Hydrology, habitat change and population demography: an individual-based model for the endangered Cape Sable seaside sparrow *Ammodramus maritimus mirabilis*

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Summary

1. Habitat destruction and fragmentation have led to precipitous declines in a number of species of concern. For these species, traditional models that group individuals into age or stage cohorts may not accurately capture the stochasticity associated with small populations. Additionally, traditional models do not explicitly incorporate landscape-level structure, which becomes increasingly important at small population sizes. Thus, for declining species, spatially explicit individual-based models (SEIBM) can be used to understand both population demography and the impacts of habitat destruction, and to guide management practices to increase the chances of species survival.

2. To gauge the impacts of changes in habitat and also demographic rates on a US endangered species, we constructed an SEIBM for the Cape Sable seaside sparrow (*Ammodramus maritimus mirabilis* Howell) of the South Florida Everglades. The model simulates temporal and spatial dynamics of individual sparrows using local GIS-based topography, vegetation and hydrology along with behavioural and demographic rates derived from field studies.

3. When adult mortality and, to a lesser extent, juvenile mortality were increased in model simulations, there was an increase in extinction risk and a decrease in population size, whereas changes in number of clutches or female mating range had little impact. In contrast to the effects of simulating changes in mortality rates, simulated landscape-level changes (increasing water levels or decreasing habitat availability) were associated with dramatic population declines and increases in extinction risk. The sparrow appears to be particularly sensitive to the loss of higher-elevation breeding habitat. These results highlight the importance of proper water- and land-use management in assuring the species' survival.

4. *Synthesis and applications.* Although changes in demographic rates affect population growth and are often the focus of conservation efforts, changes in habitat structure can also dramatically alter population viability. When both landscape-level and demographic data are available, spatially explicit models are particularly advantageous. Not only do they allow researchers and resource managers to prioritize areas for habitat restoration and species management, but they can also be used to help focus future research efforts.

Key-words: climate change, Everglades, landscape degradation, habitat fragmentation, increasing sea levels, spatially explicit individual-based model, water management

Introduction

Threatened and endangered species' viability has often been linked to habitat fragmentation and destruction (Soulé 1986; Andrén 1994; Boulinier *et al.* 1998). Both the manner in which habitat becomes fragmented and the magnitude of that

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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.* 2000; Pimm & Bass 2002). The importance of this issue for restoration of the Everglades is highlighted by the fact that the Central Everglades Restoration Plan hinges on 'getting the water right' (Lockwood *et al.* 2003). Thus understanding water flow and how species are affected by hydrological shifts can lend valuable insight into restoration and management practices for both the Everglades and other hydrology-driven systems.

In this article, we present an SEIBM for the US endangered Cape Sable seaside sparrow, *Ammodramus maritimus mirabilis*, the status of which is dependent on the plant community structure of the Everglades' marl and mixed-marl prairies and the timing of seasonal floods within these prairies (Lockwood *et al.* 2001; Pimm & Bass 2002). In general, the sparrow represents an ideal candidate for an individual-based model due to the wealth of data regarding the species and its habitat associations (Bass & Kushlan 1982; Pimm *et al.* 1995; Lockwood *et al.* 1997; Nott *et al.* 1998; Curnutt *et al.* 2000). By using an SEIBM for this endangered population, both the impacts of changes in demographic rates on population growth and changes in habitat structure can be investigated. We chose to examine four main threats to the sparrow populations: (1) changes in survival and reproduction; (2) changes in female mating range; (3) changes in water level; (4) habitat destruction. We also examined the interaction between habitat destruction and changes in male dispersal to establish new territories, which has

been shown to affect population viability for other species (With & Crist 1995; Brooker *et al.* 1999; Reed 1999). While the particular framework of the model applies directly to the sparrow population, the general approach can be, and has been, applied to both endangered and non-endangered populations (Letcher *et al.* 1998; Railsback & Harvey 2002; Stephens *et al.* 2002).

