Florida, USA, based on detections from range-wide helicopter surveys conducted since 2005.

Figure 2 Comparisons between observed Cape Sable seaside sparrow nest survival rates (black squares joined by solid lines) and predicted values from a model built exclusively using data from the large subpopulation E (crosses joined by broken lines). Upper panel shows observations and predictions for the large subpopulation E, middle and lower panels show small subpopulations C and A respectively. Dotted lines show limits of 95% null intervals generated by applying the model to bootstrap resamples of large subpopulation data (1,000 resamples of equivalent size for each datapoint).

Figure 3 Model prediction errors for nest survival rates in small subpopulations of the Cape Sable seaside sparrow, representing the proportionate difference between observed rates ($\phi$) and predictions ($\lambda$) generated using a model built from large subpopulation data, together with the 95% null interval derived by prediction bootstrapping (dotted lines). Values >0 indicate samples where model predictions exceeded observed values. Black circles show samples for individual years in subpopulation C, open squares show individual years in subpopulation A, grey circle shows pooled data from all years in subpopulation C, grey square shows pooled data from all years in subpopulation A, black diamond shows pooled data from all years and both small subpopulations.
Figure 4 Differences in nest survival rate ($S$) between small and large subpopulation datasets generated by simulation, showing how the magnitude of difference influences the detection of component Allee effects. Each point represents a dataset consisting of unbalanced samples from large (n=200) and small (n=20) subpopulations. Model prediction errors are the proportionate difference between the true nest survival rate in the small population sample ($\phi_{\text{small}}$) and the rate predicted for that sample by a model based on large subpopulation data ($\lambda_{\text{small}}$). True differences between the small and large subpopulation samples are shown on the x axis. The upper panel (a) shows 100 simulations with a component Allee effect (nest failure probability 30% higher in the small subpopulation), whilst the lower panel (b) shows 100 simulations without a true Allee effect (differences between subpopulation samples arise only from sampling error and process stochasticity). Points are labeled according to the outcome of analysis: black circles show cases where an Allee effect was inferred by both model selection and prediction bootstrapping; grey circles show cases where an effect was inferred only by model selection; open circles show cases where neither method inferred an Allee effect.

Figure 5 Effects of sample size on inferential error rates from model selection (a & b) and prediction bootstrapping (c & d) in detecting Allee effects, evaluated using simulated data. Left-hand panels (a & c) show simulated datasets simulated with a genuine component Allee effect (nest failure probability 30% higher in the small subpopulation), whilst right-hand panels (b & d) show datasets without any Allee effect (failure probability similar between subpopulations). Symbol colour highlights whether a meaningful effect was inferred (black) or not (grey) for each dataset. For model selection, Allee effects are inferred if there is a negative change in $\Delta \text{AIC}_c$ upon addition of a subpopulation term to the model. For bootstrap prediction, Allee effects are inferred if prediction errors from a model built from large subpopulation data fall
outside a 95% null interval generated from 1000 bootstrap resamples of large subpopulation data. Values in parentheses are rates of inferential error (type II in left-hand panels; type I in right-hand panels) across 100 datasets in each sample size category (large subpopulation sample=200 nests in each case).

Supporting Information

Table S1 Estimates of territory density (within study plots) in three Cape Sable seaside sparrow subpopulations (A, C and E), derived from intensive surveys.

Figure S1 Schematic diagram showing the structure of a stochastic simulation model used to generate nest encounter history datasets typical of those observed in field studies.

Figure S2 Relative performance of model selection (a & b) and bootstrap prediction (c & d) methods in detecting differences in nest survival between small and large subpopulations from simulated data, where sample size in large subpopulation is increased to 400 nests.