

**A REASSESSMENT OF FLORIDA PANTHER VIABILITY ANALYSIS AND RECOVERY EFFORTS
FROM MULTIPLE PERSPECTIVES**

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Abstract -- We used Vortex (version 7) to model Florida panther (*Puma concolor coryi*) population viability from five perspectives. Independent analyses were based on demographic inputs provided by a federal field biologist, a state field biologist, a university conservation biologist, a university landscape ecologist, and an NGO population biologist. Despite a lack of full consensus regarding the inputs and results of earlier modeling efforts (Seal et al. 1989, Seal and Lacy 1992), management of this endangered subspecies moved forward first with a plan for captive breeding and more recently with genetic restoration. Since 1994, 8 female cougars, introduced from Texas, have produced at least 13 hybrid kittens. Panther recovery has been controversial, with genetic restoration efforts being questioned by analyses which suggest that demographic stability of the population may obviate the need for such a radical approach to small population management (Maehr and Caddick 1995). Our analyses suggest that the Florida panther has a high (>0.98) probability of persisting for 100 years. However, an apparent capability for rapid population growth is countered by genetic problems that will likely become increasingly severe with time - especially beyond 100 years. Genetic erosion can be forestalled or halted by allowing for population expansion, but the conservation status of potential panther habitat in Florida is uncertain. We recommend an approach that incorporates genetic introgression, a reconsideration of rapid population growth in captivity, and an increased emphasis on expanding the current range of the Florida panther. Improvement in habitat trend data will make substantial improvements to future simulations.

what does this mean?

As more is expected of thinly allocated conservation dollars, it has become increasingly evident that the recovery of each of thousands of endangered species will not occur through individualized management plans. The debate over the value of obscure versus conspicuous species notwithstanding (Wilson 1987, Terborgh 1988), wide-ranging vertebrates, especially large carnivores, are ideally suited to serve as flagships for ecosystems and even entire landscapes. Increasingly, population viability analyses (PVAs) have been employed to model the effects of demographics, environmental variability, catastrophes, and genetics on the persistence of small populations (Shaffer 1990, Meffe and Carroll 1997:215), and have become virtual

prerequisites to recovery planning. However, there is great variation in the implementation of PVAs - whether due to the common dilemma of insufficient data (Minta and Kareiva 1994), or 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 such as the spotted owl (Strix varia) (Minta and Kareiva 1994). At worst, PVAs 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.

Conservation biology is a crisis discipline (Soule and Wilcox 1980). The accelerated global rate of modern species extinction drives the doomsday atmosphere that pervades most endangered species research and recovery efforts. Thus, population viability analyses most often refer to the future prospects of target species not as survival chances, but as extinction probabilities. Shaffer (1990:40) referred to the Florida panther (*Puma concolor coryi*) 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 is now dependent upon the success of a program to hybridize the Florida subspecies with another from Texas, a decision based in part on the results of a population viability analysis generated from the VORTEX model (Lacy et al. 1995), and concerns over possible inbreeding depression.

With the rise in popularity of PVAs (Shaffer 1990), some scientists have openly questioned the universal applicability of this approach as part of conservation planning (Caughley 1994, Harcourt 1995). Walter (1990:442) cautioned that large body size, longevity,

and low predation may be sufficient buffers against extinction for some populations such as the Socorro Island red-tailed hawk (*Buteo jamaicensis socorroensis*) which has maintained viability for more than a century despite a population that may number fewer than 50. Not only can their utility be diminished by limited data, but the interpretation of available information can be influenced by the personal perspectives of the individuals conducting a PVA (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, PVA results can easily outpace the collection of data needed to properly drive the model (Lacy et al. 1995). Caughley (1994:232) noted that most PVAs "are essentially games played with guesses," and that few have surfaced "above the grey literature." We utilized the most recent information on the Florida panther (painstakingly collected over a two-decade period) for a series of new population viability analyses, and compared them with the outcomes of PVAs conducted in 1989 and 1992 (Seal and Lacy 1989, 1992).

METHODS

We used VORTEX version 7 (Lacy et al. 1995) to model Florida panther population viability from five different perspectives. Independent analyses were based on inputs provided by a federal field biologist, a state field biologist, a university conservation biologist, a university landscape ecologist, and a non-governmental organization (NGO) population biologist. Each contributor had equal access to published, peer-reviewed literature on panther biology as well as recent unpublished agency progress reports on field studies of the south Florida panther population. Relevant references included those on genetics (Roelke et al. 1993a, O'Brien et al. 1990), general ecology (Belden et al. 1988, Dalrymple and Bass 1996, Maehr

1990, Maehr 1997a, Maehr et al 1989a, 1989b, Maehr et al. 1990a, 1990b, Maehr et al. 1991a, Maehr and Cox 1995) demographics (Barrone et al. 1994, Bass and Maehr 1991, Maehr 1997a, Maehr et al. 1991b, Maehr and Caddick 1995), and disease (Forrester 1992, Forrester et al. 1985, Glass et al. 1994, Greiner et al. 1989, Maehr et al. 1995, Roelke et al. 1993b). Each author was asked to independently provide inputs to drive the VORTEX model. Collaboration among authors was prohibited during this initial step of input preparation. These inputs were used to develop survival probabilities for each of the five models (Table 1). Each model ran for 100 years and 500 iterations. Authors were then given the results of their simulation before a series of e-mail and fax transmissions were used to develop a single, hybrid model that represented the consensus of the group. The hybrid model was then compared to the original VORTEX-based PVA that was developed in 1989 (Seal and Lacy 1989), and a subsequent analysis conducted in 1992 (Seal and Lacy 1992).

