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Florida Panther (*Puma concolor coryi*)

Using Models to Guide Recovery Efforts

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South Florida is a rapidly urbanizing region with large amounts of intensive types of agriculture such as citrus and sugarcane. This region, where the temperate and tropic regions meet, is very diverse in flora and fauna. At least 68 federally listed species occur in South Florida, including the endangered Florida panther, *Puma concolor coryi* (U.S. Fish and Wildlife Service 1999). These vulnerable species are under increasing pressure as the human population continues to increase and economic expansion is accompanied by extensive land-use alterations. Cox et al. (1994) estimated that more than 3.2 million ha (or 8 million acres) of forest and wetland habitats have been cleared in Florida to accommodate the expanding human population over the last 50 years. The human population in Florida is expected to continue its growth, reaching 17.8 million people by 2010, with about half of them living in the South Florida ecosystem (Floyd 1997).

The endangered Florida panther is the only representative of the species *Puma concolor* surviving in the eastern United States, and it survives only in a small area in South Florida. The Florida panther is an excellent example of a unique rare Florida species. The high-profile, endangered cat is a habitat generalist that ranges widely, seeking its preferred prey of deer and hogs. Panther numbers, though, are greatly reduced. As of 2001, the verifiable, by radiotelemetry and other field data, number of panthers in South Florida was 78 adults and juveniles (McBride 2001).

This species once ranged from eastern Texas and the lower Mississippi River Valley east through the southeastern states (Young and Goldman 1946). The current distribution, as indicated by radiotelemetry data, is reduced to approximately 810,000 ha in South Florida south of the Caloosahatchee River (U.S. Fish and Wildlife Service 1999). Dispersal northward, either across the Caloosahatchee River or through the urbanized areas east of Lake Okeechobee, has been very rare, often fatal, and by a few males (Maehr et al. 1992, 2002b; Maehr 1997).

This geographic isolation combined with habitat loss and fragmentation, population declines, and inbreeding have led to a decrease in the genetic variability of this species (Roelke et al. 1993). Because of its low abundance and documented traits such as heart defects, cryptorchidism, and reduced sperm viability, there was great concern that this species was suffering from inbreeding depression (Seal and Lacy 1992, Roelke et al. 1993, Barone et al. 1994). In 1995, eight female Texas cougars (*Puma concolor stanleyana*) were introduced into South Florida as part of a genetic restoration program. While this genetic restoration program may have alleviated many of the genetic issues, fragmentation and loss of habitat continue to pose the greatest threats to panther recovery.

To evaluate the viability of the current Florida panther population and to complement ongoing habitat suitability analysis, I developed a spatially explicit metapopulation model for the Florida panther in South Florida. Specifically, I wanted to evaluate the factors affecting the long-term viability of the existing South Florida panther population and explore some potential strategies for recovery of this listed species.

Methods

Since 1981, Florida panthers have been radiocollared and monitored on public and private lands throughout South Florida (Maehr 1997, Maehr et al. 2002a). A total of 108 panthers have been radiocollared and over 100 kittens marked at the den since telemetry research began (Shindle et al. 2001). Florida panther radiotelemetry data collected February 22, 1981, to March 30, 2002, are shown in Figure 44.1. These data were used to estimate survival rates and fecundity for previous viability analyses (Seal and Lacy 1989, 1992; Maehr et al. 2002a). Using these data, combined with detailed geographic information system (GIS) habitat data, I constructed female-only, stochastic, structured, spatially explicit metapopulation models for the Florida panther in RAMAS GIS (Akçakaya 2002).

RAMAS GIS provides a framework for building detailed metapopulation models with complex spatially explicit structure. It is well suited for addressing conservation and management questions for species at risk because of its close integration of demographics with habitat dynamics. Therefore, using this model, I could examine the long-term viability of the panther and explore potential recovery options, such as increasing natural dispersal and translocation.

Metapopulation Models

Linking habitat data to metapopulation models requires three key steps: identify the species-habitat relationship; locate discrete habitat patches; and estimate population- and metapopulation-level parameters. Florida panthers are habitat generalists but prefer areas with cover, such as forests, for feeding, breeding, and shelter, and they avoid urban areas (Belden et al. 1988, Kautz et al. 1993, Cox et al. 1994, Maehr and Cox 1995, Dees et al. 2001). A base map was created by lumping forest cover types from two sets of maps: the Florida water management districts land use and land cover maps for South Florida based on 1995 aerial photography data and the Florida Wildlife

