

Sources, sinks, and model accuracy

Summary

Source–sink models are a promising empirical tool for the sustainable management of animal populations across landscapes. Recent work has demonstrated a theoretical link between the demographic processes addressed in both source–sink and metapopulation models and the formation of species’ range limits. In the face of large-scale anthropogenic disturbances (e.g., increasing temperature and sea level with global climate change), conceptual range-limit models that are functionally linked to these demographic mechanisms may help predict range shifts and provide insights for the management of vulnerable populations. However, the value of such models is limited by their ability to offer precise and testable predications about how demographic parameters might respond to environmental change and thus influence population dynamics. Here, we illustrate the gulf between the promise of conceptual demographic models and the difficulty of their empirical application by developing a model of range limits for a narrowly distributed tidal-marsh songbird, the coastal plain swamp sparrow (*Melospiza georgiana nigrescens*, CPSS). We first modeled a gradient in CPSS fecundity that depends on environmental factors varying with latitude. To predict the species’ range limits we embed this fecundity gradient in Pulliam’s (1988) source–sink model. Our resulting model predicts current CPSS range limits reasonably well. However, its predictions are also subject to substantial uncertainty. Our model framework generally conforms to the conceptual unification of source–sink theory, Hutchinson’s (1957) fundamental niche, and species range limits recently expounded by Pulliam (2000).

Background

It is now clear that sources and sinks exist (Pulliam 1995) and that anthropogenic disturbance can alter the landscape distribution of sources and sinks (Pulliam 1995; Gaona *et al.* 1998; Remes 2000; Rowe and Hopkins 2003). Pulliam (1988) presented a hypothetical case in which anthropogenic destruction of a seemingly unimportant habitat (where a small fraction of the population occurred) could have disastrous consequences if the habitat is an important source. If we are to sustainably manage landscapes with mosaics of source and sink populations, we need predictive models to quantify the effect of our actions on these populations. Thus, for management, it is not sufficient for models to simply predict the existence of sources and sinks; they must also functionally link demographic rates to specific landscape features and environmental conditions. Furthermore, predictions of demographic responses to habitat alterations must be sufficiently precise to support management actions that are designed to positively influence population stability and growth. However, spatial demographic models may be subject to considerable uncertainty, even when informed by intensive monitoring data (Ettersson and Nagy 2008).

Uncertainties notwithstanding, empirical and theoretical research on source–sink dynamics continues to generate insights and novel hypotheses about the observed dynamics of spatially structured populations. As the work of Holt and colleagues has shown (Holt and Keitt 2000; Holt *et al.* 2005; Holt, Chapter 2, this volume), species' distributional limits provide a dynamic laboratory for understanding how gradients in metapopulation parameters such as occupancy, extinction, and colonization rates may limit the spatial distribution of populations. Similarly, Pulliam (2000) elaborated the relationship between resource gradients, source–sink dynamics, and a species' niche, by defining the latter as the set of environmental conditions for which $\lambda \geq 1$. By this definition, the niche is the set of all population sources ($\lambda > 1$; Pulliam 1988), although the former would also include sites for which $\lambda = 1$. This explicit and simple relationship provides a powerful conceptual approach for extending source–sink theory to investigate the relationship between environmental factors, demography, and species' range limits.

In this chapter we explore the data requirements for translating the conceptual relationship between source–sink theory and environmental factors into specific predictions about the present range limits of coastal plain swamp sparrows (*Melospiza georgiana nigrescens*, CPSS). Our primary goal is to illuminate the difficulties of using a promising conceptual model to construct an empirical model with predictions sufficiently precise to make management decisions. In keeping with classical source–sink theory, our model examines how gradients

in factors affecting fecundity may create regions where productivity exceeds mortality versus regions where extinction would occur in the absence of immigration (Pulliam 1988). At the scale of a species range, we assume that a geographic transition between these two regions (from mostly sources to mostly sinks) should determine the approximate range boundary. We recognize that while we use the term boundary, metapopulation dynamics may result in a zone of populations that wink in and out of existence, as suggested by repeat surveys of the historical range of this subspecies (Beadell *et al.* 2003).

Environmental gradients and avian reproductive success in tidal-marsh habitats

We used four latitudinal gradients in avian reproductive parameters to construct our fecundity model: clutch size, nest predation rates, nest inundation rates (due to flooding), and breeding season length. Greenberg *et al.* (2006) reviewed studies of North American tidal-marsh sparrows and found that, while clutch size and flooding rates increase with increasing latitude, nest predation rates and breeding season length generally decrease with increasing latitude. Therefore, nest predation and clutch size will result in increased fecundity with increasing latitude, while flooding rates and breeding season length will result in reduced fecundity with increasing latitude.

