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Why sparrow distributions do not match model predictions

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Abstract

A companion paper in this issue describes the mapping of Cape Sable seaside sparrow (*Ammodramus maritimus mirabilis*) habitat using satellite imagery. In general, those maps are correct. However, testing against an independent survey of the sparrow population does identify errors. Those errors fall into two categories, model errors and bird errors. The model errors result from genuine problems with the model. More interesting for conservation are the bird errors, which are more numerous. They are of two types. (1) Commission errors: some suitable habitat does not contain birds. These are areas where prior events have depleted sparrow numbers, but because the sparrows do not disperse long distances, they cannot occupy it quickly. (2) Omission errors: some birds remain in unsuitable habitat that was formerly suitable. This results from the sparrow's very high site fidelity. Often, they will not leave an area even when it is no longer suitable. The consequences of these bird errors are that some habitat and some birds are not contributing to the species' survival. Thus, an estimate of only the amount of habitat or only the sparrow population may present an overly optimistic view of the sparrow's plight.

INTRODUCTION

A companion paper (Jenkins *et al*. this issue, 29–38) uses satellite imagery and predictive models to produce maps of the habitat of the Cape Sable seaside sparrow (*Ammodramus maritimus mirabilis*). Each year, a survey of the entire sparrow population by helicopter records every bird encountered within a 200 m radius of the observer. In comparing the model's predictions to these surveys, we expect to find birds more often in areas where the model predicts more habitat. The companion paper confirms the overall predictions, but there are errors.

With *errors of omission*, we encounter birds, but the model fails to predict sufficient habitat. We consider 2 ha, the size of a typical breeding territory, to be sufficient habitat. In *errors of commission*, the model predicts sufficient habitat, but the survey finds no birds. The purpose of this paper is to examine the causes of these errors. We separate those errors due to the model from those due to inappropriate choices the birds make. We then ask, why do birds make bad choices?

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These bird errors have important consequences for conservation. Quite generally, if organisms are not occupying suitable habitat, then that habitat is not contributing to the population's survival. Thus, measuring the amount of habitat alone may give an overly optimistic view of the species' plight. Similarly, organisms in unsuitable habitat do not contribute to the population's survival because they are unlikely to produce offspring successfully. Thus, population numbers alone may also give an overly optimistic view.

If we are to prevent the sparrow's extinction, we need to know both the amount of habitat and how much of it the sparrows will actually use. The companion paper answers the former question. The errors in those predictions can help answer the latter. The first step in analyzing those errors is to separate their various types and causes.

We shall show that about one-quarter of the omission errors are model failures. More interesting are the errors attributed to the birds. The remaining three-quarters appear to be birds either occupying unsuitable habitat at the edge of densely populated areas or remaining in areas that were suitable in a previous year but are no longer so. Of the commission errors, about two-thirds appear to involve suitable habitat that birds do not occupy because prior events depleted their numbers and they cannot recolonize it quickly enough.

Before discussing these errors in detail, we must first explain how to identify them.

ERROR CAUSES

Of the 3992 survey points over 8 years, 658 have held one or more birds. The model successfully predicts that 494 (75%) should have held birds, leaving 164 (658 – 494) omission errors. Of the 3334 survey points without sparrows, the model successfully predicts that 2030 (61%) should not hold sparrows, leaving 1304 (3334 – 2030) commission errors.

Both omission and commission errors have five potential causes: bird errors, model errors, survey errors, image errors and threshold errors:

Birds may make mistakes in their choice of territories, placing them in inappropriate places or not placing them in suitable ones.

The model may incorrectly predict the habitat.

Surveyors may make errors when surveying the sparrow population, missing birds that are present or recording birds by mistake when they are absent.

The satellite image may not capture an important event affecting the habitat.

Our threshold for predicting presence, 2 ha, may be incorrect.

Threshold errors are a dilemma. Increasing the threshold increases omission errors while reducing commission errors and vice versa. We use the size of a territory (2 ha) because it is the lower limit of what the threshold can be and it is ecologically defensible. Sparrows need at least 2 ha but we do not know how much more they may need. We prefer to risk overestimating habitat than risk missing important areas. We will not discuss these errors further.

