

sus model, we gradually increased carrying capacity (K) in order to judge the subsequent affect of a growing population on heterozygosity (H) over 100 years. Increasing K from 70 to 500 resulted in an increase in H from 72.2% to 92.4%, respectively (table 14.4). If the genetic goal of panther recovery were to retain 90% of the population's initial heterozygosity (Soulé et al. 1986), then the population would need to be increased to more than 300.

Rapid recovery from a population bottleneck may be the most effective form of genetic management. Fortunately, demographic modeling suggests that the panther population could rapidly expand into additional habitat should it be made available. This focuses attention on the need for landscape management as part of Florida panther recovery, but also raises the question of whether captive breeding should be revisited as a population-expanding mechanism. This approach was abandoned, presumably, under the perception that future genetic problems could be circumvented with a large and rapid influx of genetic material from another subspecies. Our analyses suggest that genetic management alone may not be sufficient, because the introduction of Texas cougars will not increase the total population size unless there is enough habitat for such growth to occur. Thus, along with a needed increase in genetic variability, the Florida panther also requires a boost in carrying capacity.

Additional Variations on the Consensus Model

Whereas the consensus model indicates that genetics should play an increasingly important role in future management, we also recognize that the panther in south Florida has the capability for population growth. Relatively low mortality (Maehr et al. 1991a), low adult turnover (Maehr 1997b), high kitten survival (Maehr and Caddick 1995), recent records of the panther north of the population core (Layne and Wassmer 1988; Maehr et al. 1992), and recent dispersal of south Florida panthers to south-central Florida suggest that population expansion and colonization may occur even without human intervention. This led us to simulate the consensus model without the constraints of a finite range. To do this, we increased the carrying-capacity limit to 300 and kept all other model inputs constant. This resulted in the expansion of an initial population of 60 to 300 within 20 years. While this scenario may be unlikely under today's landownership and management patterns, the facilitation of panther movement between south Florida and south-central Florida, and the adoption of a statewide wildlife habitat conservation plan (Noss 1987; Harris and Atkins 1991; Cox et al. 1994; Carr et al. 1998; Hactor et al. 2000) could lead to population growth that would enhance the long-term survival of the subspecies.

Alternate Futures

We examined five possible future scenarios by altering three management and habitat variables either singly or in combination (table 14.3). The single effects of no population supplementation or 25% habitat loss over 25 years had no effect on the 100-year persistence probability of the simulated population. A combination of both 25% habitat loss and no supplementation reduced the probability of persistence for 100 years from 1.00 to 0.998. Adding the removal of panthers from the population to both habitat loss and no supplementation reduced the survival probability to 0.992. Without the influence of rapid genetic deterioration in the model, simulated populations were virtually assured of persisting for at least 100 years. Although managed genetic introgression has already occurred, even the exclusion of two supplemental females per decade from another population had little impact on the persistence probabilities predicted by the consensus model. We believe that the very minor impacts of these permutations on the consensus model are due to the robust demographics that have been exhibited by the panther over the last 15 years.

Overview of Model Results

The development of our consensus model followed a progression of simulations that were overly pessimistic with regard to Florida panther demographics (Seal and Lacy 1989, 1992). The early age of first reproduction in females, resistance to natural and artificial perturbations, and low mortality in juvenile and adult age classes were population features that required a decade for research to reveal. As recently as 1992 these parameters were considered too optimistic, and another decade transpired before panther PVA was revisited. In the short term, habitat loss had little impact on survival prospects of the Florida panther. In the long term, genetics were revealed as the most important factor leading to population decline. Simulations that projected a future with significantly higher carrying capacity resulted in larger final populations and adequate genetic variability.

The iteration of panther PVA presented here has suggested that conservation of the subspecies need not be driven by a crisis mentality with respect to short-term survival. Rather, the pursuit of efforts that facilitate real or artificial population growth should be the primary focus of agencies responsible for panther recovery. Thus, the immediate threats to the panther's future are those that reduce habitat availability or sever the connections between occupied habitat and habitat that can be colonized. If any crisis exists, it is due to the reluctance of agencies to grapple with the hurdles of not only securing existing panther habitat but

increasing its distribution. The panther population has time; its habitat does not.

