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## Evolution of Population Viability Assessments for the Florida Panther: A Multiperspective Approach

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### ABSTRACT

We conducted a population viability analysis (PVA) for the Florida panther (*Puma concolor coryi*) and compared the results with two previous PVAs conducted in 1989 and 1992 that suggested complete extinction within 100 years. Despite a lack of full consensus regarding the inputs and results of these modeling efforts, management of this endangered subspecies moved forward first with a plan for captive breeding and more recently with planned genetic introgression. Since 1994, eight female cougars, introduced from Texas, have produced at least 40 hybrid kittens. Panther recovery has been controversial, with genetic restoration efforts questioned by analyses suggesting that demographic stability of the population may obviate the need for such radical management.

We conducted another PVA that demonstrates the value of periodically updating previous analyses. We constructed independent VORTEX models based on demographic inputs provided by each author: a federal field biologist, a state field biologist, a university conservation biologist, a university landscape ecologist, and a nongovernmental-organization population biologist. Our results indicate that the Florida panther has a high (>0.98) probability of persisting for 100 years, compared to PVAs in 1989 and 1992 that predicted complete extinction. However, an apparent capability of Florida panthers for rapid population growth is countered by potential genetic problems that might become severe beyond 100 years. Genetic erosion can be forestalled or halted by allowing for population expansion, but the conservation status of panther habitat in Florida is uncertain. We recommend an approach that emphasizes the expansion of Florida panther range, incorporates controlled genetic introgression, reconsiders rapid population growth in captivity, and embraces the long-term goal of conserving the Florida panther genome with a landscape-based strategy.

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### INTRODUCTION

Wide-ranging vertebrates, especially large carnivores, are ideally suited to serve as conservation flagships and are increasingly the subject of population viability analysis (PVA). However, there is great variation in the implementation of PVAs, whether due to the common dilemma of insufficient data (Minta and Kareiva 1994; Beissinger and Westphal 1998), or due to the inconsistency with which they are applied (Backhouse et al. 1994). At best, PVAs can be used to illustrate the linkage between populations and landscapes, and can drive adaptive management on behalf of a target species (Minta and Kareiva 1994). At worst, PVAs either are not used at all, or are relied upon as fact (Reed et al. 1998) to support agency policies in the presence of extreme uncertainty or political division among managers. Not only can the utility of PVAs be diminished by limited data, but the interpretation of available information can be influenced by the personal perspectives of the individuals conducting them (Reed et al. 1998). Because PVAs can use best guesses for model inputs, and because the collection of accurate demographic data from small populations can be a slow, painstaking process (especially for naturally rare carnivores), PVA results can easily outpace the collection of data needed to properly drive the model (Lacy et al. 1995). Caughley (1994) noted that most PVAs "are essentially games played with guesses."

Shaffer (1990) referred to the Florida panther as an example of an organism whose "survival may hinge on who mates with whom," and likened its status to that of the California condor (*Gymnogyps californianus*)—a species that has recently been repatriated to the wild with captive-raised individuals. Recovery of the panther now depends on success of a program to hybridize the Florida subspecies with individuals of another subspecies from Texas (*P. c. stanleyana*), a decision based in part on the results of a PVA generated from the program VORTEX (Lacy et al. 1995), and concerns over possible inbreeding depression.

Florida panther PVAs began in the late 1980s when little was known about the demographics of the population (Seal and Lacy 1989). The first PVA in 1989 estimated that the Florida panther had a 100% chance of becoming extinct within 100 years. Captive breeding was the recommended course of action, based on speculative data. A subsequent PVA was inconclusive, suggesting complete extinction or persistence over 100 years depending upon the values used in the model (Seal and Lacy 1992). It resulted in recommendations to abandon captive breeding and to introduce genetic material from another wild population (Seal and Lacy 1992).

Now, with two decades of supporting information, we offer a third PVA based on long-term demographic research that minimizes speculation and produces results that are very different from previous efforts. This approach is unique because it allows a retrospective analysis of two previous PVAs based on 20 years of experience and because it resulted in a consensus among participants with diverse backgrounds. We offer this case study to emphasize the dangers of applying management actions based on speculative analyses, and show that PVA can be an instructive process that becomes more realistic over time with better information.