To assess the relative frequency of the remaining errors first requires a ‘field guide’ to their distinguishing characteristics.

Omission errors: where the model omits birds from places where they actually occur

Bird errors. Birds may make two kinds of omission errors, temporal and spatial. The first is where birds are in a suitable area that becomes unsuitable from 1 year to the next, but they remain there. Cape Sable seaside sparrows rarely move more than a few hundred metres between years (Lockwood *et al*., 1997, 2001; Dean & Morrison, 1998). A diagnostic of this error is the presence of birds in predicted unsuitable habitat when, in the previous year, birds were present and the model judged the habitat suitable. For example, in Fig. 1(a) the model successfully predicts sparrows in three of four sites in 1992 (yellow dots). In 1993 (Fig. 1(b)), two of these sites still contain birds but the model predicts no habitat because of flooding (red dots). These birds

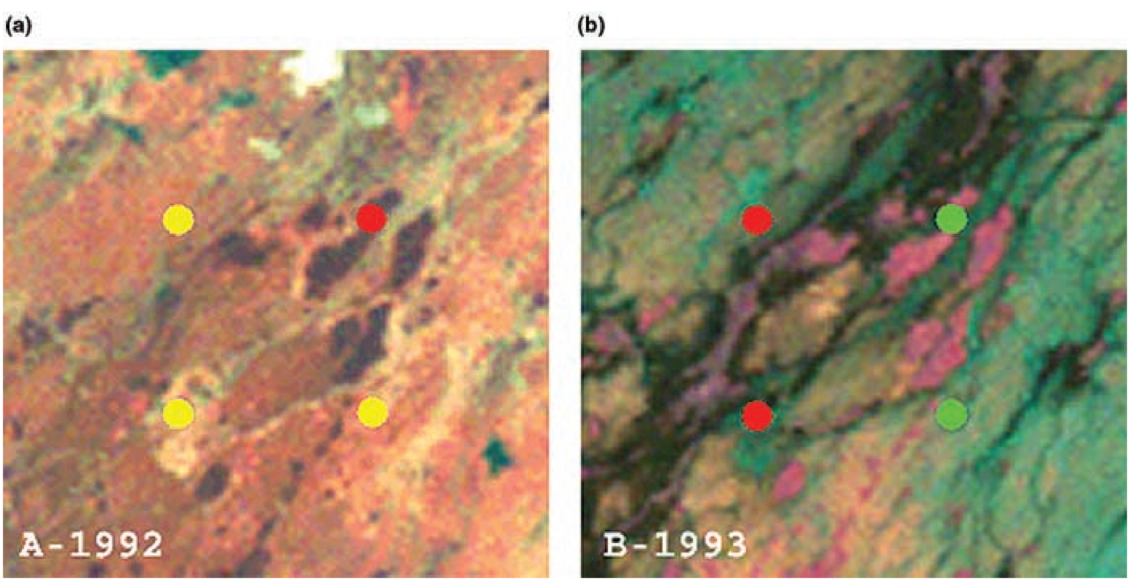

Fig. 1. Examples of *temporal bird errors* and a *bush model error*. The Landsat image in (a) is of the northern portion of population A in 1992. (b) is a 1993 image of the same area. These images are in false colour and employ three spectral bands, 5, 3 and 2 for red, green and blue respectively. In 1993, the prairies were flooded and water absorbs much of the mid-infrared light (band 5) leaving a bluish-green color. Yellow dots are survey points where the model predicts birds and they are present. Red dots are survey points where the model does not predict sparrows, but they are present. Green dots are where the model does not predict sparrows and they are not present. In 1993, two sites that had birds in 1992 still contained birds even though flooding had destroyed the habitat. The red dot in 1992 is a bush model error. Although the location appears inside a tree island, the helicopter would have landed near the trees, not within them. The model does not predict enough habitat within a 200 m radius of the survey point (all habitat < 58 m from tree islands and other bushes is excluded), but none the less, one or more birds were counted here.

