Journal of Applied Ecology 2008, **45**, 258–268 doi: 10.1111/j.1365-2664.2007.01369.x

Ammodram s mari im s mirabilis

[1]*D a f E a S d , U f Ca f a, Sa a C z, CA, USA a d D a f Ec a d E , U f C ca , C ca , IL, USA; a d* [2]*I f E a M d , U f T , K , TN, USA*

---

1. Habitat destruction and fragmentation have led to precipitous declines in a number of species of

fragmentation can prove important for determining species survival (Andrén 1994; Turner *et al*. 1994; Letcher *et al*. 1998; Wiegand *et al*. 1999). This is particularly true in a dynamic landscape where the aberrant timing of seasonal disturbances such as flooding can be detrimental to population viability (Menges 1990; Nott *et al*. 1998). When data are available, individual-based models (IBM) are ideal for exploring the interaction between habitat destruction and species behaviour (Letcher *et al*. 1998; Schmitz 2001; DeAngelis & Mooij 2005; Zollner & Lima 2005). For species whose survival and reproduction are intricately tied to spatial and temporal dynamics of their habitat, spatially explicit individual-based models (SEIBM), which are linked to community structure and behaviour, represent a promising approach for providing insight into population dynamics (DeAngelis & Rose 1992; Holt *et al*. 1995; Donalson & Nisbet 1999).

Changes in population dynamics and probability of extinction can be brought about by various means. For instance, hydrological regimes altered either by direct management or indirectly via climate change can have an adverse impact on ecosystem function, community structure and population demography (Wootton *et al*. 1996; DeAngelis *et al*. 1998; Clark *et al*. 2001; Jackson *et al*. 2001; Elderd & Doak 2006). This is particularly true within the Florida Everglades, an ecosystem driven by the timing and extent of waterflow (Curnutt *et al*. 1998; Nott *et al*. 1998; Lockwood *et al*. 2003). Currently, the altered hydrology within the Everglades, brought about by managing water for urban and agricultural purposes, may be responsible for the precipitous decline in a number of species that depend on the Everglades' complex hydrological dynamics (Beissinger 1995; DeAngelis *et al*. 1998; Nott *et al*. 1998; Curnutt

et al. 1998). Where there were gaps in the data of <10 days, water levels were estimated using linear interpolation. For a 76-day gap from April to June 1992, values were estimated using measurements taken from station P34 located in the south-eastern corner of the subpopulation's habitat. This technique was also used to fill in a gap during the spring of 1989. Additionally, no data were available for the period between January and July 1993. The data used for this period reflected the average 20-year rainfall for the area (Nott *et al*. 1998). From the data gathered at these gauges, the daily temporal trends in water depth within each 500-m-resolution cell could be modelled (for a more thorough description see Nott *et al*. 1998).

MODEL INITIAL CONDITIONS AND SPARROW LIFE HISTORY

Simulations of SIMSPAR were performed to determine how the sparrow population might respond to multiyear hydrological scenarios. The population was modelled using a daily time step during the breeding season, whereas overwinter survival was modelled as only a single time step. For each of the model runs, male sparrow

100 individuals during the simulation run. This final 100-year period was used to compare estimates of quasi-extinction probability and final mean population size, given changes in the model parameters described below.

At the beginning of each model run, a ‘seed’ population of male and female sparrows was placed within the model landscape. This population represented a combined distribution of the 1993, 1995, 1996 and 1997 sparrow surveys resulting in an initial population size of 308 individuals. Each individual’s age within the seed population was calculated using a decaying binomial representing a stable age-class distribution. Within each simulation run, sparrows were individually tracked during annual breeding seasons that varied in duration due to the hydrological history of the site. Adults had a mortality probability during winter of 0·40 unless the adult had reached the maximum age of survival (Table 1). In that case, the adult did not survive the winter. For juveniles, the mortality rate was density-dependent and ranged linearly from 0·40 to 0·42 depending on the number of territories occupied. If juveniles survived their first year, they would become part of the ‘floater’ population in the subsequent year. Reproduction, mortality and other life-cycle parameters were all modelled using values estimated from field data (Bass & Kushlan 1982; Pimm *et al*. 1995; Lockwood *et al*. 1997; Curnutt *et al*. 1998) (Table 1).