“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). Caughley (1994) provides a critical assessment of the VORTEX program in use circa 1992. The model has become widely used in recovery planning, in classroom settings, and for many individuals dealing with small populations. VORTEX, like any simulation, produces results that are only as meaningful as the inputs are accurate - even consensus among authors does not guarantee reliable results. However, we believe that the familiarity with which each author approached this project enhances the likelihood that the model results are closer to reality than previous organized efforts to predict survival probabilities of the Florida panther. The authors have a combined total of over 70 years of experience with

Florida panther issues - more than 40 years of experience were obtained in the field. Further, we believe that our approach is itself a model of the practical application of population viability analysis for many other species. A detailed description of the model can be found in Lacy et al. (1995). Key inputs of the model are listed in the accompanying tables.

Overview of Panther Status

History of Distribution - The Florida panther has been listed as a state and federally listed endangered subspecies since 1973. The species was once distributed throughout the southeastern coastal plain, but now exhibits a hyper-peninsular distribution in less than 5% of its original range in extreme south Florida. Although radio telemetry studies began in 1980¹, it was not until the end of that decade that sample sizes exceeded 10 in any given year. This was in part due to the remote and hostile nature of the landscape as well as the inherent rarity and uneven densities of the panther. More recently, successful capture efforts have been attributed to a population increase beginning in the 1980s. R. McBride (personal communication), who has systematically surveyed for panthers in south Florida since the early 1970s has observed that current centers of population abundance were virtually uninhabited two decades ago. While there is no evidence of comparable growth in the current decade, recent dispersal events suggest the potential for future population expansion outside of what is considered occupied range.

Basic Demographics - The panther currently inhabits an area of about 1.5×10^6 ha (Maehr 1990). The most recent empirically derived population estimate is 74 (9 resident males, 28 resident females, 9 transient males, and 28 dependent kittens)(Maehr et al. 1991a). A northwest to southeast gradient in panther density exists: the highest densities are associated with the

better-drained more productive soils and private lands of the upper Big Cypress basin, whereas

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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 smaller, ephemeral population inhabits the Everglades ecosystem in extreme southeastern Florida (Bass and Maehr 1991), and acts as a population sink. The larger, source population encompasses the better drained, more productive portions of the Big Cypress physiographic region in southwestern Florida (Maehr 1997a).

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Natural immigration from outside of south Florida is unknown, however, recent records of the panther exist to the north of the Caloosahatchee River (Layne and Wassmer 1988, Maehr et al. 1992). Dispersal away from the population 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. Mortality rates, litter sizes, social ecology, and patterns of land tenure are virtually identical to populations of *Puma concolor* in unhunted regions of western North America. The greatest single cause of mortality is intraspecific aggression between males (Maehr et al. 1991b). Mortality of kittens during the period following parturition to 12 months-of-age is less than 20% for both males and females (Maehr and Caddick 1995). Overall, mean annual mortality for all age and gender groups is also less than 20%. The highest mortality rates are found among non-resident, dispersing males (Maehr 1998). Females are recruited readily into the population, and they conceive their first litter at about 18 months-of-age. Average litter size is 2, but litters of 3 and 4 also occur. Males are not so readily recruited into the population. Successful breeding in males is dependent upon avoiding intraspecific aggression, winning an encounter with an older, decrepit male, and/or

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demonstrating patience and luck in waiting for the disappearance of a resident adult. Most males do not breed before 3 years-of-age. Maehr and Caddick (1995) demonstrated that the production of kittens outpaces the death of adults.

Male panthers exhibit a high incidence of deformed spermatozoa (Barone et al. 1994), and most individuals possess morphological characteristics that have been attributed to inbreeding (Belden 1986, O'Brien et al. 1990). Most Florida panthers exhibit reduced genetic variation, reduced allozyme heterozygosity, and a high rate of band sharing for DNA fingerprints (O'Brien et al. 1990). This has been used to explain testicular abnormalities, an apparent increase in atrial septal defects, and high levels of disease in the population (Hedrick 1995, Roelke and Glass 1992, O'Brien et al. 1990). However, discrepancies between field detections and subsequent necropsies suggest that atrial septal defects do not occur at the rate that has been previously suggested (Cunningham et al. *in press*). 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 indicate "depression 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. 1991b).