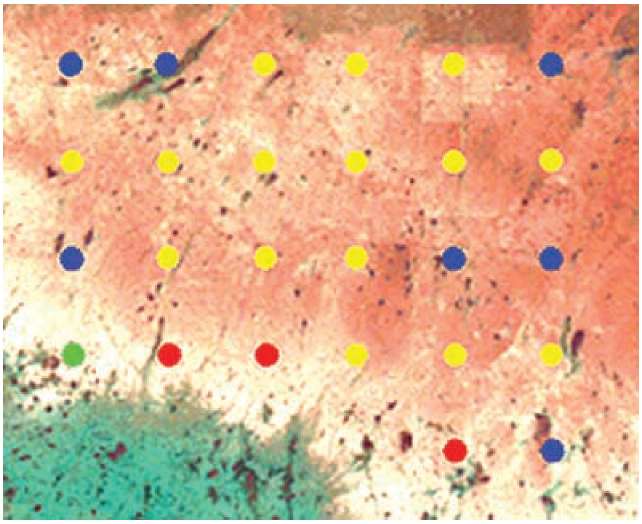

Fig. 2. Examples of *spatial bird errors*. A 1994 image of the southern portion of population B. This population is the largest and is densely populated with birds. Yellow dots are sites with birds that the model successfully predicts. Blue dots have no birds but the model predicts they should have birds. Green dots have no birds and no habitat. Red dots are sites with birds that the model predicts should not have birds. The three red dots occur in an area that usually does not hold birds and is flooded in some years. The bluish-green area in the southwest is water and the white areas along its edge are mostly periphyton, sparse vegetation and exposed limestone.

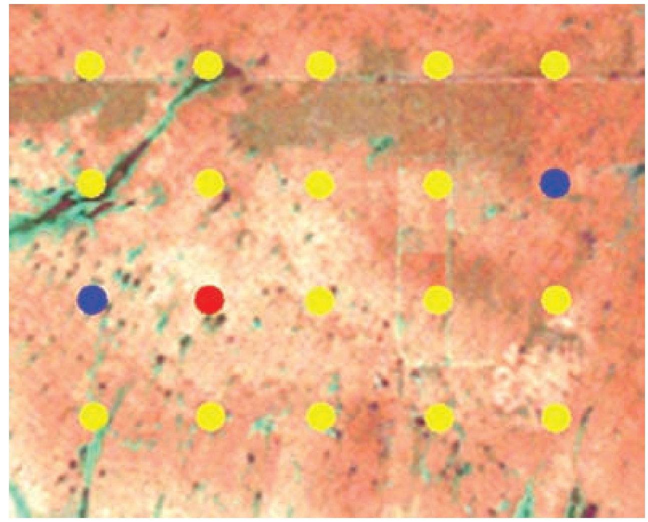

Fig. 3. Example of *prairie model error*. A 1993 image of the southern part of population B. Yellow dots are survey sites successfully predicted to have sparrows. Red dots are errors where sparrows are present but the model does not predict habitat. Blue dots have habitat but no sparrows. The red dot is a site that has birds in every year and the area surrounding it has habitat occupied by birds. Yet, the model does not classify the area as suitable in 1993 or most other years, and there is no evidence of floods or fires.

remained in the area even though suitable habitat had disappeared.

Spatial errors occur when birds in densely populated, productive habitat force other birds into adjacent marginal habitat. A diagnostic is the presence of birds in habitat the model predicts to be unsuitable with birds present in at least one adjacent point with predicted suitable habitat. These areas must also have a history of two or fewer sparrow occurrences during the study period and be near a large, presumably full population. For example, Fig. 2 shows the southern portion of population B in 1994. The model successfully predicts most sparrows, but fails to predict three sites along the southern margin.

Model errors. The model does not always successfully predict suitable habitat. Two sets of criteria distinguish model omission errors from bird omission errors. (1) *Bush model errors*: The model eliminates the area because it identifies it as having too many bushes, but it consistently has birds. This can happen when the helicopter lands outside a tree island but the target coordinate would be within it. The actual survey point would then be closer to sparrow habitat than the model predicts. Figure 1(a) shows an example of a *bush model omission error*. (2) *Prairie model errors* are areas that consistently have birds (≥ 3 times) and the model fails to predict them, but where there is no evidence of fires or floods making the habitat unsuitable. Figure 3 shows a prairie model error. The central red dot is a site that consistently holds birds, the area around it consistently has suitable habitat with birds, but the model rarely classifies this area as suitable for unknown reasons. Many errors from population A in 1992 are in this category. In that case, we have no signature of a sparse sawgrass habitat that occurred in A in 1992 and thus misclassify it as unsuitable. We explain this in detail later in the paper.

