

Demonstrating the destruction of the habitat of the Cape Sable seaside sparrow (*Ammodramus maritimus mirabilis*)

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Abstract

The Cape Sable seaside sparrow (*Ammodramus maritimus mirabilis*) is Federally protected under the Endangered Species Act of the United States of America. This legislation prohibits direct or indirect take – the killing or harming – of the protected species. In 1993 and 1995, the opening of floodgates into Everglades National Park during the normal dry season resulted in a direct take of the sparrow. The argument was also made that there was indirect take through destruction of the habitat upon which the sparrow depends. Using a combination of fieldwork and satellite image analysis, we show that the floods did damage to the habitat of the sparrow. Moreover, they did so for a period longer than the actual flooding, further increasing the sparrow's extinction risk. Recovery of the sparrow population to pre-flood levels will require an adequate and stable amount of habitat. We now have a technique for monitoring that habitat and ensuring that poor water management does not threaten it. More broadly, this technique has the potential for monitoring the habitat of many other species and avoiding another situation such as the sparrow faces.

INTRODUCTION

Countries differ in the vigour with which they protect biodiversity and in the particular laws they pass to do so. In the United States of America, one of the most effective laws is the Endangered Species Act. It prohibits direct take – the killing or harming – of Federally listed endangered species. From its inception there has also been the implication that it prohibits indirect take – through the destruction of the ecosystems on which species depend. That provision was challenged in a legal case, *Sweet Home versus Babbitt*, argued in front of the Supreme Court of the United States, on 17 February 1995. In the particular context of the spotted owl, an Oregon group challenged the responsible cabinet member, Secretary of the Interior Bruce Babbitt, arguing that only direct take violated the law and not habitat destruction. In a brief of Amici Curiae scientists, one of us (Pimm) among others (Cairns *et al.*, 1995) argued that habitat destruction is most often the cause of species endangerment and extinction.

The Supreme Court agreed with that position. In doing so, they raise a scientific question that transcends national boundaries: how are we to demonstrate that

human actions harm the habitat on which a species depends? In the case of the owl, the action – extensive logging of the old-growth forests on which the birds depend – was obvious. Of course, it need not be.

Our particular concern is the Federally listed Cape Sable seaside sparrow (*Ammodramus maritimus mirabilis*), a bird found only within the seasonally flooded marshes in the Everglades of South Florida. In previous publications, we demonstrated that unnatural flooding of its breeding habitat directly caused its precipitous decline in the western half of its range (Curnutt *et al.*, 1998; Nott *et al.*, 1998). The flooding resulted from diversion of the area's drainage, Shark River Slough, to the west of its natural path and a change in the timing of its seasonal ebb and flow. Because sparrows nest near the ground, flooding results in increased nest failure both by drowning nest contents and by increasing losses to predators (Lockwood *et al.*, 1997, 2001). Floods also do indirect harm by causing sparrows to cease courtship activities and further nesting (Lockwood *et al.*, 1997, 2001). Concomitant with those changes, areas in the east became overdrained and more susceptible to anthropogenic fires. Those fires also harm the birds and when too frequent eliminate sparrows from the area (Curnutt *et al.*, 1998).

We left open the possibility that flooding and fires also damaged the habitat and so the birds as a consequence. In this paper, we demonstrate that flooding has indeed

altered the habitat in which the sparrow occurs, in a way such as to preclude the bird's use of the habitat, and over a period longer than the flooding itself.

The paper proceeds in two stages. The first explains how we predict sparrow habitat. In brief, by precisely locating sparrow nests during the breeding season, we identify the 'spectral signatures' of their habitat on satellite images. These signatures are six-element vectors, each element representing a 'colour' – a wavelength within or beyond visual detection. The combination of these spectral signatures for a sufficient sample of habitat produces a prediction of the habitat available to the sparrows on the date of the satellite image.

The second stage is an evaluation of those predictions.

It has three parts. The first shows that we can predict habitat in years before we began intensive fieldwork and thus have no nest locations. It includes both ecological reasons and empirical evidence supporting our methods. The second is an analysis of the habitat predictions. It links water-management decisions to their effects on the habitat. The third part is a detailed technical analysis of the errors in our predictions. We identify these errors using the annual range-wide surveys of the sparrow's abundance and distribution. Some of these errors are failings of the predictive model; we argue that many more are errors the birds make for one reason or another. We discuss this analysis in a companion paper (Jenkins *et al.*, this issue, 39–46).