Future Needs

We agree with Boyce (1992) and Reed et al. (1998) that most PVAs are useful as starting points for management, but are not in and of themselves sufficient. Although our consensus simulation predicts a high probability of survival for the panther, this future is contingent upon the continued availability of habitat. Despite the relative ease with which ecological change can be determined (Harcourt 1995), habitat trend and its influence on panther population increase are the most poorly understood aspects of Florida panther conservation. There are many satellite and high-altitude images available for Florida. Yet analyses related to panther habitat have been only snapshots in time. Analyses of panther habitat change over time have yet to be done. To more accurately predict the ability of the south Florida landscape to support a panther population in the future, comparisons between aerial images over time would allow managers to measure the rate of forest retreat or expansion. Geographic information system (GIS) technology could also create an image layer of permitted construction/agricultural activities that would allow the calculation of future changes. This would enhance the accuracy of predictions resulting from future Florida panther viability analyses, and could quantitatively link ongoing panther management activities with efforts to plan a statewide ecological reserve network (Carr et al. 1998; Hactor et al. 2000). The panther, as a flagship species, could help drive the ongoing efforts to conserve and restore native landscapes in Florida and the southeastern United States.

Our simulations suggest that, even with genetic supplementation, under current conditions the south Florida panther population will have persistence problems in the long term. On the other hand, raising carrying capacity results in rapid growth in modeled populations. Without the initiation of extensive forest restoration, panther habitat availability in south Florida will, at best, remain static for the next 100 years. Thus, in situ population expansion will have to occur north of the Caloosahatchee River. If the landscape can be managed to facilitate panther movement across this landscape filter, or if panthers can be moved to potential habitat, the population will be able to increase naturally.

A Metapopulation Approach

Our final simulations examined the creation of a metapopulation by allowing the existing population to colonize vacant range. To do this, we divided existing range into the Everglades sink ($N = 10$ panthers)

and the Big Cypress source ($N = 50$ panthers), and added a new region north of the Caloosahatchee River. We believe that the recent dispersal of male panthers across the river and their use of potentially high-quality habitat (Maehr et al. 1992) suggest that this area could be colonized through dispersal from the south. With a 1% probability that an animal will disperse from either the Everglades or the Big Cypress in any direction in a given year, the Big Cypress core remained at 50, the Everglades dropped to 5, and the new population north of the Caloosahatchee River grew to 35 in 100 years. Increasing the probability of dispersal to 6% increased the total population to 100, with additional growth ($N = 44$ panthers) in the colonized area. Probability of population persistence ranged from 72 to 97% for the new population, 98 to 100% for the Big Cypress core population, and 35 to 70% for the Everglades population. Persistence of simulated Everglades populations appears dependent upon frequent rescues by the Big Cypress core population. It is unknown what panther population the landscape north of the Caloosahatchee River can support. However, analyses by Cox et al. (1994) and Maehr and Cox (1995) clearly demonstrate the potential of this landscape to support panthers.

LESSONS FROM THE PANTHER CASE STUDY

Our collaboration emphasized the advantages of multiple perspectives in developing a credible PVA. This third iteration of a VORTEX-based panther PVA also demonstrated the need to periodically revisit previous analyses, reevaluate available data, and renew simulations in light of new information, compelling trends, and new management direction. It also demonstrated that no matter how well-intended the participants of a PVA may be, they can make mistakes during the process. The results of our analyses, with or without supplementation with Texas cougars, contrasts sharply with the results of the 1989 and 1992 PVAs. The 1989 panther PVA and the version presented here have few similarities despite four of the authors being participants in both simulations.

Differences in the results of the three PVAs conducted over a decade were primarily due to the use of fewer guesses in the model inputs. Importantly, we found that kittens were surviving at a higher rate, females began breeding 1.5 years earlier than other cougar populations, and adult survival was higher. Although one of the 1992 model runs offered a very optimistic view of panther demographics, it was discarded because the consensus of experts at the time indicated that there was no way that the population could be performing so well. The performance of the Florida panther population over the last decade suggests that the earlier optimistic run was probably correct.