## OVERVIEW OF PANTHER STATUS

### History of Distribution

The Florida panther has been a state and federally listed endangered subspecies since 1973. It was once distributed throughout the southeastern coastal plain, but now is confined to less than 5% of its original range in a hyper-peninsular distribution in extreme south Florida. Radio-telemetry studies began in 1980, but it was not until the end of that decade that sample sizes exceeded ten radio-collared individuals in any given year. This was due to the remote and hostile nature of the landscape, as well as the inherent rarity and uneven distribution of the panther. More recently, successful capture efforts have been attributed to a population increase beginning in the 1980s. R. McBride (personal communication) has systematically surveyed for panthers in south Florida since the early 1970s and found that current centers of population abundance were virtually uninhabited two decades ago. While there is no evidence of comparable growth in the 1990s, recent dispersal events suggest the potential for future population expansion beyond currently occupied range.

### Basic Demographics

The panther currently inhabits an area of about 8,800 km<sup>2</sup> (Maehr 1990). The most recent empirically derived population estimate is 74 individuals (9 resident males, 28 resident females, 9 transient males, and 28 dependent kittens; Maehr et al. 1991b). Panther density follows a northwest to southeast gradient: the highest densities are associated with the better drained, more productive soils and private lands of the upper Big Cypress basin, whereas the lowest densities are associated with the poorer quality, frequently inundated soils associated with the Everglades (Maehr 1997a). This density gradient also follows a pattern of declining forest abundance. The population exists in two rather distinct subunits. A larger, source population encompasses the better drained,

more productive portions of the Big Cypress physiographic region in southwestern Florida (Maehr 1997a). A smaller, ephemeral sink population inhabits the Everglades ecosystem in extreme southeastern Florida (Bass and Maehr 1991).

There is no known natural immigration from outside of south Florida. However, there are recent records of panthers north of the Caloosahatchee River (Layne and Wassmer 1988; Maehr et al. 1992). Dispersal away from south Florida is unusual. During the summer of 1998 a subadult male left south Florida by crossing the Caloosahatchee River and continues to inhabit south-central Florida at the time of this writing. Since then, at least two other males have crossed this landscape filter.

Mortality rates, litter sizes, social ecology, and patterns of land tenure are similar to some populations of *Puma concolor* in un hunted regions of western North America (Lindzey et al. 1988; Anderson et al. 1989). The greatest single cause of mortality is intraspecific aggression between males (Maehr et al. 1991a). Mortality of kittens during the period following parturition to 12 months of age has been reported to be less than 20% for both males and females (Maehr and Caddick 1995). Overall, mean annual mortality for all age and sex groups is also less than 20%. The highest mortality rates are for nonresident, dispersing males (Maehr 1998). Females are readily established in the population, and they conceive their first litter at about 18 months of age. Average litter size is two, but ranges from one to four. Successful establishment of breeding males is dependent upon avoiding intraspecific aggression, winning an encounter with an older, decrepit male, and/or demonstrating patience and luck in waiting for the disappearance of a resident adult. Most males do not breed before three years of age. Maehr and Caddick (1995) found that the production of kittens outpaced the death of adults.

Male panthers exhibit a high incidence of deformed spermatozoa (Barrone et al. 1994), and both sexes possess morphological characteristics that have been attributed to inbreeding (Belden 1986; O'Brien et al. 1990). Most Florida panthers exhibit reduced allozyme heterozygosity and a high rate of band sharing for DNA fingerprints, characteristics that have been used to explain testicular abnormalities, an apparent increase in atrial septal defects, and high levels of disease in the population (O'Brien et al. 1990; Roelke and Glass 1992; Hedrick 1995). However, discrepancies between field detections and subsequent necropsies suggest that atrial septal defects are fewer than has been previously suggested (Cunningham et al. 1999). In addition, while it is true that antibodies to a number of diseases have been detected in panther serum samples (Roelke et al. 1993), such sera-positive results do not necessarily



arise from loss of genetic diversity. On the contrary, the formation of titers to viruses and other infectious diseases is more likely explained by a functioning immune system where an encounter with a potentially lethal disease is dealt with successfully and permanently. Although environmental contaminants may have contributed to demographic instability in the small Everglades segment of the panther population (Bass and Maehr 1991), infectious diseases and contamination play an insignificant role in total mortality (Maehr et al. 1991a).