It is widely accepted that habitat loss is the most significant short- and long-term threat to the population. For example, Maehr (1992:181) observed "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, will undoubtedly reduce the ability of the region to support panthers." Subsequently, Pearlstine et al. (1995:1030) suggested that an increase in citrus development in southwest Florida could reduce "potential panther habitat" by 25 to 60%. Such concerns lead 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 of the spread of agriculture, there have been no analyses that have compellingly demonstrated the influence of habitat loss on Florida panther population size. In addition, there is no evidence to suggest that panther numbers have declined during 2 decades of increasing human population and intense study (indeed, the popular, quasi-official 1980s estimate of "30-50" has been replaced by the 1990s estimate of "30-50 *adults*"). This counterintuitive conclusion may be the result of 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 percent of the total population. 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 an occurrence of habitat loss and a measurable impact on the population. Further, there may be sufficient prey resources in the landscape and adequate social flexibility in the subspecies to allow a temporarily increased concentration of individuals in the face of contracting range. Although the actual impacts of the loss in habitat would also be delayed in

this scenario, it too 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 is that panther numbers have not declined over the last 20 years because key portions of productive, occupied range have not been lost. The more serious problem is that development is, indeed, occurring, and that the loss of habitat may be in those areas where panthers live but where their presence has been undocumented or unstudied. Or, it represents potential range that could be colonized, or that could serve as an important landscape linkage to potentially colonized 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 benefitting the population. From the perspective of VORTEX, then, determining a trend in carrying capacity becomes a completely subjective process - no trend has, as yet, been empirically determined. This is where best guesses enter into the modeling process, and where modelers must become comfortable in the use of crystal balls.

Recent Panther Management - Although a number of papers and books have addressed the need for panther management to occur at the landscape level (Cox et al. 1994, Harris and Cropper 1992, Harris et al. 1996, Maehr 1990, Maehr 1997a, Maehr 1997b, Maehr and Cox 1995, Schortemeyer et al. 1991), most recovery actions have focused on the individual or population level. The two most noticeable and controversial recovery-based actions have been the initiation of a captive breeding program in 1991 and genetic introgression in 1994. Both were based, in part, on the inputs and results of earlier modeling efforts (Seal and Lacy 1989, Seal and Lacy

1992). Captive breeding was abandoned in 1994 after 10 kittens were removed from south Florida during 1991 and 1992. Since 1994, ⁵ 8 female cougars, introduced from west Texas, have produced at least ¹⁶ 16 hybrid kittens. The intent of these introductions is for 20% of the Florida gene pool to derive from Texas cougars (Seal 1994). Although breeding between Texas cougar

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females and Florida panther males has been successful, no plans have been made 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 8 females. Some of these females have now been in south Florida for more than 4 years and have produced their second F1 litters.

RESULTS and DISCUSSION

Four out of 5 independent models resulted in south Florida panther populations that maintained a >99% probability of surviving for 100 years. Mean final populations derived from these models ranged from 34 to 83 (Table 1). The single model that had a very low probability of survival (<7%) reflected demographics for residents of the Everglades only. This area represents a very large proportion (>50%) of occupied panther range, but it supports only a small segment (<10%) of the total population in south Florida. When compared to the original PVA conducted in 1989 (Table 2), only the Everglades model (federal wildlife biologist) and the 1992 PVA 'Consensus' model (Table 2) follow similar trajectories to extinction in less than 50 years (Figs. 1, 2, and 3). Inasmuch as the ultimate results are similar, the predicted extinctions appear to be driven by different input variables. Because the Everglades inputs reflect a very small initial population as well as a low carrying capacity, environmental variation and stochastic events are likely powerful influences on population performance. Further, without the possibility

of immigration from a nearby population (which is behaviorally and demographically possible, but precluded in this particular model), there is no opportunity for recolonization after an initial extinction. All of the other independent models considered the panther as a single, south Florida-wide population. In the 1989 PVA, estimates based on small sample sizes and speculation suggested mortality rates of 50% for kittens and 25-30% for older age classes. Although litter sizes were relatively large in the 1989 PVA, age at first reproduction in females was 3, and habitat loss was predicted to equal 50% (Table 1). In addition, catastrophes, which were predicted to occur infrequently, were modeled to have a greater influence on the population when they did occur than were allowed in any subsequent analyses. The 1992 'Consensus' model had slightly lower mortality rates in older panthers, but did not allow population supplementation, and precluded the possibility of litters >3 . Subsequent to the 1992 PVA, the encouraging data collected during the late 1980s and early 1990s (but not used because it was viewed as overly optimistic), continued to characterize the remainder of the decade.

Agreement Among Simulation Inputs - With the exception of the Everglades model, all independent PVAs were very similar in their basic demographic composition. While only the NGO biologist incorporated inbreeding depression, predicted a 25% loss in habitat over 25 years, and suggested that litter sizes were somewhat skewed toward 1, these factors were insufficient to drive the model to extinction (although the population declined to a mean of 34) (Table 1). General agreement among models was reflected in similar biological inputs such as age at first reproduction, age of senescence, gender ratio at birth, lack of density dependence in reproduction, and effective population size (proportion of adults breeding). The probability of catastrophe was low or non-existent in all independent simulations. All authors agreed that the

panther has exhibited resilience against natural disasters such as Hurricane Andrew (1992), periodic drought and flood, and unnatural disturbances such as highways and research disturbance.

