

Risks in large populations: the Cape Sable sparrow as a case history

Stuart L. Pimm (1)

and

Oron L. Bass Jr. (2)

(1) Department of Ecology and Evolutionary Biology

The University of Tennessee

Knoxville, TN 37996

(2) South Florida Natural Resources Center,

Everglades National Park

Homestead, FL 33034, USA.

Abstract

Very small populations — those numbering a few to a few dozen breeding pairs — often go extinct quickly. The reasons for their doing so are well-understood and relatively easy to model. Considerable experience teaches that much larger populations can become extinct quickly too. Understanding the fate of these species is the much more difficult challenge that this paper will address. The species of concern is the Cape Sable sparrow.

We explore two methods of calculating the sparrow's risk of extinction. The first employs the idea that one can characterize the natural limits of population size fluctuations over time. So armed, one can predict whether the lower limit will encompass such low levels that rapid extinction will be probable. This is a familiar recipe. We show that this method failed spectacularly even when applied to a situation where it would seem entirely appropriate. Our second method identifies the causes of the sparrow's population fluctuations. By understanding the mechanisms underlying population fluctuations we deduce an altogether bleaker picture of the bird's future.

Introduction

Very small populations — those numbering a few to a few dozen breeding pairs — often go extinct quickly. The reasons for their doing so are well-understood and relatively easy to model. Such populations suffer the problems of finding suitable mates, of many individuals dying before the next breeding season from different causes, loss of genetic variability and its deleterious consequences, and other unavoidable vagaries of birth and death. The importance of these chance factors quickly diminishes as populations become larger. Nonetheless, considerable experience teaches that much larger populations can become extinct quickly too. Indeed, we know that vertebrate populations numbering in the low thousands of breeding pairs are too rare to enjoy a secure future (Baillie and Groombridge 1996, Collar et al. 1994, Mace 1996). Understanding the fate of these species is the much more difficult challenge that this paper will address.

Large populations may be composed of many smaller partially isolated ones. If so, the balance between frequent local extinction and re-colonization from surviving populations determines the species' long-term fate (Hanski 1998). In such cases, the insights from studies of very small populations are of value (Pimm et al. 1993, Pimm and Curnutt 1994). In other cases, an inexorable decline in numbers, perhaps driven by a readily observable reduction in habitat, leads to a clear prediction of a species' demise. Yet other species may

be at risk because of the high year-to-year variability in their numbers that typify all natural populations (Pimm 1991). In nature, many individuals die from the *same* causes — bad weather, for instance. Such natural population fluctuations can prove terminal for a species that is now more geographically restricted than in the past.

The case history we shall present may be typical in requiring answers to all the questions implied by the last paragraph:

- 1 What is the spatial organization of the population? Are any of its geographically determined sub-populations small enough to warrant concerns over those “unavoidable vagaries of birth and death?”
- 2 What are the unnatural causes of population decline? How will these causes affect the population in the future?
- 3 What are the natural causes of population fluctuations and how can we anticipate to what low levels they will drive the population in the future?

The species of concern is the Cape Sable sparrow, a drab, olive-brown bird, so obscure and lacking in charisma that it was not discovered until well into this century. Some brief remarks about its natural history and that of the southern Everglades are now in order. These remarks summarize Lockwood et al. (1997), Curnutt et al. (1998), and Nott et al. (1998).

We shall then explore two methods of calculating the sparrow's risk of extinction. The first employs the idea that one can characterize the natural limits of population size fluctuations over time. So armed, one can predict whether the lower limit will encompass such low levels that rapid extinction will be probable. This is a familiar recipe. It characterizes many of the papers in this volume (references to be added at later date). One of us has devoted considerable thought to it (e.g. Pimm 1991). We shall show that this method failed spectacularly even when applied to a situation where it would seem entirely appropriate. The second method we present identifies the causes of the sparrow's population fluctuations. By understanding the mechanisms underlying population fluctuations we deduce an altogether bleaker picture of the bird's future.

The Cape Sable sparrow and the ecosystem on which it depends

Shark River Slough is the primary drainage in the southern Everglades of Florida (figure 1). To its west, lies the higher ground of the Big Cypress and, on the east, the Atlantic coastal ridge. Expanses of marl prairie lie between the main drainage of Shark River Slough and these two modest ridges. These prairies are inundated on average from three to seven months per year. They are the particular ecosystem on which this bird depends.