The PVA model presented in this paper represents an evolution in both demographic information and conservation thinking as applied to the panther. The earliest applications of VORTEX to panther persistence occurred when there was great uncertainty about panther ecology and when ex situ conservation (captive breeding) was a more popular small-population management tool. Today, panther demographics and genetics are better understood, and the management focus is on in situ conservation (reserve creation and landscape management). The PVA presented here incorporated increased initial population size, increased carrying capacity, and reduced mortality. Whether these changes are the result of improving demographic conditions in the population or they reflect an improvement in the accuracy of field data is unknown.

Our PVA model suggests that, despite a demographically secure population in the short run, genetic considerations may become more important over time. Indeed, all of the initial independent models that considered the entire south Florida population predicted a very high probability of survival for 100 years. However, genetic complications frequently drove the consensus model to extinction if it was allowed to run for 500 years. Despite the uncertainty that pertains to short-term PVAs, this exercise helped create a consensus that genetic factors must be considered in the long-term management of the subspecies.

What sets this PVA apart from earlier panther PVAs is the availability of more current data and our consensus approach. The value of a consensus goal for PVAs should not be underestimated. While previous panther PVAs were done in a group setting, neither the inputs nor the results were unanimously agreed to by participants. The five authors of this paper have a wide range of perspectives on the Florida panther and on small-population management, but this was not an impediment to developing the consensus product. This diversity of expertise was likely a key factor leading to a better analysis than could have been done by a more narrowly focused group. Perhaps the clear ground rules for participation and compromise gave all of us a sense of ownership, involvement, and bipartisanship that is not always possible with PVAs where politics can influence the outcomes.

Both previous PVAs resulted in radical, single-pronged management actions. It is clear, however, that no single approach will assure the future of the Florida panther and the Florida panther genome. We hope the PVA presented here will compel managers to consider multiple solutions to the Florida panther's small-population problem. Genetic restoration, which dominates recovery efforts today, will be successful only if it is part of a larger plan that considers demographic and landscape

concerns. Ultimately, recovery should seek to expand from the quick-fix solution of genetic introgression and embrace the long-term goal of conserving the Florida panther genome in an expanding landscape.

The subspecies' recovery plan calls for the reestablishment of at least three viable populations in the panther's historic range (U.S. Fish and Wildlife Service 1987). Thus, we recommend that future recovery efforts combine controlled genetic introgression with aggressive landscape management that provides opportunities for the panther to colonize significant new tracts of suitable habitat north of the Big Cypress source population. Should such efforts succeed and a third population be established, managers may wish to use artificial dispersal by moving individuals between populations. The movement of panthers among meta-population patches would counter some future genetics problems by increasing the effective population size, reducing male dominance, and maintaining proper sex ratios. Alleles could wink out in some patches but be "recolonized," just as natural subpopulations are by dispersers. Expanding numbers and distribution might also justify revisiting the role of recovery technologies such as captive breeding and artificial reproduction, without the anxiety created by a crisis mentality.

LITERATURE CITED

- Anderson, A. E., D. C. Bowden, and D. M. Kattner. 1989. Survival in an un hunted mountain lion (*Felis concolor hippolestes*) population in southwestern Colorado. *Mountain Lion Workshop* 3:57.
- Backhouse, G. N., T. W. Clark, and R. P. Reading. 1994. The Australian eastern bandicoot recovery program: evaluation and reorganization. Pages 252-269 in T. W. Clark, R. P. Reading, and A. L. Clarke, editors, *Endangered species recovery: finding lessons, improving the process*. Island Press, Covelo, California.
- Barrone, M. A., M. E. Roelke, J. Howard, J. L. Brown, A. E. Anderson, and D. E. Wildt. 1994. Reproductive characteristics of male Florida panthers: comparative studies from Florida, Texas, Colorado, Latin America, and North American zoos. *Journal of Mammalogy* 75:150-162.
- Bass, O. L., and D. S. Maehr. 1991. Do recent panther deaths in Everglades National Park suggest an ephemeral population? *National Geographic Research and Exploration* 7:427.
- Beissinger, S. R., and M. I. Westphal. 1998. On the use of demographic models of population viability in endangered species management. *Journal of Wildlife Management* 62:821-841.
- Belden, R. C. 1986. Florida panther recovery plan implementation: a 1983 progress report. Pages 159-172 in S. D. Miller and D. D. Everett, editors, *Cats of the world: biology, conservation, and management*. National Wildlife Federation, Washington, D.C.