Disagreement among variable inputs was more prevalent than agreement. Four of us initially chose to leave inbreeding depression out of the model because of the lack of demographic proof of its occurrence. Distribution of litter size probabilities and first year mortality were highly variable, and resulted from the individual interpretation of existing data. Starting population sizes, habitat carrying capacity, and trend in habitat availability were more subjective inputs that reflected personal perspectives of each author. The variation in most of the inputs, either demographic- or habitat-related, were within reasonable limits given the relatively small population of panthers in all of south Florida and the uncertainty in some variables. For example, the high mortality estimates provided by the university conservation biologist for males aged 2-3 stemmed from the disappearance of uncollared animals in an age and gender cohort that experiences the highest mortality in the collared population (Maehr et al. 1991b). The most uncertainty was associated with trends in available habitat. None of the initial inputs agreed on carrying capacity, in part because current population estimates are based on extrapolation (Maehr et al. 1991a), and because each of us had different visions for the trajectory of future

south Florida development.

Development of the Consensus Simulation

Reaching consensus among the 5 authors was a relatively straightforward process. For variables that have received continued research attention since earlier publications on the same subject, we relied heavily on the input from active field biologists (Land and Bass) for the most current

is this true? Do we not all feel that South Florida development will increase significantly over the next 50-100 yrs. I certainly do!

information. Thus, distributions of litter sizes, survival probabilities, and age at first reproduction were quickly resolved. Starting population size was a simple matter of using the arithmetic mean of the three values offered for the entire south Florida population. A carrying capacity that is higher than previous PVAs was based on a 20-year pattern of gradual population expansion noted by R. McBride. Under this scenario it was difficult to argue that there is a decreasing trend in habitat despite the intuitive reasoning that some forest loss must be occurring in south Florida. The consensus that population augmentation will occur and that panther removals will not simply reflects the facts that augmentation has occurred, and that captive breeding has not.

Genetic considerations - The most difficult variable to reconcile was the incorporation of inbreeding depression. However, the example of the cheetah (*Acinonyx jubatus*) notwithstanding, we all agreed that despite the apparent lack of demographic declines in the panther, genetic erosion is inevitable without immigration or rapid population growth, that some form of depression is theoretically guaranteed, and that the population is otherwise doomed to extinction (Diamond 1978).

The analyses that considered all of south Florida as a single population projected that the Florida panther is highly likely to persist for 100 years (although perhaps not in the Everglades), and three of them suggest that the population size will remain near carrying capacity. The simulation that incorporated inbreeding depression resulted in a population decline of over 30%. If allowed to run for 500 years, this model (Lacy) declines steadily to extinction (Fig. 4). Although we all recognize that demographic stability does not ensure genetic stability, most of us were reluctant to model inbreeding as an important component of simulations for the reasons

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outlined by Caughley (1994). Nonetheless, all of the simulations presented in Tables 1-3, including those that do not incorporate inbreeding depression, project considerable decay of genetic variability over the next 100 years. The loss of heterozygosity ranged from 24% in the consensus model to as high as 46% in some of the projections using input values provided independently by the authors. These losses of heterozygosity (and concomitant accumulated inbreeding) could cause a reduction in juvenile survival of 31% to 51%, if the response of Florida panthers to inbreeding is comparable to the median effect observed in a survey of 40 mammalian populations (Ralls et al. 1988). Furthermore, reductions in adult survival and fecundity resulting from inbreeding depression are often of similar magnitude as reductions in juvenile survival (Falconer 1989). Like the cheetah, the Florida panther exhibits genetic impoverishment without clear impacts on demographics (Caughley 1994). However, the much smaller panther population should be theoretically more susceptible to inbreeding effects.

Although Florida panthers exhibit morphological and physiological abnormalities (e.g., deformed tail vertebrae and cryptorchidism) that may result from past inbreeding, there is no compelling evidence that links inbreeding with demographic performance. Caughley (1994:239) suggested that in situations such as this, genetics provides "an interesting case of overdominance." However, in some species, inbreeding depression does not show up until inbreeding has accumulated to higher levels, after which rapid fitness declines can theoretically lead to extinction (Frankham 1995; Lacy and Ballou 1998). Although the Florida panther population is projected to remain demographically viable through 100 years, the population often went extinct when one of the simulations was run for 500 years (Fig. 4), presumably because of a decline in survival accompanying accumulated inbreeding. Even if the Florida

panther is found to be one of the few mammalian populations that is relatively unaffected by inbreeding, a lack of genetic diversity would reduce environmental adaptability in the taxon (Lacy 1997), and it could be questioned whether conservation objectives would be achieved if the population retained only a small portion of the gene diversity which had been present.