Methods

STUDY SPECIES

The Cape Sable seaside sparrow breeds in the short-hydroperiod marl prairies of the Everglades and Big Cypress National Preserve in South Florida (Fig. 1a). These marl prairies are composed of either dominant stands of muhly grass (*Muhlenbergia filipes*) or a mosaic of hundreds of grass species including muhly grass, thin stands of saw-grass (*Cladium jamaicense*) and black-top sedge (*Schoenus nigricans*) (Lockwood *et al.* 2003). Within these prairies, which are found on an elevational gradient between marsh and scrub/forest habitats, sparrows prefer to nest in graminoid stands composed mostly of muhly grass. These stands provide ideal nesting and foraging sites for the sparrow. The sparrow begins nesting in these prairies as the high water levels recede during the onset of the dry season around 1 March (Lockwood *et al.* 1997; J. Lockwood, personal communication). Depending on the timing of the subsequent wet season, the sparrows may be able to complete up to three broods or, in rare instances, four broods. Generally, the dry period within these prairies allows for rearing of only two broods (Lockwood *et al.* 1997, 2001). If water levels fluctuate during the breeding season, sparrow breeding can be interrupted and nests can fail (Lockwood *et al.* 1997; Nott *et al.* 1998). Thus sparrow reproduction is highly dependent on the timing and extent of flooding during the dry season, and is driven by the overall hydrological regime of the Everglades (Lockwood *et al.* 1997; Nott *et al.* 1998; Lockwood *et al.* 2003).

Currently, the sparrow's range is limited to six subpopulations. Five of the subpopulations are located along the eastern edge of the Shark River Slough (Pimm *et al.* 2002). The western subpopulation (Fig. 1), which is the focus of our modelling efforts, is located along the western edge of the Shark River Slough, and was heavily impacted during a series of dry-season anthropogenic water releases from 1993 to 1996 (Nott *et al.* 1998; Jenkins *et al.* 2003). While single-season long hydroperiods have a negative effect on sparrow breeding, they also adversely affect long-term breeding success by altering habitat structure. When wetter conditions prevail, non-breeding sparrow habitat (e.g. thick stands of sawgrass and spike rush) can encroach on breeding habitat (Ross *et al.* 2003). Given a number of decades without burning, pine stands are able to encroach and take over marl prairie habitat (Curnutt *et al.* 1998; Lockwood *et al.* 2003). Thus sparrow populations are susceptible to both short-term changes in hydrology and long-term changes in habitat structure brought about by altering hydrological dynamics and fire regimes.

THE MODEL

In order to examine the impacts of both changes in hydrology and vegetation structure on sparrow population dynamics, an SEIBM for the western subpopulation of the sparrow was constructed. The SEIBM sparrow model (SIMSPAR) is part of the Across Trophic Level System Simulation (ATLSS) effort to model the ecosystem dynamics within the Florida Everglades along with its related
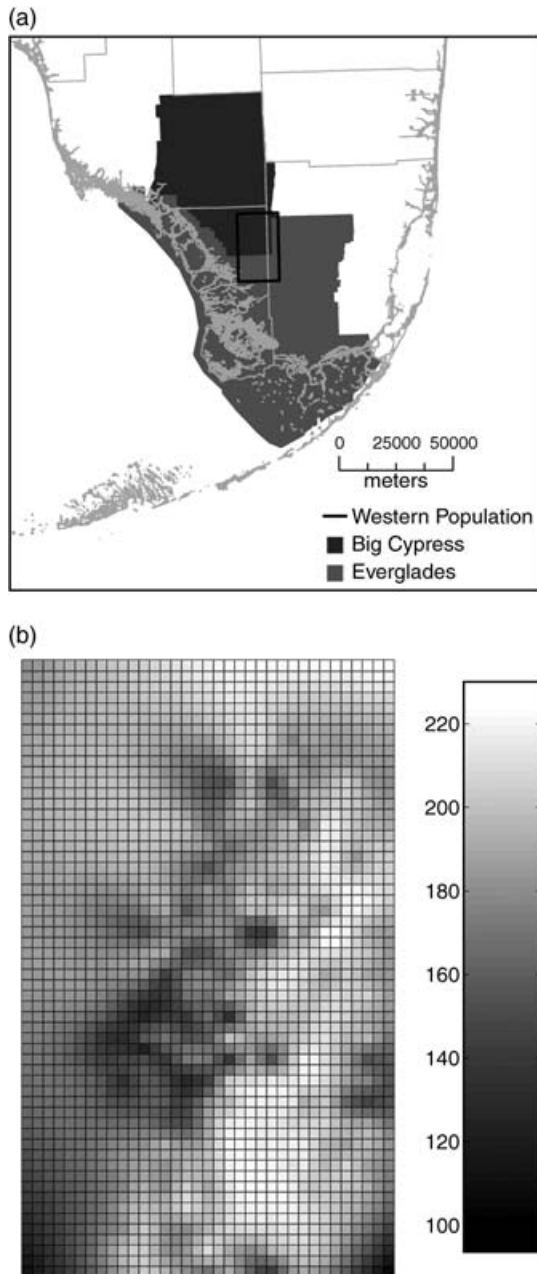
Fig. 1. Map of (a) southern Florida counties showing the boundaries of Everglade National Park, Big Cypress National Preserve, and the location of the western subpopulation of the Cape Sable seaside sparrow (black outline); (b) the associated western subpopulation's 17·5 × 25·5-km topographic map (cm above mean sea level) used in simulation runs.

