

CONSERVATION REPORT

THE AOU CONSERVATION COMMITTEE REVIEW OF THE BIOLOGY, STATUS, AND MANAGEMENT OF CAPE SABLE SEASIDE SPARROWS: FINAL REPORT

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THE CAPE SABLE SEASIDE SPARROW (*Ammodramus maritimus mirabilis*) was listed as an original member of the federal list of endangered species in 1968. It is restricted to seasonally flooded prairies of extreme southern Florida and is disjunct from all other conspecific breeding populations (Kushlan et al 1982, McDonald 1988). Since the subspecies was described in 1919, its populations have been discovered and rediscovered, often only to disappear or decline to a handful of individuals (Werner and Woolfenden 1983, Kushlan and Bass 1983). Although the sparrow historically is known from six distinct areas, at present only two of these areas support populations numbering in the hundreds or low thousands of individuals.

Debates swirl around the status of these remnant populations. The main controversy encompasses whether the sparrow, now largely restricted to Everglades National Park, is in jeopardy of global extinction and if so, what actions must be taken to prevent this from happening. In November 1998, a panel of scientists was assembled under the auspices of the Conservation Committee of the American Ornithologists' Union (AOU) to evaluate the scientific evidence relevant to this controversy. The Panel was charged with scrutinizing the evidence for the existence and probable causes of global population decline in this subspecies,

evaluating proposed management actions, and suggesting further research necessary to manage the remaining populations to maximize their chances of long-term persistence.

This document presents the conclusions of the Panel, which are based on our reading of the peer-reviewed and "gray" literature, interactions during a workshop held 9 to 11 February 1999 at Florida International University in Miami with researchers investigating the sparrow's biology, and site visits associated with the workshop. In addition, researchers provided the Panel with position papers summarizing their findings and conclusions prior to the workshop and provided information in response to specific questions following the workshop. Further information was obtained through public comment on an initial draft of this report.

THE CAPE SABLE SEASIDE SPARROW IN CONTEXT

The Cape Sable Seaside Sparrow is the only avian taxon entirely restricted to the Everglades ecosystem. Considerable evidence suggests that it is adapted to local conditions. The Cape Sable Seaside Sparrow was originally described as a distinct species, a status it officially maintained (contrary to recommendations of Griscom 1944), along with the now extinct Dusky Seaside Sparrow (*A. m. nigrescens*), until

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the 32nd supplement to the AOU check-list (AOU 1973).

The long-held view that the Cape Sable Seaside Sparrow is a separate species was presumably based on its isolation, as well as its morphological and ecological distinctiveness. Ecologically, the Cape Sable Seaside Sparrow joins the Dusky Seaside Sparrow as the only Seaside Sparrows known to have occurred in freshwater wetlands. The plumage is distinctively more olive above and streaked below compared with other Seaside Sparrows. The adaptive significance of this coloration is unknown; one possibility is that it matches the background of the greenish-gray periphyton (algae) layer that covers the soil in the marl prairies these birds inhabit. MacDonald (1988) analyzed variation in all of the recognized Seaside Sparrow subspecies and found the Cape Sable Seaside Sparrow to be, along with the Texas (*A. m. sennetti*) and Dusky subspecies, significantly smaller than other Seaside Sparrows. Robins and Schnell (1971) determined that the Cape Sable Seaside Sparrow was the most distinctive of all Seaside Sparrow subspecies in terms of overall skeletal morphology, even when characters were standardized by sternum or humerus length. This suggests uniqueness in "shape" as well as size. MacDonald (1988) analyzed sound spectrographs and concluded that both Cape Sable and Dusky seaside sparrows had songs that were distinctly more "insect-like" than songs of other Seaside Sparrows.

As of this writing, no definitive analysis exists of the relationship of Cape Sable Seaside Sparrows to other Seaside Sparrows based on molecular genetics (Avise and Nelson 1989, J. Avise pers. comm.). We note that the Dusky Seaside Sparrow was distinct from other Seaside Sparrows in many of the same ways as the Cape Sable Seaside Sparrow, yet the Dusky was not genetically distinguishable from other Atlantic Coast populations based on mtDNA markers (Avise and Nelson 1989). Recent studies of other sparrow taxa (e.g. *Melospiza melodia* and *M. georgiana*) demonstrate substantial geographically based, and presumably adaptive, morphological variation in the absence of geographic structuring in mtDNA haplotypes (Zink and Dittmann 1993, Greenberg et al. 1998). Therefore, little basis exists on which to argue against species-level recognition of a tax-

on that shows marked morphological divergence because of lack of differentiation in mtDNA (Zink and Kale 1995). In summary, unequivocal morphological, behavioral, and ecological grounds exist for recognizing the Cape Sable Seaside Sparrow as a unique subspecies that qualifies for protection under the Endangered Species Act.

As a subspecies that historically has occupied coastal marshes and inland prairies, the Cape Sable Seaside Sparrow typifies the general threats to two particularly vulnerable components of the North American avifauna. First, as a taxon with a declining number of small, local populations in *Spartina* marshes, it joins a large number of distinctive emberizid sparrows associated with coastal wetlands, including other Seaside Sparrows (McDonald 1988) and subspecies of Song Sparrows (*Melospiza melodia*), Swamp Sparrows (*M. georgiana*), Salt-marsh Sharp-tailed Sparrows (*Ammodramus caudacutus*), and Savannah Sparrows (*Passerculus sandwichensis*). Second, as a taxon restricted to prairie habitat, it joins a large number of sparrows and other birds associated with natural grasslands that are declining substantially (Knopf 1995), including several other *Ammodramus* species such as Baird's Sparrow (*A. bairdii*), Henslow's Sparrow (*A. henslowii*), and Grasshopper Sparrow (*A. savannarum*).

THE CURRENT CONTROVERSY

The current controversy centers on the scale and implications of population declines and local extirpations that have been described for this subspecies. Curnutt et al. (1998) and Nott et al. (1998) suggest that recent population declines are the direct result of water management practices that have altered the greater Everglades ecosystem. Such an anthropogenic decline, if true, is all the more significant considering the recent extinction of the Dusky Seaside Sparrow, which was generally acknowledged to have resulted from habitat mismanagement (Walters 1992).

Flooding and fire are the major explanations for the putative decline in Cape Sable Seaside Sparrows (Curnutt et al. 1998, Nott et al. 1998). The prairie habitat that supports remaining populations is naturally prone to both. However, researchers hypothesizing anthropogenic decline note the increasingly restricted distri-

bution of the sparrow to a few habitat patches (Werner and Woolfenden 1983), along with human-caused changes in flooding and fire regimes (Curnutt et al. 1998, Nott et al. 1998), as factors that combine to threaten remaining populations. Specifically, emergency releases of water into the western portion of Everglades National Park appear to increase the frequency and duration of flooding of the western population of sparrows during the breeding season. At the same time, structures restricting water flow to the east create unnaturally frequent fire-prone conditions in the prairies inhabited by northeastern populations (USDI 1998).

The potential for human influences on Cape Sable Seaside Sparrow populations, particularly through catastrophic fire and the incursion of exotic trees (see Werner and Woolfenden 1983), has been discussed since the subspecies' discovery. The potential problems of habitat fragmentation and increased frequency and extent of catastrophic, dry-season fire were described by Werner and Woolfenden (1983). Kushlan et al. (1982) prepared a management plan that, although not advocating any drastic management actions, suggested that fire, flooding, and the encroachment of trees (particularly exotics) were threats in need of continued monitoring. Unnaturally frequent flooding and fire were cited by Post and Greenlaw (1994) as threats to the prairie habitat of the Cape Sable Seaside Sparrow.

Concern about the threats facing the sparrows has heightened dramatically in recent years, coinciding with an unusually wet period in the Everglades system. Based on monitoring reinstated in 1992 of both habitat and populations, an alarm was sounded about the effect of the high water years of 1993 to 1995 on the western Everglades (Orians et al. 1996). Recently, Curnutt et al. (1998) and Nott et al. (1998) suggested that Cape Sable Seaside Sparrows face imminent jeopardy of extinction owing to increased risks from flooding and fire that result from the shunting of water from east to west within the Everglades.

W. Post (pers. comm.) argues that the Cape Sable Seaside Sparrow is not in imminent jeopardy. He suggests that local declines, if real, are a natural consequence of the highly dynamic and vagile nature of the subspecies' population dynamics. As a subspecies adapted to habitats that are subjected to a highly unpredictable

disturbance regime, populations may shift locations, disappearing from and reappearing in particular habitat patches. Post further suggests that the primary native habitat of the Cape Sable Seaside Sparrow, like other Seaside Sparrows, was coastal *Spartina* marshes. Indeed, it was in such habitat that the species was first discovered and subsequently extirpated on Cape Sable. According to Post's hypothesis, the disappearance of suitable *Spartina* habitat owing to both natural and anthropogenic causes has restricted the Cape Sable Seaside Sparrow to suboptimal inland prairie habitat. A similar argument was made by Post (pers. comm.) in relation to the decline of the Dusky Seaside Sparrow.