In four broad steps we use what we know about the breeding biology of the CPSS and latitudinal gradients in tidal-marsh sparrow reproduction to predict the location of the CPSS southern range boundary.

1. We first develop a mathematical model that predicts seasonal fecundity as a function of specific CPSS traits.
2. We incorporate the four latitudinal gradients into this model to generate a fecundity curve, dependent on latitude.
3. To relate this fecundity curve to population growth rate, we embed the model within Pulliam's (1988) source–sink model to create a niche model for the CPSS.
4. Finally, we use this niche model to predict where population growth falls below replacement in the absence of immigration: the putative southern range boundary.

Our objectives are to explore the following questions.

- Given what we know about CPSS fecundity (*Seasonal fecundity model*) and latitudinal gradients in reproductive parameters for tidal-salt-marsh sparrows, what is the optimal breeding latitude for the CPSS (*Fecundity curve*)?

- Does this optimum occur within the current range of the CPSS?
- When combined with plausible values for survival probabilities, can a simple demographic model be used to predict CPSS range limits (*Niche model*)?
- If a plausible model is possible, is it feasible to estimate its parameters with sufficient precision to be able to use the model to predict range shifts resulting from natural or anthropogenic environmental change and, more importantly, for making decisions about conservation and management of this endemic subspecies (*Model precision*)?

Research methods

Study species

The coastal plain swamp sparrow (CPSS) is a recognized subspecies which is largely restricted to brackish marshes above the mean high tide line during both its breeding and non-breeding periods. Two far more widespread inland subspecies are restricted to the freshwater marshes of eastern and boreal North America. The coastal subspecies is not differentiable from those inland based on MtDNA analysis (Greenberg *et al.* 1998) or on microsatellite markers (R. Fleischer *et al.*, unpublished), but is 100% diagnosable based on its large bill and grayer/blacker coloration (Greenberg and Droege 1990): traits that the coastal endemic subspecies shares with other tidal-marsh birds (Greenberg and Droege 1990; Grenier and Greenberg 2005). Standard rearing experiments show that the morphological differences are probably genetically based (Greenberg and Droege 1990; Ballentine and Greenberg 2010). In addition to morphological differences, a number of behavioral and ecological features distinguish coastal plain birds from interior swamp sparrows (Olsen 2007), including distinctive parental behavior and vocal repertoire (Liu *et al.* 2008) as well as a smaller average clutch size (Olsen *et al.* 2008a). These considerations suggest that the CPSS is on a separate evolutionary trajectory from the inland subspecies and is worthy of conservation as a distinct evolutionary unit.

Coastal plain swamp sparrow habitat and range

Preferred marshes for the CPSS have salinities well below 10 parts per thousand (ppt) and support a relatively diverse flora of *Spartina* grasses, rushes (*Schoenoplectus* spp.), reeds (*Phragmites australis*), and shrubs (*Iva frutescens* and *Baccharis halimifolia*). The subspecies winters in a similar shrub–grass marsh community, which lies between the maritime loblolly pine (*Pinus taeda*) forests and extensive tracts of black needle rush (*Juncus roemerianus*) in the southeastern

USA. The CPSS migrates north to breed despite the presence of very similar habitat in the wintering range that lacks breeding sparrows in the summer months. Breeding populations are known in coastal marshes from northern New Jersey (40.9° N) to the southern Chesapeake shore of the Delmarva Peninsula in Maryland (38.3° N) and the upper Rappahannock River in Northern Virginia (37.9° N) (Greenberg and Droege 1990; Beadell *et al.* 2003; Watts *et al.* 2008). The subspecies completely leaves its breeding range in the fall (Greenberg *et al.* 2010) and has been found wintering from extreme south-coastal Virginia (36.7° N) to Charleston, SC (32.7° N) (Greenberg *et al.* 2007, 2010), but appears to be most common in the northern part of this coastal zone. Thus the migration, while complete, is relatively short, ranging from about 200 to 600 km. It is rather curious, then, that swamp sparrows would complete an energetically costly and risky northward migration, when the environment they leave appears structurally identical to the niche they occupy further north and possesses no obvious competitors. This seasonal within-habitat shift provides an excellent system for exploring the effects of gradients within key environmental factors on demographic processes that determine the breeding niche.