LANDSCAPE AND HABITAT CHARACTERIZATION

The western subpopulation's habitat is composed of different vegetation types in which the sparrow is known to breed and forage. Breeding territories for the sparrow are ≈100 m across and may be discrete or slightly overlapping (Pimm *et al.* 1995). During the non-breeding season, sparrows will move only a few kilometres from these sites and will often interact across breeding and natal areas (Post 1974; Werner 1975; Greenlaw 1983; Dean & Morrison 1998). Behavioural and demographic rates come from past work on population dynamics at a 500-m grid-cell scale (Lockwood *et al.* 1997; Curnutt *et al.* 1998). A grid of 500 × 500-m cells was chosen for the model's spatial resolution as it represents reasonably the area in which a group of breeding sparrows interacts.

Each 500 × 500-m grid cell for the model's vegetation layer was constructed using a composite of habitat types. These composite cells were taken from a 32 × 32-m grid-cell resolution map of vegetation types analysed by The Nature Conservancy (1993/94), over which a grid of 500 × 500-m cells was placed. The approximate locations of breeding sparrow males and their densities, which were derived from extensive field surveys in 1993 within the 500-m grid cells (Pimm *et al.* 2002), was placed on top of these two grid layers. Given known breeding locations and habitat structure, it was determined that sparrows breed only in those cells that contain a minimum of 55% of the sparrow's preferred vegetation for nesting and contain at least 10% open area (the combined coverage of marsh and nesting habitat cannot exceed 90%). Additionally, 500-m grid cells classified as containing tree or shrub coverage according to the smaller grid cells in the vegetation map (The Nature Conservancy 1993/94) were excluded from being potential breeding sites, as trees and shrubs are refuges for known predators of the sparrow (e.g. raptors). Areas that met the criteria for suitable breeding habitat were designated as potential breeding sites. Given the above criteria and using upper quartile regression (Scharf *et al.* 1998) on the number of singing males within surveyed territories (Lockwood *et al.* 1997), the maximum number of sparrow territories in a 500-m grid cell was set to four. In general, these composite vegetation maps provided the base layer for simulating the sparrow's interaction with its landscape.

TOPOGRAPHY AND HYDROLOGY

To model vegetation changes, topography and hydrology layers for the model were developed, as the Everglades' vegetation is strongly influenced by the interaction between these two factors. The topography layer of the model was calculated during the 1995 breeding season by measuring the water level at every kilometre within a 17·5 × 25·5-km area encompassing the western subpopulation's habitat, for a total of 284 sites. For each cell, the mean water depth was calculated by measuring water depth at six random points within the site. The elevation for each site was expressed as a difference between the water depth at the site and that at a nearby hydrological station, NP205, during the time of the survey. This station is located at the north-eastern edge of the habitat at ≈180 cm above mean sea level. As only every other cell within the subpopulation's habitat was sampled, values for intervening areas were derived by linear interpolation (Nott *et al.* 1998). All values were combined to create a map corresponding to the topography of the western subpopulation's habitat (Fig. 1b).