The controversy surrounding the existence and causes of a global decline in the Cape Sable Seaside Sparrow is borne from the scientific uncertainty surrounding almost every facet of the biology of this difficult-to-observe subspecies. The controversy has been nurtured further by the possible implications that changes in habitat management have to the ecology of the Everglades ecosystem and to the economic base of people living in the vicinity.

Scientific uncertainty stems, in large part, from an incomplete historical record of the subspecies' distribution and abundance. Stimson (1956) is credited with the first intensive search for populations away from the original Cape Sable and Ochopee sites. The first systematic survey of the sparrow throughout its known range was conducted in 1981 (Kushlan and Bass 1983), although extensive surveys also were conducted by Werner and Woolfenden in the mid-1970s and by Kushlan and Bass from 1978 to 1980. Information on Cape Sable Seaside Sparrows prior to the 1970s is anecdotal and fragmentary, and no systematic surveys were conducted between 1981 and 1992. Extensive research on the population biology of the subspecies began in 1992, and many of the important details of these studies are not yet published.

Given the recent reports of population declines, how probable and imminent is the extinction of the Cape Sable Seaside Sparrow under current management? This critical question is difficult to answer definitively, because many of the problems identified by researchers as contributing to the decline eventually may be alleviated by long-term changes in water man-

agement that already are planned. The emergency measures required to stabilize the population in the interim, as well as the adequacy of the planned changes, are the management issues at hand.

SEASIDE SPARROW HABITAT AND WATER MANAGEMENT IN THE EVERGLADES

Currently, the Cape Sable Seaside Sparrow is entirely restricted to marl prairies within and immediately adjacent to Everglades National Park. Outside the park, much of this distinctive prairie habitat has been converted to agricultural land, making proper management of remnant patches of prairie within the park especially critical (DeAngelis et al. 1998). In the subtropical climate of the Everglades, seasonality and year-to-year variation of rainfall greatly affect ecological systems. Short-term and long-term cycles of water levels are driven by seasonal variation in rainfall and by water management regimes. Most rain occurs during the wet season of May through September (Thomas 1974, Duever et al. 1994). Less rain falls in the other months, but the "dry season" is rarely completely dry, because winter rains periodically occur when cold fronts move southward down the Florida peninsula. The Everglades are less seasonal in rainfall, and presumably in water levels, than are many other lowland wetlands in the Neotropics (Beissinger and Gibbs 1993). Water levels and rainfall in South Florida also appear to follow longer-term drought/flood cycles with a periodicity of four to seven years (Thomas 1974, Beissinger 1986).

Water management can have important influences on the seasonality of water levels. For example, Beissinger (1986) showed that seasonal fluctuations in Lake Okeechobee water levels in the northern Everglades were small prior to the completion of the dike around the lake in 1930, but they increased greatly during the mid-1900s when large volumes of water began to be released from the lake via canals. Variation in Okeechobee's water levels has decreased again since the completion of the South Florida Water Management Project.

Under natural conditions, water in the southern Everglades comes from local precipitation and from southward flows out of Lake Okeechobee. Because of the slight tilt of the land,

and the lack of major topographic features, this water flows sheet-like across virtually the entire Everglades. Vegetation varies with subtle local differences in the annual period of flooding (hydroperiod), which are caused largely by minor microgeographic variation in topography and drainage. Marl prairie occurs within the zone intermediate between the permanently flooded sloughs and the drier pine-dominated high ground. Marl prairie is a relatively diverse floristic association dominated by grasses, sedges, and rushes growing on thin limestone soils that are seasonally flooded. Prairie occurs where the hydroperiod is four to eight months long. Where hydroperiods are longer, taller marsh grasses and sedges dominate, and where hydroperiods are shorter, prairie persists only where fire eliminates woody plants.

A core issue is the effect of water management projects in recent decades on these prairies. Water flow has been under increasing human management for nearly 100 years. With urbanization of the greater Miami area and agricultural development in areas to the north and east of Everglades National Park, the United States Army Corps of Engineers began in the 1950s to construct a series of structures and impoundments that control water flow throughout South Florida. Today, water flow into Everglades National Park is controlled by floodgates and levees in Water Conservation Areas 3A and 3B to the north. A series of floodgates (S-12s) along the east-west oriented Tamiami Trail at the north end of Shark River Slough allows managers to release water from Water Conservation Area 3A (WCA 3A) southward into the western portion of the park (Fig. 1). Water that historically would have flowed through WCA 3B into the eastern portion of the park thereby may be diverted to the west. The L-67 extension canal and levee prevent water released from WCA 3A from flowing into the eastern portion of the park (Fig. 1). Diversion of so much water to the west has reduced the average hydroperiod of the marl prairie in the northeastern portion of the park. Emergency releases of water from WCA 3A add to the flooding of areas west of Shark River Slough during years of high precipitation (Nott et al. 1998).

One of the remaining sparrow populations (Population A) is affected by flooding of these western areas, and another (Population D) is af-

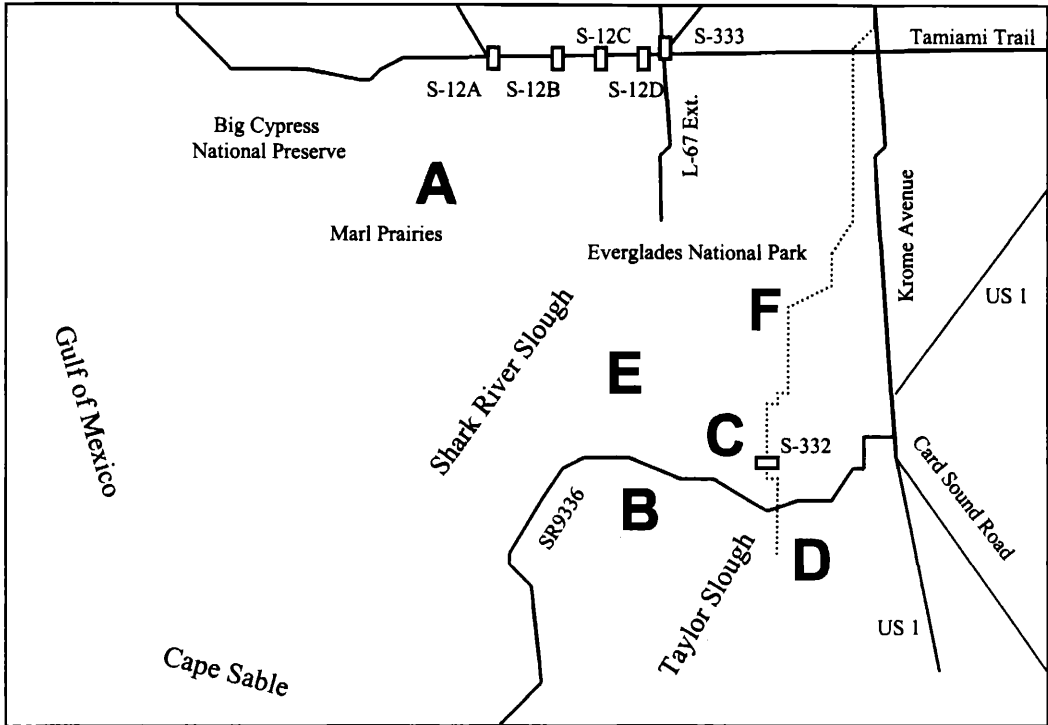


FIG. 1. Location of Cape Sable Seaside Sparrow populations A to F in Everglades National Park in relation to Shark River Slough, Taylor Slough, the S-12 floodgates (S-12A to S12D), and the L-67 extension canal and levee (L-67 Ext.). Major roads are shown for reference.

affected by additional releases of water into Taylor Slough in the southeastern portion of the park (Fig. 1). Three populations (C, E, and F) occur in the prairies that experience unusually frequent and prolonged dry conditions in the northeastern portions of the park. The remaining population (B) occurs along the Ingraham Highway in the eastern part of the park.

The new water management strategy planned for the Everglades calls for construction of new structures that will restore more natural patterns of water flow, especially increased flow into northeastern Shark River Slough and decreased flows west of Shark River Slough. Water managers have purposely prohibited significant flows into northeastern Shark River Slough because such flows would increase flooding of large areas of private land within the East Everglades (i.e. Everglades National Park Expansion Area) and would increase groundwater levels in another area of private land (known as the "8.5 square mile" area). The new plans call for purchase of these

private lands. In the interim, however, water continues to be routed west of Shark River Slough rather than into northeastern Shark River Slough. In wet years, water is either retained in Water Conservation Area 3A or released west of Shark River Slough and through a point source into Taylor Slough, resulting in flooding of those areas. Retention of water in WCA 3A produces abnormally high water levels that can prolong the flooding of tree islands (Guerra 1996). This may have adverse effects on other species of concern within the Everglades system, and on people. WCA 3A is inhabited by members of the Miccosukee tribe of Native Americans, and high water may result in flooding of culturally significant sites.

Below, we review and evaluate the scientific evidence bearing on population trends of Cape Sable Seaside Sparrows and their significance, and provide recommendations for further research. We conclude by offering short-term and long-term management recommendations based on our findings and interpretations.