- Belden, R. C., W. B. Frankenberger, R. T. McBride, and S. T. Schwikert. 1988. Panther habitat use in southern Florida. *Journal of Wildlife Management* 52:660–663.
- Boyce, M. S. 1992. Population viability analysis. *Annual Review of Ecology and Systematics* 23:481–506.
- Carr, M., P. Zwick, T. Hootor, W. Harrell, A. Goethals, and M. Benedict. 1998. Using GIS for identifying the interface between ecological greenways and roadway systems at the state and sub-state scales. Pages 68–77 in G. Evink, P. Garrett, D. Ziegler, and J. Berry, editors, *Proceedings of the International Conference on Wildlife Ecology and Transportation*. Florida Department of Transportation, Tallahassee, Florida.
- Caughley, G. 1994. Directions in conservation biology. *Journal of Animal Ecology* 63:215–244.
- Cox, J., R. Kautz, M. MacLaughlin, and T. Gilbert. 1994. *Closing the gaps in Florida's wildlife habitat conservation system*. Florida Game and Fresh Water Fish Commission, Tallahassee, Florida.
- Cunningham, M. W., M. R. Dunbar, C. D. Buergelt, B. L. Homer, M. E. Roelke-Parker, S. K. Taylor, R. King, S. B. Citino, and C. Glass. 1999. Atrial septal defects in Florida panthers. *Journal of Wildlife Diseases* 35:519–530.
- Dalrymple, G. H., and O. L. Bass Jr. 1996. The diet of the Florida panther in Everglades National Park, Florida. *Bulletin of the Florida Museum of Natural History* 39:173–193.
- Diamond, J. M. 1978. Critical areas for maintaining viable populations of species. Pages 27–40 in M. W. Holdgate and M. J. Woodman, editors, *The breakdown and restoration of ecosystems*. Plenum Press, New York, New York.
- Falconer, D. S. 1989. *Introduction to quantitative genetics*. 3d edition. Longman, New York, New York.
- Forrester, D. J. 1992. *Parasites and diseases of wild mammals in Florida*. University Press of Florida, Gainesville, Florida.
- Forrester, D. J., J. A. Conti, and R. C. Belden. 1985. Parasites of the Florida panther (*Felis concolor coryi*). *Proceedings of the Helminthological Society of Washington* 52:95–97.
- Frankham, R. 1995. Inbreeding and extinction: a threshold effect. *Conservation Biology* 9:792–799.
- Franklin, I. R. 1980. Evolutionary change in small populations. Pages 135–149 in M. E. Soulé and B. A. Wilcox, editors, *Conservation biology: an evolutionary-ecological perspective*. Sinauer Associates, Sunderland, Massachusetts.
- Glass, C. M., R. G. McClean, J. B. Katz, D. S. Maehr, C. B. Cropp, L. J. Kirk, A. J. McKiernan, and J. F. Evermann. 1994. Isolation of pseudorabies (Aujeszky's disease) virus from a Florida panther. *Journal of Wildlife Diseases* 30:180–184.
- Greiner, E. C., M. E. Roelke, C. T. Atkinson, J. P. Dubey, and S. D. Wright. 1989. *Sarcosystis* spp. in muscles of free-ranging Florida panthers and cougars (*Felis concolor*). *Journal of Wildlife Diseases* 25:623–628.
- Harcourt, A. H. 1995. Population viability estimates: theory and practice for a wild gorilla population. *Conservation Biology* 9:134–142.