The hydrology of the Everglades is driven by the interactions of topography and fluctuations in the daily water levels. The temporal dynamics of water depths for SIMSPAR were simulated using data collected from the hydrological monitoring station NP205 (Nott
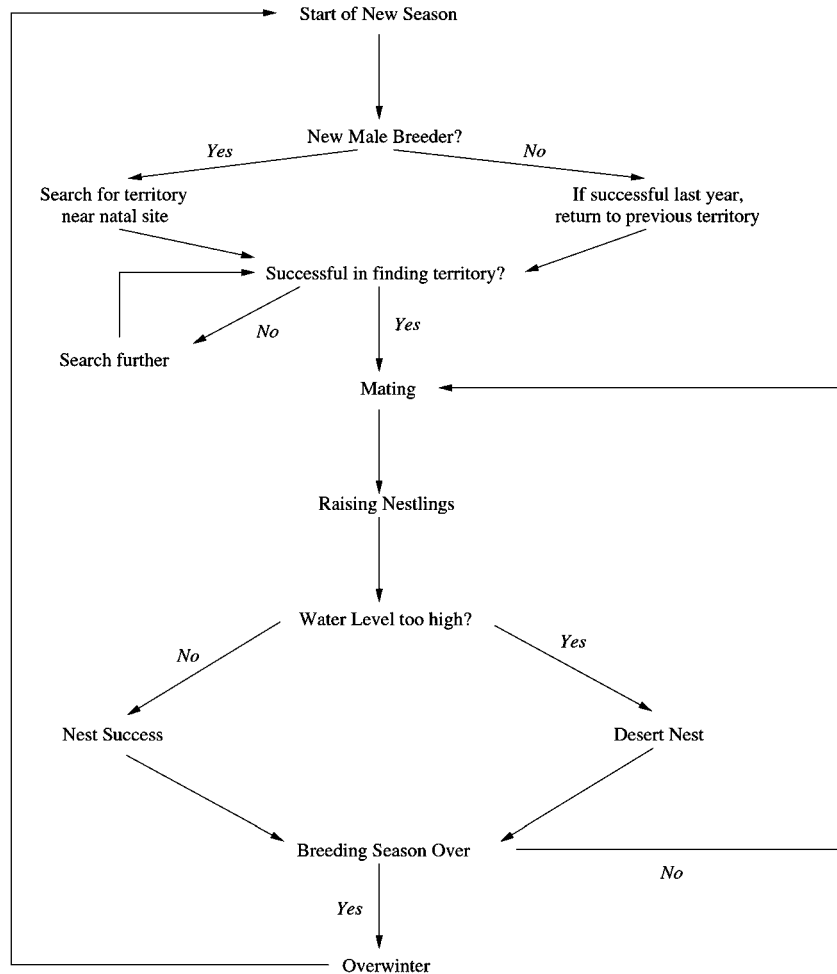
population-level impacts (DeAngelis *et al.* 1998). SIMSPAR consists of a number of modules that determine the behaviour and breeding success of sparrows moving across the landscape. Behavioural rules and demographic rates are based on direct field observations (Bass & Kushlan 1982; Pimm *et al.* 1995; Lockwood *et al.* 1997; Curnutt *et al.* 1998), while the landscape in which the sparrow moves consists of multiple layers encompassing local topography, hydrology and vegetation. SIMSPAR uses knowledge of both the species' biology and its landscape to predict the sparrow's response to changes in hydrology and vegetation.

Fig. 2. Decision-based flow chart for male sparrows during the breeding season.

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 behaviour was dependent on a series of decisions (Fig. 2) dictated by interactions with other sparrows and the environment.