RECENT POPULATION TRENDS

Published patterns.—As in most studies of avian populations, the number of adult individuals forms the core statistic for inferences concerning population health. Since the 1970s, studies of Cape Sable Seaside Sparrows have focused primarily on extensive counts of singing males, conducted at 600 to 800 points that are accessed primarily by helicopter and that cover all of the known appropriate habitat for the subspecies (Curnutt et al. 1998). Periodically, sites not known to support sparrows also have been checked for the presence of singing birds during the appropriate season. Census points are distributed systematically at grid intersections with 1 km between points. Each point is surveyed once during the morning hours (0630 to 0930) during the season of peak breeding activity (mid-March through May). The census protocol was established by Kushlan and Bass (1983) for the 1981 survey using the same helicopter-based approach followed by Werner and Woolfenden (1983) in the mid-1970s, and was used consistently for subsequent surveys between 1992 and 1998. The only change in protocol was to shift from a nonrandom order of visiting sites in 1981 and 1992 to 1994, to a stratified random sampling order for 1995 to present. The total population of territorial sparrows has been estimated by multiplying the field counts by 16. This number was originally based (Kushlan and Bass 1983) on the need to multiply by two to account for females and by eight to account for the area between census points not covered in the survey. This estimation factor was found to be approximately correct when point counts were compared with actual mapped territories on intensive study plots (Curnutt et al. 1998).

Survey points are distributed across three different areas from which Cape Sable Seaside Sparrows have been reported in recent decades. The "Ingraham" population (Population B) was discovered in the 1970s along with the other small populations (C to F) in the eastern Everglades. Since at least the 1950s, a large number of birds, originally referred to as the southern Big Cypress population, has been known to be scattered through the prairies northwest of Shark River Slough (Population A). All of these areas, A to F (Fig. 1), were thought to contain substantial numbers of

birds in the mid- to late 1970s prior to the initiation of the full population surveys described above. No evidence exists that more than a handful of birds has occurred in recent decades in either of the earliest known sites, the Ochopee prairies and the *Spartina bakeri* marshes of Cape Sable (Kushlan et al. 1982, USFWS 1998). These latter two populations are considered extirpated.

Several estimates derived from counts of singing males are critical to management decisions: (1) the global breeding population (in this case, number of territorial adults during the breeding season); (2) trends in the global breeding population; (3) spatial distribution of individuals, particularly as they are distributed among the recognized populations (A to F); and (4) the pattern of change in the local populations. Some results from the surveys (Table 1) are that (1) the estimated global breeding population declined from approximately 6,500 in 1981 and 1992 to approximately 3,000 (range 2,416 to 4,048) from 1993 to 1998; (2) recently the only populations estimated to include more than 200 adults are Population B (estimated at 1,800 birds in 1998) and one of the three subpopulations of the northeast (E, estimated at 900 birds in 1998); and (3) the other four populations are estimated to be much reduced from 1981. In the case of the western population (A), the estimated decline from more than 2,500 to a few hundred individuals occurred after the 1992 breeding season. Estimates for several of the populations (but not Population A) increased markedly between 1996 and 1998.

Declines in numbers of singing males counted were precipitous, and counts remained well below initial (i.e. 1992) levels for a number of years after the decline. The Panel can propose no credible confounding factors to explain as artifacts the large changes in numbers of singing males detected in these standardized surveys. It is possible that systematic changes in detection probability occurred, brought about by changes in bird behavior as a consequence of altered habitat condition. However, we consider this explanation to be substantially less parsimonious than a genuine decline in number of territorial males. Numbers of birds observed remained low even in years when conditions for detection were favorable (e.g. 1997), that is, when males would be expected to be active and conspicuous. Because no measures of

TABLE 1. Number of singing male Cape Sable Sparrows detected in each of six populations during extensive surveys (data provided by S. Pimm et al.). The upper number in each cell is the actual number detected, the lower is the resulting population estimate (no. detected \times 16). Data are incomplete for 1994 owing to logistical difficulties during the survey.

Popu- lation	1981	1992	1993	1994	1995	1996	1997	1998
	168	163	27	5	15	17	17	12
A	2,688	2,608	432	80	240	272	272	192
	147	199	154	139	133	118	177	113
B	2,352	3,184	2,464	2,224	2,128	1,888	2,832	1,808
	27	3	0	—	0	3	3	5
C	432	48	0	—	0	48	48	80
	42	7	6	—	0	5	3	3
D	672	112	96	—	0	80	48	48
	7	37	20	7	22	13	52	57
E	112	592	320	112	352	208	832	912
	7	2	0	—	0	1	1	1
F	112	32	0	—	0	16	16	16
	416	411	207	151	170	157	253	191
Total	6,656	6,576	3,312	2,416	2,720	2,512	4,048	3,056

uncertainty (e.g. sampling variances) have been computed for these abundance estimates, one cannot use them to draw strong inferences about population change. Nevertheless, given the consistency in sampling protocols between 1992 and 1998, we conclude that a true population decline is the most parsimonious explanation for the large declines in counts in some populations.

Improving the design and statistical analysis of the current survey.—We strongly recommend applying standard statistical inference procedures to investigation of changes in abundance using count data. The Panel was surprised that the publication summarizing population dynamics (Curnutt et al. 1998) does not include estimated variances, standard errors, and confidence intervals along with its population estimates. Here, we discuss ways to develop such estimates.

Estimates of abundance from surveys such as those conducted for Cape Sable Seaside Sparrows can be written as $N^* = C/\alpha p^*$, where N^* denotes estimated abundance, C is a count statistic (i.e. the number of birds counted at point counts), α denotes the proportion of the area of interest that is actually sampled by the point counts, and p^* is the estimated detection probability, or the probability that a bird in the area sampled is actually detected during a point count. The estimated sampling variance of the abundance estimate [$\text{var}^*(N^*)$] then contains two main components (see Thompson 1992). One of these components involves the variance

of the actual point counts. This component includes the actual variation in counts from one point to another, the fraction of the area of interest that is sampled (α), and the binomial variation associated with the detection and counting of birds. Estimation of this component will depend on the survey design. The other component concerns the estimation of detectability, p ; the various estimation methods that can be used for this purpose have associated distinctive variance estimators.

In the present case, it appears that the multiplier 16 (Kushlan and Bass 1983) used to translate counts into population estimates is based on the fraction of total area sampled and the probability of detecting birds within these areas (i.e. $\alpha p^* = 1/16$). The use of fixed-radius point counts together with GIS maps of the surveyed area should permit direct determination of α . The estimate of detection probability could be derived from comparison of point counts with "known" numbers of birds as determined by territory mapping on the intensive study areas, as suggested by Curnutt et al. (1998). Because year-to-year variation in both α and p are possible, we recommend that determination of α and estimation of p be carried out each year that a survey is conducted, or at the very least over a range of densities and conditions. It is particularly important to determine how p^* is affected by flooding and fire. Detection probabilities may vary spatially as well as temporally. Obtaining data from intensive study plots in populations A and E, as well as

existing plots in population B, is essential to evaluating the possibility of spatial variation in p^* .

Estimation of $\text{var}^*(N^*)$ involves two components as noted above. The first is based on the spatial or point-to-point variance in numbers of birds counted. Estimation of this component for the sparrow survey is not straightforward because of the systematic sampling design, but several reasonable approaches are available (e.g. Cochran 1977, Thompson 1992). This component should not be based on an assumed underlying distribution (e.g. Poisson was assumed for discussion purposes in one of the review documents) but should be computed from the raw count data. The second component, $\text{var}^*(p^*)$, will be based on the method used to estimate detection probability. If detection probability is estimated as a ratio of point counts to "known" numbers of birds (based on territory mapping), then the variance of this estimate can be obtained using standard expressions for the variance of a ratio estimator (e.g. Thompson 1992) that depend on details about how the data are aggregated for estimation.

In summary, although the count data obtained through reasonably consistent methodology suggest substantial declines in sparrow abundance, the absence of estimates of precision demands that care be exercised in interpreting these data. Raw data obtained from surveys in 1981 and 1992 to 1997 can be used to compute population estimates and related estimates of precision for each year of the survey. We recommend that such estimation be carried out, because resulting estimates of precision will be useful in providing an improved ability to assess the magnitude of historical population changes, as well as any changes in the future.

General design recommendations for future surveys.—Besides computation of estimates of precision based on existing data, the Panel suggests that several other changes be considered. Some involve the sampling of space. For example, controversy exists over potential sparrow habitat that was not sampled from 1992 to 1997 (W. Post pers. comm.). Although no specific areas of suitable but unsurveyed habitat have been identified, Post suggests that such areas occur along the inland border of the mangrove zone in extreme western Everglades. One approach to dealing with such a possibility

would involve stratification of a large area of potential habitat into adequate (i.e. likely to contain some sparrows) and poor (unlikely to contain sparrows) habitat strata. The "adequate habitat" stratum could be sampled at high intensity (i.e. α would be high for this stratum), whereas the "poor habitat" stratum would be sampled at a much lower intensity, reflecting the low probability of birds inhabiting this stratum.