Survey errors. Survey omission errors involve false detections of sparrows. They would appear as birds in locations unusual for sparrows, probably as a single bird, and occurring only in 1 year. We have no examples of these errors. Surveyors only count sparrows if they sing and surveyors are very familiar with the sparrow's song from years of experience. In addition, no other bird in the prairie has a similar song. We will not discuss them further. (The distant songs of red-winged blackbirds and meadowlarks can sometimes fool the inexperienced and we give no guarantees that others who count sparrows for other projects do not make mistakes.)

Image errors. Image omission errors occur when image problems cause a suitable area to be classified as unsuitable. They have two sources. Clouds in the satellite imagery may obscure suitable habitat in a survey area. Therefore, before our analyses we remove any survey point that is cloudy in the satellite image. It is also possible that habitat suitability will change between the image date and the survey date. For example, if an area is under water on the image date, the model will not classify it as suitable. However, if the water recedes before the survey it may become suitable and we will have an omission error. Evidence of flood between the survey and image dates identifies these errors. To avoid

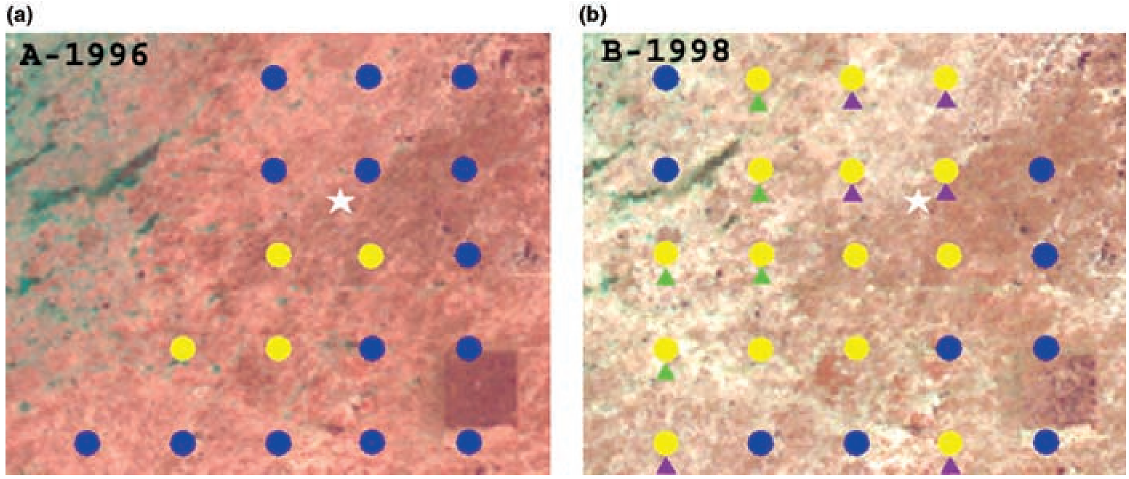

Fig. 4. Examples of *bird commission errors* and *bush model commission errors*. Landsat images from 1996 (a) and 1998 (b) of the northern part of population E. Yellow dots are sites with predicted habitat and sparrows present. Blue dots have predicted habitat but no sparrows. Fires in 1989 and flooding in 1993 and 1995 reduced this population to only four sites in 1996. As the floodwaters receded the habitat recovered, but a large amount remained unoccupied in 1996. By 1998, the population had expanded into six new sites predicted to be habitat in 1996 and 1998 (purple triangles). In addition, as the western area dried out, the habitat recovered and sparrows have been expanding westwards (green triangles) into areas that were flooded, and so unsuitable, in 1996. Intensive fieldwork at a remote camp (white star) supports these results. This site is very densely populated and has the highest nest success rate of the three populations monitored (Lockwood *et al.*, 2001). The blue dots in the easternmost column are bush model commission errors. Bushes fragment the area too much to support sparrows, but the model fails to exclude it. The square feature in the southeast corner is an abandoned tomato field dating from the mid 1970s. The ploughing and fertilizer permanently changed the area from prairie to shrubs.

such errors, all images in this study are during or within 3 weeks of the survey dates. We find no image errors and will not consider them further.