Currently, nearly all the overland flow in the Shark River Slough drainage originates from the four S-12 gated spillways at the northern boundary of Everglades National Park (figure 1). The east-west distribution of these

structures covers about half of the pre-drainage expanse of Shark River Slough. Previously, most of the overland flow occurred toward the *eastern* edge of Shark River Slough, the S-12 structures are on the *western* edge. This artificial hydrology affects the two expanses of marl prairie on either side of the slough in opposite ways.

The western marl prairies naturally remained dry for much of the year. They were inundated seasonally by rainfall and overflow from the slough. They are now subject to the vagaries of water releases from the S-12 structures.

The southeast corner of the Florida peninsula held the largest expanse of marl prairie. Bounded by the eastern edge of Shark River Slough, it spread southeast, encompassing the southern terminus of the Atlantic coastal ridge. It ended at the thin line of mangroves along the northeastern shore of Florida Bay. To the north, the marl prairies once extended in a long arm to central Dade County. This expanse of potential sparrow habitat suffered two major assaults. The more drastic was the conversion of the eastern portion of prairies to residential and agricultural lands.

Much of the remaining prairie, at and around the eastern boundary of Everglades National Park, is over-drained and subject to frequent fires. Fires in the wet season (June to October) are caused by lightning strikes and are generally small and patchy because the ecosystem is already wet. They can occur throughout the region. Those at the end of the dry season, (March to

late May) are frequently caused by human carelessness and tend to burn large areas along the Everglades eastern boundary.

Curnutt et al. (1998) estimated that the total proportion of destroyed or degraded original prairie may be close to 50%. As for many species for which we must assess the risk of extinction, the ultimate cause of endangerment is the massive reduction in suitable habitat.

The sparrow is considered to be a subspecies (*Ammodramus maritimus mirabilis*) of the widespread seaside sparrow, albeit an ecologically and geographically distinct one. It is not a "seaside" sparrow ecologically as it inhabits freshwater rather than saltwater marshes. In addition to its unique habitat, it is geographically isolated. The nearest surviving subspecies, *A. m. peninsulae* is 300 km to the north. Although first discovered in 1918 on Cape Sable, vegetation changes after the massive hurricane of September 1935 made the Cape unsuitable for it.

The U. S. Fish and Wildlife Service included the subspecies in the first list of endangered species on March 11, 1967, (32 Federal Register 4001). Its restricted range and the fate of the population on Cape Sable were the primary justifications. The subsequent rapid extinction of the Dusky seaside-sparrow (*A. m. nigriscens*) in northern Florida lent support to that decision.

Bass and J.A. Kushlan conducted the first extensive sparrow survey in 1981 (Bass and Kushlan 1982). We repeated the survey in 1992 and annually

thereafter. Across a 1 km x 1 km grid of more than 600 sites, we record the number of sparrows seen or heard within a 10 minute interval. We take particular care to visit all locations that might hold sparrows and do not observe birds at most of the sites we survey. 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 on our 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 and on the assumption that one female accompanies each singing male. Work on our intensive study plots confirms this calibration (Curnutt et al. 1998).

Using this calibration, we estimated that the total population of this species was over 6000 in both 1981 and 1992. The birds are not distributed continuously, but are grouped into six sub-populations of varying sizes (figure 1). Sub-population A (west of Shark River Slough) was the most numerous in 1981 (~2700 birds) and B held fewer birds (~2300). Sub-population B beat A into second place in 1992 (~3000 versus ~ 2600). Sub-population E consistently held ~600 birds. The other three sub-populations held between 100 and 400 birds, though none were seen in F in 1992.

What is the likelihood that this species will become extinct?

Risk analysis 1: a phenomenological approach

Other things being equal, populations that are highly variable in their numbers from year to year are more likely to go extinct than less variable ones (Pimm 1991, Pimm et al. 1988). The causes of population variability are diverse and they operate at different scales (Pimm 1991). So how do we estimate this variability? Complete, range-wide surveys with associated estimates of population size will often be all the information available to those who estimate risk. (For many species, we lack even this knowledge.) Long-term studies to assess population variability directly will be a luxury afforded very few ecologists. They might, however, have access to long-term data on closely related, or at least ecologically similar species.