Another consideration is the sampling design itself. Historically, surveys have been based on a systematic design with point counts conducted at either 0.8 km or 1 km perpendicular distances in a checkerboard pattern. Such a design was selected because information on large-scale bird distribution was considered to be an important product of the survey (J. Kushlan pers. comm.). If abundance estimation now is the primary goal of the survey effort, however, then a simple, random, or stratified random design might be more efficient and would permit straightforward estimation of variances. If continued collection of information about large-scale distribution remains a priority, then the current systematic design should be retained.

In addition to the sampling of space, it also is possible to consider ways of estimating detection probability. If territory mapping is to be continued in the future for reasons other than estimation of p , and if it is sensible to regard bird numbers obtained from such exercises as approaching true numbers, then it is reasonable to take advantage of these data for estimation of detection probability. Details of this calibration as described by Curnutt et al. (1998) are not entirely clear to us (e.g. it was not clear why the average of counts at four different survey points was compared with the numbers of birds indicated by territory mapping on a single, intensive study plot). In any case, we recommend that standard point counts be conducted each year within intensive study plots in which actual bird abundance is documented through territory mapping, so that direct estimation of detection probability is possible. If territory mapping on intensive study plots is to be discontinued, or it is not thought to provide an accurate estimate of abundance, then other methods for estimating detection probability, and hence bird abundance or density, may merit consideration. Distance sampling using var-

iable circular plots (Buckland et al. 1993) and double-observer sampling (original aerial survey approach of Cook and Jacobson [1979] modified for point counts by Nichols et al. [2000]) both provide reasonable approaches to estimating the probability of detecting single males. (They do not, however, address the problem of detecting birds that do not sing, see below.) We note that detection probability cannot be estimated well simply from replicate counts (by the same or different persons) at the same point(s).

We strongly recommend that estimation of sampling variances accompany future abundance estimates, and that estimation of detection probability be incorporated directly into the survey design. Sparrow surveys clearly require substantial expense and effort, and it is a reasonable expectation that these efforts yield inferences about variation in sparrow abundance over space and time. Such inferences should incorporate estimates of precision that properly account for possible spatial variation in counts, as well as detection probability and variation associated with its estimation.

Beyond singing male surveys.—Three specific concerns have been raised about reliance on surveys of singing males (W. Post pers. comm.). First, singing is highly affected by both endogenous and environmental factors, potentially making detection probabilities low and variable. To partially address this concern, the Panel recommends that playback of song or other vocalizations, which is a standard method in single-species studies, be incorporated into the survey work. This could be accomplished by adding a short playback session at the end of each standard point count. For example, application of playback to standard 10-min point counts has been shown to double the detection probability for forest birds such as Scarlet Tanagers (*Piranga olivacea*; K. Rosenberg, J. Lowe, and A. Dhondt unpubl. data). Such a design would allow for the continued gathering of data comparable to earlier parts of the study. We further recommend that playback be investigated in pilot studies of variance in detection probability conducted in intensive study plots.

Second, the adult population at any one time may include birds that do not attempt to breed but nonetheless are alive and part of the future breeding population (i.e. floaters). The importance of understanding the population dynam-

ics of floaters has been emphasized by Verner (1985) and others. In the Cape Sable Seaside Sparrow, floaters may be more numerous in years in which suitable habitat is reduced or at non-peak periods of activity during the breeding season.

Third, the number of males attempting to attract mates may not indicate the number of females actually engaged in reproductive activity. In fact, singing rates actually may be higher for unmated birds (Post 1974), resulting in temporal changes in detection probability associated with changes in the proportion of birds that are paired. For most demographic models, the number of breeding females, not territorial males, is the most relevant statistic.

The so-called floater question is amenable to investigation through color marking of individuals on intensive study plots. Flush-netting methods and radio tracking of individuals may help determine the size of any nonbreeding component of the population. If numbers of floaters can be estimated reasonably on the intensive study plots, then it would be possible to include this component in the estimation of detection probability. The size of a floater component, and its variation in response to temporal changes in habitat quality, are important to population modeling (see below), as well as to interpreting variation in the size of the breeding population.

Reliance upon singing males rather than on females, although common in avian survey work, is problematic. In the case of the Cape Sable Seaside Sparrow, it may be possible to monitor the number of nesting females over large areas to complement surveys of singing males. Females of at least one other subspecies of Seaside Sparrow are known to give a "nest departure" call (McDonald and Greenberg 1991), i.e. females utter a series of chip notes almost every time they leave the nest from bouts of brooding or incubation. This call is given throughout the day and under a wide range of conditions. Nest departure often follows a predictable schedule during incubation, and determining the departure schedules of females may enable the design of a vocalization-based survey that provides a more direct index of nesting activity and permits estimation of female detection probability and abundance. Effort should be made to determine if female Cape Sable Seaside Sparrows reliably display this behavior and

whether this behavior could serve as the basis for improved estimation of the breeding population.

Conclusions about population trends.—Having explored ways to improve survey techniques, the Panel emphasizes that we view as parsimonious and reasonable the conclusion that Population A experienced a dramatic decline during the 1990s, and that eastern Populations C, D, and F are smaller now than they were in 1981. However, we strongly recommend that point-count data be analyzed statistically using an approach that accounts for relevant sources of variation (spatial variation, variable and unknown detection probabilities), because results of such analyses will provide a basis for stronger scientific inferences than can be made at present.

Future monitoring should be extensive and should provide coverage of existing potential habitat. Given the potential for Cape Sable Seaside Sparrows to shift breeding locations, broad geographic coverage is essential. Future monitoring also should deal explicitly with uncertainty in point-count data associated with spatial variation in bird density and variation in detection probability. The Panel envisions a double-sampling approach in which intensive study plots are established at a subset of the points selected for sampling in the extensive survey. Work on these intensive plots would be used not only to estimate detection probability, but also to assess numbers of nonbreeding floaters, to explore the incorporation of female nest departure calls into the survey design, and possibly to estimate vital rates using marked individuals and nests. Intensive study plots already have been established (S. Pimm pers. comm.), and some of the above data have been gathered from them. The Panel recommends that this effort be expanded and increased as outlined above.

CAUSES OF POPULATION CHANGES

The Panel considered several proposed explanations for changes in the distribution and numbers of Cape Sable Seaside Sparrows. We address them here in sequence, beginning with those we view as most likely to have affected population changes in the past 10 years.

Flooding.—A wealth of published information (e.g. Kushlan et al. 1982, Werner and Wool-

fenden 1983, Curnutt et al. 1998, Nott et al. 1998) indicates that the Cape Sable Seaside Sparrow is extremely sensitive to variations in the nature and quality of its breeding habitat. It was clear to the Panel, both from the literature and on the site visit, that relatively small changes in hydrology, especially water depth and hydroperiod, can produce critical changes in habitat quality that are visible even to the untrained eye. A fundamental feature of the subspecies' biology—nest placement—causes this sensitivity. Cape Sable Seaside Sparrows place their nests just above the bases of clumps of wet-prairie vegetation (most often, now at least, in tussocks of muhly grass [*Muhlenbergia filipes*]; Werner 1975). Placement of a nest too low in vegetation exposes the nest to the ever-present risk of flooding. If the nest is placed too high, the vegetation is too sparse to support the nest or to shield it from predators and the elements.

Uncertainty exists over precisely how high above ground (and especially standing water) the sparrows will build nests. Nott et al. (1998) cite a "10 cm rule" for maximum water depth over which the birds will initiate nesting, based on absence of singing activity during surveys when water depth exceeded that level. In modeling population dynamics, Nott (1998:81) uses a 5-cm threshold of water depth for male singing and nest building. Even the small sample of nests analyzed by Dean and Morrison (1998) is sufficient to demonstrate that some nesting may occur when average water depth exceeds these thresholds. Thus, the Panel recognizes some risk in over-interpreting a hard criterion for acceptable water levels when these are measured over a grid of 0.5 to 1 km in scale. Because of variability in topography and vegetation, apparently some suitable nesting sites for sparrows may remain in generally inundated habitat, and these sites can be essentially invisible to large-scale measurements of water depth.

The Panel reached two conclusions about this problem. (1) The relation between water level and nesting activity deserves further research, mainly to better define the correlation between water levels measured at large scales and sparrow productivity. (2) A better understanding is necessary to evaluate the effects of water level during the 1990s. The 1990s represent an unusually rainy period in the Everglades, and during this period managers frequently were

TABLE 2. Percent of habitat available for brood production for Cape Sable Seaside Sparrow population A.

	1977 to 1992		1993 to 1996	
	One brood	Two broods	One brood	Two broods
<i>n</i> (years)	16	16	4	4
Median	91	36	16	5
Mean	74	44	16	7
SD	29	28	14	8
Range	15–100	0–100	0–33	0–18

concerned about high water levels. Data provided by Nott et al. (1998) allow one to assess the scale of water-level fluctuations during this period and their likely effects on sparrow reproduction. Although one might quibble about details and causes, it is clear from these data that the magnitude and duration of flooding changed substantially west of Shark River Slough, and that these changes likely had a major influence on Population A.