Commission errors: where the model predicts birds in places where they are absent

Bird errors. Bird commission errors stem from the sparrow's limited dispersal. Fires or floods can eliminate sparrows from an area and damage the habitat. Thereafter, the habitat may recover, but the birds may take several years to reoccupy it. Areas of predicted suitable habitat that appear in 1 year, and then become occupied by sparrows in future years, confirm this bird error. So, too, do areas that had habitat and sparrows in the past, have predicted suitable habitat now, but which the bird do not occupy. Figure 4 shows an example from population E. In 1996, only four sites (yellow dots) held birds while most of the suitable habitat was unoccupied. By 1998, the sparrows had expanded to occupy 11 additional sites.

Model errors. In model commission errors, the model predicts there should be birds, but the survey finds none. These errors have four causes. (1) *Bush model errors* result when the area has too many bushes, but this is undetectable with the satellite imagery. We identify these using qualitative vegetation records from the extensive survey and aerial photography when available. (2) *Fire model errors* result when the area burns too frequently. We calculate the burn frequency using fire maps from 1980 to 1999. Sites burning in the previous year or three or more times during the previous 10 years identify fire model errors. (3) *Data model errors* result from insufficient data to rule out model error when it may be a bird or survey error. (4) The cause may be unknown. The absence of sparrows at a survey point and most adjacent survey points in every year distinguishes these last two from bird commission errors. Because the sparrow population has been monitored only for a short period, some suitable areas may never have had sparrows simply by chance. Thus, we probably overestimate model commission errors.

Figure 5 shows examples of *bush* and *fire model commission errors*. In the bush example (a), the model regularly classifies an area in population E as suitable habitat but it rarely has birds. Examination of the vegetation records from the helicopter survey shows that 11 of the 16 sites in error contain vegetation that renders the area unsuitable. In the fire example (b), the model classifies most of population F as suitable. However, this area has a much higher fire frequency than elsewhere in the park, rendering it unsuitable for sparrows.

Survey errors. The survey does not always detect birds when they are present. The principal explanations are (1) the birds do not always sing; (2) birds move about their territories and will sometimes be beyond detection distance during the survey. When this happens, and the model classifies the habitat suitable, we get a commission error. These errors are indistinguishable from other commission errors because we do not know which survey points really had birds. If we did, then we would correct them.