Seasonal fecundity model

To estimate the number of young produced per female during a breeding season (seasonal productivity) for female CPSS we adapted the regular Markov chain model developed for dickcissel (*Spiza americana*) and eastern meadowlark (*Sturnella magna*) by Etterson *et al.* (2009). Thus our breeding season model is a generalization of Markov chain methods for estimating avian nest survival (Etterson and Bennett 2005), which in turn are a generalization of standard methods for estimating nest survival (Mayfield 1975; Johnson 1979; Bart and Robson 1982). The form of the model we use here employs six parameters, which are

- m_p the daily probability that a nest is destroyed through predation
- m_f the daily probability that a nest is destroyed through flooding
- a the age (in days since the first egg was laid) at which fledglings leave a successful nest
- w_s the expected time required between fledging and the first egg in a subsequent nesting attempt
- w_f the expected time required between failure and the first egg in a subsequent nest
- T the length of the breeding season, defined as the amount of time separating the first egg of the first nest (among all females) and the first egg of the last nest of the season (again among all females).

Analysis of the resulting Markov chain model gives the expected number of successful broods per female (b) in a typical breeding season (Etterson *et al.* 2009; see Eq. (13.A1.2) in the Appendix to this chapter) To estimate seasonal fecundity (β) we estimated mean clutch size per nest (c) and assumed negligible hatching failure and equal ratio of male to female offspring so that $\beta \approx \frac{bc}{2}$.

We parameterized our seasonal fecundity model using nest data from a breeding population of CPSS at Woodland Beach, Delaware, that has been intensively monitored for the last 7 years (Olsen 2007; Olsen *et al.* 2008a, 2008b; Liu *et al.* 2008; Greenberg *et al.* 2006, 2007; Etterson *et al.* 2007). Greenberg *et al.* (2006) had already reported values for CPSS at Woodland Beach for clutch size, predation rates, flooding rates, and breeding season length (c , m_p , m_f , and T). These were used in our present model with transformations described in the next section (equations are provided in the Appendix to this chapter). Because nests were monitored daily and females were color-banded, we were able to estimate the remaining three parameters (a , w_s , and w_f) as the simple mean observed values, under the assumption that females did not disperse off the study site between nesting attempts and intermediate nests were not missed. The behavior of female swamp sparrows allows assumptions regarding our nest-locating ability that are much safer than for typical grassland-nesting songbirds, because females utter a distinctive series of call notes whenever they leave the nest during nest building, egg incubation, and nestling brooding (McDonald and Greenberg 1991). Over all years we located nests 3.6 ± 0.3 days (mean \pm SE) after the start of incubation ($n = 275$), for those nests for which clutch completion date could be calculated (by laying or hatching date). Thus we are confident that we did not miss many nesting attempts.

The fecundity curve

Of the seven parameters required for our seasonal fecundity model (m_p , m_f , a , w_s , w_f , T , and c), Greenberg *et al.* (2006) published estimates of four (m_p , m_f , T , and c) derived from 12 breeding populations of three species of tidal-marsh sparrows distributed from 29.8° to 43.6° N latitude (Gulf County, Florida, to Scarborough Marsh, Maine; see Table 13.1). We used their data to estimate gradients in m_p , m_f , T , and c by first logit transforming (m_p , m_f) or log transforming (T , c) the observed values to express them on the continuum, and then estimating linear regressions of the transformed data on latitude. Full details of the transformations and regressions are provided in the Appendix.

TABLE 13.1. *Estimated sampling variance, confidence intervals (degrees latitude) and width (km) of the southern distributional limit of coastal plain swamp sparrows (CPSS) for assumed levels of precision (coefficient of variation, CV) of estimated input parameters.*

CV	Southern limit		
	Variance ¹	95% CI (° lat.)	Width (km)
0.01	44.57	24.52–50.70	2,914
0.001	2.76	34.36–40.86	723
0.0001	0.26	36.61–38.61	222

¹ Estimated sampling variance around the predicted location of the southern range limit of the coastal plain swamp sparrow.

The niche model

To expand our fecundity model to predict the population growth rate of CPSS across its range, we embedded our estimated fecundity curve (above) within a simple, two-stage population projection model assuming constant survival among habitats (Pulliam 1988).

$$\lambda = P_A + P_J\beta \quad (13.1)$$

where P_A and P_J are the annual adult and juvenile survival probabilities, respectively, and β is the annual per-female rate of production of female offspring (from the fecundity model above).