Using a single estimate of abundance plus a surrogate estimate of year-to-year variability to predict risk of extinction is a familiar tactic. As for many other threatened species, there are no long-term data on year-to-year changes in Cape Sable sparrow populations, or indeed on other seaside sparrows. There are, however, substantial long-term records of grassland sparrow numbers in the Breeding Bird Survey. These BBS data are obtained from point counts — a method very similar to the survey method we employ — and grassland sparrows from prairie states are broadly similar in their life history characteristics.

Curnutt et al. (1996) used BBS data on 10 North American grassland finches

(Fringillidae) to explore how populations behave simultaneously in space and time. Two well-known relationships guided this exploration. The first is the power law relating variance of population abundance over time to average abundance across a species' geographic range (Maurer 1994). The second relationship examined the increase in a population's variability at a single location over time (Pimm and Redfearn 1988). Curnutt et al. asked how abundance, variability, and increase in variability change over a species' geographic range and with respect to one another.

For all but one of the species they analyzed, variability increased more slowly than expected with increasing abundance across the species' range. Were relative variability to be independent of abundance, the slope of the logarithm of standard deviation versus the logarithm of abundance would be unity. Most of the species had slopes of ~ 0.7 . Simply, where a species is less common — typically at the edge of its range — it will be relatively more variable.

Let us put this average slope into more accessible terms. For a normally and independently distributed, (statistical) population, a sample of 10 observations will span values encompassing approximately ± 1.5 standard deviations of the mean.

First, consider one of the larger sub-populations (A or B) and suppose we actually counted 200 birds, ($\log 2.3$) leading to an estimate of 3200 individuals.

The log of the standard deviation of this population should be $0.7 \times 2.3 = 1.6$, and so the standard deviation should be ~ 41 . A range of plus or minus $41 \times 1.5 (= 61)$ would have the population varying between 140 and 260 counted birds or between an estimate 2240 and 4160 birds. This approximately two-fold span of values over a sample of ten points — a decade. It fits comfortably with the experiences of those who count common birds over such intervals.

Now consider a site where the species is much rarer: say a mean count of 10 birds and so an estimate 160 birds. Using the same logic, it would have a standard deviation of 5 and so abundances should span from 18 (an estimate of 288 birds) down to a count of 2 (an estimate of 32 birds). This is a much greater span of values than in the previous example (a factor of nine, versus a factor of about two). It is large enough that local extinctions might occur naturally at least intermittently over the span of a decade or two. Mean population counts below 10 should experience regular periods when the birds would not be counted — and where they might indeed be locally extinct.

We have not missed the significance of the assumptions of normal and independently distributed population sizes in the previous two paragraphs' analysis. The population count in one year is likely to be dependent, probably strongly so, on that of the previous year. As a consequence, for most populations, estimates of the variability of population abundances increase with increased length of record (Pimm and Redfearn 1988).

This was the case for the grassland sparrows too. Curnutt et al. (1996) found that of the seven species with at least 10 sampling locations of continuous data over 20 years, six showed significant increases in variability over all time periods. These increases in variability over time would mean that not only would we expect a sample of twenty years to encompass a wider range of standard deviations than the samples of ten years exemplified above, but that the standard deviation will itself be larger.

We will not rework the example of how large is the envelope of population fluctuations with the added complication of increasing variability over time. More rigorous discussions of population extremes appears elsewhere (Lande 1993, Ariño and Pimm, 1995). Incorporating these details does not alter the general conclusions:

(1) The two largest sub-populations are large enough that given normal year-to-year variability seen in other grassland sparrows, we should not expect dangerously low populations within a century (or indeed a much longer interval).

(2) In contrast, the smaller sub-populations might well fall below levels where we could not likely count them — and where those unavoidable vagaries of birth and deaths may well doom them to at least local extinction.

Thus, local sub-populations may become extinct, but at least one of the three larger sub-populations (A, B, or E) should be available to naturally re-stock them. This is an entirely comforting conclusion. It stems from a rough-and-ready estimate of risk, but one certainly appropriate to the amount of information at hand.

The conclusion was rudely shocked in April 1993. The western sub-population, for which the preceding calculation suggests might vary two-fold over a decade, in fact declined to one seventh of its 1992 abundance in the spring of 1993. It has remained at low levels since then. Population D in the southeast corner of the species' range nearly disappeared and the populations in the northeast (C and F) also declined. Curnutt et al. (1998) provide a detailed analysis to show that these declines were statistically highly improbable given what we know about year-to-year variation in other sparrow populations.