At workshops held in 1991 and 1992, it was recommended that some pumas from Texas be released in south Florida to restore genetic variability and reverse existing inbreeding (Seal et al. 1992). The subsequent releases of female Texas cougars in Florida will partly accomplish this. However, even in the simulations which included continued releases of unrelated females (two per decade, or about one per generation), the populations lost 24-28% of their heterozygosity over 100 years. Thus, the population in south Florida would appear to be too small to avoid considerable losses of genetic variation unless there is a steady inflow of unrelated animals. These would, of necessity, be from a different subspecies. To prevent significant future losses of the genetic diversity still present in the Florida panther, the population would have to be expanded several-fold. The size necessary to meet any specific genetic objective could be estimated with further modeling. **(Bob, is there some simple rule of thumb that could be used to suggest a rough genetic target based on what we know about panther genetics today? Also are we doing a disservice by not performing a sensitivity analysis?)** Rapid recovery from a population bottleneck is often 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 not only should focus attention on the need for landscape management as part of Florida panther recovery, but also raises the question of whether or not 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 unrelated genetic material. Our analyses suggest that genetic management alone is not enough, because the introduction of Texas cougars will not increase the total population size unless there is enough space for such growth to occur.

The models presented in this paper represent an evolution in both demographic information and conservation thinking as applied to the panther. The earliest applications of VORTEX to panther survival occurred when there was great uncertainty about panther ecology and when *ex situ* conservation was a more popular small population management tool. Today, panther demographics and genetics are largely understood, and the management focus is on *in situ* conservation. The most recent iterations of the model have 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. Regardless, these trends are reflected in the consensus "hybrid" simulation. This model suggests that genetic considerations will become more important over time. Indeed, although all of the initial independent models that considered the entire south Florida population predicted a very high probability of survival for 100 years, genetic complications drove the NGO population biologist model to extinction if it was allowed to run for 500 years. This exercise helped create the consensus among us that genetic factors must be considered in the long-term management of the subspecies. Thus, inbreeding depression and 3.14 lethal equivalents were used in the "hybrid" model.

Variations on the Consensus Model - While the consensus model acknowledges the likelihood that genetics will play an increasingly important role in future management, we also recognize

that the south Florida panther population has the capability for significant growth. Relatively low mortality (Maehr et al. 1991b), low adult turnover (Maehr 1997), 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 the recent dispersal of a south Florida panther to south central Florida, suggest that population expansion and colonization may occur even without human intervention. This lead us to simulate the "hybrid" model without the constraints of a finite range. To do this, we removed the carrying capacity limit and left all other model inputs alone. This resulted in the expansion of an initial population of 60 to 300 in about 20 years. While this scenario is unlikely under the constraints of today's land ownership and management patterns, the facilitation of panther movement between south Florida and south central Florida, and the enlistment of potential panther habitat into a statewide conservation plan (Carr et al. 1998, Cox et al. 1994, Noss 1987) could lead to population growth that would enhance the long term survival of the subspecies.

Although the results of our modeling efforts are based on nearly two decades of intensive field studies, and we have confidence in the predictions of the "hybrid" simulation, it is not possible to accurately predict changes in future management and human population trends. We tested other futures by altering three management and habitat variables either singly or in combination (Table 3). The single effects of no population supplementation or 25% habitat loss over 25 years had no effect on the survival probability of the simulated population. A combination of both 25% habitat loss and no supplementation reduced the probability of survival from 1.00 to 0.998. Adding the removal of panthers from the population to both habitat loss and no supplementation reduces the survival probability to 0.992. Without the influence of rapid

genetic deterioration in the model, simulated populations are virtually assured of survival 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 survival probabilities of the "hybrid" consensus model.

Future Needs - We agree with Reed et al. (1998), and Boyce (1992) 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. Florida is rich with satellite, and high altitude images of the state. And yet, analyses related to panther habitat are merely snapshots in time. Time-series analyses of panther habitat change have yet to be done. To more accurately predict the ability of the south Florida landscape to support a future panther population, comparisons between temporally separated aerial images could allow managers to measure the rate of forest retreat or expansion. Geographic information system (GIS) technology could also create an imaging 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 greenways system. 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, the south Florida panther population will have long-term persistence problems. On the other hand, the lifting of carrying capacity limits results in rapid growth in modeled populations. Without the initiation of extensive forest restoration, 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 more panther movement across this landscape filter, or if panthers can be moved to potential habitat, the population will be able to increase naturally. Our final simulations examined the creation of a metapopulation by allowing the population to colonize vacant range. To do this we divided existing range into the Everglades sink ($N=10$) and the Big Cypress core ($N=50$), and added a new region north of the Caloosahatchee River. We believe that the recent dispersal movements of a panther across the river and his 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 remains at 50, the Everglades drops to 5, and the new population grows to 35 in 100 years. Increasing the probability of dispersal to 6% increases the total population to 100, with additional growth ($N=44$) in the colonized area. Probability of population persistence ranges from 72% to 97%, for the new population, 98% to 100% for the core population, and 35% to 70% for the Everglades. Survival of simulated Everglades populations appears dependent upon frequent rescues by the population core. Of course, it is unknown to what degree the landscape north of the Caloosahatchee River can support a panther population. However, analyses by Cox et al. (1994), and Maehr and Cox (1995) clearly demonstrate the potential for

this landscape to support the species.