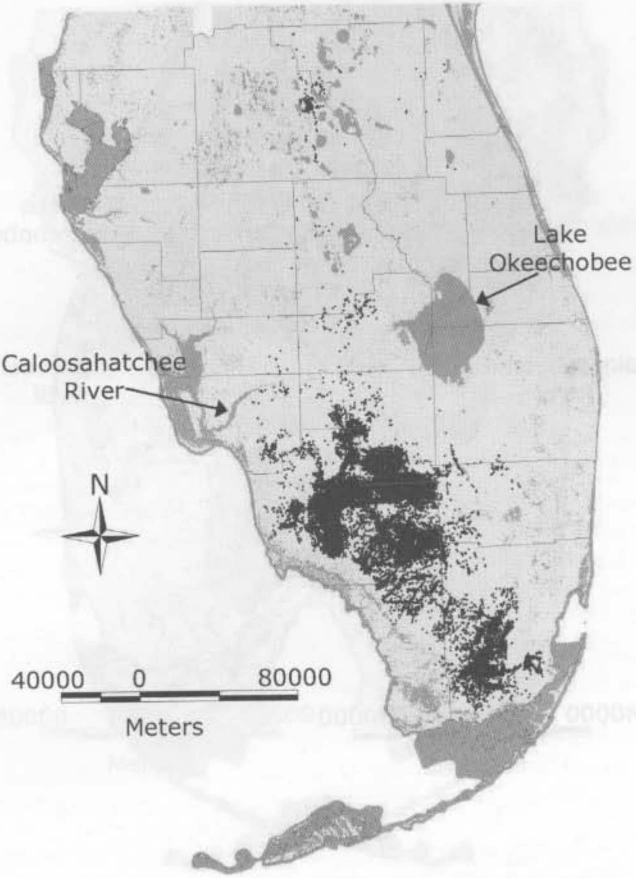

Figure 44.1 Florida panther radiotelemetry data (*black dots*) collected February 22, 1981, to March 30, 2002, by personnel from the Florida Fish and Wildlife Conservation Commission, Big Cypress National Preserve and Everglades National Park (U.S. Fish and Wildlife Service 2002).

Commission's land use and land cover map developed by Kautz et al. (1993) from 1985–1989 Landsat satellite TM imagery updated to 1996 using change detection analysis (U.S. Fish and Wildlife Service 2002). Forest cover patches smaller than 2 ha were eliminated, and a nonurban land cover buffer of 200 m (based on the spatial accuracy of the telemetry data; Belden et al. 1988) was added for each forest patch. Suitable habitat for the Florida panther was assumed to occur in patches greater than 2 ha in size, within 100 m of forest and more than 300 m from urban areas, based on the relationships described in Maehr and Cox (1995). The result was a map of potential panther habitat, as shown in Figure 44.1. The smallest density estimate for panthers is one panther per 110 km^2 of optimal habitat (Maehr et al. 1991). Extracting all forest patches greater than 110 km^2 in size and grouping contiguous patches together created a map of large suitable habitat patches (Figure 44.2) (U.S. Fish and Wildlife Service 2002).

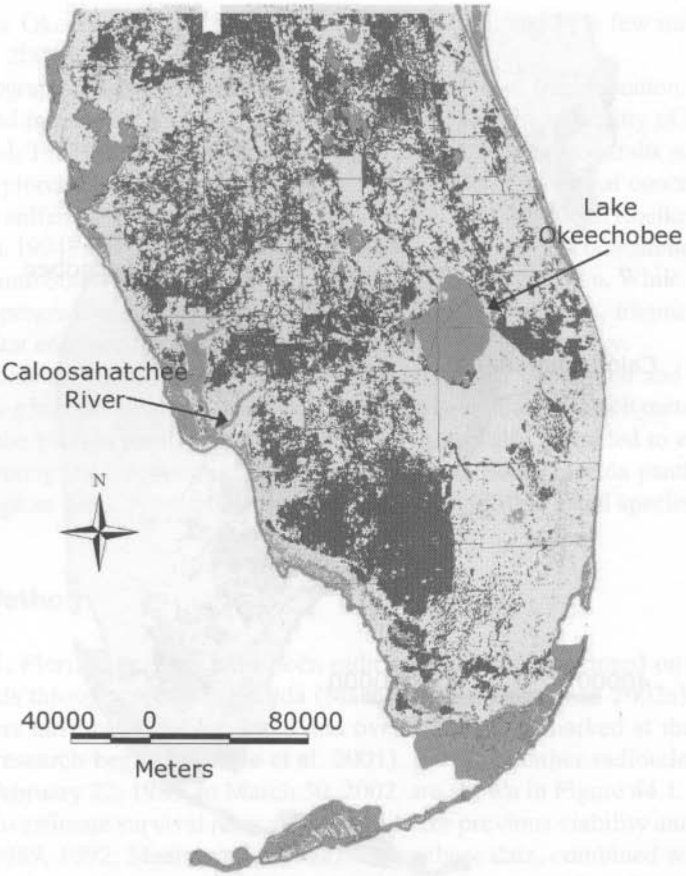

Figure 44.2 Potential panther habitat (*black areas*) in Florida based on Florida Fish and Wildlife Conservation Commission 1985–1989 Landsat data (updated to 1995–1996), combined with Florida's water management districts' 1995 data as forest patches greater than 2 ha in size plus a nonurban buffer of 200 m (U.S. Fish and Wildlife Service 2002).