Male dispersal to establish new territories consisted of a self-avoiding random walk across the landscape, with distinct responses by the individual to habitat and non-habitat cells. Throughout the simulation, all non-habitat cells were avoided by dispersing males and thus were considered reflecting boundaries. At the beginning of the breeding season, individual males would search the cell they currently occupied for available nesting habitat. If the cell contained no available habitat, the male would randomly disperse within a predefined search range (e.g. a 500-m range was used in the base model) to another habitat cell and test it for availability. If the tested cell contained no unoccupied territories or had been degraded during a particular simulation run (see Methods, Landscape level changes), the individual would begin searching again but would avoid all cells he had previously visited. The male continued testing the habitat until a vacant breeding territory was found. A mortality probability of 10% was

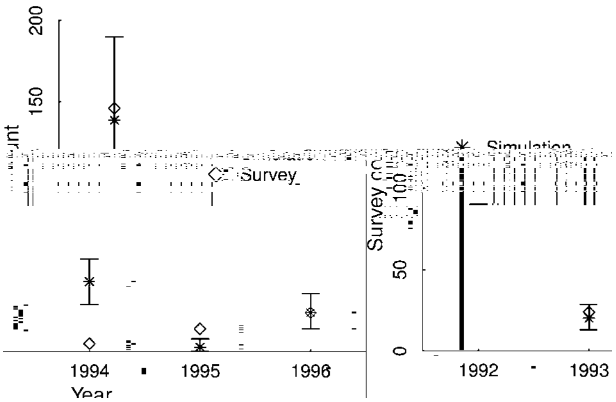

Fig. 4. Comparison of population surveys with simulated results (±95% CI) for 250 simulations using base model parameters and the entire 21-year hydrological sequence.

In order to gauge the ability of the model to forecast population dynamics, we first compared simulated model survey output with survey data for the sparrow. These initial runs used field estimates at their base values (Tables 1 and 2) and consisted of 250 replicates of 21-year runs. Each replicate used the entire long-term hydrological sequence in chronological order. When compared with the five complete population surveys conducted between 1992 and 1996, these simulation runs showed a good correspondence between simulation results and population surveys (Fig. 4). The one notable exception was for 1994, when a number of sites went unsurveyed and the field survey was considered incomplete (Pimm *et al.* 2002).

MODEL ANALYSIS

To examine the potential effects of changes in the landscape and the population's susceptibility to changes in demographic rates, a number of landscape-level, demographic and behavioural parameters were varied from baseline values (Table 2).

CHANGES IN DEMOGRAPHY AND FEMALE MATING RANGE

Demographic parameters were either increased or decreased anywhere from 5 to 50% from the field estimated base levels (Table 2). In terms of number of nesting attempts, the maximum number of clutches attempted was decreased from three to two in order to simulate an overall decrease in breeding-season length that may occur during wet years (Nott *et al.* 1998). This decrease could simulate either a possible alteration in water-management practices or changes in overall timing of the wet season due to climate change. Juvenile and adult mortality rates were also varied. To determine the impact of changes in adult mortality, adult mortality was varied from 0·40 to 0·56 using 0·04 intervals. The same values were used for minimum juvenile mortality and linearly increased to 0·02 above the minimum when all territories within a cell were occupied (linear density-dependent juvenile mortality). In general, understanding the role of all demographic parameters varied is essential for understanding the life history of this species and helping to direct future research efforts.

The effect of female mating range on population growth was also examined. Despite considerable efforts to determine the various life-history parameters important for sparrow population dynamics, there is still considerable uncertainty surrounding female mating range (Lockwood *et al.* 2001). In order to investigate the impact of mating range, we varied the ability of female sparrows to find a mate from a base model range of 4 to 1 km (Table 2). Thus by using an SEIBM, differences in behaviour or uncertainty surrounding these estimates can be translated into changes in population dynamics.