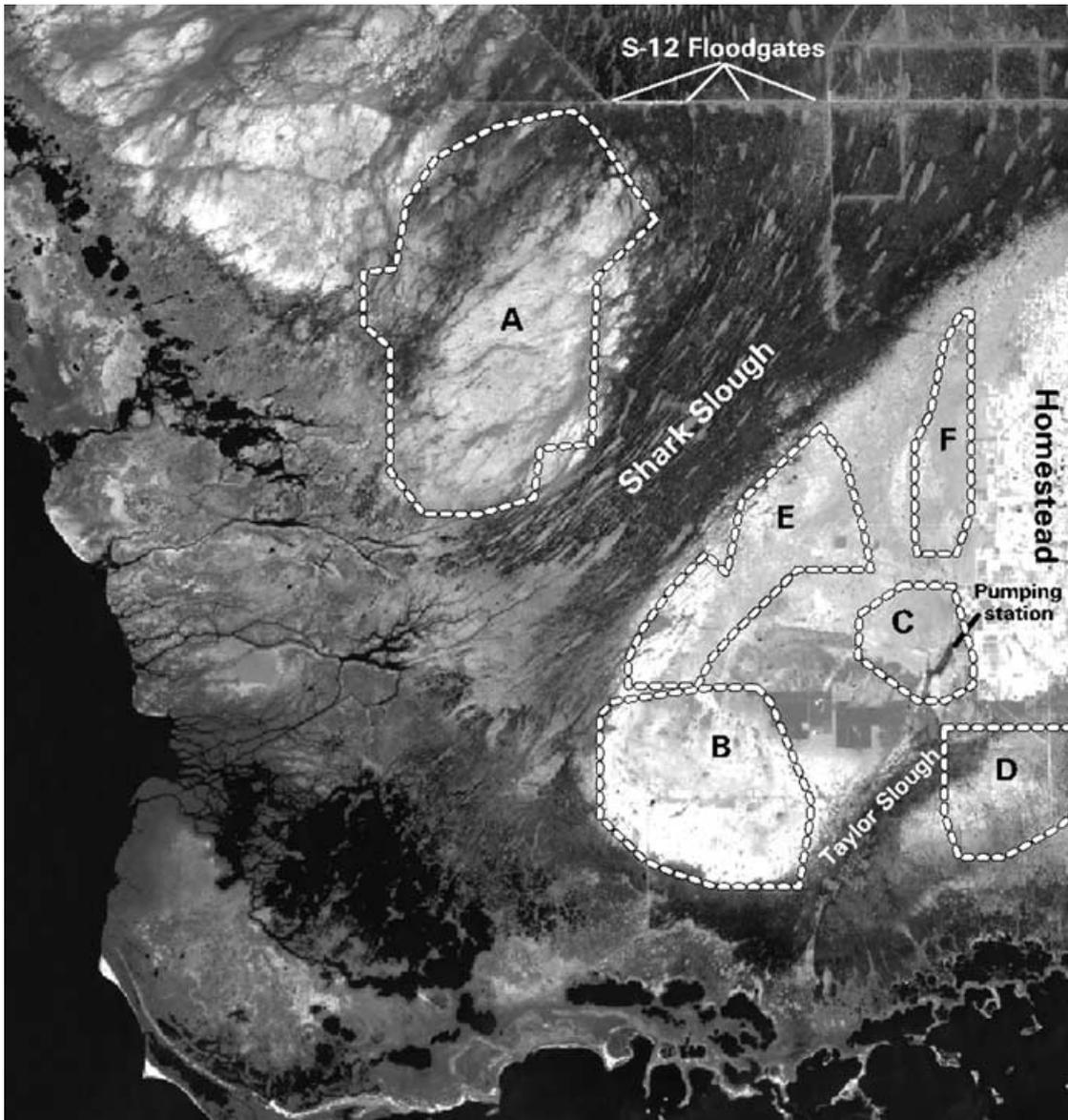


Fig. 1. Location of sparrow populations (A–F) in Everglades National Park. Water enters the park from two sources, the S-12 floodgates and a pumping station north of Taylor Slough. The S-12 floodgates are west of the natural entry point for water into the ecosystem. The tree islands, which appear as pale, teardrop shaped objects amid the darker, flooded areas of Shark Slough, illuminate the natural flow path. Whenever the S-12s open, they flood population A. Additionally, shifting of water to the west causes population F to become drier and to suffer an increased fire frequency. The pumping station north of Taylor Slough affects the water levels in populations C and D. Heavy pumping results in the complete flooding of D and the southeastern portion of C. Floods have less effect on populations B and E.

We will present two key results.

(1) Across the 8 years of the study, large year-to-year fluctuations in predicted habitat confirm the culpability of water managers. Flooding in 1993 and 1995 greatly reduced the habitat predicted to be suitable for the sparrow compared to 1992. This is a formal, technical demonstration of the figures presented by Nott *et al.* (1998), inferring dry prairies in 1992 and extensively flooded prairies in 1993 and 1995, from the colours of the published images.

(2) The predicted suitable habitat west of Shark River Slough was at a low ebb in 1995 and had recovered slowly, but consistently, since then until 1999. This formal, technical demonstration matches the subjective opinion expressed by Bass & Pimm from their visual inspections during the annual surveys of the sparrow population. By 1999, the predicted suitable habitat had not yet recovered to its pre-flood state. However, the habitat is recovering faster than the bird populations. It is the repetition of precisely such a scenario that could lead to the species' extinction (Pimm & Bass, 2002).

Neither of these results is a surprise, for they were suggested by previous papers (Curnutt *et al.*, 1998; Nott *et al.*, 1998). None the less, we consider the details presented here to be important in both a national and a broader context. Importantly, our data conclude that water-management practices have damaged huge areas of vegetation across Everglades National Park, and have done so for extensive periods of time and in a way that jeopardizes the survival of a Federally listed species. This constitutes a take. Moreover, it is one that is independent of, and lasts longer than, the direct effects of flooding. Crucially, these data are independent of – and so additional to – all other conclusions that we have drawn in previous papers (Curnutt *et al.*, 1998; Nott *et al.*, 1998).

More broadly, we have used satellite imagery to predict potential habitat and its fluctuation from year to year, and have calibrated these changes against known bird numbers. This is a singular result with few, if any, precedents.

THE CAPE SABLE SEASIDE SPARROW, ITS HABITAT AND ITS HISTORY

The approximately 2000 pairs of Cape Sable seaside sparrows live entirely within 500 km² of Florida's Everglades. The birds live in six populations separated to various degrees by the area's main drainage, Shark River Slough, and areas of unsuitable habitat (Fig. 1).