As runs are stochastic, a single SIMSPAR simulation consisted of a set of 100 runs, each 150 years in length, in order to calculate mean responses to changes in model parameters (Fig. 3). For each simulated year, a single, year-long hydrological sequence was chosen randomly from the 21 years in the long-term hydrological sequence.
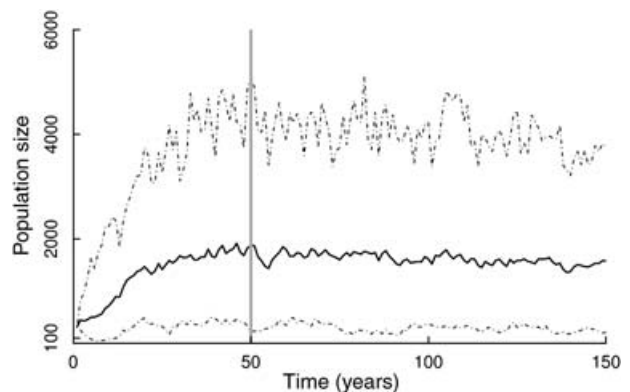

Fig. 3. Mean (solid line) and 95% CI (dashed lines) for a single set of 150-year simulation runs (*n* = 100) using the field-derived estimates of the base model parameters. Quasi-extinction risk was set at 100 individuals. Simulation results prior to the dark grey line in the figure constitute the burn-in phase of the model and were discarded.

This year-long sequence was then used to drive daily fluctuations in water levels during a single breeding season. While this does not preserve between-year autocorrelation in water levels that are present across the entire long-term sequence, it does preserve within-year autocorrelation. The first 50 years of a simulation constituted a burn-in phase to allow the population runs to stabilize. During the subsequent 100 years, populations were considered extinct if they dropped below

Table 1. Main parameter values for initial runs of the SEIBM

Life cycle parameter	Default value
Maximum age	5 years
Juvenile mortality	0·40–0·42 per year (density-dependent)
Adult mortality	0·40 per year
Nesting	7 days
Fledging age	33 days
Clutch probability	2 : 0·16 3 : 0·48 4 : 0·36 (number of eggs : probability)
Sex ratio (male : female)	0·5 : 0·5

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 associated with each dispersal step. During the search, if no unvisited cells were available, the male would become an unmated floater for the breeding season. For unmated females, their mating ranges were limited to 4 km in order to look for available singing males as mates. As males are dispersing to establish new territories in an unfamiliar landscape, we assumed that males would incur the added mortality penalty due to the cost of territory establishment. By contrast, females move to territories that contain good breeding habitat in response to male mating calls and therefore would not incur a mortality penalty due to territory establishment. The movement patterns for the model are all based on parameters derived from telemetry studies (Dean & Morrison 1998; Lockwood *et al.* 2001). However, given the limited number of individuals radio-collared in the telemetry study (Dean & Morrison 1998), there is some uncertainty in the estimates of male dispersal distance, and considerable uncertainty in female mating range estimates; we explore these below (see Model analysis).

During the start of the breeding season (set to 1 March in the model), males would begin singing to attract mates. If a male was able to find a suitable territory and attract a mate, the pair would begin nesting. The height at which the pair built their nest was randomly chosen from a set of 460 measured nest heights (J. Lockwood, unpublished data). These nests were abandoned if the overall height of the water in the 500-m grid cell rose above the nest during a breeding attempt (Fig. 2). The number of eggs in a single clutch was randomly drawn from a distribution of known clutch sizes. The maximum number of clutches during the breeding season is directly affected by the length of the dry season. The sparrow needs 30–40 days to complete a nest cycle (Lockwood *et al.* 1997) and, on average, mating pairs produce two clutches during the season (Lockwood *et al.* 1997, 2001). A three-clutch breeding season necessitates an uninterrupted period of 90–120 dry days, and represents a good breeding year. This was used as the base value for our model runs (Table 2).