Using the map of large suitable habitat patches, I delineated discrete populations in RAMAS GIS based on distribution of suitable habitat. This resulted in a metapopulation structure that grouped cells that were within normal dispersal distance into the same population (Figure 44.3). There were 10 potential populations in the model, but currently only the two populations south of the Caloosahatchee River (nos. 9 and 10 in Figure 44.3) are occupied by panthers. These two currently occupied populations are spatially distinct and have only infrequent dispersal among them.

Carrying capacity of each population was based on home range size (one panther per 110 km^2) (Maehr et al. 1991) and habitat area. The dispersal values among populations were based on the distance among populations and the dispersal patterns documented from telemetry studies (Shindle et al. 2001, Maehr et al. 2002b). For models that focused only on the existing panther populations (South Florida), only populations south of the Caloosahatchee River were considered.

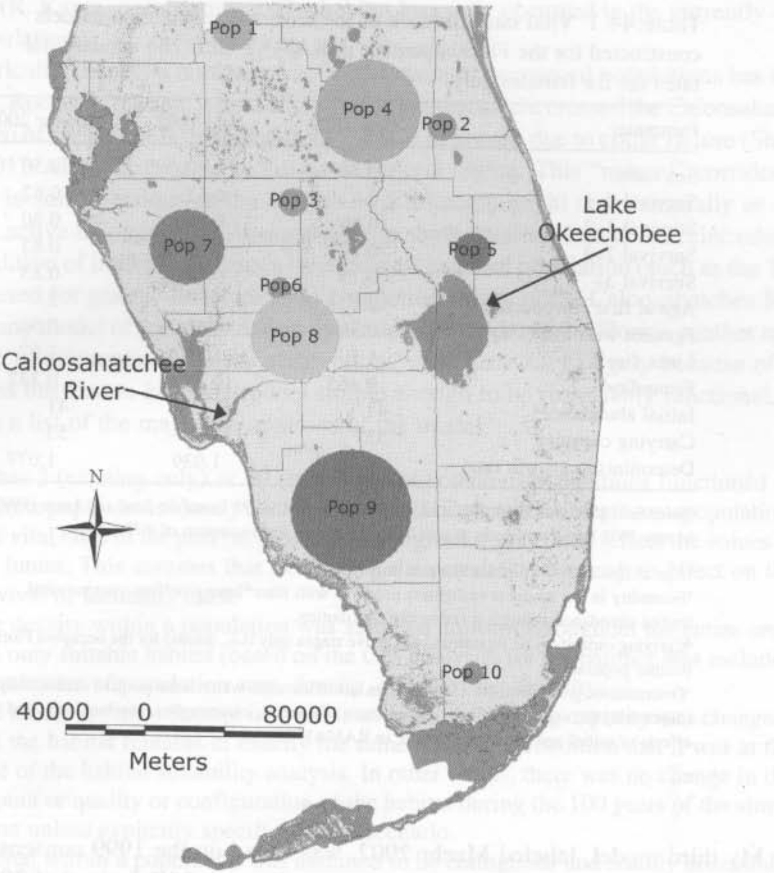

Figure 44.3 Metapopulation structure developed for the RAMAS GIS panther metapopulation model, based on the potential panther habitat (forest patches greater than 2 ha with a 200-m nonurban buffer). Only populations 9 and 10 on this map are currently occupied by Florida panthers.

For comparison, I constructed three general single-sex models, shown in Table 44.1. My Seal 1989 model was based on the analysis by Seal and Lacy (1989), except that annual juvenile mortality was updated based on more recent field data to 38% (D. Land, pers. comm.) instead of 50%. In this three-stage model, annual survival for young adults and adults is 70% and 75%, respectively. On average, females begin reproduction in their third year or later and have a 50% chance of breeding in a given year. Fecundity in this model, based on the product of the probability of breeding, average litter size, and average first-year survival, was 0.375.

I based the second model, labeled Seal 1992, on the analysis by Seal and Lacy (1992) except that juvenile mortality was also updated to 38% instead of 20%. In this two-stage model, annual survival for adults was 80%. On average, females began reproduction in their second year or later and had a 50% chance of breeding in a given year; fecundity in this model was 0.310.