Bass & Kushlan (1982) conducted the first extensive sparrow survey in 1981. We repeated the survey in 1992 and annually thereafter (Pimm & Lockwood, 2000). Across a 1 km² grid of more than 600 sites, we record the number of sparrows seen or heard within a 7 minute interval. We take particular care to visit all locations that might hold sparrows and do not observe birds at most of the sites surveyed. This suggests that we do not miss many (if any) sites that hold birds.

To estimate the actual numbers of sparrows from the number we observed in the survey, we multiply each singing male by 16. This correction is based on the range at which we can detect the sparrow's distinctive song – a circle with a radius of 200 m or one eighth of a square kilometre – and on the assumption that one female accompanies each singing male; Curnutt *et al.* (1998) provide details.

Using this calibration, we estimated the total breeding population was over 6000 in both 1981 and 1992. Of the six populations, A (west of Shark River Slough) was the most numerous in 1981 (~2700 birds) and B held fewer birds (~2300). Population B held more than A in 1992 (~3200 versus ~2600). Population E held ~700 birds. The other three populations held between 30 and 400 birds.

Table 1 lists the numbers of survey points and birds heard during each yearly survey. The number of survey points ranges from 225 to 1003. Table 1 lists from 225 to 722 because we exclude some outlying areas that hold few, if any birds. These include Cape Sable itself where the bird was first collected and where habitat changes have subsequently made the location unsuitable. Some of the earlier surveys deliberately explored areas thought unlikely to hold birds to confirm they did not. In 1992, for instance, the survey extended across much of the deep-water areas of Shark River Slough. Recent surveys (1997 to 1999) count at every location that has held birds in the past or that we think is even remotely potential habitat. For quantitative habitat comparisons, we demarcate populations by drawing a polygon around all survey points that ever have birds or that were in the 1997–99 surveys (Fig. 1).

Populations A and B were the two largest populations in 1981 and 1992 and consequently contain most of the survey points (Table 1). In 1994, the survey was incomplete. Populations C, D and F have no survey results and A and E are incomplete. The 1996 survey was incomplete for population F.

Although populations A and B were of similar size in 1981 and 1992, floods during the breeding seasons of 1993, 1994 and 1995 prevented the birds from nesting across much of population A. Like other small-bodied passerines, the yearly adult mortality rate is about 40%, so only a few birds survived to the drier conditions of 1996 (Lockwood *et al.*, 2001). Population B remained relatively constant throughout the study period. Populations C and D had moderate numbers of birds in 1981, but during this study period consistently have few birds.

Population E had two subpopulations in 1992. We speculate this was the result of a very large fire in 1989. Much of the middle and southern portions of the population area burned, while the northern portion was undamaged. Birds are present in the northern sub-population every year of the survey. In 1995, opening of the S-12 floodgates flooded part of this subpopulation and there was an associated decline in numbers. Since then, the northern sub-population has been increasing and expanding southward. The southern sub-population held 20 birds in 1992, but since then has fared poorly owing to flooding.

Table 1. Number of birds heard (top) in number of survey points (bottom) in each population in each year. These numbers are subsets of the full survey done each year because we exclude some areas that rarely, if ever, have birds. NS means there was no survey; INC means the survey was incomplete.

Birds heard

	1981	1992	1993	1994	1995	1996	1997	1998	1999
A	156	146	24	5/INC	14	24	17	11	25
B	147	199	154	139	133	118	177	113	128
C	27	3	0	NS	0	3	3	5	9
D	25	7	6	NS	0	5	3	3	11
E	42	37	20	7/INC	22	13	52	57	48
F	7	2	0	NS	0	1/INC	1	1	1
Total	404	394	204	151	169	164	253	190	222

Points surveyed

	1981	1992	1993	1994	1995	1996	1997	1998	1999
A	338	347	333	95/INC	280	167	210	263	297
B	137	146	123	121	118	130	135	136	133
C	40	41	35	NS	26	38	34	40	39
D	67	67	54	NS	21	57	45	50	50
E	73	79	59	9/INC	57	63	65	77	88
F	41	42	41	NS	24	11/INC	34	32	36
Total	696	722	645	225	526	466	523	598	643

Population F is always small, probably because of frequent fires (Curnutt *et al.*, 1998).

Floods and fires directly harm the birds and their nests. The question we ask here is whether they have also harmed the habitat on which the birds depend. If so, a second question follows: how quickly does the habitat recover? Clearly, the birds cannot recover until their habitat does.

STAGE I: PREDICTING THE HABITAT

To produce a map of a species' habitat using satellite imagery, we need to incorporate all the features of the species' natural history that are identifiable on an image. For the sparrow, our field experiences suggest a minimum of three features: vegetative structure, proximity to bushes, and patch size.

Our first stage is to identify what spectral responses correspond to suitable sparrow habitat. Different vegetative structures give different spectral responses or *signatures*. Even in the gray-scale image in Fig. 1, it is possible to distinguish between the wetter vegetation in the central part of Shark River Slough and the drier prairies on either side. In colour (see Curnutt *et al.*, 1998) and at a finer resolution, it is possible to distinguish many other more subtle vegetative features.

We located 261 nests using a Global Positioning System (GPS) and matched each nest to its corresponding pixel on the satellite images. The resolution of these images – the pixel size – is 29 × 29 m. These nest pixels form the basis of the prediction of sparrow habitat.