It is widely accepted that habitat loss is the most significant short- and long-term threat to the Florida panther. For example, the recent southward retreat of the state's freeze line has placed new pressures on southwestern Florida's wildlands to produce citrus. This, in addition to other intensifying agricultural practices and urbanization, will undoubtedly reduce the ability of the region to support panthers (Maehr 1992). Subsequently, Pearlstine et al. (1995) suggested that an increase in citrus development in southwest Florida could reduce "potential panther habitat" by 25 to 60%.

Such concerns led to the development of an interagency planning document to stem panther habitat loss (Logan et al. 1993). Curiously, while such reports are remarkably detailed and accurate in their portrayal of Florida's rapidly increasing human population and the spread of agriculture, no analyses have compellingly demonstrated the influence of habitat loss on Florida panther population size. In addition, there is no evidence, despite intense study, to suggest that panther numbers have declined during two decades of increasing human population. Indeed, the popular, quasi-official 1980s estimate of "30 to 50" has been replaced by the 1990s estimate of "30 to 50 *adults*." This counterintuitive result may be caused by several factors. First, panther numbers might actually be declining, but intensive monitoring and capture activities maintain a static study sample that may be an increasingly large percentage of the total population. In the absence of density-dependent adjustments this scenario seems unlikely, however, because there have not been concurrent declines in other demographic variables that would suggest a shrinking population. Second, because panthers reproduce relatively slowly and because there is little turnover in the adult segment of the population, there may be a lag between habitat loss and a measurable impact on the population. Furthermore, there may be sufficient prey resources in the landscape and adequate social flexibility in the subspecies to allow a temporary increased concentration of individuals in the face of contracting range. The impacts of loss of habitat would also be delayed in this scenario. This explanation also seems unlikely

because the basic shapes and sizes of home ranges have not changed since the inception of telemetry studies in 1980 (Maehr 1997a).

Perhaps the most likely scenario for why panther numbers have not declined over the last 20 years is because key portions of productive, occupied range have not been lost. The more serious potential problem is that loss of habitat to development is occurring in areas where panthers live but are not documented. Alternatively, lost habitat may be potential range that could be colonized, or that could serve as an important landscape linkage to potential habitat. At best, the loss of peripheral and dispersal habitat could limit the ability of the population to increase.

Despite the lack of specific data to demonstrate a negative impact of habitat loss on panthers, it must be presumed that current patterns of expanding human presence in south Florida are not benefiting the population. For the input requirements of VORTEX, then, determining a trend in carrying capacity becomes a matter of judgment. No trend has, as yet, been empirically determined. This is one example where best guesses enter into the modeling process.

#### **Recent Panther Management**

Although a number of authors have addressed the need for panther management to occur at the landscape level (Maehr 1990; Schortemeyer et al. 1991; Harris and Cropper 1992; Cox et al. 1994; Maehr and Cox 1995; Harris et al. 1996; Maehr 1997a,b), most recovery actions have focused on the individual or population level. The two most controversial recovery-based actions have been the initiation of a captive-breeding program in 1991 and purposeful genetic introgression in 1994. Both were based, in part, on the inputs and results of earlier modeling efforts (Seal and Lacy 1989, 1992). Captive breeding was abandoned in 1994 after ten kittens were removed from south Florida during 1991 and 1992. Since 1994, eight female cougars introduced from west Texas have produced at least 40 hybrid kittens. The intent of these introductions is for 20% of the Florida gene pool to be derived from Texas cougars (Seal 1994). Although breeding between Texas cougar females and Florida panther males has been successful, no plans had been made as of early 2000 to remove the Texas animals from the population. This is a potentially important issue inasmuch as the original recommendations called for a one-time infusion of genetic material from the original eight females. Some of these females have been in south Florida now for more than four years, and have not only produced their second  $F_1$  litters but have produced 75% pure Texas offspring as the result of backcrossing.

## METHODS

The PVA exercise we present here takes advantage of this history and as such represents a mature synthesis not possible for most PVAs. Most PVA efforts are too recent to allow such a retrospective analysis of their strengths and weaknesses. We used VORTEX version 7 (Lacy et al. 1995) to model Florida panther population viability independently from the different perspectives of the five authors: a federal field biologist, a state field biologist, a university conservation biologist, a university landscape ecologist, and a nongovernmental-organization population biologist. "The VORTEX program is a Monte Carlo simulation of the effects of deterministic forces as well as demographic, environmental, and genetic stochastic events on wildlife populations" (Lacy et al. 1995, 4). Key inputs of the model are listed in table 14.1.