The case for massive disruption of sparrow breeding because of flooding rests on several implications in Nott et al. (1998), especially data provided in their figure 2 and table 1. (We assumed that the expressions "dry" and "wet" used in reference to water levels describe levels below or above, respectively, a hard criterion such as 5 cm or 10 cm, because these are elsewhere stated to be critical for sparrow breeding. We also assumed that the authors correctly assessed such conditions as permitting or not permitting breeding, respectively.) Nott et al. (1998: table 1) analyzed topographic variation in Area A by comparing water depths at 284 census points in 1995 with water levels at monitoring station NP205 taken on the same date. Table 2 summarizes the percent of Area A that these authors deemed to be sufficiently dry for a sufficiently long period (see caveat above) to permit the production of one or two broods between 1977 and 1996.

Persistently high water levels over the period 1992 to 1996 were sufficient to have nearly precluded successful breeding during both 1993 and 1995. Even during 1994 and 1996, acceptable water depths were available for first clutches in less than one-third of the area (27 and 33%, respectively), and almost no habitat remained at acceptable water levels to allow second broods. Over the 16-year period preceding 1993, typically 70 to 90% of Area A was available for first broods and 35 to 45% for second broods (Table 2). Comparable percentages from

1993 to 1996 were 15% and 4 to 7%. Even assuming perfectly synchronous onset of breeding during these years, and allowing for microsite variation that would have permitted limited nesting when the area as a whole was unsuitable, productivity of Population A from 1993 to 1996 would have been only a small fraction of its average during the previous 15 years.

Deep water in Area A during the period of inundation between 1993 and 1996 renders moot the question of precisely which habitat acceptability rule one applies based on nest heights. During this period, water levels in most of the area were well above the acceptable range. Data in Lockwood et al. (1997) suggest that even where sites are available for nesting, high water levels may result in elevated predation and hence reduced nesting success. Evidence for this further effect of flooding is inconclusive, however, in contrast to evidence that reproduction is reduced when water levels exceed typical nesting heights.

In short, we find the evidence convincing that successful breeding in Population A was substantially reduced throughout the period from 1993 to 1996 compared with earlier years, and reproduction may have been essentially nil during at least two of these years (1993 and 1995). For a small, sedentary songbird, such a significant reduction in reproductive output can be expected to result in reduction of overall population size.

Even before the manipulations by the Corps of Engineers, the Everglades ecosystem experienced substantial temporal variation in rainfall and water levels (Blake 1980, Beissinger 1986, Beissinger and Gibbs 1993, Deuver et al. 1994). Is it likely that increased water levels, which appear to have caused cessation of nesting and concomitant decline in Population A, resulted simply from natural variation in climate? Elevated water levels in the area of Population A occurred during a series of uncom-

monly wet years in South Florida, and no doubt this contributed greatly to the problem.

Nott et al. (1998) attempted to isolate the effects of water discharges into Everglades National Park through the S-12 structures by sequentially removing through regression the effects of base water level at the beginning of the season and rainfall during the season. Residual water depth after removing these two factors was significantly correlated with discharges from S-12A. Contributions of discharges from the remaining three S-12 structures were not examined.

Although correlational analyses of this sort do not yield strong inferences, the Panel views as reasonable Nott et al.'s (1998) conclusion that the concentrated releases of water from the S-12 structures from 1992 to 1995, above and beyond existing water depth and seasonal rainfall, directly led to the deep-water conditions west of Shark River Slough. These in turn probably caused habitat in the range of Population A to be unsuitable for breeding, and we conclude that this likely played a major role in the apparent decline of Population A.

Good evidence also exists that extended hydroperiods result in vegetation changes that reduce habitat suitability for the sparrows, specifically the conversion of prairies or marshes dominated by muhly to those dominated by sawgrass (Kushlan et al. 1982, Armentano et al. 1995, Nott et al. 1998). This may have played a role in the decline of Population A, but it is better illustrated by changes in Population D in the Taylor Slough region. In fact, Kushlan et al. (1982) predicted that such a habitat conversion, and accompanying decline in sparrow numbers, would occur in Population D owing to the construction of a pumping station immediately upstream in Taylor Slough. Nott et al. (1998) presented evidence that the increased hydroperiods resulting from releases from the pumping station have indeed resulted in the predicted change in vegetation. Survey results provide evidence of the predicted decline of the sparrow population (Table 1).

In some ways, effects of extended hydroperiod on vegetation may be more important than effects on sparrow reproduction. That sawgrass-dominated prairie is unsuitable habitat for sparrows is evident from Nott's (1998) work on habitat use as a function of vegetative composition generally, as well as information about

Populations A and D specifically (Nott et al. 1998). Muhly prairie can withstand deep inundation, and even whole years with little or no dry period, as long as these are interspersed with years in which winter drying occurs (Kushlan et al. 1982). Because muhly prairie can recover following a return to shorter hydroperiods (Nott 1998), chronic alteration of hydroperiod rather than occasional flood events are the most problematic in bringing about changes in vegetation. If water management produces long hydroperiods in Area A frequently enough to alter its vegetation, as has occurred in Area D, then sparrow survival and reproductive rates will be moot because the habitat will be unable to support successful reproduction regardless of how many birds might be in the area.

Fire.—Compared with the role of water levels, the effects of fire on population sizes through the 1990s have been minor. We agree, however, that the *potential* capacity of fire to affect sparrow populations and habitats remains large. No catastrophic population declines in the past decade can be directly ascribed to fire. Nevertheless, it appears likely that populations in northeastern Everglades National Park, especially Population F, may be prevented from growing by the extremely high frequency of arson-caused fires during the dry season (Curnutt et al. 1998). The Ingraham fire burned part of the area occupied by population B in 1989. Survey data only three years later (1992) provide evidence that this major fire did not have a catastrophic effect on Population B (Table 1).

The Panel concludes that in the short term, loss of populations to catastrophic fire is possible but unlikely, even under current water management practices. Risk of catastrophic fire will be greatly reduced by increased flows into northeastern Shark River Slough, and the potential for catastrophe increases the longer these larger flows are delayed. When fires occur, as with the Ingraham fire, damage is likely to affect a portion of a population rather than eliminate all of it. However, fire does have potentially important effects on population dynamics through altering habitat suitability. Curnutt et al. (1998) provide convincing evidence that fires are much more common in areas at the eastern edge of Everglades National Park where the habitat frequently is dry, and where exposure to humans is especially great.

At issue is whether such effects played a significant role in the decline of the small northeastern populations (C and F) and whether they might threaten the larger one (E). Unfortunately, the survey technique is not sensitive enough to permit a direct approach to this question.

Disagreement exists about the effects of fire on sparrow populations. Abundant evidence points to a short-term negative effect of burning on sparrow numbers (Werner 1975, Taylor 1983, Werner and Woolfenden 1983, Curnutt et al. 1998). Burned habitat is avoided for up to a year, and numbers then increase over the next several years. There are conflicting reports about the duration of the effect and subsequent deterioration of habitat in the continued absence of fire. Werner (1975) suggested that use of otherwise suitable habitat declines to abandonment after six years without fire. However, Taylor (1983) reported sparrows in sites that were unburned for more than a decade. Curnutt et al. (1998) pointed out that many birds in the largest and most productive population (B) nested during the mid- to late 1990s in areas that had not burned since the Ingraham fire in 1989. Curnutt et al.'s (1998) cross-sectional analysis suggests that sparrow numbers increase for up to 10 years after fire. However, their analysis (see figure 5) was handicapped in that it did not control for site effects. Many differences besides fire frequency and time since last fire exist among sites that were compared. Moreover, little question exists that at some timescale, fire is necessary for continued occupancy of a site by Cape Sable Seaside Sparrows because it inhibits invasion by woody plants (Craighead 1971). The aversion of sparrows to woody vegetation in their nesting habitat, and resulting loss of habitat to invasion of woody vegetation, is well documented (Werner 1975, Werner and Woolfenden 1983, Nott 1998).

Numerous factors complicate analysis of the effects of fire frequency on habitat and sparrow populations. Areas with deeper soil appear to recover more rapidly from a fire (Taylor 1983, Curnutt et al. 1998) and to build up excess fuel sooner (A. Mayer unpubl. data). Fires set by humans in the dry season often burn wider areas more intensively than do lightning-caused fires during the wet season.

The long-term role of fire should be investigated through a series of longitudinal studies within sites of known fire history having dif-

ferent hydrology and soil depths. Use of prescribed burning as an experimental treatment likely will be necessary to accomplish this. Recently established intensive study plots in population E could be employed for this purpose. The Panel recommends a collaborative effort involving plant ecologists, ornithologists, and habitat managers, and employing intentional burns in the experimental design, to identify how soil, hydrology, and fire interact in affecting the dynamics of Cape Sable Seaside Sparrow populations.