The second stage involves the proximity to bushes. Predators, such as red-shouldered hawks (*Buteo lineatus*), perch on bushes and shrubs when looking for prey, such as the sparrow. Nesting close to bushes probably exposes sparrows to an increased risk of predation. So we ask: how close to bushes do the birds nest? After answering that question, we eliminate areas that are too close.

In the third stage, we eliminate patches of habitat that are too small to hold a breeding territory (~2 ha).

Predicting habitat 1: obtaining the spectral signatures

This stage has three parts. First, we correct the satellite images so the GPS data will match up correctly with the image. Second, we make spectral signatures of suitable sparrow habitat using the nest pixels. Last, we apply these spectral signatures to the image to map the habitat.

Images and rectification. We use Landsat Thematic Mapper (TM) images taken during the breeding seasons of 1992 to 1999. When possible, these are from April or May, the months of peak breeding activity. In 1996, no cloud-free image was available in April or May and we used one from 21 March. In 1997, all images in the breeding season were cloudy. Images are from the following dates: 13 May 1992, 14 April 1993, 1 April 1994, 6 May 1995, 21 March 1996, 14 May 1998, 17 May 1999.

Landsat TM images consist of seven spectral bands ranging from blue (0.45–0.52 μm) to thermal (10.4–12.5 μm). Because the prairie is essentially at thermal equilibrium, using the thermal band reduces the accuracy of our results. We eliminate it from our analyses.

Original Landsat images have some misalignments and distortions that we must first correct. This correction process, known as rectification, smoothly stretches the image to produce a least square fit to a set of control points. We defined 66 control points that we could unambiguously identify both on the satellite image and on the ground or accurate maps. We recorded the coordinates of these, using a differentially corrected GPS accurate to < 2 m in accessible areas and 1:24,000 quadrangle maps in inaccessible areas. The difference between the predicted positions of the control points and

their true values had a root mean square error of 2.9 m, that is, 10% of the linear dimension of a pixel.

Making spectral signatures. Using the GPS, we took coordinates for 261 nests from 1996 to 1999. We eliminate nest locations judged to be of questionable accuracy and those closer than one pixel (29 m) to a road. Presence of a road within a pixel contaminates the spectral signature. This leaves 232 usable nests. For each year, we discard nest locations if they fall on clouds, shadows or other features corrupting the image.

Using only the nest pixel provides no information on the spectral characteristics of the surrounding habitat within the sparrow's territory. Sparrows defend homogeneous territories of about 2 ha (Werner, 1975; Lockwood *et al.*, 1997, 2001). Ideally, we would have precise maps of sparrow territories and build spectral signatures from those. However, in most cases we only know the nest location. Therefore, we need to select pixels that adequately represent the true territory.

Our field experience, including mapped territories, suggests that sparrows do not define their territories or place their nests in a consistent pattern. Territories can be irregular in shape and have a nest anywhere, even at the boundary. This suggests that using a regularly defined territory, such as a circle centred on the nest, may not identify the pixels most representative of the true territory. We assume sparrows place their nest in a spectrally typical part of the territory. We then select the 25 contiguous pixels (2.1 ha) having the minimum Euclidean spectral distance from the nest pixel over all spectral bands. Contiguous pixels touch along one of the four sides, but not diagonally.

Making and summing classifications. For a particular nest and its associated 25 pixels, the model calculates the minimum and maximum value within each of the six spectral bands. This produces a six-dimensional box within which all enclosed pixels are suitable habitat. This is one sparrow's opinion of suitable habitat. We can do

this for all available nests and territories and combine those opinions in a large variety of ways. Predictions based on few nests will probably perform less well than those based on many nests. Moreover, in some years we have no nests at all. To get the largest samples we could combine nests from different years. This runs the risk of combining years where the birds placed their nests in different places because of different water conditions. To resolve such difficulties, we compare and contrast the predictions they produce. This we will do, but first we must explain the final two stages.

Predicting habitat 2: the bush layer

Sparrows do not nest near bushes, presumably because of increased predation risk. Using aerial photography of the intensive study plots, we measured the distance of 235 nests and 235 random points from the nearest bush. Figure 2(a) shows the frequency distribution of these nests and random points and Figure 2(b) their cumulative frequency distributions. The distribution of nests shows a shift away from bushes when compared to the randomly selected locations. Sparrows place very few nests within 29 m of a bush, or one pixel on the satellite image (Fig. 2(a)). We also find fewer nests within 58 m and 87 m (two to three pixels) than one expects from random placement, though there are some (Fig. 2(a)). In Fig. 2(b), the nests curve has a much shallower slope than the random-points curve below 40 m, suggesting that sparrows do not randomly place nests until at least 40 m. As a compromise between excluding too much sparrow habitat and including too many areas too close to bushes, we eliminate classified habitat within two pixels (~58 m) of a bush.

Bushes are high in chlorophyll – they are green – compared to the buff tones of the prairie grasses. The satellite images capture such visually obvious features. Because of the large spectral differences between bushes