Each contributor had equal access to published, peer-reviewed literature on panther biology as well as to recent unpublished agency progress reports from field studies of the south Florida panther population. Relevant references included those on genetics (O'Brien et al. 1990; Roelke et al. 1993), general ecology (Belden et al. 1988; Maehr et al. 1989a,b, 1990a,b, 1991b; Maehr 1990, 1997a; Maehr and Cox 1995; Dalrymple and Bass 1996), demographics (Bass and Maehr 1991; Maehr et al. 1991a; Barrone et al. 1994; Maehr and Caddick 1995; Maehr 1997a), and disease (Forrester et al. 1985; Greiner et al. 1989; Forrester 1992; Roelke et al. 1993; Glass et al. 1994; Maehr et al. 1995). Each author independently provided inputs to drive the VORTEX model on a standardized form. Collaboration among authors was prohibited during this initial step of input preparation. Each model was then run on the same computer by the senior author.

Author inputs were used to develop persistence probabilities for each of the five models (table 14.1). Each model ran 500 iterations of simulations for 100 years. Authors were then given the results of their simulation before a series of E-mail and fax transmissions were used to develop a consensus model for the group. Each author was then able to view the inputs of the other authors and reconsider the variables entered into his original simulation. Where discrepancies were more than slight, each author was asked to justify the variable in question. When a single view did not prevail, compromise was sought by averaging the five versions of the contentious variable. Results of the consensus model were then compared (table 14.2) to the original VORTEX-based PVA that was developed in 1989 (Seal and Lacy 1989), and to a subsequent analysis in 1992 (Seal and Lacy 1992).

Six other simulations based upon the consensus model were also run. Scenario 1 excluded population supplementation. Scenario 2 retained

Table 14.1 Comparison of VORTEX Model Inputs Provided Independently by the Five Authors and the Outputs Generated from These Simulations

Model Inputs and Output	Originator of Variable Estimates for the VORTEX Simulation				
	Population Ecologist (Lacy)	State Field Biologist (Land)	Federal Field Biologist (Bass)	University Landscape Ecologist (Hactor)	University Conservation Biologist (Maehr)
<i>Inputs</i>					
Inbreeding depression?	Yes	No	No	No	No
Lethal equivalents	3.14	—	—	—	—
% due to recessive lethals	50	—	—	—	—
Reproduction correlated with survival?	Yes	No	No	No	No
Polygynous mating system?	Yes	Yes	Yes	Yes	Yes
Age 1st female reproduction	2	1	3	2	2
Age 1st male reproduction	4	3	2	3	3
Maximum individual age	12	12	12	9	12
Reproduction density dependent?	No	No	No	No	No
Sex ratio at birth	50:50	50:50	50:50	50:50	50:50
Maximum litter size	4	4	2	3	4
% females with litter/year	50	50	50	60	50
SD of above	20	5	10	10	5
% litter of size 1	32.5	17.5	50	20.0	10.0
% litter of size 2	40.0	50.0	50	50.0	50.0
% litter of size 3	20.0	30.0	—	30.0	30.0
% litter of size 4	7.5	2.5	—	0	10.0
Female mortality in year 1	26.5	20	0	20	20
SD in female mortality, year 1	6.625	2.0	4	10.0	5.0
Female mortality in year 2	10.1	—	0	10	20
SD in female mortality, year 2	2.5	—	4	5.0	5.0
Female mortality in year 3	—	—	0	—	—
SD in female mortality, year 3	—	—	4	—	—
Female mortality in adults	10.1	17	25	20	20
SD in female mortality, adults	2.5	3.0	4	5.0	10.0
Male mortality in year 1	26.5	20	0	20	20
SD in male mortality, year 1	6.625	10.0	6	10.0	5.0
Male mortality in year 2	21.7	15	0	20	50
SD in male mortality, year 2	5.425	3.0	6	5.0	5.0
Male mortality in year 3	21.7	15	—	20	60
SD in male mortality, year 3	5.425	3.0	—	5.0	5.0

(continued)