Table 44.1 Vital rates for each of the three metapopulation models constructed for the Florida panther in RAMAS GIS. The annual vital rates are for females only.

Parameter	Seal 1989	Seal 1992	Maehr 2002
Sex ratio	0.50	0.50	0.50
Survival 0–1	0.62	0.62	0.62
Survival 1–2	0.70	0.80	0.80
Survival 2–3	0.70	0.80	0.83
Survival 3+	0.75	0.80	0.83
Age at first reproduction[a]	3	2	2
Females with litter (%)	0.50	0.50	0.50
Litter size	1.50	1.00	1.07
Fecundity[b]	0.465	0.310	0.332
Initial abundance[c]	41	41	41
Carrying capacity[d]	53	53	53
Deterministic growth rate[e]	0.985	1.039	1.077

Note: Seal 1989 based on Seal and Lacy (1989); Seal 1992 based on Seal and Lacy (1992); Maehr 2002 based on Maehr et al. (2002a). See text for discussion of differences.

[a] Age at first reproduction for females only.
[b] Fecundity in the model is (daughters only): % with litter*litter size*first-year survival.
[c] Initial abundance assumes a stable age distribution.
[d] Carrying capacity is on reproductively active stages only (i.e., adults) for the occupied Florida panther populations.
[e] Deterministic growth rate (or λ) is the finite rate of increase, which is the result of matrix analysis (eigenanalysis) ignoring density dependence, dispersal, catastrophes, stochasticity, and the effects of initial age/stage distribution, in RAMAS GIS.

My third model, labeled Maehr 2002, was based on the 1999 consensus model in Maehr et al. (2002 a) except that juvenile mortality was 38% instead of 20%. This was a two-stage model with young adult and adult survivals of 80% and 83%, respectively, and a fecundity of 0.332. Breeding was possible at 2 years of age or older, as in the Seal 1992 model.

Simulation Scenarios

The baseline version of each model had no catastrophes or epidemics, no change in habitat quality or amount, and a ceiling type of density dependence (maximum density 1/110 km^2). All models began with a stable age distribution. Variants of these models had different density dependence or none, various levels of habitat loss, intermittent catastrophes or epidemics, or scheduled translocations or reintroductions. I assumed that the existing South Florida panther population consisted of 41 females in two populations south of the Caloosahatchee River (populations 9 and 10 in Figure 44.3) and that the populations north of the river were "empty" or unpopulated at the start of the simulations, except when a hypothetical fully populated metapopulation was modeled. Each simulation was run with 10,000 replications for 100 years.

For models that included habitat loss, I used a 1% reduction in habitat for each of the first 25 years of the 100-year simulation. This rate of habitat loss corresponds to the estimated rate of loss from 1986 to 1996 for five southwest counties based on land use changes (R. Kautz, pers. comm.). The habitat loss only occurred in the currently occupied populations.

Historically, dispersal northward out of the currently occupied populations has rarely occurred. Recently, though, three collared male panthers have crossed the Caloosahatchee River; two of the panthers died, and third's fate is unknown due to collar failure (Shindle et al. 2001). All three crossed in the same general region. This "natural" corridor was included in some versions of the models as if a female might cross naturally or is assisted by active management. Alternatively, in some versions I modeled reintroduction as the addition of individuals from a hypothetical external population (such as the Texas cougars used for genetic restoration) to populations north of the Caloosahatchee River.

As in any model of metapopulation dynamics, the model of the Florida panther makes a number of assumptions. These assumptions were necessary largely because of data limitations but also to keep the model simple enough to be reasonably functional. Following is a list of the major assumptions of the model:

1. Either 2 (existing only) or 10 (existing plus potential) populations functioned as discrete populations loosely connected through dispersal, forming a metapopulation.
2. The vital rates of the past (as measured through telemetry data) reflect the values in the future. This assumes that monitoring the population has had no effect on the survival or fecundity rates.
3. The density within a population was assumed uniform throughout the entire area, and only suitable habitat (based on the GIS analysis) for the panther was included in estimates of population area, density, and carrying capacity.
4. The model assumes (except in the scenarios where carrying capacity was changed) that the habitat remains in exactly the same shape and condition that it was at the time of the habitat suitability analysis. In other words, there was no change in the amount or quality or configuration of the habitat during the 100 years of the simulation unless explicitly specified in the scenario.
5. Habitat within a population was assumed to be contiguous and readily accessible.
6. Dispersal was considered as permanent movement of a proportion of individuals from one population to another in a single year. This was dependent on the distance among the populations, although travel across the Caloosahatchee River was very infrequent.
7. For the purposes of reproduction, mates were assumed to be readily available and non-limiting.
8. The density ceiling only applied to adults to simulate territoriality.