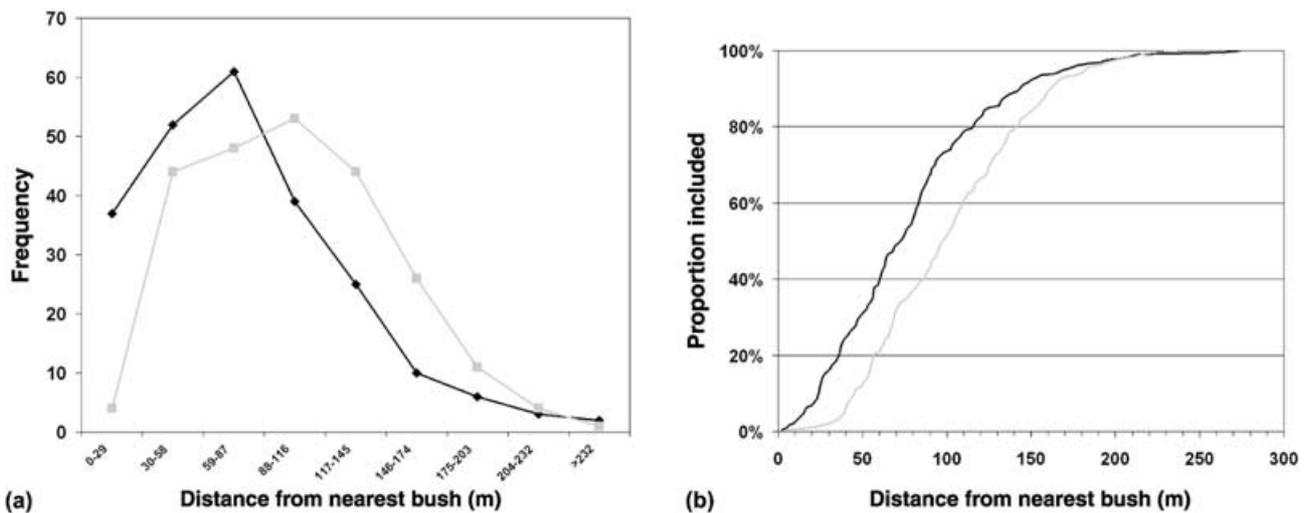


Fig. 2. Distance of nests (gray) and random points (black) from the nearest bush. (a) The frequency distribution of the distances of 235 sparrow nests and 235 random points from the nearest bush. Each bin in the distribution is 29 m, the size of a satellite-image pixel. (b) The cumulative frequency distribution of those same points. In each study plot, we generated random points equal in number to the number of nests. A Kolmogorov–Smirnov test shows the distributions to be different ($P < 0.0001$).

and other prairie vegetation, we use the ISODATA algorithm (Jensen, 1996) to find automatically the signatures corresponding to bushes. Accuracy assessment with aerial photography shows this method has an error rate of 8% for commission errors and 29% for omission errors. It detects most large bushes and clusters of smaller bushes, but misclassifies areas with only a few small bushes.

Predicting habitat 3: eliminating small habitat patches

Because sparrows need enough suitable habitat for a breeding territory, we eliminate patches of habitat smaller than 25 pixels (~2 ha). We use 25 pixels to be consistent with the territory size used in making signatures.

STAGE II: EVALUATING THE PREDICTIONS

Any attempt at prediction begs two questions: 'of what?' and 'by what?' The first answer is simple – sparrow habitat. It is the second that is more subtle. Certainly, we could predict sparrow habitat in each population in each year from nest locations in each population and in each year. But prediction usually seeks efficiency. Ours is the ability to predict habitat in all populations in all years from a sample of nests that are only from the more accessible populations and only from some of the years. The first part of the evaluation stage explores how accurately we can do this.

The second part is an analysis of the habitat predictions within each population. It links water-management decisions to their effects on the habitat and the population.

The third part is a detailed and technical analysis of the errors in our predictions. We defer discussion of this to a companion paper (Jenkins *et al.*, this issue, 39–46).

Each of these components uses the annual range-wide surveys of the sparrow's abundance and distribution. Tests in the intensive study areas indicate an observer can hear a singing sparrow up to 200 m away – an area of about 13 ha (Pimm & Lockwood, 2000). We calculate how much predicted suitable habitat is within a circle of 200 m radius about the survey point. If the model predictions are good, then the survey should find birds more often in areas where the model predicts more habitat. In a graph of sparrow presence versus amount of habitat predicted (Fig. 3(a)) there should be few sparrows below a minimum threshold for predicting presence and many sparrows above the threshold. We use the size of a breeding territory (2 ha) as the threshold.

Predicting habitat in years without enough nests

We only have nest locations from 1996 onwards, and 1996 and 1997 have too few nests for good results. However, we need to predict habitat from 1992 onwards. An efficient solution would allow the use of nests from

all available years on every year's imagery. This provides a large sample size and allows predictions in every year. Both ecological and empirical evidence support this alternative. An inefficient solution would obtain if there were large variations in nesting habitat from year to year. If sparrows did not nest in similar places each year, then a nest in 199x would not likely be within a territory in 199y.

The ecological evidence is the consistency of habitat within our study sites. They are primarily in areas that have not flooded or burned since 1992. A criterion for originally selecting these locations was that they had a consistent sparrow population and thus suitable habitat. Therefore, we posit that areas in which sparrows nested during the detailed studies, 1996–99, were also suitable habitat in prior years. Sparrows do nest in similar places each year, so a nest in 199x would almost certainly be within a territory in 199y.

Figure 3 (b–d) shows the empirical results supporting this assumption. These graphs compare using nests from 1998, 1999 and from all years on various years' imagery. (We have too few nest locations in 1996 and 1997 to separate them out.)

Ideally, the graphs would all be comparable to Fig. 3(a), showing a positive relationship between habitat predicted and probability of finding birds. Below some threshold amount of habitat (the vertical line), there would be insufficient habitat to hold birds. Should we find birds in such areas we would have an *omission error*. (Our model errs in omitting places where birds occur.) Above this threshold we should find birds, and were we not to find them we would have a *commission error*. Ideally, both omission and commission errors would be small, with a sharp transition about the threshold. In reality, the graphs are more variable, but the relationship still holds.