Conclusions - Our analyses emphasize the advantages of multiple perspectives in developing a credible PVA. This third iteration of a VORTEX-based panther PVA also demonstrates the need to periodically revisit previous analyses, re-evaluate available data, and renew simulations in light of new information, compelling trends, and new management direction. The results of our analyses, with or without supplementation with Texas cougars, are antithetical to the results of the 1989 and 1992 PVAs. The results of each previous analysis resulted in radical, single-pronged management actions. It is clear, however, that there is no single approach that will assure the future of the Florida panther and the Florida panther genome. What sets this PVA apart from earlier panther simulation efforts is not only the use of more current data, and a consensus among participants, but that it is a compelling statement for a manifold approach. Indeed, just as we developed an ideal hybrid simulation, future panther recovery efforts will likely be most successful if they combine a variety of management approaches. The single genetic restoration approach that dominates recovery efforts today will be most successful only if it is part of a plan that also considers demographic and spatial concerns. Thus, we recommend that future recovery efforts combine controlled genetic introgression with:

- 1) reconsideration of captive breeding to rapidly expand population numbers, and
- 2) aggressive landscape management that provides opportunities for the panther to colonize significant new tracts of suitable habitat north of the population core (Maehr 1997). This will require the renewal of linkages with zoological parks, and an increase in efforts to not only refine our knowledge of potential habitat, but to describe the trend in habitat availability.

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Table 1. Comparison of VORTEX model inputs provided independently by the five authors.

Model Variable	Originator of variable estimates for the VORTEX simulation				
	NGO population biologist	State field biologist	Federal field biologist	Academic landscape ecologist	Academic conserv. biologist
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 1 st female reproduction	2	1	3	2	2
Age 1 st male reproduction	4	3	2	3	3
Maximum individual age	12	12	12	9	12
Repro. density dependent?	No	No	No	No	No
Gender ratio at birth	50:50	50:50	50:50	50:50	50:50
Maximum litter size	4	4	2	3	4
% females w/litter/year	50	50	50	60	50
S.D. 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
F mortality in year 1	26.5	20	0	20	20
F mortality in year 2	10.1	-	0	10	20
F mortality in year 3	-	-	0	-	-
F mortality in adults	10.1	17	25	20	20
S.D. in F mortality year 1	6.625	2.0	4	10.0	5.0
S.D. in F mortality year 2	2.5	-	4	5.0	5.0
S.D. in F mortality year 3	-	-	4	-	-
S.D. in F mortality - adults	2.5	3.0	4	5.0	10.0
M mortality in year 1	26.5	20	0	20	20
M mortality in year 2	21.7	15	0	20	50
M mortality in year 3	21.7	15	-	20	60
M mortality in adults	21.7	20	66	20	20
S.D. in M mortality year 1	6.625	10.0	6	10.0	5.0
S.D. in M mortality year 2	5.425	3.0	6	5.0	5.0
S.D. in M mortality year 3	5.425	3.0	-	5.0	5.0
S.D. in M mortality - adults	5.425	3.0	6	5.0	10
Number of catastrophes	0	0	0	2	1

Prob. for catastrophe 1	-	-	-	0.05	0.02
Prob. for catastrophe 2	-	-	-	0.01	-
Repro. rate for catastrophe 1	-	-	-	0.80	.98
Repro. rate for catastrophe 2	-	-	-	0.50	-
Survival for catastrophe 1	-	-	-	0.80	0.95
Survival for catastrophe 2	-	-	-	0.50	-
% of adult males breeding	100	50	100	50	40
Starting population size	50	50	6	60	70
Habitat carrying capacity	50	60	8	70	85
S.D. of carrying capacity	0	5	2	10	5
Change in habitat	Lost	0	0	Lost	0
# of years of habitat loss	25	0	-	20	0
% habitat change per year	1	0	-	-1.5	0
Will panthers be removed?	No	No	No	Yes	No
At what annual interval?	-	-	-	1	-
For how many years?	-	-	-	10	-
# male cubs removed/year	-	-	-	1	-
# female cubs removed/year	-	-	-	1	-
Population augmentation?	Yes	Yes	Yes	No	No
If yes, at what interval?	20 years	10 years	10 years	-	-
For how many years?	100 years	100 years	100	-	-
# males added	0	0	1	-	-
# females added	6	1	2	-	-
Expected heterozygosity	0.682	0.597	0.659	0.537	0.635
Number of extant alleles	6.38	4.58	3.89	3.58	4.68
Prob. of surviving 100 years (500 iterations)	0.998	1.00	0.0689	.998	1.00
Mean final population	34.19	59.41	5.52	50.24	83.29
Mean time to extinction	-	-	7.13 years	-	-

Table 2. Variable comparison between the 1999 hybrid simulation and the original 1989 Florida panther population viability analysis.

