

# Importance of estimating dispersal for endangered bird management

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## Abstract

Endangered species recovery plans are frustrated by small, spatially structured populations where understanding the influence of birth, death, and dispersal is difficult. Here we use a spatially explicit, long-term study to describe dispersal in the Cape Sable seaside sparrow (*Ammodramus maritimus mirabilis*). Since 1990, this species declined > 50%. It occurs as several geographically isolated subpopulations in the Florida Everglades. We characterize dispersal, recognizing that our sampling, as well as the species' distribution, is spatially heterogeneous. The annual movements of juveniles and adults are statistically heavy-tailed. That is, while most individuals are recaptured locally, a significant portion exhibit long-distance dispersal. Individuals move between subpopulations to distances > 30 km. Not accounting for the spatial heterogeneity of sampling or the species range itself underestimates dispersal and can lead to ineffective management decisions. Recovery focused on translocation will be less successful than strategies that protect habitat and increase breeding.

## Introduction

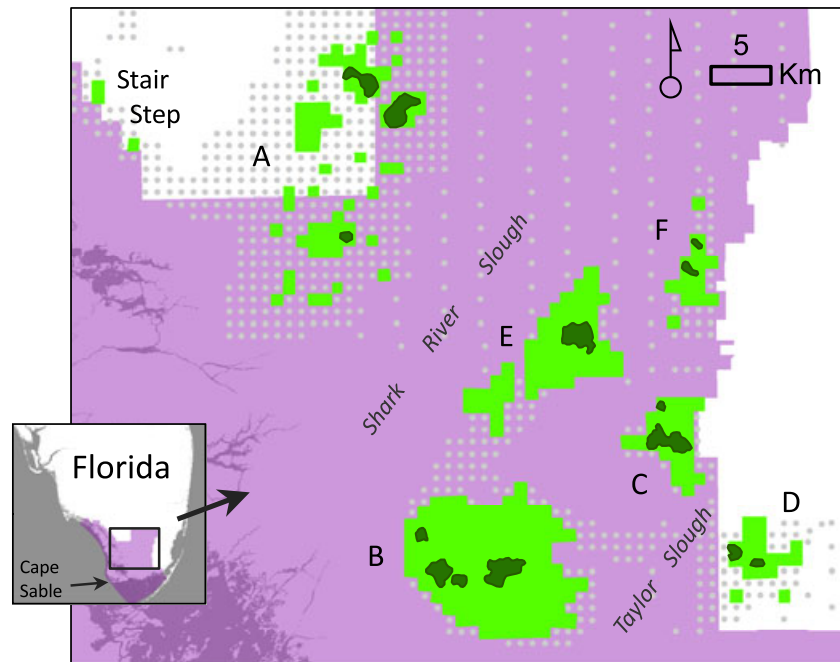
Population parameters of birth and death rates are essential elements in understanding the fates of species, especially endangered ones. However, population persistence is driven as much, if not more, by dispersal events as it is by births and deaths (Wahlberg *et al.* 1996; Van Houtan *et al.* 2007). Empirical studies of dispersal between subpopulations of endangered species are few. They demand marking efforts of individuals in the various subpopulations extensive enough in space and time to capture dispersal events between them. For endangered species, by force of circumstance, marking large numbers of individuals will generally be difficult. The statistical issues associated with modeling dispersal, especially the frequency of long-distance dispersal, are equally daunting (Clark *et al.* 1999; Hastings *et al.* 2005).

Most dispersals are local. For the small sample sizes involved with endangered species, one is likely to observe only such events. Using only these observations biases understanding population dynamics (Koenig *et al.*

1996). Simple models severely underestimate the frequency of long-distance dispersal events. That is a concern given that such rare events may drive population dynamics (Nathan *et al.* 2003). The failure to represent dispersal correctly for threatened species raises important conservation issues, not merely statistical ones (Walters 2000). Management lies at the core of decisions made on behalf of endangered species. Clearly, the individual small subpopulations of an endangered species can have high risks of extinction. Indeed, they might not be self-sustaining and only persist through continued immigration. If such a subpopulation becomes extinct, is it prudent to attempt to translocate individuals from another subpopulation to rescue it? Or is it better to not intervene and focus resources on population centers?

The answer to these questions depends, in part, on the likelihood of long-distance dispersals. Here, we report a geographically extensive, long-term study of the Cape Sable seaside sparrow (Lockwood *et al.* 1997; Curnutt *et al.* 1998; Nott *et al.* 1998; Lockwood *et al.* 2001; Pimm *et al.* 2002; Baiser *et al.* 2008; Boulton *et al.* 2009).