LANDSCAPE-LEVEL CHANGES

Changes in the amount of available breeding habitat as well as habitat configuration can have a dramatic effect on the sparrow population. Breeding habitat degradation can result from increases in overall water level, through either changes in management regimes, or rising sea levels due to global warming (Nott *et al.* 1998). The vegetation in which the sparrow breeds also depends on the impacts of long-term flooding and fire regimes (Mayer 2000; Lockwood *et al.* 2003), which, in turn, may alter breeding success. Thus breeding sites may also decrease by direct degradation of breeding habitat due to changes in vegetation type and structure. This landscape-level degradation may occur randomly across the landscape, but probably occurs systematically depending on the breeding sites' topography and proximity to other non-breeding habitat types. Overall, changes in water level throughout the breeding season and alteration of breeding habitat represent two of the greatest threats to the sparrow (Nott *et al.* 1998; Lockwood *et al.* 2001; Pimm & Bass 2002; Lockwood *et al.* 2003).

Rising water levels

To examine the impacts of changes in water level, the water level within each landscape cell was either increased or decreased over the entire length of the simulation run. These increments varied from 12 cm below to 12 cm above the current level. For example, if a current cell contained 15 cm of water on a particular day, water levels in that cell would be anywhere from 3 to 27 cm during these modified runs. Throughout a single simulation, background water levels would increase or decrease on a daily basis depending on the local hydrology (see Topography and hydrology).

Habitat change and male dispersal

In all likelihood, sparrow habitat would not degrade randomly across the landscape. The habitat on the edge of the landscape would have a greater probability of shifting to unsuitable habitat due to its closer proximity to unsuitable habitat types. The breeding habitat sites that are located near unsuitable habitat could be invaded either by shrubs/trees or by wet marsh species, depending on whether the habitat was located at high or low elevations, respectively. Depending on water- and fire-management regimes, the invasion of tree species such as cypress and wet marsh species such as sawgrass could occur either separately, affecting only high- or low-elevation sites, or simultaneously, affecting both high- and low-elevation sites. While degradation of the habitat would more than likely take place over the long term (≥10 years) (Ross *et al.* 2000) and not immediately affect the sparrow population, the effects of a changing landscape on the sparrow population are central to understanding population dynamics and identifying potential management actions.

To determine the differential effects of a systematic invasion of both shrubs/trees and wet marsh vs. random invasion, a factorial set of simulations were conducted by degrading the habitat in one of four ways: random degradation; habitat-based degradation by shrub/tree invasion; habitat-based degradation by marsh encroachment;

and habitat-based degradation with both shrub/tree invasion and marsh encroachment. Random degradation consisted of randomly picking available cells within the habitat and decreasing the number of breeding territories by one. For the habitat-based method, a cell in the landscape matrix was chosen at random. If the cell contained suitable breeding habitat, it was degraded only if the breeding habitat was adjacent to unsuitable habitat. All eight cells adjacent to the target cell were searched for unsuitable habitat. The algorithm searched the landscape until the required percentage of the habitat had been degraded.

Species may respond to habitat degradation by increasing dispersal distances, which allows individuals to locate increasingly isolated patches of preferred habitat (With & Crist 1995). This change in behaviour may offset habitat degradation. Additionally, the effects of behavioural changes due to changes in habitat on population dynamics may be extremely important for understanding population persistence (Brooker *et al*. 1999; Reed 1999). Thus, to explore the possible interactions between habitat degradation and behavioural modification, both the percentage of degradation and the effective dispersal range of male sparrows to establish new territories were varied in tandem. Available breeding habitat decreased by 10, 30 or 50%, while male dispersal distance was varied between 500 and 2000 m at 500-m intervals (Table 2). We present only the results from the 500- and 2000-m simulations, as they elucidate the general pattern. The 1000- and 1500-m dispersal distances represent intermediate effects. Thus, within the SEIBM, we were also able to examine the impact of habitat change as it relates to potential behavioural responses.

ANALYSIS OF MODEL RESULTS

For each of the individual simulations outlined above,

Table 3. Impact of changes in female mating range, male dispersal, demographic rates and habitat-based parameters on the Cape Sable seaside sparrow