Results

Under assumptions of no change in habitat and no catastrophes, the models suggest that the Florida panther was likely to persist (i.e., probability of extinction >0) over the course of the 100-year simulation. For the Seal 1989 model, the probability of extinction was 78.5% in 100 years, with a mean final abundance of 3.5 females (Figure 44.4). Also, the probability of a large decline in abundance (50%) was 94.1%. Under this model any perturbation such as habitat loss or catastrophes greatly increased the probability of extinction and resulted in mean final abundances near 0.

The probability of extinction for the existing panther populations in South Florida (Figure 44.4b) was quite low under both the Maehr 2002 and Seal 1992 models: ap-

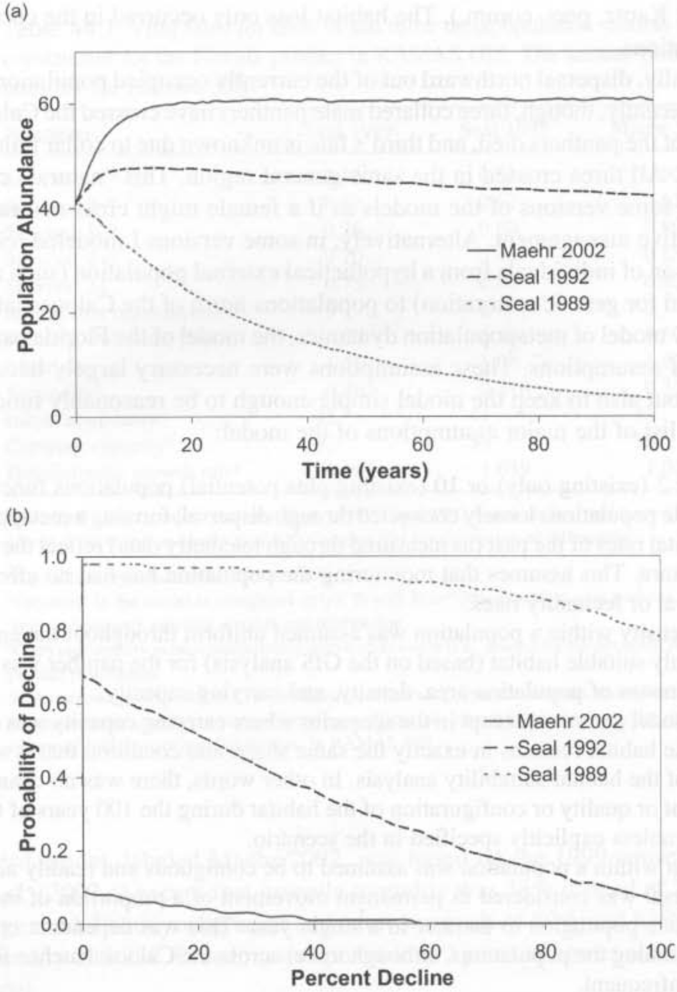

Figure 44.4 Three Florida panther metapopulation models for only the currently occupied South Florida populations: **(a)** mean final abundance over time and **(b)** probability of a decline, as a percentage of the initial abundance. The models assume no habitat changes and no catastrophes.

proximately 2% under Maehr 2002 and 5% under Seal 1992. However, the probability that the population size will decline was much greater. For example, there was a 9% probability and a 20% probability that the number of panthers would decline by half for the Maehr 2002 and Seal 1992 models, respectively. The mean final abundance of females, shown in Figure 44.4a, was 42.3 females and 51.2 females for the Seal 1992 and Maehr 2002 models, respectively. When the model included all of the potential populations north of the Caloosahatchee River (assuming these potential populations are unpopulated at the beginning of the simulation) and allowed infrequent distance-dependent dispersal among all of the populations, the probability of extinction was reduced (by 1%–2%); the probability of a 50% decline was reduced (by 5%–9%); and the mean final abundance was much larger (111%–220%), as shown in Figure 44.5.