Model Variable	Origin of Inputs			1999 Hybrid Simulation
	1989 Panther PVA Workshop	1992 Panther PVA 'Consensus'	1992 Panther PVA 'Optimistic'	
Inbreeding depression?	Yes	Yes	No	Yes
Lethal equivalents	3.4	3.0	-	3.14
% due to recessive lethals	50	50	-	50
Reproduction correlated with survival?	Yes	Yes	No	No
Polygynous mating system?	Yes	Yes	Yes	Yes
Age 1 st female reproduction	3	2	2	2
Age 1 st male reproduction	3	2	2	4
Maximum individual age	10	12	12	12
Repro. density dependent?	No	No	No	No
Gender ratio at birth	50:50	50:50	50:50	50:50
Maximum litter size	5	3	3	4
% females w/litter/year	50	50	50	50
S.D. of above	1	0	0	10
% litter of size 1	20	25	25	17.5
% litter of size 2	30	50	50	50.0
% litter of size 3	30	25	25	30.0
% litter of size 4	20	-	-	2.5
F mortality in year 1	50	50	20	20
F mortality in year 2	30	20	20	20
F mortality in year 3	25	-	-	-
F mortality in adults	25	20	20	17
S.D. in F mortality year 1	5	0	0	6
S.D. in F mortality year 2	3	0	0	3
S.D. in F mortality year 3	3	-	-	-
S.D. in F mortality - adults	3	0	0	3
M mortality in year 1	50	50	50	20
M mortality in year 2	30	20	20	30
M mortality in year 3	25	-	-	30
M mortality in adults	25	20	20	15
S.D. in M mortality year 1	5	0	0	6
S.D. in M mortality year 2	3	0	0	5
S.D. in M mortality year 3	3	-	-	5
S.D. in M mortality - adults	3	0	0	5
Number of catastrophes	2	0	0	1
Prob. for catastrophe 1	0.01	-	-	0.5
Prob. for catastrophe 2	0.02	-	-	-
Repro. rate for catastrophe 1	0.50	-	-	0.95
Repro. rate for catastrophe 2	0.30	-	-	-
Survival for catastrophe 1	0.50	-	-	0.95

Survival for catastrophe 2	0.80	-	-	-
% of adult males breeding	100	50	50	50
Starting population size	45	50	50	60
Habitat carrying capacity	45	50	50	70
S.D. of carrying capacity	1	0	0	5
Change in habitat	Lost	Lost	No	No
# of years of habitat loss	50	25	-	-
% habitat change per year	1.0	1.0	-	-
Will panthers be removed?	Yes	No	No	No
At what annual interval?	1	-	-	-
For how many years?	3	-	-	-
# male cubs removed/year	0	-	-	-
# female cubs removed/year	1	-	-	-
Population augmentation?	No	No	No	Yes
If yes, at what interval?	-	-	-	10 years
For how many years?	-	-	-	100 years
# males added	-	-	-	0
# females added	-	-	-	2
Expected heterozygosity	0	0	0.594	0.759
Number of extant alleles	0	0	4.02	8.91
Prob. of surviving 100				
years (500 iterations)	0	0	0.998	1.00
Mean final population	0	0	47.44	65.72
Mean time to extinction	23.13	43.71	-	-

Table 3. Hybrid simulation compared to 4 variations in management trajectory.