Parameter	Quasi-extinction probability (95% CI)	Final Mean population size	Percentage of Base model
Base model	12 (6, 18)	1598 ± 13·1	100
Clutch number (*D*)	13 (7, 20)	1391 ± 10·4	87
Female mating range (*D*)	15 (8, 22)	1166 ± 10·0	73
Juvenile mortality (*I*)	19 (12, 27)	1390 ± 12·0	87
Adult mortality (*I*)	22 (14, 31)	1020 ± 8·0	64
500-m male dispersal			
Shrub/tree invasion	18 (11, 27)	851 ± 6·6	53
Marsh encroachment	17 (10, 26)	856 ± 7·4	54
Shrub/tree and marsh	23 (15, 32)	929 ± 8·2	58
Random degradation	23 (15, 31)	953 ± 7·4	60
2000-m male dispersal			
Shrub/tree invasion	69 (60, 78)	1018 ± 12·0	64
Marsh encroachment	53 (43, 63)	1158 ± 12·9	72
Shrub/tree and marsh	52 (41, 62)	957 ± 11·4	60
Random degradation	52 (41, 62)	891 ± 11·6	56

Demographic and changes in female mating range represent either an increase (*I*) or decrease (*D*) by 30% in the model's default parameter values. For 500-m and 2000-m male dispersal, 30% of the habitat was degraded. Second column, probability of quasi-extinction (bootstrapped 95% CI) of <100 individuals; third column, mean final population size (±95% CI); fourth column, final population size as a percentage of the default model or base model (no change in any parameters).

Increasing adult mortality had by far the largest impact on quasi-extinction risk and population size, in terms of the demographic and behavioural parameters that we examined (Fig. 5; Table 3). However, there was a great deal of overlap in the 95% CI for all demographic and behavioural parameters. The impact of changes in adult mortality was largely reflected in the final population size. An increase in juvenile mortality had little effect on either metric, except at the higher levels of mortality examined. If management efforts focus on increasing the number of clutches during the breeding season, there could be positive effects on sparrow populations. However, these results highlight the importance of adult mortality for determining long-term population size and potential extinction risk.

LANDSCAPE-LEVEL CHANGES

Increasing the average water level throughout the breeding season increased quasi-extinction risk and decreased final population size dramatically (Fig. 5d,h). When we decreased the water level, there was no discernible impact on either metric. The rise in extinction risk and decline in final population size became readily noticeable with as little as a 4 cm increase in water levels. With an increase of 12 cm in average water level, quasi-extinction risk was >75%. This dramatic decrease in population and increase in extinction risk resulted from a decline in breeding sites and lack of recruitment due to nest desertion. These results highlight the importance of 'getting the water right' (Lockwood *et al*. 2003).

Confronted with a degraded landscape, how did changing the dispersal distance of individual male sparrows searching for suitable habitat affect population size? Increasing male dispersal distance to establish new territories increased quasi-extinction risk, but had varying effects on final population size (Fig. 6; Table 3). At high levels of habitat degradation, the difference in quasi-extinction risk becomes even larger when comparing between dispersal distances (Fig. 6a vs. b). At low levels of habitat degradation and high dispersal, final population size was greater than at low dispersal distances, while the opposite held true at the highest level of degradation (Fig. 6c vs. d). Thus, at high levels of degradation, increasing dispersal distance allows some individuals to find distant good patches in which to breed. However, when a male settles in habitat that is at a greater distance from other breeding habitats, he may have problems encountering a mate. Overall, increasing dispersal distance can have negative consequences on population survival via an increase in extinction risk.

Additionally, at high levels of degradation and longer male dispersal distances, the means by which habitat becomes degraded appears to become important. If habitat is degraded by the encroachment of forest, the extinction risk rises more quickly when males disperse further (Fig. 6b) than if the habitat was degraded by other means (e.g. marsh encroachment). However, there is considerable overlap in the 95% CI when comparing across type of degradation. The mechanism of habitat degradation also affects final population size, with forest encroachment having a greater negative effect (Fig. 6). Overall, this suggests that there could be a three-way interaction between percentage of habitat degraded, male dispersal distance, and type of degradation. However, the percentage of habitat degraded overwhelmingly drives the pattern with regard to quasi-extinction risk, and appears to be the major factor responsible for declines in final population size.