Other possibilities.—One interpretation of the historical record of habitat distribution of the Cape Sable Seaside Sparrow is that the current plight of the sparrow results from its extirpation from the now largely nonexistent *Spartina bakeri* habitats that once occurred along the Everglades-marine interface at the turn of the century (W. Post pers. comm.). According to this hypothesis, the population might be larger and more productive if the habitat that it once occupied on Cape Sable was still available and sparrows still lived there. However, the recent productivity of birds in good habitat (Lockwood et al. 1997, Dean and Morrison 1998) is fully comparable to that of other populations of this species (e.g. Post et al. 1983) and appears adequate to support a thriving population. The data required to determine how demography in *Spartina* prairie compares with that in muhly prairie do not (and probably never will) exist, but no direct evidence of any kind exists that muhly prairie represents suboptimal habitat.

All known threats to the Cape Sable Seaside Sparrow involve alteration of habitat. The Panel encountered no evidence that the bird's population is being affected by other biotic factors (e.g. unusual new predators, diseases, or competitors) or abiotic factors. The Panel explicitly considered the possibility that Hurricane Andrew, which roared through most of the range of the sparrow in 1992, caused the decline, especially in Population A. However, we find Curnutt et al.'s (1998) arguments that Andrew was not a primary factor in the decline of Population A to be reasonable. Most important, Population A continued to decline for years after Andrew, whereas Population B received only slightly less extreme wind conditions than did Population A, but exhibited no decline.

Conclusions.—The Panel concludes that population declines of the Cape Sable Seaside Spar-

row occurred largely as a result of reduced habitat suitability. Habitat degradation owing to invasion by exotics and by woody vegetation, which was of great concern in the early 1980s (Kushlan et al. 1982), does not appear to threaten areas where sparrows live currently. In contrast, the other threats to habitat quality identified in the 1980s, fire and flooding (Kushlan et al. 1982), indeed appear to have wrought the damage it was feared they might. Declines of Populations A and D likely can be attributed to extended hydroperiods that suppressed reproduction and produced adverse changes in vegetation. Populations C and F appear to be depressed by reductions in habitat quality resulting from fire. Abnormally high fire frequency in these areas is the direct result of reduced hydroperiods and proximity to humans.

RISK OF EXTINCTION

The current risk of extinction of the Cape Sable Seaside Sparrow needs to be assessed carefully because of recent declines of some of its populations, and because of the recent extinction of its close relative, the Dusky Seaside Sparrow. We will discuss extinction risk with respect to current water management and plans for new water management described in the Introduction. Because the new plan stipulates that some of the water currently held in WCA 3A will instead flow through WCA 3B into northeastern Shark River Slough, we assume that Populations A and D will experience extended hydroperiods less often under the new plan than under current management. We further assume that Populations C, E, and F will experience dry conditions less often.

Although the new water management plan is scheduled to be implemented in only five years, many obstacles to its implementation exist (e.g. land acquisition, construction of new structures), and if the previous 50 years of Everglades history are any indication, delays are likely. Therefore, risk of extinction in the interim cannot be ignored. The key element for the sparrows is that flow patterns produce hydroperiods similar to those that characterized the marl prairies prior to management of water by humans. Flows west of Shark River Slough and into Taylor Slough must be reduced, and flows into northeastern Shark River Slough increased, to accomplish this. The adequacy of

the new water management plan depends on the extent to which the desired hydroperiods are actually produced. In the interim, the best alternative to reduce risk of extinction of the sparrow is to restore the required flow patterns to the maximum extent possible using existing structures. Recognizing the reluctance of managers to adopt this alternative, we evaluate risk of extinction over the short term for two additional scenarios.

The first scenario is "status quo" management. We consider the data collected during the last two decades to reflect biological consequences of status quo management. The second scenario is to retain water in WCA 3A in wet years rather than allow emergency releases through the S-12 structures into the area west of Shark River Slough. We assume in this second scenario that Population A would not be subjected to extended hydroperiods such as those that occurred from 1993 to 1996, whereas in the first scenario these events will continue to occur when rainfall is sufficient. We further assume that Populations C, E, and F will continue to experience dry conditions unusually frequently in both short-term scenarios.

Here, we review aspects of demography relevant to extinction risk and then evaluate previous efforts to model extinction risk. Finally, we address the following questions: (1) Will the planned changes in flow patterns result in minimal extinction risk for the Cape Sable Seaside Sparrow? (2) What is the relative risk resulting from the two short-term management scenarios? Components of the second question include the risk to Populations C, E, and F resulting from unusually frequent and prolonged dry conditions, the risk to Populations A and D of continued releases of water into their habitat, and the risk to Population B of catastrophic fire.

Key features of demography.—To evaluate the potential threat that factors such as flooding and fire represent to the continued existence of the Cape Sable Seaside Sparrow, we must gauge the sparrow's capacity to respond to these threats. Many other species in the Everglades ecosystem (e.g. Snail Kites [*Rostrhamus sociabilis*] Beissinger 1986, Takekawa and Beissinger 1989; Wood Storks [*Mycteria americana*] Ogden 1996) have the capacity to move considerable distances in response to degradation of habitat. If Cape Sable Seaside Sparrows were

facultatively nomadic, they might be able to move to better conditions when flooding or fire degrades their habitat, perhaps returning when conditions improve. Indeed, Post and Greenlaw (1994) refer to the Seaside Sparrow as a catastrophe-prone species with such abilities. Thus, it is especially important to examine dispersal behavior in evaluating extinction risk.

The history of the patchy and apparently dynamic distribution of the Cape Sable Seaside Sparrow (e.g. Kushlan et al. 1982) suggests some ability to colonize newly available habitat as traditional areas become unsuitable. Inferences from historical distributions, however, must be weighed against the finding by Dean and Morrison (1998) that radio-tagged birds, even juveniles, show limited dispersal. The Panel was impressed by this team's abilities to account for and maintain radio-tracked birds through many cycles of transmitter replacement and bird movements of up to 7 km (T. Dean unpubl. data). Telemetry data suggest that when habitat remains in good condition the birds are quite sedentary, and that even dispersing juveniles only rarely cross the kinds of barriers that separate different populations (Dean and Morrison 1998). Sample size for juvenile birds remains small, however ($n = 11$; T. Dean unpubl. data). Another piece of evidence that adult sparrows have limited capacity for large-scale movements is that no compensating increase occurred in any of the other populations after flooding of the habitat of Population A. The birds that disappeared from Population A did not appear to move elsewhere en masse.

Although no evidence of rapid shifts in distribution through mass movements exists, gradual shifts could occur through population extinction and recolonization events. Without better information on survival during flooding and fire episodes (see below), it is not possible to determine precisely how prone the Cape Sable Seaside Sparrow might be to local extinction events. The historical extinctions at Cape Sable and Ochopee involved changes in vegetation that rendered habitat unsuitable (Kushlan et al. 1982); hence, they have little bearing on assessing the vulnerability of sparrow populations to stochastic fluctuations in vital rates. The accuracy of population estimation is not known, so it is not possible to determine whether recent apparent extinction and recolonization events involving small populations (i.e. C, D, and F; see Table 1) were real or reflected sampling error.

Telemetry data suggest that recolonization ability is limited in terms of distance and frequency. No movements between populations have been observed, nor have movements been observed beyond barriers such as tree islands and sloughs, although movements over continuous habitat of distances as large as those that separate Populations B to F have been documented (Dean and Morrison 1998). The available data suggest that emigration from good habitat probably is not frequent enough for one to assume with any confidence that the various populations are linked as a single metapopulation, in which populations are routinely "rescued" from extinction by emigration from other populations (Stacey and Taper 1992). However, occasional movements that could result in recolonization cannot be ruled out.

More problematic are movement patterns in response to adverse conditions, such as fires or floods. Movement patterns are known to change in response to such events in other Seaside Sparrows (Post and Greenlaw 1994). Unfortunately, no relevant data exist for the Cape Sable Seaside Sparrow. Moreover, its distinctive habitat and nonmigratory tendencies make it easy to imagine that this population does not share these habits with more northerly ones. It may be possible to evaluate the degree of isolation among the various Cape Sable Seaside Sparrow populations by examining genetic relationships among them. If sparrows are to be trapped for other research purposes, then blood, and perhaps tissue, should be taken to pursue this possibility.

We further recommend that experimental studies be conducted in which movements of individuals following burning and flooding are monitored using telemetry. In the case of fire, this could be incorporated into the longitudinal studies using prescribed fire recommended above. In the case of floods, the study could be coordinated with planned water releases. These studies would allow researchers to measure for the first time the movements of birds faced with degraded habitat. To date, all telemetry work has been done in the relatively stable and suitable Ingraham population area. These studies would also enable evaluation of variation in detection probabilities (see above) and

survival (see below) under adverse (but not uncommon) conditions.

Limited dispersal and a dynamic spatial history need not represent a paradox. Over long time scales, rare long-distance movements of juveniles are capable of producing considerable range dynamics. However, Cape Sable Seaside Sparrows in the late 1990s appeared to live in an ecosystem with less total habitat, and perhaps less variety, than that in which the taxon probably evolved. Marl prairies have been reduced by development, chronic flooding, and invasion of woody vegetation, and *Spartina* habitat has been nearly eliminated by invasion of mangroves and changes in salinity (USDI 1998, W. Post pers. comm.). Thus, whatever capacity the species may have to shift its distribution to match changes in habitat suitability is now constrained by limited habitat availability. The capacity for colonization of new habitat patches probably exists, but the Panel sees no scientific rationale for gambling on a still unproven potential for long-distance movements as a responsible strategy for protecting the sparrow from population collapses in the few usable habitat patches that remain.