Table 2. Parameters used in examining how sparrows respond to changes in female mating range, demographic rates, landscape attributes and male dispersal to establish new territories

Parameter level	Parameter varied	Values
Demography and female mating range	Maximum number of clutches	2 and **3**
	Female mating range	1, 2, 3 and **4** km
	Juvenile mortality	**0·40**, 0·44, 0·48, 0·52 and 0·56
	Adult mortality	**0·40**, 0·44, 0·48, 0·52 and 0·56
Landscape level	Changes in water level	–12 to 12 (**0** cm)
Landscape and male dispersal (varied factorially)	Degradation of habitat	**0**, 10, 30 and 50%
	(a) Random	
	(b) Systematic – shrubs/trees invasion	
	(c) Systematic – marsh encroachment	
	(d) Systematic – both	
	Bachelor male dispersal	**500**, 1000, 1500, 2000 m

Random degradation habitat algorithms chose breeding sites regardless of location; habitat-based degradation algorithms chose only breeding sites next to unsuitable habitat. Model default parameters based on field-derived estimates are in bold.
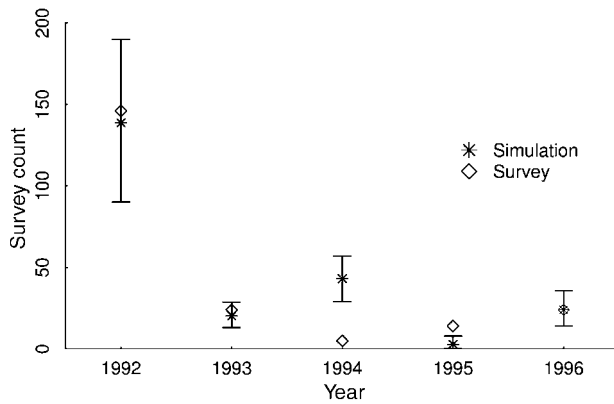
Fig. 4. Comparison of population surveys with simulated results (±95% CI) for 250 simulations using base model parameters and the entire 21-year hydrological sequence.

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;
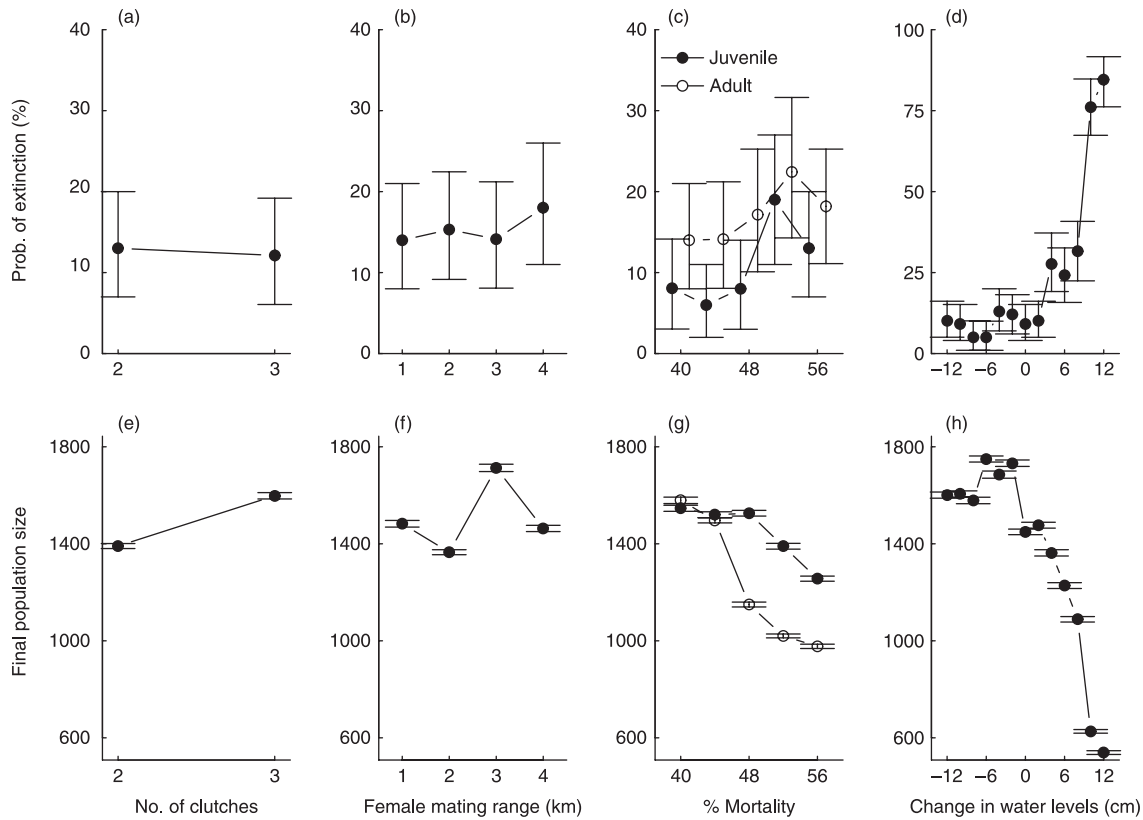
Fig. 5. Probability of extinction (a–d) and final mean population size (e–h) for number of clutches, female mating range, adult and juvenile mortality, and changes in water level, respectively, throughout the breeding season (±95% CI). Data for juvenile and adult probability of extinction are jittered to show overlapping points. Note the change of scale in extinction probability for changes in water level.