- Harris, L. D., and K. Atkins. 1991. Faunal movement corridors in Florida. Pages 117–134 in W. E. Hudson, editor, *Landscape linkages and biodiversity*. Island Press, Covelo, California.
- Harris, L. D., and W. Cropper. 1992. Between the devil and the deep blue sea: implications of climate change for Florida's flora and fauna. Pages 309–324 in R. Peters and T. Lovejoy, editors, *Global warming and biological diversity*. Yale University Press, New Haven, Connecticut.
- Harris, L. D., T. S. Hootor, D. S. Maehr, and J. Sanderson. 1996. The role of networks and corridors in enhancing the value and protection of parks and equivalent areas. Pages 173–197 in R. G. Wright, editor, *National parks and protected areas: their role in environmental protection*. Blackwell Scientific, Cambridge, Massachusetts.
- Hedrick, P. W. 1995. Gene flow and genetic restoration: the Florida panther as a case study. *Conservation Biology* 9:996–1007.
- Hootor, T. S., M. H. Carr, and P. D. Zwick. 2000. Identifying a linked reserve system using a regional landscape approach: the Florida ecological network. *Conservation Biology* 14:984–1000.
- Lacy, R. C. 1997. Importance of genetic variation to the viability of mammalian populations. *Journal of Mammalogy* 78:320–335.
- Lacy, R. C., and J. D. Ballou. 1998. Effectiveness of selection in reducing the genetic load in populations of *Peromyscus polionotus* during generations of inbreeding. *Evolution* 52:900–909.
- Lacy, R. C., K. A. Hughes, and P. S. Miller. 1995. VORTEX: a stochastic simulation of the extinction process: version 7 user's manual. IUCN/SSC Conservation Breeding Specialist Group, Apple Valley, Minnesota.
- Layne, J. N., and D. A. Wassmer. 1988. Records of the panther in Highlands County, Florida. *Florida Field Naturalist* 16:70–72.
- Lindzey, F. G., B. B. Ackerman, D. Barnhurst, and T. P. Hemker. 1988. Survival rates of mountain lions in southern Utah. *Journal of Wildlife Management* 52:664–667.
- Logan, T., A. C. Eller Jr., R. Morrell, D. Ruffner, and J. Sewell. 1993. Florida panther habitat preservation plan. Florida Panther Interagency Committee and U.S. Fish and Wildlife Service, Gainesville, Florida.
- Maehr, D. S. 1990. The Florida panther and private lands. *Conservation Biology* 4:167–170.
- . 1992. Florida panther. Pages 176–189 in S. R. Humphrey, editor, *Rare and endangered biota of Florida*, vol. 1, *Mammals*. University Press of Florida, Gainesville, Florida.
- . 1997a. The comparative ecology of bobcat, black bear, and Florida panther in south Florida. *Bulletin of the Florida Museum of Natural History* 40:1–176.
- . 1997b. *The Florida panther: life and death of a vanishing carnivore*. Island Press, Covelo, California.
- . 1998. The Florida panther in modern mythology. *Natural Areas Journal* 18:179–184.
- Maehr, D. S., R. C. Belden, E. D. Land, and L. Wilkins. 1990a. Food habits of panthers in southwest Florida. *Journal of Wildlife Management* 54:420–423.
- Maehr, D. S., and G. B. Caddick. 1995. Demographics and genetic introgression in the Florida panther. *Conservation Biology* 9:1295–1298.