Survival estimates for the niche model

To estimate P_A we used 6 years of mark–recapture data (2002–2007, $n = 385$) for breeding adult CPSS at Woodland Beach, Delaware. We estimated separate apparent survival rates (ϕ) and recapture rates (p) for males ($n_m = 234$) and females ($n_f = 151$). Parameter estimates were generated using the “recapture-only” model in the program MARK (White and Burnham 1999). Preliminary demographic modeling of our Woodland Beach population suggested that the resulting female apparent survival rate (ϕ_f), in combination with other model parameters, would project a declining population at Woodland Beach. We suspected that this result was due to greater dispersal bias in the apparent survival estimate for females than for males, rather than a true difference in survival, and so we analyzed the population model (Eq. 13.1) twice, using each survival value (ϕ_f and ϕ_m) in turn for P_A .

We do not know juvenile survival rates in CPSS. Of 540 nestlings banded over the course of the study, we relocated only 34 after their hatch year. Therefore we solved for potential values of juvenile survival by fitting the niche model to the known northern range boundary of CPSS. In other words, we used the niche model to determine what value (if any) of P_j would result in a predicted value of $\lambda = 1$ at the northern range boundary (40.87° N). If this problem has a solution, then there will be a corresponding point further south at which, again, $\lambda = 1$, which we define to be the niche model's prediction of the location of the southern boundary. The precision analysis described below is a hypothetical exercise conducted under the assumption that the input parameters and model predictions, derived as described above, are correct.

Model precision

We used the Delta method (Daley 1979; Houllier *et al.* 1989) to discover how precisely the output metric (the location of the southern distributional limit, where $\lambda = 1$) would be estimated, conditional on hypothesized values for the estimated coefficients of variation of input parameters. The same question can be stated in a form akin to a power analysis: how precisely must the input parameters be estimated to predict the southern distributional limit to a given level of precision? We analyzed the model with the coefficients of variation in all input parameters set to three hypothetical levels of precision (0.01, 0.001, 0.0001). Equations are provided in the Appendix. Our precision analyses incorporate some variation due to fixed environmental effects (the latitudinal gradients), but we do not consider random environmental effects (environmental stochasticity).

Results

Annual apparent survival for males swamp sparrows was 0.52 (SE, CV: 0.04, 0.08) and 0.45 (0.07, 0.16) for females. Recapture probability for males was 0.67 (0.06, 0.09) and 0.43 (0.10, 0.23) for females. Mean age at fledging (a) was 22.3 (0.13, 0.006) days after the first egg was laid. The mean time between failure and the first egg of a replacement clutch (w_f) was 10.6 (0.88, 0.08) days, and between fledging and the first egg of the next nest (w_s) was 11.9 (1.4, 0.12) days. The estimated gradients in clutch size (c), breeding season length (T), flooding (m_f), and predation (m_p) are depicted graphically in Figure 13.1. As expected, predicted values of clutch size and flooding risk increased with latitude, whereas breeding season length and predation rate decreased with latitude (Fig. 13.1).

Maximum estimated reproductive success occurred at 39.68° N latitude, at which point the fitted estimate was approximately 1.67 female offspring per

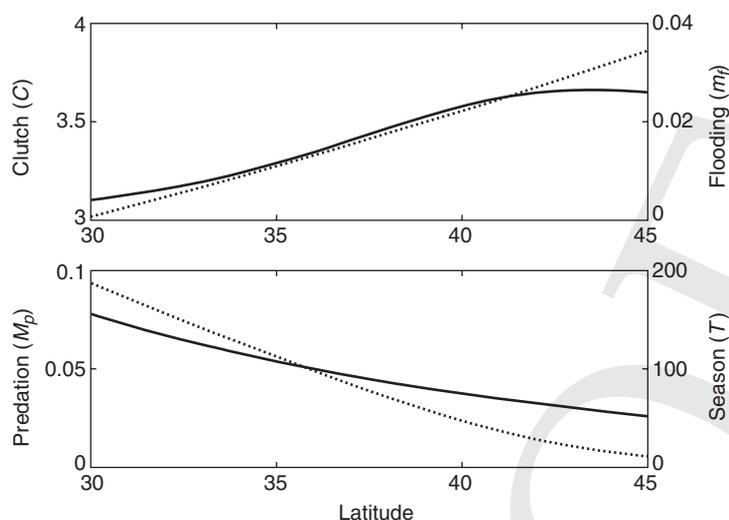


FIGURE 13.1. Estimated latitudinal gradients in clutch size (top, solid line), daily probability of inundation (top, dashed line), daily probability of predation (bottom, dashed line), and breeding season length (bottom, solid line).