The shock was particularly painful to one of us (Pimm), because he had spent much of the previous decade in cataloging and analyzing natural year-to-year variation in population sizes for conservation ends (Pimm 1991). Moreover, he was a founding partner, with John Lawton, (Ascot, UK) in the effort to provide the catalogue of >2000 long-term time series (now available at <http://www.sw.ic.ac.uk/cpb/cpb/gpdd.htm>). A central objective of this compilation is to provide conservation biologists an accessible set of estimates of natural population variability for population risk assessments.

Worse still was that the assumption of natural variability seemed a particularly sensible one. The Cape Sable sparrow is found almost entirely within Everglades National Park and Big Cypress National Preserve. These adjacent protected areas are very large by the standards of the hemisphere. Only about twenty national parks in Central and South America are as large or larger (Mayer and Pimm 1998). If the method of "use natural variability to calculate risk of extinction" should apply anywhere, this bird in these National Parks could seem to be a good candidate. Why did this approach fail?

Risk analysis 2: a mechanistic approach

Our surveys showed that the sparrow declined dramatically since 1992 on the western side of Shark River Slough (sub-population A). It has declined similarly since 1981 in the northeast of its range (C, F) and in the southeast (D). Only sub-populations B and E have remained more or less constant. The key results of Curnutt et al. (1998), Nott et al. (1998) and Lockwood et al. (1997) are these:

- 1 The massive decline in A was a consequence of the inundation of the breeding habitat during the dry season by managed flows over the S12 structures in 1993, 1994 and 1995.
- 2 The decline in most of C and all of F is due to the very high fire frequencies these areas over the last decade or more. We erect the

plausible hypothesis that the high fire frequency is due in part to the high incidence of unplanned human ignitions in the areas adjacent to the park. Moreover, we assert that unnaturally low levels of water permit high fire frequencies during the breeding season. Water that would have naturally flowed through north-east Shark River Slough is diverted to the west through the S-12s and prevented from flowing to the east by a barrier: the L67-extension.

- (3) The decline in the lower part of C and in D is due to managed changes in the water levels that have locally converted the seasonally flooded prairies that the birds favor to near continuously flooded, sawgrass-dominated marshes that the birds avoid.

For this step in risk assessment, we will postpone the longer-term changes in vegetation effected by changes in hydrology and fire frequencies. The central feature of our model of risk assessment is the availability of suitable breeding habitat. Our studies show this varies considerably from year to year. We combine this feature with a simple demographic model of the sparrow.

The Cape Sable sparrows lay an average of 3.2 eggs per clutch (Lockwood et al. (1997). Only about 90% of these hatch. However, to be conservative, we assume that all do. (Some of the failures to hatch involve nest losses to predators. Following this, the birds usually re-lay a clutch.) Some 62% of the first clutch hatchlings survive to fledge, and 49% of second clutch hatchlings survive. To be conservative, we round these numbers up to 65% and 50%.

Above 50% of the adult birds survive from year to year (Lockwood and Okines, in preparation). Using this figure is also very conservative, for it is based mostly on territory holding males — the easiest birds for us to catch and band. First year birds do not survive as well as these adult males.

Under the best of circumstances, these parameters allow the population to increase by a factor of 1.8 from one year to the next. Unfortunately, a variety of factors prevent all the birds in a population from producing two or even one brood each year. It is the magnitude of these risk factors that determine each population's fate. They differ among populations, so we will model each in turn.

Sub-population A west of Shark River Slough.

This population sits on a low ridge and it is particularly vulnerable to flooding. Water depths of more than a few centimeters prevent breeding or terminate it if it has already started (Lockwood et al. 1997). Nott et al. (1998) calculated the extent of available breeding habitat for each of the last 20 years, classifying the areas into those that remain dry enough for just one brood to be raised, and those that could produce two. It is a simple matter to calculate how many sparrows would be produced each year from the breeding and survival parameters scaled by the available habitat.