Our modelling reveals that the western subpopulation of sparrows is vulnerable to changes in demographic rates, and affected even more dramatically by changes in habitat structure. Negative changes in demographic rates generally decrease population size and increase extinction risk. However, habitat-based changes, combined with potential changes in male dispersal distance to establish new territories, decrease population size and increase extinction risk to a much greater extent than do demographic challenges of realistic magnitudes (Table 3). By far the greatest risk to sparrow populations is small increases in water level throughout the habitat (Fig. 5d,h). Habitat degradation (either direct or through an increase in water levels) will place the population at much greater risk than negative changes in the demographic (or other) parameters that we examined. To counteract this vulnerability, environmental management could increase the population's viability by assuring that sparrow habitat is maintained and that untimely releases of water into sparrow habitat do not occur during the breeding season. Overall, this analysis highlights the contribution of various behavioural and demographic parameters to the sparrow's population growth and, particularly, its vulnerability to changes in breeding habitat due to direct habitat degradation or water management. Below, we discuss our results with reference to the sparrow's biology and their management implications.

CHANGES IN DEMOGRAPHY AND FEMALE MATING RANGE

For the sparrow, the uncertainty surrounding female mating range may be less important to population dynamics than other demographic parameters examined in the model (Table 3). In general, changes in maximum number of clutches and female mating range should not be the primary focus of management and/or research. In contrast to the above, juvenile and adult mortality can have a greater impact on population dynamics and can have major implications for population persistence (Table 3).

LANDSCAPE-LEVEL CHANGES

As water level rises, a precipitous decline occurs in sparrow numbers, as an increase in water level delays the onset of the breeding season, reduces its duration, and increases the frequency of nest drowning (Lockwood *et al*. 1997). A decrease has the refugia to which to retreat in wetter years. In general, the sparrows exist in a highly dynamic landscape. The importance of the landscape for sparrow survival is seen in the sparrow's response both to overall landscape level changes (e.g. water level) and to direct degradation of the habitat.

Habitat degradation, whether by changes in available habitat or increases in water level, had a much larger impact on final population size and quasi-extinction risk when compared with changes in demographic and behavioural parameters in the model. Additionally, that the mechanism of habitat degradation (e.g. random vs. tree/shrub invasion) affects extinction risk demonstrates the importance of realistic models of habitat change. The impacts of the type of degradation may be even more important for species that are highly dependent on the stochastic nature of landscapes, and we would expect to see even stronger effects for these species. The model also highlights the sparrow's vulnerability to increases in water level, whether due to managed releases of water from other parts of the Everglades or a global rise in sea level. Either pathway leads to increased degradation of the sparrow's breeding habitat, resulting in population declines and increased extinction risk. With improvements in Everglades' water management and the a2(9(ter)]al par)7-92.8(r)12.9(9(teconn r)35rs)6e-eeed-

Brooker, L., Brooker, M. & Cale, P. (1999) Animal dispersal in fragmented habitat: measuring habitat connectivity, corridor use, and dispersal mortality. *Conservation Ecology*, **3**.

Caswell, H. (2001) *Matrix Population Models: Construction, Analysis, and Interpretation*. Sinauer Associates, Sunderland, MA, USA.

Clark, M.E., Rose, K.A., Levine, D.A. & Hargrove, W.W. (2001) Predicting climate change effects on Appalachian trout: combining GIS and individual-based modeling. *Ecological Applications*, **11**, 161–178.

Curnutt, J.L., Comiskey, J., Nott, M.P. & Gross, L.J. (2000) Landscape-based spatially explicit species index models for Everglades restoration. *Ecological Applications*, **10**, 1849–1860.

Curnutt, J., Mayer, A., Brooks, T. *et al*. (1998) Population dynamics of the endangered Cape Sable seaside sparrow. *Animal Conservation*, **1**, 11–22.

Dean, T. & Morrison, J. (1998) *Non-Breeding Season Ecology of the Cape Sable Seaside Sparrow (*Ammodramus maritimus mirabilis*): 1997–98 Field Season Final Report*. US Fish and Wildlife Service, Washington, DC.

DeAngelis, D.L. & Mooij, W.M. (2005) Individual-based modeling of ecological and evolutionary processes. *Annual Review of Ecology, Evolution and Systematics*, **36**, 147–168.

DeAngelis, D. & Rose, K. (1992) Which individual-based approach is most appropriate for a given problem? *Individual-Based Approaches in Ecology* (eds D. DeAngelis & L. Gross), pp. 67–87. Chapman & Hall, New York.

DeAngelis, D.L., Gross, L.J., Huston, M.A. *et al*. (1998) Landscape modeling for Everglades ecosystem restoration. *Ecosystems*, **1**, 64–75.