female (Fig. 13.2a). Thus, maximum fecundity was predicted to occur within CPSS current range, 37 km north of our Woodland Beach site (39.35° N). With this fecundity curve (Fig. 13.2a) and assuming $P_A = \phi_m$, a juvenile survival value of $P_j = 0.288$ results in a niche curve for which $\lambda = 1$ at 40.87° N (Fig. 13.2b). On the latter curve, the southern latitude at which $\lambda = 1$ occurs at 38.53° N, close to the most southern (38.07° N) known breeding population of coastal plain swamp sparrows (Fig. 13.2b). For $P_A = \phi_f$ and $P_j = 0.288$, the niche curve is entirely below unity (Fig. 13.2b). However, assuming $P_A = \phi_\beta$ a juvenile survival value of $P_j = 0.328$ results in a niche curve for which $\lambda = 1$ at 40.87° N (not pictured). On the latter curve, the southern latitude at which $\lambda = 1$ occurs at 38.52° N, again very close to the most southern (38.07° N) known breeding population.

The difference between the niche curve (Fig. 13.2b) with $P_j = 0.288$ and $P_A = \phi_m$ versus $P_A = \phi_f$ can serve as a natural perturbation analysis. Thus, a 13% reduction in adult survival is enough to drive the entire growth rate curve well below sustainability. A similar perturbation in the opposite direction would result in a distribution that is far too large (not pictured). Similarly, the results of the power analysis suggest that the southern boundary may be very difficult to locate with confidence, even with very precisely estimated input parameters (Table 13.1). Even with presumed coefficients of variation (CV) of 10^{-5} , this model can only predict the location of the southern range limit to within 222 km (Table 13.1).

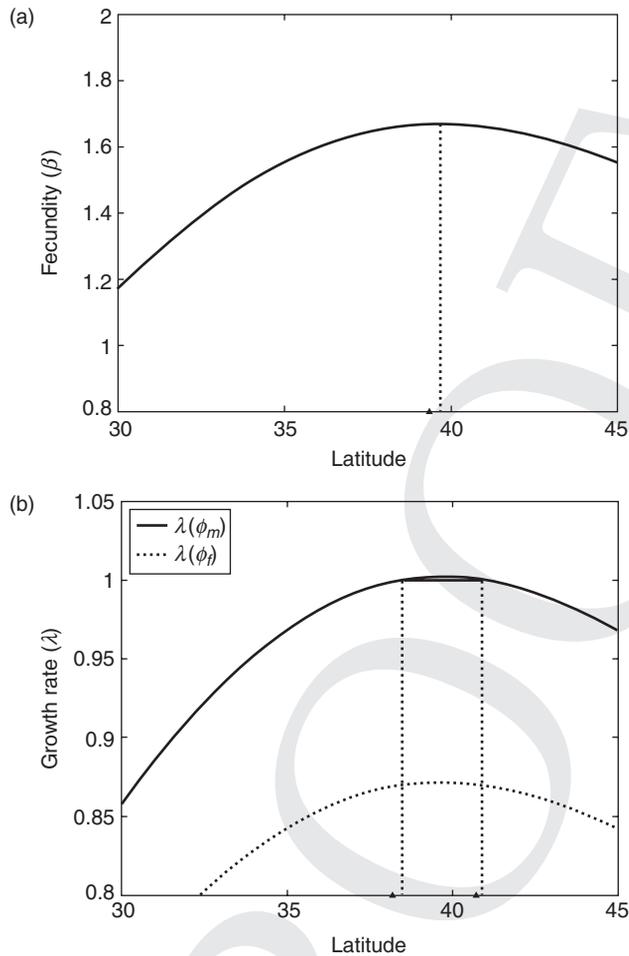


FIGURE 13.2.

(a) Estimated number of female offspring fledged per female as a function of latitude. Vertical dotted line shows the optimal breeding latitude (maximum predicted fecundity). The triangle on the horizontal axis is placed at the latitude of our Woodland Beach, DE, study site. (b) Estimated population growth rate for different values of annual adult survival predicted as a function of latitude. Vertical dotted lines, topped by horizontal line at $\lambda = 1$, indicate points of intersection of the growth rate curve with the line $\lambda = 1$. The triangles on the latitude axis indicate northernmost and southernmost known breeding populations of CPSS.