**Figure 1** The 1994–2008 distribution of Cape Sable seaside sparrows in Everglades National Park (purple) in south Florida. Light green cells are the 1 km<sup>2</sup> regions where sparrows were detected in point-count surveys during the period of record (grey circles are census points where sparrows were never detected during this period). Outlined dark green shapes are minimum convex polygons of intensive mark-recapture study sites. These sites are distributed across all six currently extant sparrow subpopulations A–F.



We show that the statistical description of dispersal distances is heavy-tailed. That is, simple characterizations of movement will not describe long-distance movements well. Long-distance movements from large populations add individuals to smaller peripheral populations in sufficient numbers that likely prevent their foundering. When populations are reduced, their smaller satellite populations can become extinct as a consequence. This study aims to characterize dispersal to understand how it can affect the population dynamics of an endangered passerine bird. In answering these questions for the Cape Sable seaside sparrow, we shed light on the broader issue of what role accurate estimates of dispersal distances play in core conservation management decisions for threatened vertebrates.

Everglades National Park and Big Cypress National Preserve in southwest Florida (Figure 1) hold most remnant populations of the species. The Florida Everglades is a subtropical wetland of global importance and was placed under protection as a national park in 1947 (Douglas 1947). In the early 1900s, the ecosystem was regularly inundated by Shark River Slough, which swelled to 90 km wide, flooding large areas for 3–7 months annually. This changed in the 1950s when the Army Corps of Engineers built a vast infrastructure to manage water flow to the Everglades; keeping some areas unusually flooded and constricting water flow to other areas.

The Cape Sable seaside sparrow, originally listed as an endangered species by the U.S. government in 1967, breeds in low-lying, dry prairie before the late-spring

rains. Its breeding success is correlated with water levels as low-lying nests easily flood (Baiser *et al.* 2008). Its range once encompassed six subpopulations (A–F) and some peripheral ones, including Cape Sable, where the bird was first collected. Of these, A, west of Shark River Slough and B, and E east of the Slough were the three largest (Figure 1). Unprecedented, managed floods across the Park's northern boundary during 1993–1996 reduced subpopulation A to <5% of its previous size. This caused a 50% decline in the species' entire population, which once exceeded 6,000 birds (Curnutt *et al.* 1998; Nott *et al.* 1998). Conservation concerns about the species, especially given the risk of stochastic events such as catastrophic prairie fires led to management decisions to protect the remaining birds in the most isolated subpopulation A (Pimm & Bass 2002).

This analysis addresses the following questions: (1) does the Cape Sable seaside sparrow show evidence of long-distance dispersal? (2) do juveniles disperse further than adults? (3) how does dispersal influence the spatial structure of the subpopulations? and (4) what management actions follow from these results?

## Methods

### Study area and data collection

In 1981, and annually between 1992–2008, Everglades National Park biologists conducted point count surveys to establish the sparrow's distribution (Jenkins *et al.*

2003a, b). Surveys took place April–May each year and occurred at 1 km intervals in areas considered potential habitat—and in many adjacent prairie habitats as well (Kushlan & Bass 1983). All birds detected within a 200 m radius of the survey location were recorded. From these surveys, the remnant population was classified into six subpopulations (Curnutt *et al.* 1998). From 1994 to present, intensive capture–recapture studies took place at study plots where logistically feasible (Figure 1). (This still included remote sites only accessible by helicopter.) From April to June each year, researchers captured sparrows with mist nets and tagged birds with uniquely numbered aluminum bands, installing color bands to facilitate visual resights. This combined tagging allowed both net recaptures and resights to provide 769 successive locations for sparrows after their initial release. Further details are provided elsewhere (Boulton *et al.* 2009).

### Dispersal kernel analysis

We analyzed census data from point count and capture–recapture surveys to model dispersal. Point count surveys established the known distribution of the species during the capture–recapture effort (i.e., 1994–2008). This distribution is considerably smaller than the 1981 range reflecting reductions in the number of occupied survey sites. From the point count data, we generated a grid of the species' occurrence with a 1-km<sup>2</sup> resolution. Each cell in this grid is centered on a census location and represents the detected presence/absence at that point in that year. The resulting map served as the greatest possible extent where the species was detected, after 1993. The capture–recapture database identifies 14 separate plots when minimum convex polygons consider locations within 750 m to be in the same plot.