Figure 3(b) shows the results of using 1998 nests to make signatures and predict habitat on 1998 imagery. It gives a strong, but variable, increase in the proportion of survey points with birds as the amount of predicted habitat increases, as expected. When using 1998 nests on non-1998 images a similar pattern occurs. Thus, 1998 nests predict habitat just as well in other years as they do in their own. Using 1999 nests on the 1999 image and other years gives a similar result (Fig. 3(c)). Thus, 1999 nests work as well.

We offer no formal tests of what we mean by predictions 'working well.' For one prediction to be better than another, it would have to predict fewer sites holding birds when there was only a small area of classified habitat and more sites when there was a large area of classified habitat. Inspection of the figures shows that the lines cross repeatedly, with no tendency for within-year predictions (1998 nests on 1998 image, 1999 nests on 1999 image) to be consistently better. Indeed, to the extent we might claim any consistency it is for nests from all years to predict a given image better than the nests from its year. Thus for the 1999 image (Fig. 3(c)), using nests from all years predicts fewer sites with birds when there is less classified habitat and more sites with

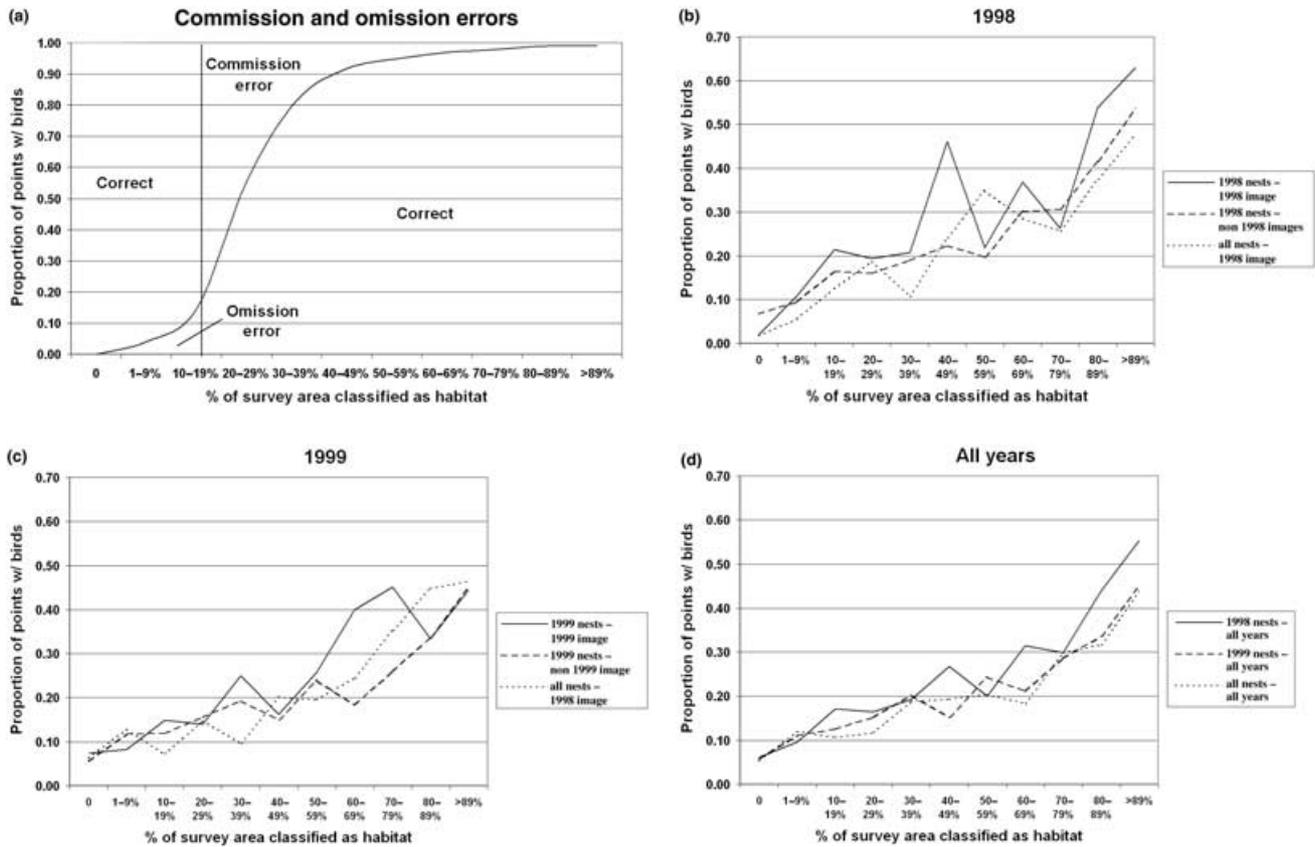


Fig. 3. The proportion of survey sites containing one or more sparrows as a function of the percentage of the survey area that the model predicts to contain suitable sparrow habitat based on different sets of nests. (a) Ideally, there will be a threshold below which we do not find birds and above which we do. We use the size of a breeding territory (2 ha or 16%) as the threshold. (b–d) In reality, the results have noticeable variability, but do show a positive relationship between the prediction of habitat and the presence of sparrows. Lines represent predictions from different combinations of nest (1998, 1999 or all years) and imagery (nest year or non-nest year). All years is a summation of the results from every year’s imagery using a given set of nests.

birds when there is more classified habitat than do the 1999 nests alone.