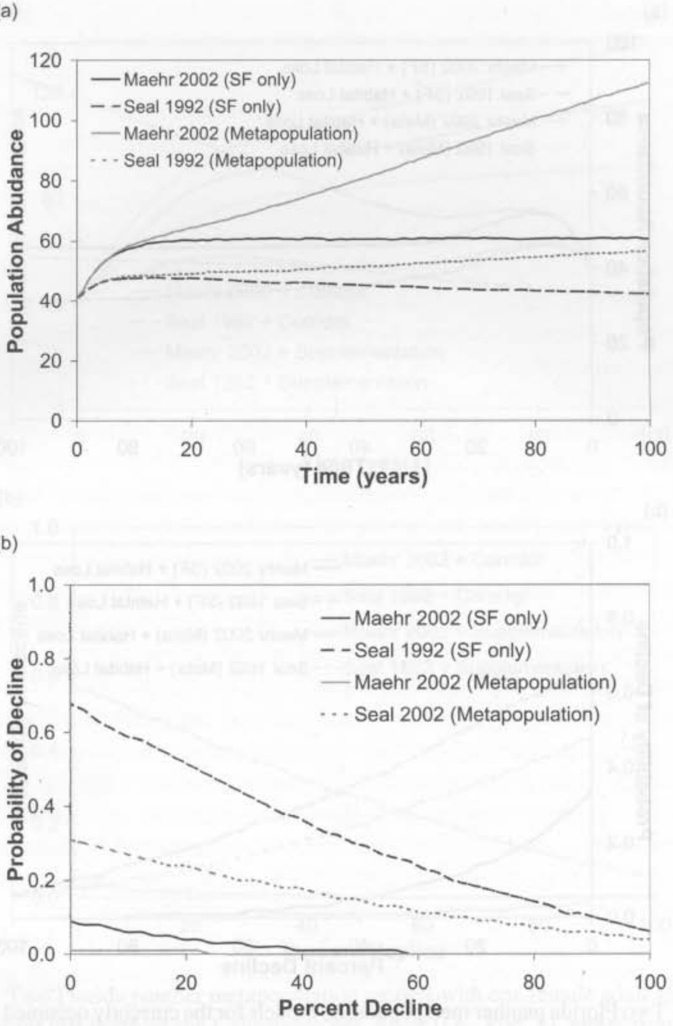

Figure 44.5 Two Florida panther metapopulation models for only the currently occupied South Florida populations (SF only) or all potential populations (Metapopulation): **(a)** mean final abundance over time and **(b)** probability of a decline, as a percentage of the initial abundance. The models assume no habitat changes and no catastrophes.

If 25% of the habitat is lost over the first 25 years of the simulation (i.e., 1% lost per year), the probability of extinction is increased approximately 1% (Figure 44.6a). The mean final abundance with habitat loss, though, is reduced by 26% to 37.9 and 31.2 females for the Maehr 2002 and Seal 1992 models, respectively. Similarly, the probability of extinction is only slightly increased when all potential populations are included and if habitat loss is restricted to the two southern populations (Figure 44.6b). Even with the additional populations, though, the mean final abundance with habitat loss is reduced by 19% to 24%, compared to the same models without the habitat loss.

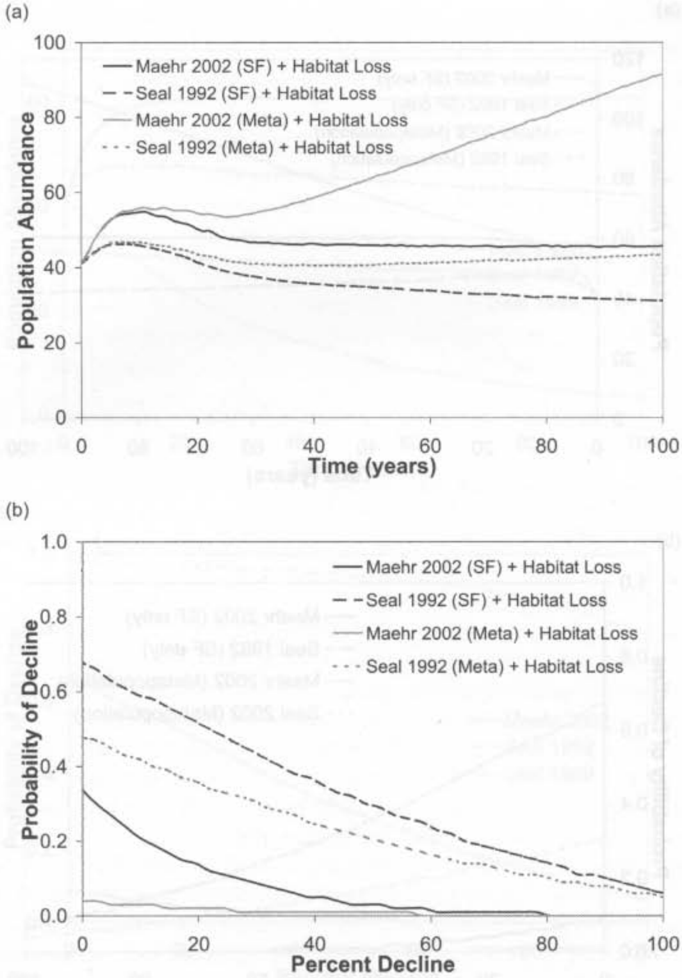

Figure 44.6 Two Florida panther metapopulation models for the currently occupied South Florida populations (SF) or all potential populations (Meta), with and without habitat loss: **(a)** mean final abundance over time and **(b)** probability of a decline, as a percentage of the initial abundance. Habitat loss, when included, was modeled as a 1% loss of habitat, in the currently occupied populations only, for the first 25 years of the 100-year simulation.