We computed travel distances from capture locations, using two-dimensional data to derive a univariate quantity. A dispersal kernel is the probability density function that corresponds to the  $x$  and  $y$  distances. We seek the probability density function of the amplitude,  $r$ , or the distance from the origin to a successive location ( $x, y$ ) using  $r = (x^2 + y^2)^{0.5}$ . We therefore model dispersal using amplitude kernels that are closely related to, but distinct from, dispersal kernels (Van Houtan *et al.* 2007). Having determined the species distribution, the areas sampled, and the distances traveled, we then considered different mechanistic models of dispersal.

The normal, or Gaussian, distribution describes an individual whose movement appears to drift randomly away from its place of origin. This random walk is the diffusion model and populations that diffuse through space will spread across landscapes slowly. The second model we considered was the negative exponential distribution.

This model describes unidirectional movement with a constant probability of stopping at each step, or directional flight. This model has a slower decay than diffusion and will subsequently observe longer flights. In both the Gaussian and exponential models, long-distance movements are somewhat constrained. Heavy-tailed probability functions, can accommodate distances both near and far. This family of models assumes a combination of local and long-distance stochastic forces and expects that a few individuals fly long distances (Viswanathan *et al.* 1996). Heavy-tailed dispersal models describe populations that can spread relatively rapidly through space and time.

We described diffusion with the Rayleigh probability distribution:

$$g(r) = \left(\frac{r}{\alpha^2}\right) \exp\left(-\frac{r^2}{2\alpha^2}\right), \quad r \geq 0, \quad \alpha > 0 \quad (1)$$

where  $\alpha$  is the scale parameter, or average dispersal distance.

For the negative exponential distribution,  $r$  is a special case of the gamma distribution. This distribution has the probability density function:

$$g(r) = \frac{1}{\alpha\Gamma(\beta)} \left(\frac{r}{\alpha}\right)^{\beta-1} \exp\left(-\frac{r}{\alpha}\right), \quad r \geq 0, \quad \alpha > 0 \quad (2)$$

where  $\alpha$  is a scale parameter,  $\beta$  is a shape parameter of the kernel, and  $\Gamma$  represents the gamma function. In this instance,  $\beta = 2$ , for the gamma distribution takes the exponential form.

For the heavy-tailed model, we used the log hyperbolic secant ("log-sech") distribution (Halley & Inchausti 2002). The amplitude kernel such that  $r$  has a log-sech distribution is

$$g(r) = \frac{2/(\pi br)}{(r/\alpha)^{1/b} + (r/\alpha)^{-1/b}}, \quad r \geq 0, \quad \alpha, b > 0 \quad (3)$$

where  $\alpha$  is the scale,  $b$  is a shape parameter, and  $\beta$  is the tail index. Here  $\beta = 1 + 1/b$  as the log-sech has the form  $f(r) \approx (2/\pi br)(\alpha/r)^\beta$  for large values of  $r$ . Unlike the previous models, the tail index parameter allows the rate of decay to vary more flexibly. When  $\beta = 2$  the distribution reduces to the better-known Cauchy form, though  $\beta$  can lie anywhere in the range  $(1, \infty)$ .

Population occurrence and sampling is patchy (Figure 1). Accurate characterizations of dispersal should account for sampling bias (Van Houtan *et al.* 2007) as well as the patchy distribution across a heterogeneous landscape (Smith *et al.* 2002). The probability of observing a recapture,  $\Pr(r_i|c)$ , depends on the model,  $\Pr(c|r_i)$ , and the spatial sampling effort at that distance,  $\Pr(w_i)$ . Using ArcGIS (ESRI 2008), we calculated  $\Pr(w_i)$  as the area the mark-recapture plots sample divided by the species range area. We did this for each of the 14 plots, in 100 m annuli that radiate from each plot's center. We weighted

averages of values across all plots according to the number of observed recaptures in that plot. This provided a single value for each annulus of the amplitude data,  $w(r_i)$ , across the landscape. We incorporated this into a likelihood model that estimates model parameters given the data:

$$L = \prod_{i=1}^n \left[ \frac{w(r_i)g(r_i)}{\int_0^{r_{\max}} w(r)g(r)dr} \right] \quad (4)$$