Discussion

Our model results show the promise of applying source–sink theory to predicting species’ distributions. The shape of the niche curve (Fig. 13.2a) confirms that the latitudinal gradients in fecundity (nest predation, nest inundation, clutch size, and breeding season length) are a coherent and sufficient explanation for the breeding range limits of CPSS (Fig. 13.2b). The maximum

of the fecundity curve occurs within the heart of the breeding range of the subspecies. The value(s) of P_j required to fit the niche model to the northern boundary are plausible and the resulting estimates of the location of the southern range limit are about 60 km from the location of the southernmost known breeding population. Thus our model demonstrates the kind of insights that can be gained through the unification of source–sink theory with the Hutchinsonian niche concept (Hutchinson 1957) to predict species distributional limits, as suggested by Pulliam (2000).

However, our model is subject to considerable uncertainty at many scales. Large sensitivities result in large variance around the projected location of the southern boundary. Relatively small perturbations in survival result in large shifts in the growth rate curve (Fig 13.2b), and power analyses suggest that enormous effort would be required to estimate the range limit to within 200 km. The former result is a good example of the relative importance of the sensitivities. Our growth rate model (Eq. 13.1) is more sensitive to changes in survival than fecundity. This also highlights the importance of careful management of this subspecies because small anthropogenic effects on survival (e.g., changes in predator communities near human habitation, increased risk during migration near human structures, decreased wintering habitat quality, or increased frequency or intensity of winter storms) could have a large impact on the species' extinction probability. This exercise, then, directs our future research attention toward understanding the causes of mortality throughout the year, including potential gradients in survival.

Fortunately, there are good reasons to believe that our estimates of uncertainty are conservative. First, our application of the Delta method did not incorporate covariances among model parameters, many of which are likely to be negative if there are life-history tradeoffs, say between survival and reproduction. Negative covariances among estimated parameters will necessarily reduce the estimated model variance because the squared sensitivities (see Appendix) are necessarily positive. Second, our model included no population regulation, whether in the form of density dependence, habitat saturation, or dispersal limitation, any of which would create negative feedbacks that would also serve to reduce the total variance (assuming a projection model with a stable equilibrium).

A useful generalization to our conceptual model would be to include mechanistic explanations for the observed latitudinal gradients. For example, the clutch-size gradient we report is not unique to tidal-marsh sparrows. It is a well-known gradient, which applies quite generally across avian taxa (Skutch 1949), that has been hypothesized to result from diverse causes, including global gradients in ambient temperatures during laying (Stoleson and Beissinger 1999; Cooper *et al.* 2005; Olsen *et al.* 2008a), nest predation pressure (Eggers

et al. 2006; Greenberg *et al.* 2006, Olsen *et al.* 2008a), and concentrated resource pulses at higher latitudes (Rabenold 1979; Ricklefs 1980). In contrast to clutch size, nest predation rates vary negatively with latitude (Ricklefs 1969, but see Martin 1996). While most latitudinal comparisons of nest predation rates involve temperate–tropical comparisons, decreased predation rates on artificial nests have been found along latitudinal gradients within the temperate zone (Andrén *et al.* 1985; Berg *et al.* 1992) and the latter authors hypothesized that these changes were due to changes in the nest-predator community with latitude. The gradient in breeding season length (T) reported by Greenberg *et al.* (2006) also generalizes beyond tidal-marsh sparrows, especially for re-nesting and/or multiple-brooded birds (e.g., James and Shugart 1974) and is probably ultimately caused by a combination of temperature and food availability (Immelmann 1973), although its proximate control is strongly influenced by endocrine response to changes in photoperiod (Hahn *et al.* 2004).

Another useful model generalization would be to incorporate annual variation in demographic parameters, in particular in response to the projected effects of climate change (changes in sea level and resulting effects on nest flooding rates, and increased temperature effects on clutch size). Other mechanisms generating our gradients and, in turn, our latitude-specific fecundity rates are also likely to vary between years. In years with abundant food resources, the breeding season will be longer, and birds will attempt more nests and experience greater fecundity (Nagy and Holmes 2004). In bad years they will attempt fewer nests and experience lower fecundity. Similarly, nest predation rates in this system vary from year to year (Etterson *et al.* 2007; Olsen *et al.* 2008a). These factors are also likely to vary locally around the large-scale latitudinal trends. In comparison with the models of Holt and colleagues (Holt and Keitt 2000; Holt *et al.* 2005), the productivity gradients we have described are best considered as gradients in extinction probability (or its complement), but other processes such as colonization rates probably also influence habitat occupancy near the range boundary. Taken together, these observations suggest that the distribution of CPSS sources and sinks is probably quite dynamic and characterized by shifting source–sink dynamics near the range boundary. Repeat survey data from near the southern range limit also support this hypothesis (Beadell *et al.* 2003).