How a species responds to adverse conditions depends on productivity and survival rates within populations, as well as movement between populations. Species with high population growth rates potentially can recover quickly from population declines and can expand rapidly after recolonization. Nesting success of the Cape Sable Seaside Sparrow is low, but this is offset to some degree by the potential for multiple brooding. Dr. Julie Lockwood and collaborators have collected data on nesting success from intensive study plots (Lockwood et al. 1997, J. Lockwood unpubl. data). Nests of this species are difficult to find and can be logistically challenging to monitor, so sample sizes are still small. Nevertheless, several patterns emerge. First, the Mayfield success estimate for first nests that were initiated during the dry season in March was 43% ($n = 40$), a typical value for a passerine. Second, nesting success appeared to decline as the breeding season advanced, a pattern seen in many avian species. Second broods that were initiated at the end of the dry season in late April and May were less than half as likely to fledge young as first broods (16%, $n = 11$). Nesting failure resulted predominantly from predation on eggs

or young, or flooding. A few individuals attempted third broods under highly favorable conditions (Lockwood et al. 1997). Fire and flooding can reduce the number of nesting attempts and, if severe enough, can terminate reproduction completely. Fledging success averaged three young per successful nest under all conditions (Lockwood et al. 1997).

Data on survival of breeding males also are available from intensive study plots. Resightings of more than 100 birds banded from 1992 to 1998 suggested a 50% survival rate (S. Pimm unpubl. data). However, this estimate was not corrected for the probability of resighting. M. Nott (unpubl. data) recently applied Cormack-Jolly-Seber methods to estimate probabilities of resighting and survivorship, obtaining an estimate of 56% for survival of adult males from these same resighting data. This result should be considered preliminary, because the analyses have not been published nor made available for examination.

Little else is known about survival rates of Cape Sable Seaside Sparrows. Data from juveniles and females are insufficient to estimate survival rates accurately. Survival estimates for juveniles represent a critical research need. Variation in survival is poorly described, even for adult males. Data from small samples suggest that survival of breeding males is substantially higher than 60% under favorable conditions (Werner and Woolfenden 1983), and survival of nonbreeding males may be substantially lower than that of breeding males (S. Pimm unpubl. data). Annual variation and other forms of heterogeneity in survival rates have not been described. It is especially important to know if survival is reduced by the same factors that reduce productivity, that is, flooding and fire. Studies of movements in response to fire and flooding recommended above also could provide valuable information on the effects of these events on survival. As data from intensive study plots accumulate, we also recommend that survival analyses examine differences among individuals of different social status (i.e. breeders vs. nonbreeders) and among populations. Currently, sample sizes and data appear insufficient to permit robust analyses of this type.

The effect that water management has on the capacity for multiple brooding by Cape Sable Seaside Sparrows is a critical issue. To further

TABLE 3. Estimates of lambda (geometric rate of population change) for Cape Sable Seaside Sparrows based on various levels of annual survival and numbers of nesting attempts per year. Populations are stable when lambda = 1 and decline when lambda < 1. Calculations assume age of first breeding at one year, three young raised per successful brood, an equal sex ratio at fledging, and that third broods have the same success rate as second broods but are attempted by only one-third of the adults (Lockwood et al. 1997, Lockwood unpubl. data). Mayfield success of first and second broods was 43% and 16%, respectively.

No. nesting attempts/year	Survival rate		
	50%	55%	60%
0	0.50	0.55	0.60
1	0.82	0.91	0.99
2	0.94	1.04	1.13
3	0.98	1.08	1.18

assess the significance of this issue for population behavior, we collated various parameter estimates to create a simple model of Cape Sable Seaside Sparrow demography in the Everglades (Table 3). The objective of this exercise was to evaluate the relationship between level of multiple brooding and rate of population change (lambda). We developed a two-stage-class prebreeding population model with a one-year time step and (lacking data on juvenile survival) no differences in survival between juveniles and adults. Although there is a large degree of variation in model outcomes, several conclusions emerged. First, lack of nesting has a dramatic effect on population behavior (as expected), but the opportunity to attempt a second brood may have a substantial effect as well. Indeed, it is conceivable that the opportunity to attempt a second brood could make the difference between a declining and an increasing population. Second, survival rates required to achieve a stable population in the absence of multiple brooding may be unrealistically high. Even though we used juvenile survival rates that are probably too high, within the range of existing estimates of adult survival, lambda only exceeds one if there are multiple broods (Table 3). Recall, however, that under favorable conditions, adult survival occasionally might be higher than the values we used in the model.

If reproduction and survival are correlated (i.e. good years have high reproduction and high survival, and bad years suffer the reverse),

then sparrow populations are capable of a "boom and bust" life history that characterizes other Everglades species (e.g. Beissinger 1995). Populations may suffer "bust" years when conditions are poor, productivity is negligible, and numbers decline, but populations also may be able to increase rapidly when favorable conditions allow for pairs to raise more than one brood.

The potential for considerable variability in vital rates complicates evaluation of extinction risk. The range of conditions the sparrows regularly encounter no doubt includes conditions conducive to both population growth and population decline. However, it is impossible to determine the relative frequency of periods of growth and periods of decline without better estimates of vital rates, and especially without a better understanding of how these rates vary in response to environmental conditions.

Modeling extinction risk.—The likelihood that population fluctuations driven by flooding and fire events will result in extinction of sparrow populations in the absence of immigration has been explored through population modeling. These attempts are preliminary and suffer from insufficient data to estimate demographic parameters and associated variation, as discussed above. Nott (1998) developed a spatially explicit, individual-based model (SIMSPAR) in which population dynamics are linked to habitat condition. SIMSPAR is data-demanding, but data available for modeling habitat occupancy and nesting density as a function of habitat condition appear to be sufficient to draw preliminary conclusions. Habitat classification is based on remote sensing data, and Nott (1998) described clear relationships between habitat and numbers of breeding sparrows. Nott (1998) modeled availability of habitat classified as suitable as a function of flooding and fire history and validated this component of the model by demonstrating that birds have not been detected at survey locations classified as unsuitable. The availability of data on habitat and bird distribution makes this component of SIMSPAR effective. The model appears capable of predicting habitat availability with reasonable accuracy.

In contrast to the habitat portion, parameterization of the demographic portion of the model exceeds current knowledge of sparrow demography. Moreover, until more is known

about the effects of habitat condition and breeding status on movement and survival, it is not clear that modeling of sparrow demography needs to be either individual-based or spatially explicit. In the meantime, it might be useful to simplify SIMSPAR's demographic subroutine. Finally, a complete sensitivity analysis has not been performed, making it unclear how much the model's results are affected by variation in some of the poorly known parameters.

Nott's (1998) model is a considerable achievement in integrating habitat and population dynamics and will be of general interest to modelers. However, its current application in the Everglades ecosystem should be limited to evaluating the comparative effects of different management scenarios and environmental fluctuations on availability of suitable sparrow habitat. It is premature to use this model to generate specific probabilities of extinction (Beissinger and Westphal 1998). SIMSPAR also may be a useful tool for helping to set research priorities. A thorough sensitivity analysis can be used to identify parameters that contribute the most to population behavior and thereby identify where limited research funds should be expended to improve the model's predictive capability.

The Panel concludes that, for now, the type of simple deterministic matrix model developed by S. Pimm (unpubl. data) is as appropriate for examining population behavior as is more complex modeling, at least until more demographic data are available. Pimm's model has not been well documented, and several of the parameter values employed require more rigorous examination. To date, the model has been used primarily to explore the capacity for flooding and fire to negatively affect population behavior through depression of survival and reproduction (USDI 1998). The results suggest that flooding poses a significant threat to Population A, and fire to the northeastern populations, but not to Population B. Pimm's model has not been used to explore how population behavior depends on values of demographic parameters, as we did in Table 3. This type of model will be most useful in evaluating potential effects of different management scenarios and alternative demographies, rather than attempting to estimate extinction risk. As additional data required for more complex models

become available, it may be possible to employ first a stochastic matrix model and eventually SIMSPAR for these purposes.

Perhaps the strongest conclusion that one can draw from modeling efforts to date is that they portray how flooding and fire, if they are frequent enough and have strong enough effects on reproduction and survival, might cause major population declines. Furthermore, the magnitude of effects and frequencies required are realistic, at least for some portion of the domain of possible mortality and reproductive rates. With this in mind, we now return to the issue of extinction risk under different water management strategies.

Conclusions about extinction risk.—The capacity for recolonization is one factor determining the significance of the extinction of a particular population. Recolonization of Population A is most problematic because of its isolation from the other populations by distance and barriers, especially Shark River Slough. Populations B to F are in much closer proximity but are still separated by barriers, albeit less-significant ones. Our first conclusion, then, is that extinction of Population A may pose greater problems for future management than will extinction of the other small populations (C, D, and F).