Donalson, D.D. & Nisbet, R.M. (1999) Population dynamics and spatial scale: effects of system size on population persistence. *Ecology*, **80**, 2492–2507.

Dunning, J.B., Stewart, D.J., Danielson, B.J. *et al*. (1995) Spatially explicit population models: current forms and future uses. *Ecological Applications*, **5**, 3–11.

Elderd, B.D. & Doak, D.F. (2006) Comparing the direct and community-mediated effects of disturbance on plant population dynamics: flooding, herbivory and *Mimulus guttatus*. *Journal of Ecology*, **94**, 656–669.

Greenlaw, G. (1983) Microgeographic distribution of breeding seaside sparrows on New York salt marshes. *The Seaside Sparrow, Its Biology and Management*. Occasional Papers 1983–85, pp. 99–114. North Carolina Biological Survey, Raleigh, NC, USA.

Holt, R.D., Pacala, S.W., Smith, T.W. & Liu, J. (1995) Linking contemporary vegetation models with spatially explicit animal population models. *Ecological Applications*, **5**, 20–27.

Jackson, R.B., Carpenter, S.R., Dahm, C.N. *et al*. (2001) Water in a changing world. *Ecological Applications*, **11**, 1027–1045.

Jenkins, C.N., Powell, R.D., Bass, O.L. & Pimm, S.L. (2003) Demonstrating the destruction of the habitat of the Cape Sable seaside sparrow (*Ammodramus maritimus mirabilis*). *Animal Conservation*, **6**, 29–38.

Letcher, B.H., Priddy, J.A., Walters, J.R. & Crowder, L.B. (1998) An individual-based, spatially-explicit simulation model of the population dynamics of the endangered red-cockaded woodpecker, *Picoides borealis*. *Biological Conservation*, **86**, 1–14.

Lockwood, J., Fenn, K., Curnutt, J. *et al*. (1997) Life history of the endangered Cape Sable seaside sparrow. *Wilson Bulletin*, **109**, 720–731.

Lockwood, J., Fenn, K., Caudill, J. *et al*. (2001) The implications of Cape Sable seaside sparrow demography for Everglades restoration. *Animal Conservation*, **4**, 275–281.

Lockwood, J., Ross, M. & Sah, J. (2003) Smoke on the water: the interplay of fire and water flow on Everglades restoration. *Frontier in Ecology and the Environment*, **1**, 462–468.

Mayer, A. (2000) *Cape Sable seaside sparrow* (Ammodramus maritimus mirabilis) *habitat and the Everglades: ecology and conservation*. PhD thesis, University of Tennessee, Knoxville, TN, USA.

Menges, E.S. (1990) Population viability analysis for an endangered plant. *Conservation Biology*, **4**, 52–62.

Morris, W. & Doak, D. (2002) *Quantitative Conservation Biology: Theory and Practice of Population Viability Analysis*. Sinauer Associates, Sunderland, MA, USA.

The Nature Conservancy (1993/94) *Southeastern Region Classification Scheme. International Classification of Ecological Communities: Terrestrial Vegetation of the Southeastern United States*. The Nature Conservancy, Chapel Hill, NC, USA.

Nott, M.P., Bass, O.L., Fleming, D. *et al*. (1998) Water levels, rapid vegetation changes, and the endangered Cape Sable seaside-sparrow. *Animal Conservation*, **1**, 23–32.

Pimm, S. & Bass, O. (2002) Range wide risks to large populations: the Cape Sable sparrow as a case history. *Population Viability Analysis* (eds S. Beissinger & D. McCullough), pp. 406–424. University of Chicago Press, Chicago, IL, USA.

Pimm, S., Balent, K., Brooks, T. *et al*. (1995) *Cape Sable Sparrow Annual Report*. Technical Report. National Biological Service/National Park Service, Homestead, FL.

Pimm, S.L., Lockwood, J.L., Jenkins *et al*. (2002) *Sparrow in the Grass. A Report on the First 10 Years of Research on the Cape Sable Seaside Sparrow (Ammodramus maritimus mirabilis)*. Technical report. National Park Service, Homestead, FL.

Post, W. (1974) Functional analysis of space-related behavior in the seaside sparrow. *Ecology*, **55**, 564–575.