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, population response was quantified by two different metrics: (1) probability of quasi-extinction; and (2) final population size. Quasi-extinction was defined as the probability of dropping below 100 individuals in the population. Confidence intervals for the probability of extinction were obtained by bootstrapping 100 models runs from the simulation of interest, calculating the probability of extinction for the boot-strapped sample, and repeating for 5000 iterations. Regardless of quasi-extinction levels, the same qualitative results were obtained. All simulations of the model were conducted in MATLAB ver. 6·1 (2001) (Math Works, Inc., Natick, MA, USA).

Results

CHANGES IN DEMOGRAPHY AND FEMALE MATING RANGE

Increasing mortality, whether juvenile or adult, or decreasing the number of clutches, resulted in an increase in quasi-extinction risk and a decrease in final population size (Fig. 5). However, changing female mating range had very little impact on extinction risk and final population size. Additionally, the magnitude of the effect varied greatly (Fig. 5; Table 3) across both female mating range and demographic parameters.

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.
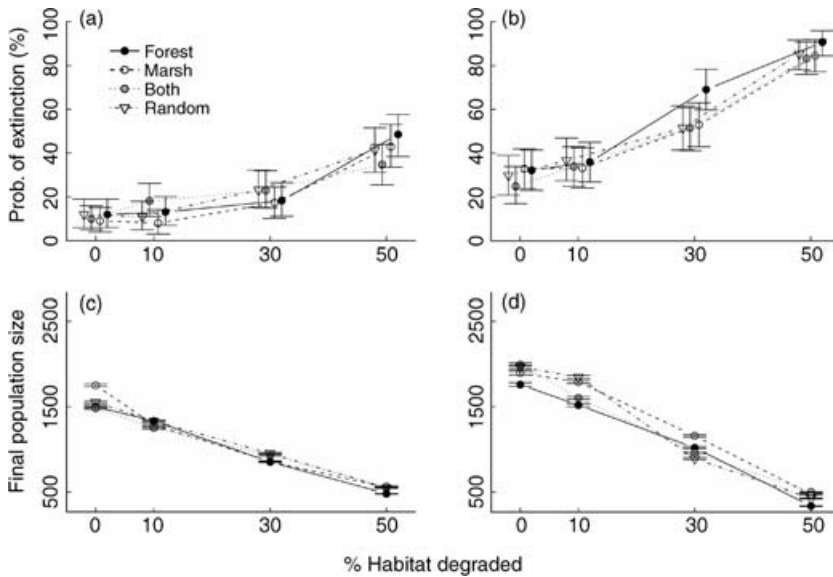
Fig. 6. Probability of extinction (±95% CI) and final mean population size (±95% CI) for male dispersal distance to establish new territories of 500 m (a,c) and 2000 m (b,d), respectively. The four degradation types are random (triangles), shrub/tree invasion (forest, black circles), marsh encroachment (marsh, open circles) and both shrub/tree and marsh encroachment (both, grey circles). Data for probability of extinction are jittered to show overlapping points.