- Maehr, D. S., and J. A. Cox. 1995. Landscape features and panthers in Florida. *Conservation Biology* 9:1008–1019.
- Maehr, D. S., E. C. Greiner, J. E. Lanier, and D. Murphy. 1995. Notoedric mange in the Florida panther (*Felis concolor coryi*). *Journal of Wildlife Diseases* 31:251–254.
- Maehr, D. S., E. D. Land, and M. E. Roelke. 1991a. Mortality patterns of panthers in southwest Florida. *Proceedings of the Annual Conference of Southeastern Fish and Wildlife Agencies* 45:201–207.
- Maehr, D. S., E. D. Land, and J. C. Roof. 1991b. Social ecology of Florida panthers. *National Geographic Research and Exploration* 7:414–431.
- Maehr, D. S., E. D. Land, J. C. Roof, and J. W. McCown. 1989a. Early maternal behavior in the Florida panther (*Felis concolor coryi*). *American Midland Naturalist* 122:34–43.
- . 1990b. Day beds, natal dens, and activity of Florida panthers. *Proceedings of the Annual Conference of Southeastern Fish and Wildlife Agencies* 44:310–318.
- Maehr, D. S., J. C. Roof, E. D. Land, and J. W. McCown. 1989b. First reproduction of a panther (*Felis concolor coryi*) in southwestern Florida, USA. *Mammalia* 53:129–131.
- Maehr, D. S., J. C. Roof, E. D. Land, J. W. McCown, and R. T. McBride. 1992. Home range characteristics of a panther in south central Florida. *Florida Field Naturalist* 20:97–103.
- Minta, S. C., and P. M. Kareiva. 1994. A conservation science perspective: conceptual and experimental improvements. Pages 275–304 in T. W. Clark, R. P. Reading, and A. L. Clarke, editors, *Endangered species recovery: finding lessons, improving the process*. Island Press, Covelo, California.
- Noss, R. F. 1987. Protecting natural areas in fragmented landscapes. *Natural Areas Journal* 7:2–13.
- O'Brien, S. J., M. E. Roelke, J. Howard, J. L. Brown, A. E. Anderson, and D. E. Wildt. 1990. Genetic introgression within the Florida panther (*Felis concolor coryi*). *National Geographic Research and Exploration* 6:485–494.
- Pearlstone, L. G., L. A. Brandt, W. M. Kitchens, and F. J. Mazzotti. 1995. Impacts of citrus development on habitats of southwest Florida. *Conservation Biology* 9:1020–1032.
- Ralls, K., J. D. Ballou, and A. Templeton. 1988. Estimates of lethal equivalents and the cost of inbreeding in mammals. *Conservation Biology* 2:185–193.
- Reed, J. M., D. D. Murphy, and P. F. Brussard. 1998. Efficacy of population viability analysis. *Wildlife Society Bulletin* 26:244–251.
- Roelke, M. E., and C. M. Glass. 1992. Strategies for the management of the endangered Florida panther (*Felis concolor coryi*) in an ever shrinking habitat. Pages 38–43 in R. E. Junge, editor, *Proceedings of the American Association of Zoo Veterinarians and the American Association of Wildlife Veterinarians*. St. Louis, Missouri.
- Roelke, M. E., J. S. Martenson, and S. J. O'Brien. 1993. The consequences of demographic reduction and genetic depletion in the endangered Florida panther. *Current Biology* 3:344–350.
- Schortemeyer, J. L., D. S. Maehr, J. W. McCown, E. D. Land, and P. D. Manor. 1991. Prey management for the Florida panther: a unique role for managers. *Transactions of the North American Wildlife Conference* 56:512–526.
- Seal, U. S. 1994. A plan for genetic restoration and management of the Florida panther (*Felis concolor coryi*). Report to the U.S. Fish and Wildlife Service. Conservation Breeding Specialist Group, SSC/IUCN, Apple Valley, Minnesota.
- Seal, U. S., and R. Lacy. 1989. Florida panther population viability analysis. Report to the U.S. Fish and Wildlife Service. Captive Breeding Specialist Group, SSC/IUCN, Apple Valley, Minnesota.
- . 1992. Genetic management strategies and population viability of the Florida panther (*Felis concolor coryi*). Report to the U.S. Fish and Wildlife Service. Captive Breeding Specialist Group, SSC/IUCN, Apple Valley, Minnesota.
- Shaffer, M. L. 1990. Population viability analysis. *Conservation Biology* 4:39–40.
- Soulé, M. E., M. E. Gilpin, W. Conway, and T. Foose. 1986. The millennium ark: how long a voyage, how many staterooms, how many passengers? *Zoo Biology* 5:101–113.
- U.S. Fish and Wildlife Service. 1987. *Florida panther (Felis concolor coryi) recovery plan*. U.S. Fish and Wildlife Service, Atlanta, Georgia.