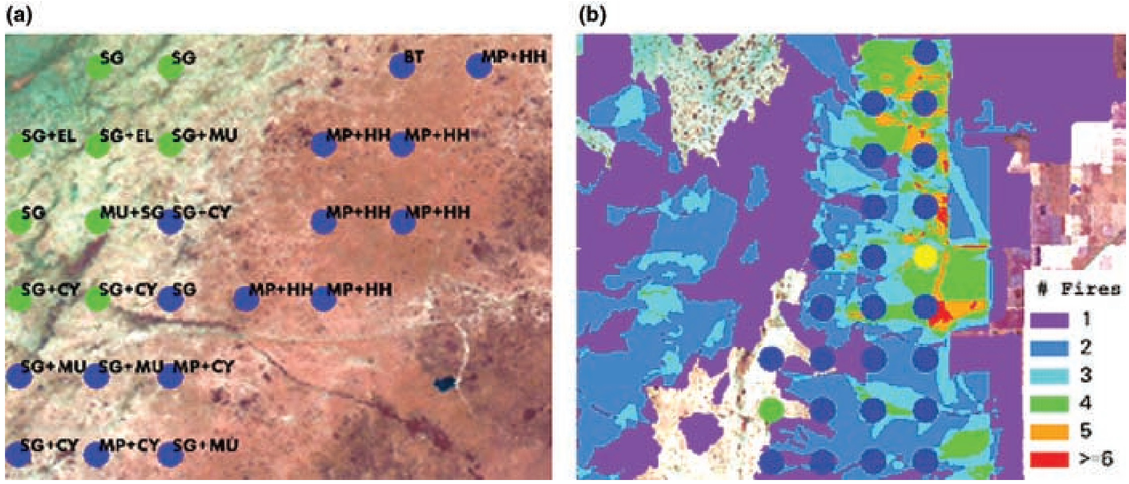

Fig. 5. Examples of *model commission* errors. (a) The southwestern portion of population E in 1998. This area rarely has sparrows, yet the model classifies it as suitable habitat in every year. Inspection of the vegetation records from the extensive survey show that many of these sites contain hardwood hammocks or cypress trees, which render the habitat unsuitable for sparrows. In particular, scattered cypress trees are not evident on the Landsat images (pixel size 30 m × 30 m) though they are evident on more finely resolved aerial photographs. SG = *Cladium jamaicensis* (sawgrass), EL = *Eleocharis cellulosa*, MU = *Muhlenbergia filipes* (muhly), CY = cypress trees, MP = mixed prairie, BT = *Schoenus nigricans* (black-top sedge), HH = hardwood hammock. (b) Population F in 1998 with fire frequency overlain. Population F has had very few birds throughout the study period, yet the model consistently classifies it as habitat. However, this area has had a much higher fire frequency over the past 20 years than the rest of the park. Most of the survey sites in population F, which cover all areas potentially holding sparrows, have a fire frequency of three or higher, compared to two or less for most of the park. Because the model does not include fire, it fails to account for its effect on the sparrow population.

By comparing the results of two coincidental surveys in 2000, Pimm (2000) estimated that sparrows were probably present at 34 sites in addition to the 165 sites at which the survey actually detected them. Scaling this proportion to the previous years suggests that birds should have been present at 794 sites (= (199/165) *658) and so missed at 136 sites. With this correction, there should have been only 3198 sites without sparrows, and the model prediction of 2194 sites leaves an error rate of 31% versus an original 34%. Given the small number of these errors relative to bird and model commission errors, it is unlikely they alter any conclusions. We will not discuss them further.

Image errors. Image commission errors result when habitat changes from suitable to unsuitable between the image and survey dates. This may happen because of fire or flood damage. Evidence of fire or flood between the image date and the survey date identifies these errors. We find no image commission errors.

RESULTS OF ERROR ANALYSIS

The 164 omission errors

Table 1 lists the classification of omission errors by year and by type, noting in which population the majority occurs.

Temporal bird omission errors have their highest proportions, relative to the number of points with birds, in the flood years of 1993 and 1995 and are primarily in population A, 52 of 79 (Table 1). Population B has the second highest absolute number (12), but few relative to the number of survey points with birds (364). Population D has eight and is the second highest relatively (22 points with birds).

Flooding directly caused the high error rates in 1993 and 1995. Most of the errors are in population A, 19 of 24 and 10 of 15, respectively. In both years, opening of the S-12 flood control structures during the breeding season flooded potential habitat in the western portion of the park. Related flooding also caused four errors in population D in 1993.

Spatial bird omission errors are almost entirely in populations B and E, 27 and seven respectively from a total of 38. This is not surprising, as these two populations have had most of the birds since 1992 (Table 1 in companion paper). These bird errors typically occur along the southern and western edge of population B, and the northern portion of population E. These are areas with a sharp division from the dry prairies to wetter slough habitats dominated by sawgrass.

Model omission errors are only in populations A and B. Most of these errors, 41 of 47, are in population A in 1992, and most of those are in the western half of the population. The 1981 survey also found birds in this western area. Flooding in 1993 caused these birds to disappear. A possible explanation for birds being present, but the model failing to classify the habitat, is that the habitat is genuinely different from that after the floods. Vegetation records from the 1992 survey support this conclusion. In 1992, 72% of the error points in population A have sparse sawgrass (*Cladium jamaicensis*) as

Table 1. The three types of omission errors and the total number of points where birds were encountered in each year. Points with birds, but where clouds obscured the satellite image, are not included. Numbers in parentheses indicate a population when it contains at least two-thirds of the errors.