Table 1. Areas suitable for breeding, sparrow numbers and the production of young for two scenarios of water delivery

Scenario 1				Scenario 2				Year
% area 2 nd brood	% area 1 st brood	Adults	Young	% area 2 nd brood	% area 1 st brood	Adults	Young	
11	100	2000	2256	11	100	2000	2256	1977
59	94	2128	3085	59	94	2128	3085	1978
55	88	2606	3532	55	88	2606	3532	1979
23	42	3069	1905	23	42	3069	1905	1980
74	100	2487	4059	74	100	2487	4059	1981
18	72	3273	2922	18	72	3273	2922	1982
0	15	3098	483	0	100	3098	3222	1983
11	27	1791	660	11	100	3160	3564	1984
63	93	1225	1803	63	93	3362	4946	1985
35	56	1514	1306	35	100	3500	4620	1986
23	33	1410	743	23	100	3500	4284	1987
37	63	1077	1024	37	63	3500	3329	1988
100	100	1050	1933	100	100	3415	6283	1989
35	100	1492	1969	35	100	3500	4620	1990
20	99	1730	2058	20	99	3500	4164	1991
56	95	1894	2720	56	95	3500	5026	1992
0	4	2307	96	0	100	3500	3640	1993
18	27	1202	510	18	27	3500	1487	1994
0	0	856	0	0	100	2493	2593	1995
9	33	428	178	9	33	2543	1056	1996
11	100	303	342	11	100	1800	2030	
59	94	322	467	59	94	1915	2776	
55	88	395	535	55	88	2345	3178	
23	42	465	289	23	42	2762	1714	
74	100	377	615	74	100	2238	3653	
18	72	496	443	18	72	2945	2630	
0	15	469	73	0	100	2787	2899	
11	27	271	100	11	100	2843	3207	
63	93	186	273	63	93	3025	4451	
35	56	229	198	35	100	3500	4620	
23	33	214	113	23	100	3500	4284	
37	63	163	155	37	63	3500	3329	
100	100	159	293	100	100	3415	6283	
35	100	226	298	35	100	3500	4620	
20	99	262	312	20	99	3500	4164	
56	95	287	412	56	95	3500	5026	
0	4	349	15	0	100	3500	3640	
18	27	182	77	18	27	3500	1487	
0	0	130	0	0	100	2493	2593	
9	33	65	27	9	33	2543	1056	

Table 1 shows two scenarios for the sparrow numbers. Under scenario 1, the left two columns show the available habitat (as a percentage) under the water conditions that prevailed during the years 1977 to 1996. These estimates, from Nott et al. (1998), come from our detailed knowledge of the area's topography and the height of the water that prevailed during the breeding season.

The sparrow numbers start with a guess of 2000 birds in 1977 and follow deterministically thereafter. For example, all 2000 birds had the chance to raise one brood, but only 11% of them were in places dry enough to raise a second. The model predicts that 2256 young would be produced that season. By season's end there would have been 2000 + 2256 birds (=4256), and, with a 50% chance of survival, 2128 birds at the start of the next season.

We do not attempt to fine-tune the parameters to the known census data. Nonetheless, with a guess of 2000 birds in 1977, the census results fit the model's predictions quite closely. There are high numbers in 1981 and slightly lower numbers in 1992. While the predicted population numbers are much higher in 1993 than actually observed — this makes sense too. We only observe singing birds. Birds neither sing nor nest when the water levels are high. By the time the water levels receded in 1996, the number of predicted survivors matches the number of birds we observed.

These estimates provide an important check on the survival parameter of 0.5. Were this parameter much higher (say 0.6 or higher) then the population in

1996 would have been much higher than actually counted. Were the parameter much lower, the population would already be extinct.

The catastrophic years of 1983, 1984, 1986, 1987, 1993 and 1995, were not *naturally* bad years. They corresponded to deliberate, massive dry season releases of water through the S12s into Everglades National Park (Nott et al. 1998).

A second validation of the model and its parameters requires the sparrows to do well in the absence of these unnatural events. Were the sparrows predicted to decline, then we might suppose the model must err in not allowing the birds to recover quickly enough. Scenario 2 runs this "what if" alternative. If, during the catastrophic years, the sparrows habitat had not been flooded early in the season and if 100% of the habitat had been available for one brood, then the population would have thrived. Indeed, it would have often reached the model's population ceiling of 3500 birds. (We estimate the ceiling based on the maximum available habitat and typical maximum observed densities.)

Thus calibrated, we run our model for another 20 years. It re-cycles the exact patterns of habitat availability, whereupon, the population declines towards extinction within fifty years (figure 2a). What if water were not released? The population dips below its population ceiling periodically, but persists indefinitely (figure 2a).

The populations in north-east Shark River Slough

Managed high water levels are not an issue in the other populations; indeed, it is the shortage of water that is the problem. Here, frequent fires burn the prairies, in some areas, annually. We do not find birds in areas that are burned as often as once every two years (Curnutt et al. 1998). To be conservative, we assume that a burned area prevents breeding in only the next breeding season and that fires kill no adults.