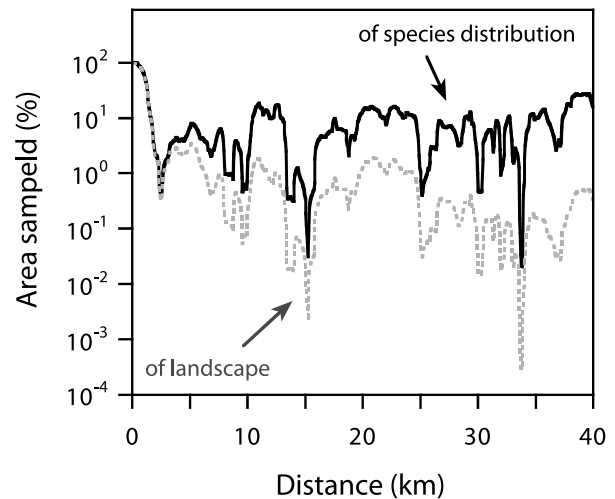
We used maximum likelihood methods to compare the Rayleigh, Gamma, and log-sech models using the corrected Akaike information criterion ( $AIC_c$ ). An optimization model from  $10^5$  Monte Carlo simulations locates the parameters yielding the minimum  $AIC_c$  (Van Houtan *et al.* 2007). Although we considered all time intervals between captures, we derived dispersal curves using only movements between years as per its classic definition (Greenwood & Harvey 1982; Fahrig 2007). We furthermore made demographic distinctions, separating annual movements in the hatching year (natal dispersal) from those in successive years (breeding dispersal). We rank all models according to their  $\delta AIC_c$  values and Akaike model weights (Williams *et al.* 2001).

## Results

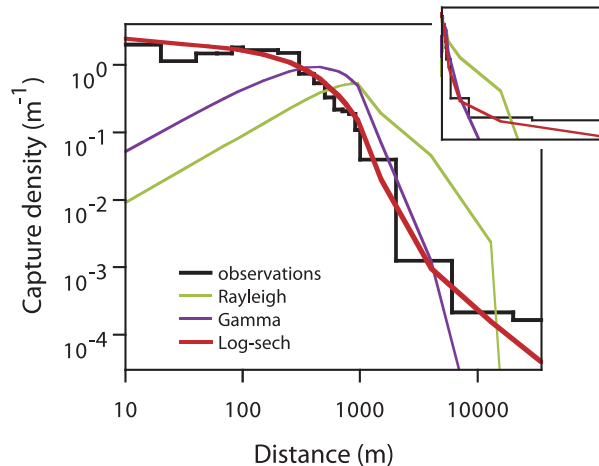
Figure 1 maps the area of the known distribution of the Cape Sable seaside sparrow from 1994 to present. Light green grid cells are the extent of occurrence of the species determined from point count surveys. Dark green polygons are the 14 intensive study plots. Most populations are on the south or east side of the Shark River Slough, with the B subpopulation being the most populous, and geographically contiguous, cluster.

Figure 2 shows the spatial sampling effort, displaying the area sampled by the recapture plots as a function of: (1) the species distribution, and (2) the percentage of the entire landscape. Importantly, the sampling effort is not constant. If the sampled area is compared to the entire landscape, there is a steep and then fluctuating decay from the origin. If the sampled area is a function of the known distribution, the effort declines to 3 km, then gradually increases out to 40 km because the available habitat declines with distance. This latter calculation forms the  $w(r_i)$  for the likelihood model.

Figure 3 compares three models of dispersal to the empirical observations of sparrow recaptures. Only the heavy-tailed log-sech distribution (red line) describes the empirical observations (black line) across the entire span of dispersal distances. The MLE fitting procedure, for the Rayleigh and Gamma models, in its attempt to



**Figure 2** Spatial sampling effort was determined as a percentage of the current Cape Sable seaside sparrow geographical distribution. Not all distances are equally sampled, nor are they equally likely to contain sparrows. We thus calculated 100-m annuli from each plot centroid, determining the area sampled, area of the known distribution, and total area in each annulus. Data from all 14 census plots were added to achieve a single corrective value,  $Pr(w_i)$ , of the sampled species distribution for fitting distance kernels.



**Figure 3** Heavy-tailed dispersal is the highest-ranked model in describing interannual movements of Cape Sable seaside sparrows, and is the only model that accommodates both local and long-distance flights. This histogram is the recapture distances from all tagged individuals in comparison to the best fit for each of the three dispersal models we considered. On the log-log scale, recaptures have a roughly constant density out to  $\sim 300$  m and then decline roughly linearly. The x-axis is the distance a marked individual moved from the location of recapture to its previously known location. The height of each bar is the number of individuals observed in that interval divided by the width of bar, and thus the total area under the black line is the total number of individual recapture events ( $n = 769$ ). The bin intervals for the histogram are chosen for visual clarity and affect neither model fitting nor model selection. Inset graphic plots the same figure on a log-linear scale, constraining the same axis limits.