Owing to the uncertainties about population dynamics, it is difficult to evaluate the viability of particular sparrow populations individually, or the subspecies collectively. However, the combination of empirical work and modeling results makes a convincing case that continued releases of water into habitat occupied by Population A pose a significant risk to that population's continued existence. We conclude that under the current water management strategy, near-term extinction of Populations A and D are real possibilities. We further believe that retaining water in WCA 3A rather than releasing it west of Shark River Slough and into Taylor Slough in wet years will substantially reduce the risk of extinction of Populations A and D.

The case for risks posed by fire is less compelling. Population B remained large after the major fire of 1989, and Pimm's (unpubl. data) modeling supports the notion that population fluctuations caused by fire likely are insufficient to cause extinction of Population B. The temporary reduction in productivity and habitat suitability caused by fire has greater consequences for the smaller northeastern popu-

lations (C, E, and F) than for Population B. In these cases, extinction risk is a function of the nature and duration of interim water management. Population E may be large enough to withstand adverse effects of fire over the short term, even if the "short term" turns out to last somewhat longer than anticipated. We conclude that extinction of Populations C and F is conceivable under both of the short-term scenarios we evaluated, if interim water management persists substantially longer than anticipated, but that recolonization of these populations, should they go extinct, also appears to be a realistic possibility.

Thus, we perceive Populations A and D, and possibly C and F, to be at risk under both of the short-term scenarios. The risk of extinction of the total population obviously is increased by the reduction of the number of large populations from three to two. Establishment of a new large population to replace an existing one seems to us a remote possibility, given the current lack of suitable unoccupied habitat. Gambling on being able to first create a large area of new habitat and then successfully establish birds there, when no candidate areas have been identified, is too risky a strategy to be seriously entertained. The best available means to reduce the risk of extinction of the Cape Sable Seaside Sparrow is to retain and recover Population A. Population E should be monitored carefully while interim water management remains in place, because the persistence of this population also is important to the future of the sparrow.

We further conclude that the new water management plan will reduce extinction risk to the sparrow. The reductions in risk achieved will depend on the extent to which alteration of flows west of Shark River Slough, in Taylor Slough, and in northeastern Shark River Slough produced by new structures and policies result in hydroperiods that mimic historic ones. If the distribution of water levels is as anticipated, the risks imposed by flooding and fire after implementation should be lower than at any time in recent history. A possible additional risk we perceive under the new water management plan is loss of habitat to encroachment of woody vegetation. This means that the new management regime must involve periodic fire.

MANAGEMENT RECOMMENDATIONS

Our main conclusions are that (1) extended hydroperiods result in changes in vegetation and suppressed reproduction and thus represent a serious threat to Cape Sable Seaside Sparrows; (2) changes in water management are required over the short term to prevent such extended flooding; and (3) the new management plan will alleviate this problem. A previous panel of scientists reached these same conclusions (Orians et al. 1996). The management recommendations below follow from these conclusions.

Long-term management.—The amount of prairie habitat under protection within Everglades National Park appears to be sufficient to support a self-sustaining population of Cape Sable Seaside Sparrows. Indeed, the total population size attained at times within this habitat, estimated at 6,000+, may be larger than that of many other populations of the species in other regions. The evidence is clear that some of the remaining habitat has been degraded in recent years by frequent fires and extended hydroperiods, but it is also clear that the habitat can recover once these effects are removed. The new water management scheme promises to reduce these effects and to restore degraded habitat. From the perspective of Cape Sable Seaside Sparrow management, we strongly endorse this new scheme and urge that it be implemented with all possible speed. To maximize benefits to the sparrow, this plan should be implemented in such a way that hydroperiods in the prairies occupied by sparrows match historic ones as closely as possible. Once the new plan is implemented, monitoring and fire management will be the predominant management activities. Habitat loss to encroachment by woody vegetation must be prevented, perhaps through a prescribed burning program based on improved information about optimum burning intervals.

The natural population dynamics of the sparrow may be sufficient to fill the available suitable habitat provided under the new water management scheme. This process promises not only to preserve the remaining large populations (B and E), but also to recover the small populations (A, C, D, and F) to higher levels. Recovery of these currently small populations to historical levels is desirable for long-term

sustainability of the Cape Sable Seaside Sparrow. If population growth does not occur as anticipated once the habitat has recovered, translocation of individuals may be necessary. Translocation is appropriate only where unoccupied habitat has been restored to optimal conditions for sparrows. Currently, such habitat may exist within Population A and perhaps at Ochopee (Kushlan et al. 1982, Nott 1998). Additional unoccupied suitable habitat may arise as a consequence of improvements in habitat conditions when the new management plan is implemented.

Short-term management.—Retaining Population A until the new water management plan is implemented at some future date is a major concern. Our recommendations about interim management are based solely on the requirements of Cape Sable Seaside Sparrows and ignore politics and the needs of other species inhabiting the Everglades. This approach befits the charge of the Panel. The best alternative is to reduce flows west of Shark River Slough and into Taylor Slough, and increase flows into northeastern Shark River Slough, to the extent possible using existing structures. This alternative would benefit Populations C, D, E, and F, as well as A. If this approach is not adopted, then releases of water west of Shark River Slough through the S-12 structures should be closely regulated. In relatively dry years, releases could occur as in the past, but our recommendation for wet years is that some water normally released into Everglades National Park under existing policy instead be retained in WCA 3A. Specifically, we recommend that water be managed to enable high productivity until Population A has recovered to at least 1,000 breeding birds. A dry period of 50 to 60 days beginning 15 March is the minimum required to ensure reasonable productivity, and a period of 80 days is preferable. A dry period of 50 to 60 days should allow most females to complete one brood, and a few to complete two, whereas an 80-day dry period should allow most females to complete two broods (Nott et al. 1998).

In wet years, maintaining dry conditions in Population A will mean retaining water in WCA 3A rather than releasing it west of Shark River Slough. After Population A has recovered, S-12 releases could be allowed in wet years. These should not occur in consecutive

years, or more often than about two years in five. It might even be possible to release water one year in five prior to recovery of Population A without jeopardizing recovery. Obviously, such releases do not benefit the sparrow and would have to be justified in terms of other considerations that outweigh harmful effects on Population A. Similarly, each year managers will have to weigh potential increases in productivity of sparrows resulting from extending the dry period from 60 to 80 days (Table 3) against the consequences of retaining water in WCA 3A. The latter will be more severe in wetter years. Evaluating the biological consequences of retaining water in WCA 3A is beyond the charge of the Panel (see Armentano 1996 and references therein). We note that whatever adverse effects occur should be short-lived, because the need to store water in WCA 3A will cease with adoption of the new long-term water management scheme.

Releases of water into Taylor Slough should be regulated similarly to releases west of Shark River Slough to avoid extirpation of Population D. We conclude that extinction of Population D does not put the Cape Sable Seaside Sparrow in imminent danger of extinction, but managers may prefer the actions necessary to retain this population over those that will be required to restore it, should natural recolonization not occur. If retaining Population D is treated as a priority, then a recovery criterion based on habitat condition should be developed for that population, and releases of water into Taylor Slough should be prevented until the criterion is achieved.

That fire might be too infrequent to prevent invasion of woody vegetation is unlikely in the short term. Therefore, we recommend a policy of prevention and suppression of dry-season fires until the new management plan is in effect. We do recommend, however, that prescribed burning during the wet season be a component of this policy. If managers elect not to increase flows into northeastern Shark River Slough prior to implementation of the new management plan, then Populations C and F will remain at risk owing to adverse effects of fire on habitat quality. Under these conditions, we do not recommend any effort to save them other than fire suppression, nor do we recommend translocation of individuals from other populations to them. As long as abnormally

frequent dry conditions continue to prevail, translocation efforts will, in our opinion, be futile. Efforts to restore Populations C and F, should they be extirpated, should be delayed until historic flow levels are restored to north-eastern Shark River Slough. However, more aggressive management of Population E should be designed and implemented, should monitoring indicate substantial declines in that population.

Captive breeding.—Note that we do not include captive breeding among our management recommendations. Captive breeding represents a rescue operation (Snyder et al. 1996), and the Cape Sable Seaside Sparrow is not yet in need of rescue. The Panel views captive breeding as risky, unnecessary, premature and distracting at this time. The hope is that the management recommended will be sufficient to ensure that captive breeding will never be required.

Recovery team.—Finally, we strongly recommend that a Federal recovery team be appointed for the Cape Sable Seaside Sparrow to advise local managers. The Everglades is not a static system, and new challenges can be anticipated. A recovery team would serve as a valuable advisory group as new issues arise. Among its members should be an avian population or conservation biologist, ornithologists who have studied the Cape Sable Seaside Sparrow, a botanist specializing in wetlands, and a hydrologist. Such a group is needed to continue the task of evaluating relevant scientific information that we have attempted here, and to assist managers in maintaining compliance with the species' recovery plan (USFWS 1998).

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