We have not undertaken a formal statistically analysis of the size distribution of fires. However, from inspection, it appears that at about 10% of the area will burn each year and that one year in ten as much as 90% will be burned. We assume a random proportion of burned areas each year, chosen with equal probability (figure 2, bottom right). The conservative assumption is that the proportion of area burned in one year is statistically independent of the proportion in the previous years. We suspect that there is some serial correlation — as there is in most climatic time series — leading to runs of “bad” fire years.

Figure 2b shows the results of five sample simulations. In all cases, the population declines towards extinction, most within 50 years. Interestingly, the populations decline at a rate consistent with our census data of this population over the last 16 years.

The population in the south-east

This area does not burn regularly; yet in 1989 nearly half of it burned as a consequence of a massive, dry-season fire. Such fires can burn huge areas in the Everglades. One, to the north of the sparrow habitat, burned 1000 square kilometers in April 1999. The policy of Everglades National Park is not to allow such fires to cross the park roads that divide this population into three pieces. Nonetheless, fires of this size are hard to control in practice.

We model this episodic burning with a statistical distribution (see figure 2 bottom right) that allows severe burns in a few years — but never ones that burn more the 95% of the habitat. In most years, only a small fraction of the habitat is unavailable because of fires. To be conservative, we allow two broods in areas not burned. We have excellent breeding data for this area and not all birds complete a second brood before rising water levels terminate breeding.

The sample of five simulations (figure 2c) shows a slow, but consistent decline to extinction. We have explored a variety of other statistical distributions of fire sizes. (The distribution we employ here has a single parameter to describe the how frequent large fires will be.) The one we show in figure 2c seems plausible in terms of the Park's fire history. Moreover, it generates a year to year relatively variability in sparrow numbers that is in excellent agreement with what one observes for other well-known grassland

sparrow populations (see above; Curnutt et al. 1996). Less frequent serious fires generate population fluctuations that are too small to be realistic.

Conclusions

Our results provide both specific and general conclusions.

For the sparrow, we conclude that the population west of Shark River Slough will decline to extinction if the pattern of managed flows over the S12s for the last 20 years repeats itself. If breeding season flows over the S12s are stopped, this population will flourish. The declines of the populations in the north-east have declined to near extinction. These declines will continue unless the fire regimes are changed. On its own, the population in the south-east (B) runs the risk extinction because of episodic, large-scale fires.

Our models omit some obvious features. We have not included the effects of prolonged inundation or of frequent fires on the vegetation. These processes alter the vegetation in ways that preclude the birds use of areas for several years (Curnutt et al. 1998, Nott et al. 1998). Incorporating these impacts would likely lead to even greater concerns about the sparrow's future. Nor have we included details about the birds' movements and dispersal — though Nott (in preparation) will do so.

The predictions of the current models arise from our knowledge of the bird's breeding biology and of the area's water and fire regimes. They are not “curve fitting exercise” to the census data. Importantly, the results predict the timing

and magnitude of the changes in those data. This confirms that the models are both sensible and sufficiently complete to capture the essential features.

The predicted decline to extinction of population B is a prediction of future events and thus one not confirmed by our short-term data. Notice a subtle problem: if the currently least affected population (B) is doomed, why does it hold so many sparrows? Should it not have gone extinct earlier? There are two non-exclusive answers. The first is that it, too, is affected by episodic fires — such as the 1989 Ingraham fire — that might be relatively recent phenomena, brought on by management changes, and likely to be outside its previous experience. The second is that the sparrow has become locally extinct on occasion and then be re-colonized from other populations.

This second possibility makes good sense. Years of naturally high water west of Shark River Slough would harm the population there. There would be concomitant flooding the north eastern populations and that would suppress the frequency of natural fires there and so their spread to the south-eastern populations. In contrast, in dry years, the population west of Shark River Slough would be expected to flourish, even if the eastern populations ran higher than average risks due to fires. Simply, a high-risk year west of the slough would be a low-risk year east of the slough, and vice versa. A complete exploration of these possibilities will require a combined water and fire model.

Nonetheless, we offer the following tentative conclusion: The Cape Sable sparrow will only survive if it has at least three healthy populations. To implement this requirement, the breeding areas west of Shark River Slough must not be flooded in the breeding season and water levels should be raised in the northeast of Shark River Slough to reduce the incidence of fires there.