**Table 1** Full model results for the dispersal kernel analysis. A variety of metrics rank the log-sech model highest among the candidate models, no matter how the data are grouped. We constrained the time step between captures to 1 year to match the common time scales of population parameters. *K* is the number of parameters, *LL* is the log-likelihood,  $\delta AIC_c$  is the relative *AIC<sub>c</sub>* among compared models, and  $\omega_i$  is Akaike weight

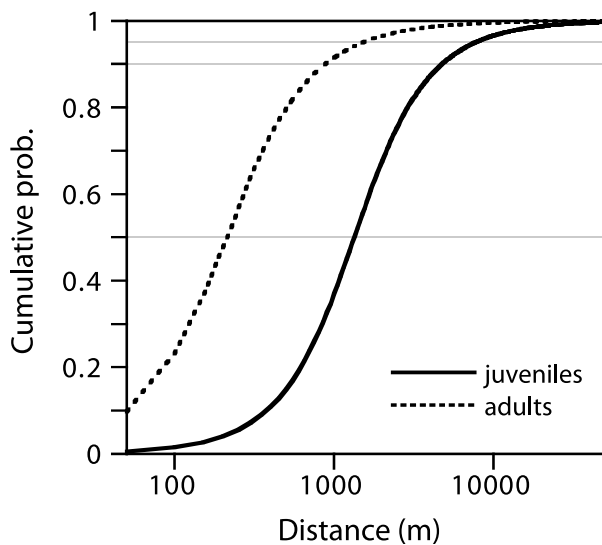
Data category	Observations	Rayleigh				Gamma				Log-sech				Log-sech parameters	
		<i>K</i>	<i>LL</i>	$\delta AIC_c$	$\omega_i$	<i>K</i>	<i>LL</i>	$\delta AIC_c$	$\omega_i$	<i>K</i>	<i>LL</i>	$\delta AIC_c$	$\omega_i$	$\alpha$	$\beta$
All data	769	1	-6,814	2,939	0	1	-6,115	1,539	0	2	-5,344	0	1	389	1.88
Adults (annual)	160	1	-1,880	1,624	0	1	-1,230	323	0	2	-1,068	0	1	211	2.29
Juveniles (annual)	89	1	-742	146	0	1	-687	38	0	2	-667	0	1	1,345	2.37

accommodate the long distances in the data, grossly underestimates recaptures > 1 and < 5 km. This effect holds under a variety of circumstances—when the data are all lumped together, when only annual time steps are considered, and when juveniles and adults are considered separately.

Table 1 lists the parameters,  $\delta AIC_c$  values, and Akaike weights for all models. The log-sech is the highest-ranked model, in each case yielding a model weight of “1.” In terms of the dispersal ability, there are nine instances of sparrow captures beyond 10 km, five beyond 20 km, and two beyond 30 km—the latter being almost the entire length of the species’ global distribution. Eight individual

birds flew to subpopulations where they were not born, and three of those individuals flew across Shark River Slough.

Figure 4 displays the cumulative dispersal probability for adults and juveniles, when the time between captures is constrained to contiguous years, i.e., annual dispersal. As expected, natal dispersal (annual movement in first year) is often to greater distances than breeding dispersal (annual movements by adults). The distances that capture 50%, 90%, and 95% of the recaptures are listed, showing that 50% of juveniles disperse almost 1,337 m in their first year. In the same time frame, for adult birds, half of the individuals are recaptured within 211 m of their previous breeding location. These numbers indicate, especially for the juveniles, that the recovery of the Cape Sable seaside sparrow is likely not limited by the species’ ability to disperse.



**Figure 4** Natal dispersal of juveniles (*n* = 89) is to greater distances away from their original capture location (graph origin) than annual dispersals of adults (*n* = 160). The cumulative probability function was derived from the highest ranked dispersal model of the three we considered (log-sech, see text for details). Horizontal grey lines are the distances that capture 50%, 90%, and 95% of each demographic group. Our model estimated that half of juveniles would be captured beyond 1,337 m, 10% beyond 4,738 m, and 5% beyond 7,658 m. Adults do not fly as far, with the respective distances being estimated at 211, 878, and 1,508 m.