The latter considerations are a good reminder that our model, while geographically explicit, was not fully spatially explicit because it did not incorporate dispersal probabilities. Doing so would likely increase the variance (except where dispersal limitation is involved in population regulation, as described above). We know very little about dispersal in CPSS, except that juvenile return rates are very low and males are more philopatric than females (as evidenced by the differences in recapture rate, $\hat{p}_m \gg \hat{p}_f$), both of which are common passerine patterns (Greenwood 1980; Clarke *et al.* 1997). Uncertainties surrounding

the incorporation of dispersal into spatially explicit models has been a contentious topic (Mooij and DeAngelis 2003; Etterson and Nagy 2008) and a thorough exploration is outside the scope of this chapter. Further, estimation of dispersal rates is very difficult in birds, even with banded populations (Clobert and Lebreton 1991; Robinson and Hoover, Chapter 20, this volume). However, the configuration of habitat in CPSS may be particularly conducive to dispersal estimation because tidal salt-marsh is found in a narrow curvilinear band along the eastern North American seaboard. Thus the problem of relocating marked individuals may be relatively easier with CPSS.

As we continue to modify species' environments on continental and global scales, we need spatial demographic models to guide management and remediation efforts. Our model of coastal plain swamp sparrows is a promising example of how conceptual models of source–sink dynamics, when linked to empirical factors that determine vital rates, can be useful in planning and managing habitat at large spatial scales. However, our results also suggest that much more work should be done to reconcile the promise of spatial demographic models within the often large uncertainties surrounding their outputs. We believe this question should be at the forefront of the study of spatial demography.

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Appendix

Our fecundity model treats seasonal productivity as a regular homogeneous Markov chain with transition matrix (\mathbf{M}) in the following form:

$$\mathbf{M} = \begin{bmatrix} 0 & \mathbf{0} & 0 & 0 & \mathbf{0} & 0 & \mathbf{0} & 0 & \mathbf{1}_1 \\ s_a & \mathbf{0} & 0 & 0 & \mathbf{0} & 1-s_a & \mathbf{0} & 0 & 0 \\ \mathbf{0} & \ddots & \mathbf{0} & 0 & \mathbf{0} & \vdots & \mathbf{0} & \mathbf{0} & \mathbf{0} \\ 0 & \mathbf{0} & s_1 & 0 & \mathbf{0} & 1-s_1 & \mathbf{0} & 0 & 0 \\ 0 & \mathbf{0} & 0 & \mathbf{1}_{w_s} & \mathbf{0} & 0 & \mathbf{0} & 0 & 0 \\ 0 & \mathbf{0} & 0 & 0 & \ddots & 0 & \mathbf{0} & 0 & 0 \\ 0 & \mathbf{0} & 0 & 0 & 0 & \mathbf{1}_{w_s-w_f} & \mathbf{0} & 0 & 0 \\ \mathbf{0} & \mathbf{0} & \mathbf{0} & \mathbf{0} & \mathbf{0} & \mathbf{0} & \ddots & \mathbf{0} & \mathbf{0} \\ 0 & \mathbf{0} & 0 & 0 & \mathbf{0} & 0 & \mathbf{0} & \mathbf{1}_2 & 0 \end{bmatrix} \quad (13.A1.1)$$

In Eq. (13.A1.1) each row or column corresponds to a single day. Thus each transition probability in the matrix describes the probability of being in a given state (column) on a given day conditional on the state (row) the female was in the previous day. The daily survival parameters (s_i) are the complement of the sum of all daily failure probabilities (m_p, m_f, m_o ; see below) and the subscript on s indicates the daily ageing of the nest up to a , at which age it fledges. The subdiagonal of ones (i.e., [$1_{w_s}, \dots, 1_{w_s-w_f}, \dots, 1_2$]) incorporates the periods of time required between a failed nest (w_f) versus a successful nest (w_s) and the first egg in the next nesting attempt. Bold zeros in the matrix (Eq. 13.A1.1) represent portions of the matrix that, when expanded to the same dimension as the corresponding ellipses, are vectors or submatrices of zeros of the appropriate dimension (Ettersson *et al.* 2009).