Figure 3(d) shows a summation of results from using 1998, 1999 and all nests to map sparrow habitat. Again, none of the curves differs substantially or consistently from the others. These results indicate the year of the nest does not alter the efficacy of the predictions. Probably, nest locations are consistently good habitat, at least within the time span of this study.

We conclude that nests from 1 year are usable for making habitat signatures in other years. To gain the maximum sample size we use all nests to map habitat in each year. This provides the opinions of the most sparrows and thus predicts the most habitat.

Habitat analysis

To estimate the total potential habitat, we combine the final habitat classifications for all years. Looking at the six populations together, we estimate 459 km² held potential habitat in 1 or more years. Among the populations, A and B have the most with 138 km² (30% of the total) and 116 km² (25%) respectively. Population E

is third with 82 km² (18%), and C, D and F have 31 km² (7%), 54 km² (12%) and 38 km² (8%) respectively.

Not all of these areas will be suitable habitat each year. In any given year, floods, fires and other environmental factors reduce the potential habitat, leaving a currently suitable subset. Looking at the average amount of this suitable habitat reveals a different pattern than looking at only potential habitat. Overall, the habitat suitable for the birds each year averages 240 km² (52% of the potential). Population A averages 38 km², just 28% of its potential, reflecting the large amount of habitat destroyed by floods in 1993 and 1995 and the slow recovery thereafter. Population D, also affected by flooding, averages just 20 km² (37%). Populations B and E are relatively consistent and have the highest average amount of habitat with 85 km² (73%) and 54 km² (66%) respectively. Populations C and F average 19 km² (61%) and 23 km² (61%) respectively.

How much of this suitable habitat do the birds occupy in a particular year?

Figure 4 shows the predicted amounts of suitable habitat and their variation from year to year as well as estimates of the area occupied by sparrows. To calculate the

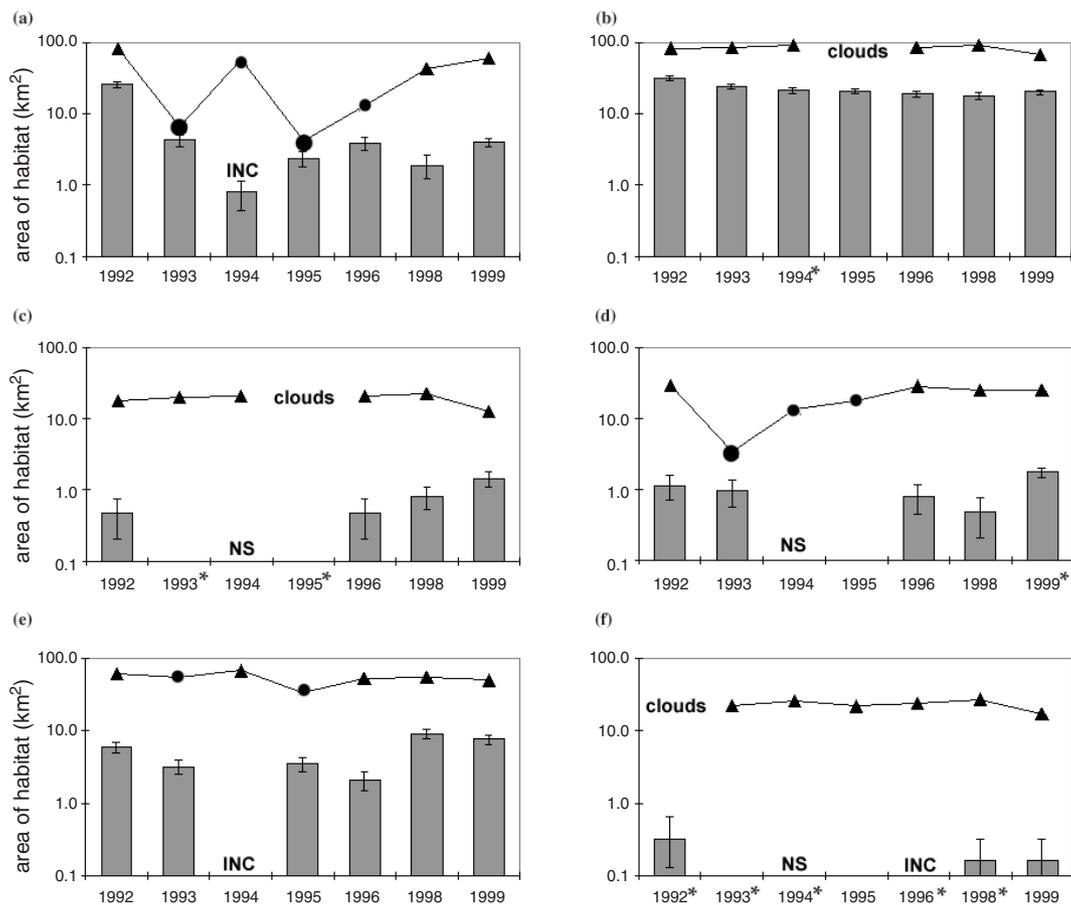


Fig. 4. Area (km²) occupied by sparrows (columns) and area of suitable habitat (lines). We calculate the occupied area by multiplying the number of birds counted in the survey (Table 1) by 8 to estimate the total number of breeding territories, equivalent to breeding males. Each territory is 2 ha or 0.02 km². The y-axis is a logarithmic scale. Bars are \pm one standard error. Triangles = no flooding; small circles = moderate flooding; large circles = extensive flood. * indicates years with fire(s) in that population. NS = no survey; INC = incomplete survey.

occupied area, we take the number of birds heard on the survey in each population (Table 1), multiply by eight territories (for the survey counts only one territory in eight – see above) and then by 2 ha, the average size of a territory. For example, in 1992, we counted 146 birds in population A, and estimate the population as $146 \times 8 = 1168$ territories, that should occupy $2336 \text{ ha} = 23.36 \text{ km}^2$. The predicted suitable habitat for that population in that year was 82 km^2 .