### Discussion

Our study shows that Cape Sable seaside sparrows can disperse across Shark River Slough and between the several discontinuous subpopulations east of the Slough, including dispersing to distances beyond 30 km. Fitting dispersal models to these data views these observations in light of how likely we would be to capture sparrows moving these distances while taking into account the amount of effort we put into sampling the subpopulations as well as the known distribution of the species. Our results provide new and important information for conservation management of this species and offer recommendation for population assessments for other threatened species.

Sparrow dispersal distances are heavy-tailed. There are few other empirical studies for comparison with other passerines, or for species thought to be sedentary, or for protected birds. This result, however, matches the conclusion that local dispersal generally underestimates how far individuals can travel and therefore will not accurately describe the species’ ability to expand in space and

time. This is a key aspect of population assessments and recovery plans for federally endangered species. Second, sparrow juveniles (which are predominantly banded in the nest) travel much further than individuals caught as adults (which are mostly banded on their breeding territories). We estimated that about half of all juveniles will travel more than 1.4 km, 5% flew more than 7.6 km, and some traveled almost the entire span of the species' known range (Figure 4). As we constrained the possible dispersal locations to the known distribution after 1993 (Figure 2), these figures are conservative.

How do these models match our field observations of the subpopulations over time? The largest subpopulations, B and E, average about 2,500 and 500 individuals, respectively, over the last decade (Pimm *et al.* 2002). About 40% of adults die each year (Boulton *et al.* 2009). At replacement rates, this survival rate implies that 1,000 and 200 sparrows must be new territory holders in B and E, respectively. This provides some measure of the numbers of first-year individuals looking for new territories annually that settle successfully to breed. Perhaps even more individuals (adults dispersing after failed breeding attempts), will search for new territories too. Our results show that individuals can disperse between subpopulations and our models predict that this will involve substantial numbers of juveniles and some adults each year.

This would have likely once been the case for subpopulation A and the small and isolated Stair Step populations to its west (Figure 1). However, when subpopulation A was reduced from >2,500 birds prior to 1993 to <400 birds since 1999, the number of colonists it could have provided to the Stair Step population would likely have been reduced accordingly. The extinction of that population may well be a simple consequence of that reduced flow of colonists. If so, the population would not be viable without colonists and so not a candidate for birds to be translocated there.

Our results highlight the importance of estimating dispersal curves for threatened species. Contrast our results with a simple characterization of the empirical dispersal data without considering the sampling effort, the species distribution, and using normal statistics. If we had lumped all the dispersal data together, the mean ( $\mu = 583$  m) and standard deviation ( $s = 2,313$  m) of observed dispersal distances would have provided confidence interval estimates suggesting 99.9% of individuals do not fly beyond 860 m. This distance is within most of the intensive study plots and certainly within all of the subpopulations, which is predicted when a variety of functions is considered (Koenig *et al.* 1996). Simple characterizations of the data underestimate the species' dispersal ability and might encourage management actions such as transloca-

tion efforts to reestablish previously occupied areas. Our estimation of dispersal that considers the patchy effort of sampling, the heterogeneous distribution of the species across the landscape, as well as demographic differences in dispersal indicates the Cape Sable seaside sparrow disperses to long distances (Figure 3) even across unsuitable habitat (Figure 1).

There is nothing particularly unusual about this species' life history (e.g., nonmigratory, socially monogamous, open-cup nest). Thus, our results documenting long-distance dispersal add important evidence that suggests, when properly modeled, long-distance dispersal may be consistently found even in species considered to be poor dispersers. This insight is exactly what we found in a previous study of understory forest birds in the Brazilian Amazon (Van Houtan *et al.* 2007). To conservation biologists, our results suggest that even a species that has experienced a marked decline in abundance and occupancy across its entire range will continue to disperse over long distances.

The management implications cannot be overstated. Translocation of populations might be touted as a solution to recover sparrows, as it has for many other threatened species from areas where they were extirpated (Armstrong & Seddon 2008). Even though translocation can be a successful management strategy (Van Houtan *et al.* 2009) it might not always be warranted. Our analysis suggests that translocations are not warranted as sparrows move between their main subpopulations in a nontrivial manner. Instead, the evidence indicates that efforts to boost population growth rates in existing populations should be emphasized. This refocuses attention on water management regimes and protecting critical sparrow habitat, both in the existing subpopulations and in unoccupied habitat.

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