If one female adult, each year, crossed the Caloosahatchee northward at a natural corridor, the mean final number of females increased substantially from the initial two southern populations (Figure 44.7a), and the probability of extinction decreased (Figure 44.7b) with the Maehr 2002 set of parameters. With the corridor, the number of females increases as the northern populations are filled, increasing by 66 additional panthers. It is interesting to note that, with the Seal 1992 set of parameters, the increase in the mean final abundance is not present at the end of the 100 years and the probability of extinction actually increases slightly. In contrast, with either the Seal 1992 or the Maehr 2002 parameters, if the additional female adult added to the population north of

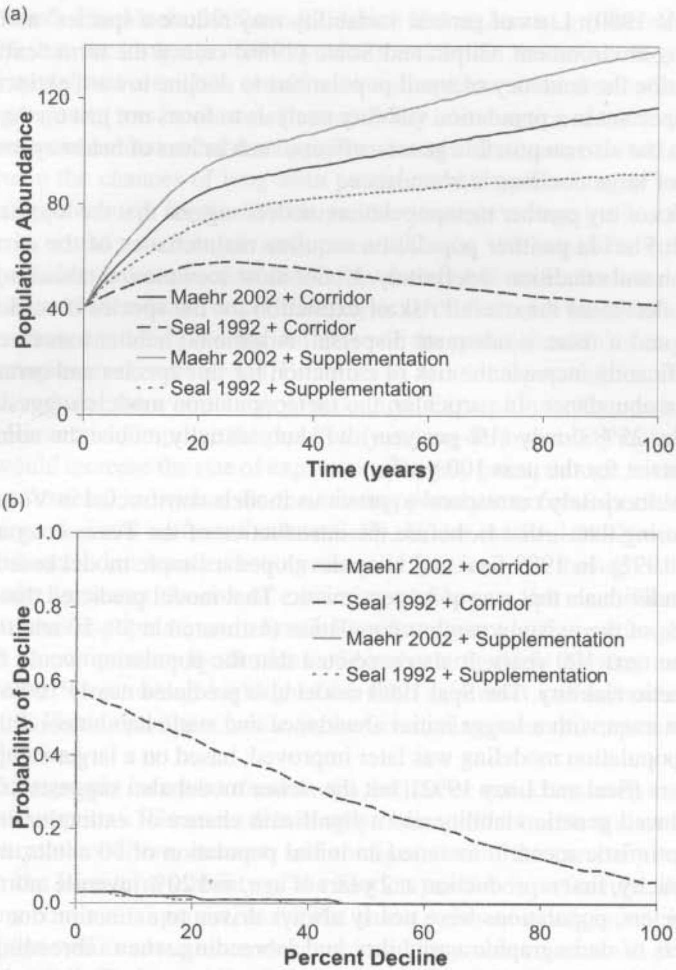

Figure 44.7 Two Florida panther metapopulation models with one female adult annually added to the population just north of the Caloosahatchee River (i.e., Pop. 8), either from the existing occupied southern populations (Corridor) or from a external source (Supplementation): **(a)** mean final abundance over time and **(b)** probability of a decline, as a percentage of the initial abundance.

the Caloosahatchee River was introduced from a population external to existing populations, such as from a captive Florida panther population, the reintroduction reduced the probability of extinction to 0 (Figure 44.7b). Reintroduction increased the number of females at the end of the 100 years by 78 to 87 (Figure 44.7a).

Discussion

Small populations, in general, are susceptible to a number of problems such as inbreeding depression, genetic drift, Allee effects, population bottlenecks, and catastrophic effects (Soulé 1980). Loss of genetic variability may reduce a species' ability to adapt to a changing environment. Gilpin and Soulé (1986) coined the term "extinction vortex" to describe the tendency of small populations to decline toward extinction. Therefore, it is important in a population viability analysis to focus not just on the probability of extinction but also on possible genetic effects, such as loss of heterozygosity, and the probability of large declines in abundance.