Figure 4 hints at an important and plausible pattern, though one about which our small sample size (six populations) precludes drawing strong inferences. Populations with frequent disturbances support fewer birds, even after the immediate impact of the disturbance. Populations A, B, D and E demonstrate this relationship with respect to floods (circles in Fig. 4). Populations A, D and E suffer varying degrees of flooding and support fewer sparrows, whereas B is not flooded and supports many sparrows relative to the suitable habitat available. In populations C and F, fire (asterisks in Fig. 4) is the dominant influence. Our habitat estimates do not reflect fire's influence, but the relationship to sparrows is clear. Sparrows do not live in areas that burn frequently.

Population A has the largest fluctuations in habitat (Fig. 4). Flooding reduced habitat from 82 km^2 in 1992 to 7 km^2 in 1993, a 91% decrease. Simply, most of the area was underwater. In the same years, the area occupied by sparrows declined from 26 km^2 to 4 km^2 . In 1994, the water level was lower than in 1993. As a result, the habitat rebounds to 58 km^2 , 71% of pre-flood levels. However, most of this habitat was again flooded soon after the image date and sparrow breeding again failed (Nott *et al.*, 1998). The occupied area stayed extremely low at less than 1 km^2 . The 1995 flood reduced the suitable habitat to just 9 km^2 .

In 1996, the water level on the image date was almost the same as in 1994 (4 cm higher). Yet, the predicted habitat in 1996 was only 25 km^2 compared to 80 km^2 in 1994. Our personal observations explain the large difference. Even though the area was not flooded, plant cover was very sparse and a thick layer of periphyton covered much of what had been sparrow habitat. The thick mat was a consequence of nearly 3 years of constant inundation.

In the following years, the water remained low and a slow recovery of sparrow habitat ensued. This suggests

the prairie was able to recover quickly from the single flood in 1993, but 3 sequential years of unnatural flooding caused long-term damage from which the habitat had yet to recover after 4 years. The sparrow population shows little recovery with occupancy in 1999 of only 4 km² of the 60 km² available. There appears to be a significant lag-time between habitat recovery and population increases.

Population B is largely unaffected by flooding and is not subject to frequent fires. It is the only population with a relatively constant amount of habitat and number of birds.

Population C shows a relatively constant amount of habitat, but few birds. In 1981, it had 4 km² of occupied habitat. Then, between 1990 and 1995 nearly the entire area burned one or more times. Consequently, the population had dropped to an undetectable level by 1993 and did not appear again until 1996. Since then, the population has increased slightly but it is still at a precariously low level.

Population D suffered a large decline in habitat because of flooding in 1993, going from 30 km² in 1992 to 3 km² in 1993. It continued experiencing moderate flooding until 1996. Since then, the amount of habitat has been relatively constant but the location has varied. This population had high occupancy in 1981 but relatively few birds in 1992, possibly because of a large fire in 1990. The floods from 1993 to 1995 depressed the population even further. Since 1996, the population has remained small.

Population E had a small decrease in habitat from the 1993 flood, and the 1995 flood caused a decline from 68 km² in 1994 to 34 km² in 1995. The occupied area stayed relatively low from 1992 to 1996, ranging from 2 to 6 km², probably owing to the flooding in 1993 and 1995. In 1998 and 1999, the occupied area increased to 9 km² and 8 km² respectively. This higher occupancy may result from the consistent amount of habitat since 1996, but the population needs further monitoring for confirmation.

Population F shows a small but constant amount of habitat. However, this area burned every year from 1981 to 1994 and again in 1996 and 1998. Consequently, sparrows never occupy most of the habitat.

CONCLUSIONS

Species do not survive in isolation from their environment. They need healthy ecosystems containing sufficient habitat to maintain their populations. If we are to preserve species, we must identify changes in ecosystems that lead to habitat losses and link them to particular causes.

For the Cape Sable seaside sparrow, water management caused direct harm by the opening of the S-12 floodgates in 1993 and 1995 before the birds west of Shark River Slough had time to rear their first clutch of young. The inability to breed in those years resulted in a rapid decline in the population.

However, the damage was even more extensive. This flooding indirectly harmed the birds by destroying their habitat, and it did so for a period longer than the actual flooding. During the floods, suitable habitat declined dramatically, especially in the west, and was at a minimum in 1995. Since then, it has recovered slowly, but had not returned to pre-flood levels by 1999. As long as suitable habitat is not consistently available, we cannot expect the sparrow population to recover from its flood-induced crash. Indeed, the population has yet to show any significant increase.

The sparrow clearly cannot cope with ecosystem changes such as those imposed by water managers in 1993 and 1995. One of the two main populations is already at a dangerously low level. Another year of flooding could result in extinction of this population. Moreover, the species' long-term survival is now dependent on a single large population (B). If this population experiences a catastrophic event, such as a fire, then the entire species would face extreme risk of extinction.

It is vital that we manage the Everglades in a manner that will enable recovery of the western population. This recovery cannot happen without an adequate and stable amount of habitat. We now have a technique for monitoring that habitat and ensuring that poor water management does not threaten it. More broadly, this technique can potentially monitor the habitat of many other species and avoid another situation such as the sparrow faces.

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