	Bird errors (temporal)	Bird errors (spatial)	Model errors	Total	Points with birds
1992	14 (12 in A)	4 (4 in B)	42 (41 in A)	60 (53 in A)	163
1993	24 (19 in A)	10 (9 in B)	1	35	99
1994	0	4 (4 in B)	0	4	62
1995	15 (10 in A)	5	1	21	47
1996	9 (8 in A)	3 (3 in B)	0	12	70
1998	1	6	0	7	108
1999	16	6	3	25	109
Total	79 (52 in A)	38 (27 in B)	47 (41 in A)	164 (95 in A)	658

their primary vegetation. In all of the intensive study sites, muhly grass (*Muhlenbergia filipes*) dominates or there is a mixed prairie with no dominant species. Thus, we can get no spectral signature for the sparse sawgrass habitat type.

Comparing the points that have birds and sparse sawgrass in 1992 to their vegetation in 1999 shows that this area has changed significantly from its pre-flood condition. *Cladium jamaicensis* now dominates only 18 of the 41 sites and most of those also have long hydroperiod species such as *Eleocharis cellulosa*. *Eleocharis cellulosa* is the dominant species in 12 other sites. In addition, the average percent ground cover increases from 62.8% to 87.8% ($P < 0.01$). This suggests that flooding changed the overall vegetation to the detriment of the sparrow. Moreover, the birds seen in later years do not occur in the western area but only in the eastern half where the model does predict habitat.

Population B has six errors, but also has 55% of the total survey points with birds. It is also the best-studied population. Thus, it is the easiest place to identify model errors.

The 1304 commission errors

Table 2 shows the number of commission errors by year and type, noting the populations in which the greatest number occurs.

Bird commission errors are relatively low in the flood years of 1993 and 1995 (Table 2). They have the fewest errors relative to the number of survey points without birds, and thus potentially in error. The incomplete survey in 1994 makes it artificially low in errors. The floods primarily reduce suitable habitat, and thus bird commission errors, in populations A and D (Fig. 4 in Jenkins *et al.*, this issue, 36). The highest proportions of bird commission errors are in dry years after the floods recede (1996, 1998 and 1999). This reflects a lag time between recovery of the habitat in A and D, and recovery of the sparrow population.

In 1993 and 1995, population A has two and four errors respectively, indicating an absence of open habitat. In 1994, there is a quick recovery of habitat, but after the 1995 flood the habitat recovery is much slower. Thereafter, a steady upward trend is evident, going from four survey points in 1995 to 63 in 1999.

The 1993 flood caused a large decrease in open habitat in population D, going from 39 bird commission errors to four. The 1995 flood had less impact. From the satellite images, it is clear that while the 1995 flood was more extensive in population A than the 1993 flood, it was less extensive in the region of population D. This may be due to less movement of water down the L-31W and C-111 canals, which flow into population D.

The other populations have a higher elevation, protecting them from flood damage. Population B consistently has many bird commission errors, but it is also the largest area of habitat.

Model commission errors show both temporal and spatial biases. They are higher in 1992 both in raw number (158) and proportionally (24% of survey points w/o birds) than any other year. This high error rate is entirely accountable for by population A. In 1992, population A has 101 commission model errors whereas the average

Table 2. The two types of commission errors and the corresponding number of points where birds were not encountered in each year. Points without birds, but where clouds obscured the satellite image, are not included. Numbers in parentheses indicate the populations containing the most errors.

	Bird errors	Model errors	Total	Points without birds
1992	139 (39 in B, 39 in D)	158 (101 in A)	297	653
1993	113 (39 in B)	50 (22 in A)	163	638
1994	58 (45 in B)	23 (23 in A)	81	163
1995	51 (10 in B, 19 in E)	33 (11 in F)	84	427
1996	139 (59 in B)	59 (17 in E)	198	394
1998	161 (52 in B)	66 (22 in F)	227	510
1999	159 (63 in A)	95 (45 in A, 22 in F)	254	549
Total	820 (281 in B)	484 (234 in A, 90 in E)	1304	3334

for other years is only 22. However, this is probably an overestimate. Some of them may be bird commission errors. We propose two possible explanations.

The first explanation stems from a lack of data before 1992. For many places, 1992 was the only year of the study that they potentially had suitable habitat because of the 1993 and 1995 floods. If the model predicts an area suitable only in 1992 and it has no birds, we do not know if it had birds in previous years or would have had birds in the absence of flooding in the following years. Thus, an area may be suitable habitat and have had birds for the last 10 years, but by chance had no birds in 1992. However, we only know that it has no birds in 1992, and thus it is impossible to rule out model error.