Discussion

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 in water level, surprisingly, had little effect on population size and extinction risk. This is due to the fact that a drop in water level did not make additional suitable habitat available for breeding, as all suitable habitat was already open for breeding. If the drop in water level resulted in a change in habitat availability by converting unsuitable breeding habitat to suitable breeding habitat, decreasing water levels through management actions could potentially increase population sizes and decrease extinction risk. However, it appears more important to ensure that water levels do not rise dramatically, as this could result in almost immediate extinction for the western subpopulation of the sparrow.

A closer examination of habitat degradation and male sparrow dispersal demonstrates not only that degrading habitat has a highly negative impact on sparrow populations, but also that the means by which habitat is degraded may play an important role in terms of extinction risk and population size. The comparison of degradation treatments shows that degradation of the habitat by invasion of shrubs/trees, particularly at high levels of degradation, has the greatest effect on population size and potentially negative effects on extinction risk (Fig. 6). Open, higher elevation sites, which stay relatively dry in extremely wet years, may offer important refugia for the population to breed during the years when adverse breeding conditions such as high water levels persist. Thus, when these high-elevation sites are invaded by shrubs/trees and subsequently degraded, the population no longer

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 assurance of the continued quality of breeding habitat, the sparrow populations may well be able to increase in size.

All models contain limitations and can be improved. For the sparrow SEIBM, we have taken a probabilistic approach to modelling sparrow behaviour. By examining male dispersal and territory establishment using a game-theoretical approach (e.g. see review by Sutherland 2006), we may continue to refine our understanding of the interaction between species behaviour and habitat structure. Additionally, we chose not to explicitly model the impacts of fire on vegetation structure, which in turn can affect population dynamics (Lockwood *et al.* 2003). However, we did consider the impacts of fire suppression via shrub/tree encroachment on breeding habitat. Resolving these limitations and examining subsequent changes in model predictions is a potential focus of future modelling and research efforts.

Conclusions

By linking behaviour to a spatially explicit landscape, we were able to tease apart the impacts on population growth of changes in behaviour, demographic rates and habitat structure. In general, spatially explicit models often focus on random degradation or random placement of habitat across the landscape (Boswell *et al.* 1998; Schiegg *et al.* 2002; West *et al.* 2002). As we have shown, at higher levels of habitat fragmentation, modelling realistic patterns of habitat degradation can become ever more important. Increasingly in ecology and conservation, population dynamics appear to be dependent on both landscape-level (Dunning *et al.* 1995; Holt *et al.* 1995; Letcher *et al.* 1998) and behavioural processes (Reed 1999). However, for the sparrow, landscape-level processes have a greater effect on population viability than the demographic or behavioural processes examined. We caution, how-

ever, that the magnitude of change may not be directly comparable between landscape-level and demographic as well as behavioural parameters. In fact, by modelling the landscape, due in part to the wealth of data collected regarding the sparrow, we are able to provide a richer analysis of possible threats and management options. Only through increasing our understanding of these interactions may we be able to guide management and conservation efforts for rare and endangered species.

In general, individual-based models represent an important tool for understanding the importance of individual variation and for linking behaviour, species survival and habitat structure (DeAngelis & Mooij 2005). For some species, IBM or SEIBM may be the only means to examine the links between habitat and population dynamics, especially when experiments are not possible due to limited number of individuals (Letcher *et al.* 1998) or the scale of the potential experiment (Turner *et al.* 1994). IBM may also provide a framework in which to develop hypotheses for field experiments or management guidelines (Schmitz 2001). While we often rely on models that group individuals into broad subclasses or age groups (Caswell 2001; Morris & Doak 2002), we may be gaining limited understanding of population dynamics as they relate directly to habitat change. This may be the only option for species for which data are limited, but for a number of species that have been well studied (such as the Cape Sable seaside sparrow), SEIBM can provide considerable insight into species–habitat relationships. For these species (Turner *et al.* 1994; Letcher *et al.* 1998; Railsback & Harvey 2002; Stephens *et al.* 2002), there is ample evidence that landscape matters and changes in habitat structure have important impacts on population dynamics.

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