The results of my panther metapopulation models suggest that the long-term survival of the South Florida panther population requires maintenance of the current habitat configuration and condition indefinitely. Under most scenarios, establishing additional populations decreases the overall risk of extinction for the species if sufficient habitat is available and if there is adequate dispersal. Additional habitat loss or catastrophes would significantly increase the risk of extinction for this species and certainly lead to a decrease in abundance. In particular, the metapopulation models suggest that reducing habitat by 25% slowly (1% per year) will substantially reduce the number of panthers that persist for the next 100 years.

These results closely correspond to previous models constructed in Vortex based on early monitoring data—that is, before the introduction of the Texas cougars (Seal and Lacy 1989, 1992). In 1989 Seal and Lacy developed a simple model based on a small number of individuals that was quite pessimistic. That model predicted that there was a 100% chance of the existing panther population (estimated at 30–50 adults) becoming extinct in the next 100 years. It also predicted that the population would have greatly reduced genetic viability. The Seal 1989 model also predicted nearly 100% probability of extinction even with a larger initial abundance and static habitat conditions.

Panther population modeling was later improved, based on a larger sample of monitored panthers (Seal and Lacy 1992), but the newer model also suggested that the panther had reduced genetic viability and a significant chance of extinction in 100 years. The most optimistic scenario assumed an initial population of 50 adults, no change in carrying capacity, first reproduction at 2 years of age, and 20% juvenile mortality. Under these parameters, populations were nearly always driven to extinction due to the interacting effects of demographic variability and inbreeding when inbreeding effects on juvenile mortality were similar to those seen in other mammals (Ralls et al. 1988). The Captive Breeding Specialist Group recommended an introduction of genetic material from another population, which was later implemented using Texas cougars (Seal and Workshop Participants 1994). In the Seal 1992 model in RAMAS GIS, similarly, there was only a small chance (less than 5%) of extinction under static habitat conditions, and perturbations such as habitat loss significantly increased the probability of a decline from initial abundance.

Maehr et al. (2002a) developed a panther model using a consensus approach for parameter estimation. The model, run in Vortex, resulted in a 99% or greater probability of the panther population persisting for the next 100 years, although the final median population sized varied, depending on the conditions. For example, a 25% loss in habitat (over 25 years) did not increase the probability of extinction, but the final population size was 46.7 panthers compared to 65.6 panthers without habitat loss. The results for the Maehr 2002 model were very similar, with a greater than 99% probability of persistence over 100 years but reduced population sizes with habitat loss.

These models suggest that the probability of a large decline is likely for the Florida panther population unless the population increases substantially in size or its growth rate is increased. The Maehr 2002 model, which had an annual growth rate of approximately 7.7%, has the lowest probability of extinction and the largest mean final abundance. The model was also quite sensitive to assumptions about density dependence. If the carrying capacity was increased, the probability of extinction also decreased. Therefore, restoration of habitat or habitat improvement to make it more suitable for panthers would increase the chances of long-term panther viability. Two major issues complicate habitat improvement for the Florida panther, though: a large portion of the habitat that panthers currently used is privately owned (Maehr 1990), and the currently unoccupied, but suitable, habitat north of the Caloosahatchee River is characterized by a high degree of fragmentation based on a GIS analysis (U.S. Fish and Wildlife Service 2002).

Based on these modeling results and those of the past, a number of important management strategies are recommended. Establishing additional populations, all other things being equal, reduces the overall risk of a decline. Expansion to the north of the Caloosahatchee River could improve the probability of long-term viability and sustainability; a corridor would increase the rate of expansion. The key point, though, is that there must be sufficient "excess" individuals in the existing populations for dispersal, or the probability of large declines increases substantially. Under the Seal 1992 model, a simple corridor, with one adult female moving annually (naturally or through active management), actually increases the risk of extinction and lowers the mean final abundance. The current panther populations in South Florida may not be large enough or growing fast enough to compensate for the loss of panthers regularly moving north over the Caloosahatchee River, which highlights the need to protect and enhance the existing populations of Florida panthers, while further evaluating potential expansion habitat in unoccupied areas.

Habitat loss greatly increases the risk of a decline or extinction even under the most optimistic assumptions. These models clearly indicate that unless we are able to safeguard the current condition, amount, and configuration of the currently occupied panther habitat, the long-term viability of the Florida panther is not secure. While Florida panthers may continue to persist, as habitat is lost, without management interventions the populations will become more vulnerable to the problems of small populations—for example, inbreeding and Allee effects, as the number of individuals dwindles. It cannot be overemphasized that these models assume that there will be no loss of habitat (unless specifically mentioned), no degradation in quality, no difficulties in finding mates, no additional human-induced mortality, and no intermittent catastrophic events. In addition, if recovery goals are to expand the population of panthers, more habitat will be needed to allow for population expansion and subsequent dispersal.

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