The second explanation is that sparrows were using a sparse sawgrass habitat in the west rather than muhly and mixed prairie habitats as in the east. Because the sparse sawgrass habitat no longer exists, we have no data to indicate if it may have been more suitable, and perhaps favoured by the sparrow. If that were true, we would expect the sparrows to occupy the sparse sawgrass habitat before they expanded into the muhly and mixed prairie habitats.

Population E has a high number of model errors concentrated in the central region. The model consistently finds the area suitable but we never find sparrows. However, in 1981 the northern sparrow subpopulation did extend farther southwest into this habitat than in 1992 and later years. In addition, a small subpopulation of sparrows occurs near the southwestern end of this 'misclassified' habitat in 1992. A possible explanation for this split population is a very large fire in 1989. This fire burned much of population E, but left the far northern and southern portions of the range intact. Then in 1993, flooding eliminated the southwestern subpopulation. The combination of the 1989 fire and 1993 flood may have left population E with only a small northern subpopulation. Thus, this area may be suitable, but sparrows have yet to recolonize it. Without survey data during this period, it is impossible to confirm this scenario and rule out model errors.

Population F, and to a lesser extent population C, have many commission model errors because of high fire frequency. Fires exclude sparrows in two ways: (1) frequent fires prevent the vegetation from becoming thick enough to support a sparrow nest, supply adequate food resources or provide adequate cover from predators; (2) fires during the breeding season interrupt nesting, reducing total fecundity. The model captures some fire effects via vegetation changes that are visible in the satellite image. However, the lack of an explicit fire component causes the model to predict habitat in areas unable to support a sparrow population.

CONCLUSIONS

We find that our model is an accurate tool for understanding the dynamics of Cape Sable seaside sparrow habitat. The model error rates are low, 7% for omission errors and 15% for commission errors. Moreover, these are probably overestimates. Most omission errors result from an inability to map a sparse sawgrass habitat that existed in population A in 1992. We know of no other occurrence of this habitat. Excluding population A in 1992 leaves a model omission error rate of just 1%.

Two factors reduce the model commission error rate. First, many commission errors are also from population A in 1992. We suspect the birds preferred the sparse sawgrass habitat in the west and occupied it before occupying the habitat in the east. The lack of survey data before 1992 makes it difficult to confirm this scenario. Second, we undoubtedly miss some birds in the survey for reasons described earlier. Considering these two factors reduces the model commission error rate to 10%.

Most errors result from water managers forcing conditions on the sparrow to which they are not adapted. These 'bird errors' result from the sparrow's strong site fidelity and its inability quickly to occupy newly available habitat (Lockwood *et al.*, 1997, 2001; Dean and Morrison, 1998). It cannot cope with the habitat variability that resulted from floods in 1993 and 1995.

Bird omission errors result primarily when floods destroy habitat from beneath the sparrow. Because of the sparrow's strong site fidelity, it will stay even when the habitat disappears. This means birds have little chance to survive and reproduce unless the habitat returns quickly. Such was not the case for population A where floods in 1993 and 1995 caused damage that had yet to fully recover by 1999.

Bird commission errors are a direct measure of the open habitat into which the sparrow population can grow. As no organism is 100% efficient in occupying its habitat, we should expect there always to be some open habitat. Indeed, most of the populations have a relatively constant amount. However, the 1993 and 1995 floods meant there was essentially no open habitat in population A. Simply, there was not enough habitat to support the sparrow population and it declined dramatically. Thereafter there is a steady increase in open habitat. However, the sparrow's low population growth rate means it may take another decade, under optimal conditions, for this population to return to pre-flood numbers.

Poor water management decisions have resulted in the effective sparrow population and amount of suitable habitat to be lower than they first appear. The consequence is that a species already threatened with extinction is actually in a more perilous situation than previously thought. As long as water management such as occurred during this study period continues, the Cape Sable seaside sparrow faces an unnaturally high risk of extinction. To prevent the sparrow's extinction, water managers must ensure both that suitable habitat is present and that the sparrows are able to occupy it.

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