The general conclusion for conservation is that species even within one of the hemisphere's largest national parks — and possibly its best funded— are not immune to massive anthropogenic impacts from outside them.

Everglades National Park is not large enough for calculations of risk based on natural population fluctuations to be sensible. Such calculations demonstrable give the wrong answer for the Cape Sable sparrow.

Critics may counter that this is a special case. The species occupies a wetland and wetlands are uniquely vulnerable to the vagaries of water flows upstream. Perhaps; but we are not convinced. Other large parks have unique problems that cross their boundaries. Fire, and our inclination to suppress small fires and so risk catastrophic ones, is an example that comes to mind for many parks in the western USA, for example.

We argue that even for the largest protected areas, we must develop mechanistic models of what causes populations to decline. Unless we do so, we will not predict future risks adequately.

References

- Ariño, A. and S. L. Pimm. 1995. On the nature of population extremes. *Evolutionary Ecology* **9**:429–443.
- Baillie, J. and B. Groombridge. 1996. 1996 IUCN red list of threatened animals. The IUCN Species Survival Commission, Gland, Switzerland.
- Bass, O. L., Jr., and J. A. Kushlan. 1982. Status of the Cape Sable sparrow. Report T-672, South Florida Research Center, Everglades National Park, Homestead, Florida, USA.
- Collar N. J, M. J. Crosby, and A. J. Stattersfield. 1994. Birds to Watch 2. BirdLife International, Cambridge, UK.
- Curnutt, J. L., S. L. Pimm, and B. A. Maurer. 1996. Population variability of sparrows in space and time. *Oikos* **76**:131–144.
- Curnutt, J. L., A. L. Mayer, T. M. Brooks, L. Manne, O. L. Bass, Jr., D. M.
- Fleming, M. P. Nott, and S. L. Pimm. 1998. Population dynamics of the endangered Cape Sable seaside-sparrow. *Animal Conservation* **1**:11–20.
- Hanski, I. 1998. Metapopulation dynamics. *Nature* **396**: 41–49.
- Lande, R. 1993. Risks of population extinction from demographic and environmental stochasticity and random catastrophes. *American Naturalist* **142**: 911–927.

Lockwood, J. L., K. H. Fenn, J. L. Curnutt, D. Rosenthal, K. L. Balent, and A. L. Mayer. 1997. Life history of the endangered Cape Sable seaside-sparrow. *Wilson Bulletin* **109**: 234-237.

Maurer, B. A. 1994. Geographical population analysis: tools for the analysis of biodiversity. Blackwell Scientific, Oxford, UK.

Mayer, A. L., and S. L. Pimm. 1998. Integrating endangered species protection and ecosystem management: the Cape Sable seaside-sparrow as a case study. Pages 53-68 *in* G. M. Mace, A. Balmford, and J. R. Ginsberg, eds. Conservation in a changing world. Cambridge University Press, Cambridge, UK.

Nott, M. P., O. L. Bass, Jr., D. M. Fleming, S. E. Killeffer, N. Fraley, L. Manne, J. L. Curnutt, T. M. Brooks, R. Powell, and S. L. Pimm. 1998. Water levels, rapid vegetational changes, and the endangered Cape Sable seaside-sparrow. *Animal Conservation* **1**:21-29.

Mace, G. M. 1994. Classifying threatened species: means and ends. *Philosophical Transactions of the Royal Society (London)* **B 344**:91-97.

National Research Council. 1992. Scientific bases for the preservation of the Hawaiian crow. National Academy Press, Washington, D.C., USA.

Pimm, S. L. 1991. *The Balance of Nature? Ecological issues in the conservation of species and communities.* University of Chicago Press, Chicago, Illinois, USA.

Pimm, S. L., H. L. Jones, and J. M. Diamond. 1988. On the risk of extinction. *American Naturalist* **132**:757–785.

Pimm, S. L., J. M. Diamond, T. R. Reed, G. J. Russell, and J. Verner. 1993. Times to extinction for small populations of large birds. *Proceedings of the National Academy of Sciences (USA)* **90**:10871–10875.

Pimm, S. L., and A. Redfearn. 1988. The variability of animal populations. *Nature* **334**:613–614.