Note that the parameter T does not appear in the transition matrix. It is used to impose a plausible biological limit on the number of nests a female can attempt in a breeding season, without assuming a fixed number of nesting attempts per female per season (e.g., Grzybowski and Pease 2005). The expected number of successful broods (b) a female will raise during a breeding season lasting T days is the expected number of times the female passes through the state of having just fledged a nest (row 1) conditional on having started the season with the laying of her first egg (row $a+1$) in her first nest. This quantity can be obtained from the fundamental matrix, Z , of \mathbf{M} , where $Z = [I - (\mathbf{M} - A)]^{-1}$, $A = \lim_{t \rightarrow \infty} (\mathbf{M}^t)$, and I is the identity matrix of the same dimension as \mathbf{M} (Kemeny and Snell 1983). Thus:

$$E(b) \rightarrow z_{a+1,1} + \alpha_1(T-1) \quad (13.A1.2)$$

The arrow in Eq. (13.A1.2) indicates that this formula is asymptotically valid.

The data provided by Greenberg *et al.* (2006) required transformation before they could be used in the above fecundity model. First, we converted the reported overall nest survival rates (S , which were already corrected for

discovery bias) to site-specific daily nest survival rates, s , using the equation $s \approx \sqrt[4]{S}$. Next we estimated the probability that an unsuccessful nest failed due to predation versus other causes (P_p) as the simple proportion of depredated nests among all failed nests (after Etterson and Stanley 2008). Then the maximum likelihood estimates of the daily probabilities of failure due to predation (m_p) versus flooding and other causes ($m_f + m_o$) are given by $m_p = P_p(1-s)$ and $m_f + m_o = (1-P_p)(1-s)$ (Etterson and Stanley 2008). After estimating the above site-specific probabilities, we transformed them to the real number scale using the logit transformation and performed linear regression on the logits. For example, to estimate a nest survival gradient, we fitted the equation:

$$\log\left(\frac{s}{1-s}\right) = \alpha_0 + \alpha_1 * \text{latitude} \quad (13.A1.3)$$

The resulting regression coefficients (α_i) describe the gradients, and the latitude-specific probabilities can be obtained by exponentiating. A similar equation was fitted to the predation gradient (m_p). The flooding gradient (including some failures due to other causes) was estimated as the complement of the sum of the daily survival probability and the daily probability of nest predation (i.e., $m_f + m_o \approx 1 - s - m_p$). Clutch size (c) and breeding season length (T) were log-transformed to the real scale and then regressed on latitude, as above.

For the analysis of Pulliam's model (Eq. 13.1), we make use of the sensitivities and elasticities of λ to changes in the demographic parameters. The sensitivities are:

$$\text{a. } \frac{\partial \lambda}{\partial \beta} = P_J, \quad \text{b. } \frac{\partial \lambda}{\partial P_A} = 1, \quad \text{and} \quad \text{c. } \frac{\partial \lambda}{\partial P_J} = \beta. \quad (13.A1.4)$$

The elasticities are:

$$\text{a. } e_{P_J} = \frac{P_J \beta}{\lambda}, \quad \text{b. } e_{P_A} = \frac{P_A}{\lambda}, \quad \text{and} \quad \text{c. } e_{\beta} = \frac{P_J \beta}{\lambda}. \quad (13.A1.5)$$

To estimate sampling variance in the population growth rate, we used the Delta method (Daley 1979; Houllier *et al.* 1989):

$$\text{var}(\lambda) \approx \left(\frac{\partial \lambda}{\partial \theta}\right)^T \text{cov}(\theta) \left(\frac{\partial \lambda}{\partial \theta}\right). \quad (13.A1.6)$$

In Eq. (13.A1.6), θ is a column-vector of model parameters. For the survival parameters, the partial derivatives of λ with respect to θ are the sensitivities (Eq. 13.A1.4a,c). However, for fecundity we used the second-order sensitivities of λ to the regression coefficients (the α_i from Eq. (13.A1.3), which were obtained using the product rule; Caswell 2001). The matrix $\text{cov}(\theta)$ is the

variance–covariance matrix of estimated parameters. When the covariances are zero, Eq. (13.A1.6) can be reformulated using the elasticities (Eq. 13.A1.5):

$$\text{var}(\lambda) \approx \lambda^2 E_{\theta}^2 CV_{\theta}^2. \quad (13.A1.7)$$

In Eq. (13.A1.7), E_{θ}^2 is a row-vector of squared elasticities and CV_{θ}^2 is a column-vector of squared coefficients of variation. We derived Eq. (13.A1.7) to allow the sampling variance of the estimated population growth rate to be expressed conditionally on similarly scaled hypothetical levels of precision in the estimated input parameters.