Pimm, S. L., and J. Curnutt. 1994. The management of endangered birds. Pages 227–244 *in* C. I. Peng and C. H. Chou, eds. *Biodiversity and terrestrial ecosystems* (Monograph Series, no. 14). Institute of Botany, Academia Sinica, Taipei.

Figure legends

Figure 1. Map of Everglades National Park and adjacent areas showing features mentioned in the text.

Figure 2. (a) Top left. Simulated population numbers with and without unnatural dry season releases of water into Everglades National Park across the S-12 structures. With the releases the sparrow population west of Shark River Slough is driven to extinction. Without them, it can frequently reach the maximum number (3500 birds) allowed by the simulation. The extent of available habitat is as described in table 1 and it cycles every 20 years (b) Top right. Five simulated populations with the extent of available habitat chosen at random from an even distribution (see figure at bottom left). Fires in the region have a pattern of habitat destruction that seems similar to this. (c) Bottom left. In the southeastern population, most of the habitat is available in most years: the typical pattern of burns is for only small fires. However, there are occasional very large fires (see figure at bottom left.) Five simulated populations under this fire regime all tend to decline in the long term, because of runs of bad fire years.

Figure 1

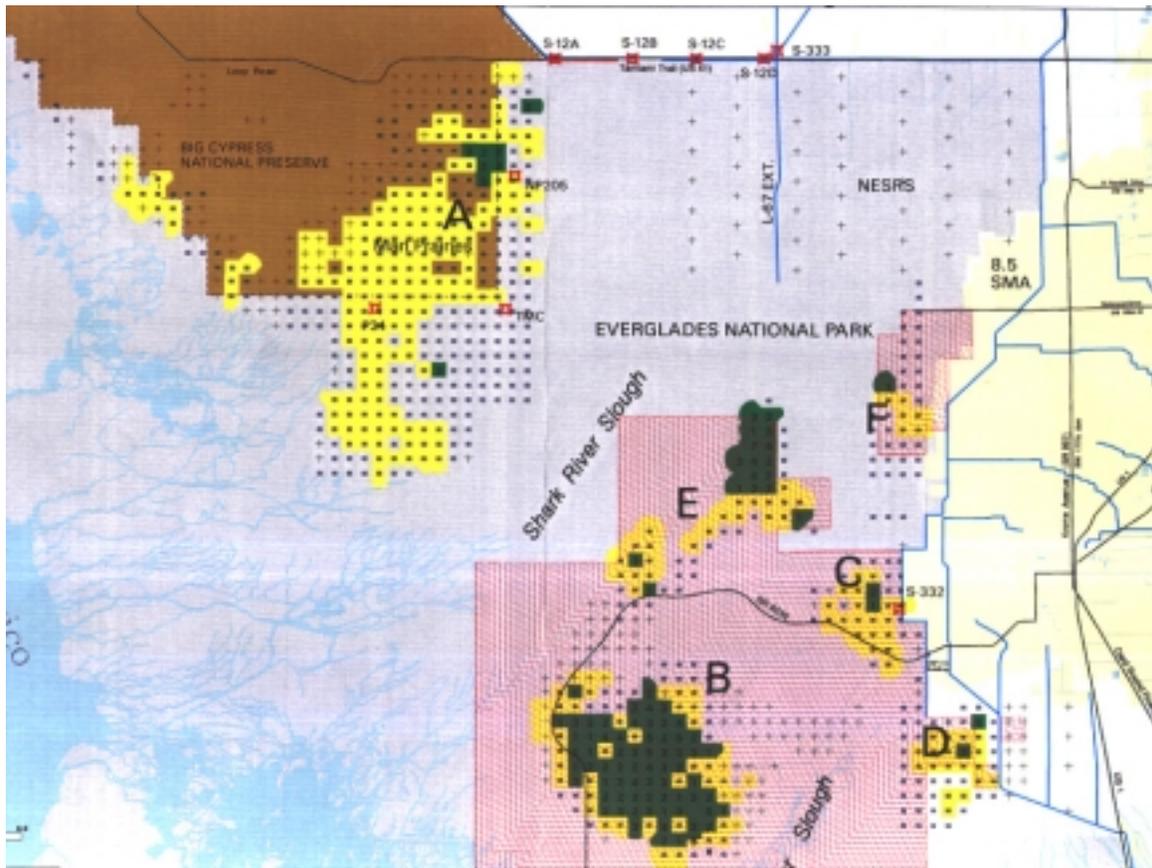


Figure 2