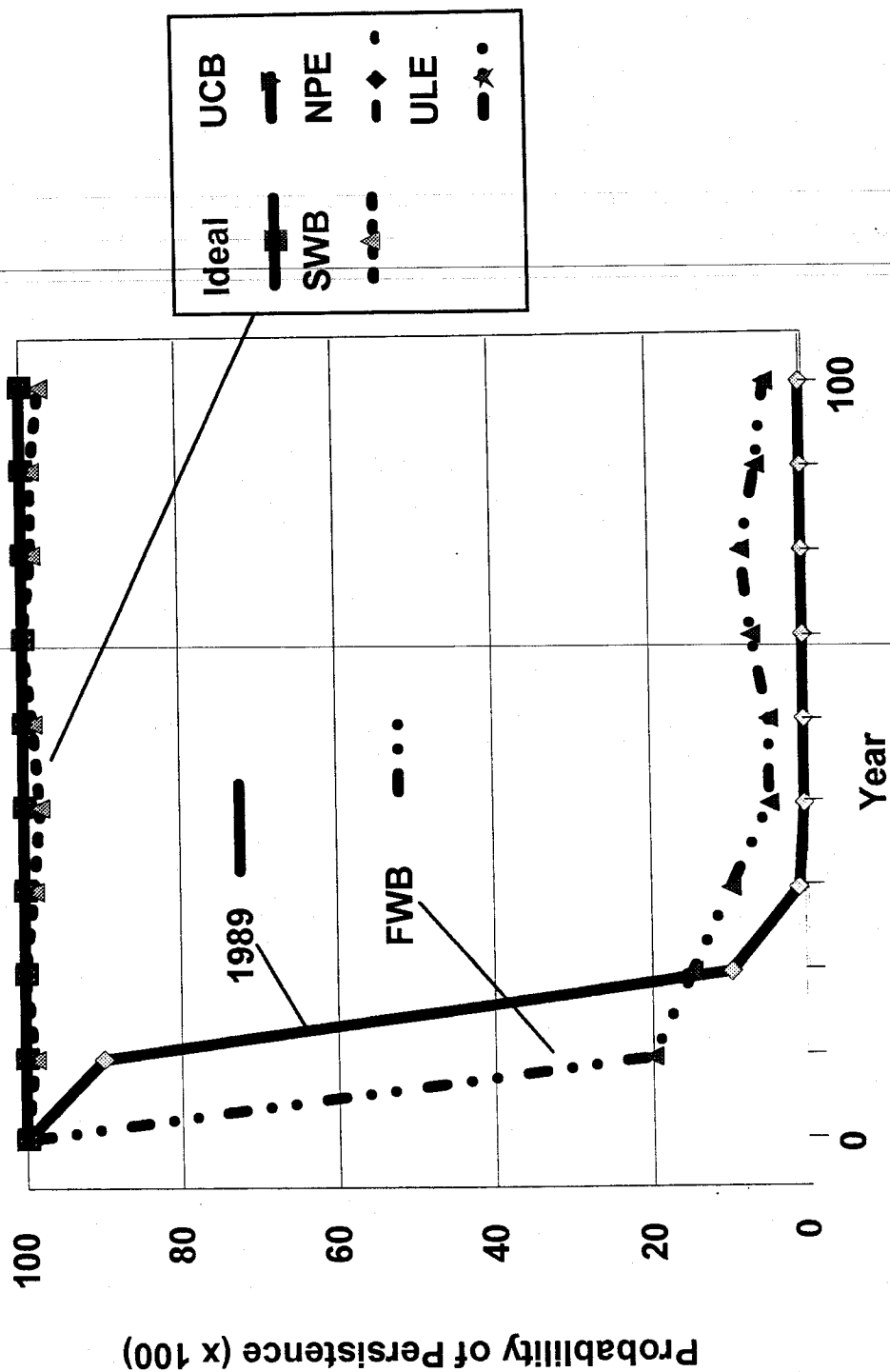
Model Variable	Simulation Variation				
	Hybrid simulation	No cats added	25% habitat lost	25% loss, no cats added	25% loss, no cats added, cats removed
Inbreeding depression?	Yes	Yes	Yes	Yes	Yes
Lethal equivalents	3.14	3.14	3.14	3.14	3.14
% due to recessive lethals	50	50	50	50	50
Reproduction correlated with survival?	No	No	No	No	No
Polygynous mating system?	Yes	Yes	Yes	Yes	Yes
Age 1 st female reproduction	2	2	2	2	2
Age 1 st male reproduction	4	4	4	4	4
Maximum individual age	12	12	12	12	12
Repro. density dependent?	No	No	No	No	No
Gender ratio at birth	50:50	50:50	50:50	50:50	50:50
Maximum litter size	4	4	4	4	4
% females w/litter/year	50	50	50	50	50
S.D. of above	10	10	10	10	10
% litter of size 1	17.5	17.5	17.5	17.5	17.5
% litter of size 2	55	55	55	55	55
% litter of size 3	25	25	25	25	25
% litter of size 4	2.5	2.5	2.5	2.5	2.5
F mortality in year 1	20	20	20	20	20
F mortality in year 2	20	20	20	20	20
F mortality in year 3	-	-	-	-	-
F mortality in adults	17	17	17	17	17
S.D. in F mortality year 1	6	6	6	6	6
S.D. in F mortality year 2	3	3	3	3	3
S.D. in F mortality year 3	-	-	-	-	-
S.D. in F mortality - adults	3	3	3	3	3
M mortality in year 1	20	20	20	20	20
M mortality in year 2	30	30	30	30	30
M mortality in year 3	30	30	30	30	30
M mortality in adults	15	15	15	15	15
S.D. in M mortality year 1	6	6	6	6	6
S.D. in M mortality year 2	5	5	5	5	5
S.D. in M mortality year 3	5	5	5	5	5
S.D. in M mortality - adults	5	5	5	5	5
Number of catastrophes	1	1	1	1	1
Prob. for catastrophe 1	0.5	0.5	0.5	0.5	0.5
Prob. for catastrophe 2	-	-	-	-	-
Repro. rate for catastrophe 1	0.95	0.95	0.95	0.95	0.95
Repro. rate for catastrophe 2	-	-	-	-	-
Survival for catastrophe 1	0.95	0.95	0.95	0.95	0.95

Survival for catastrophe 2	-	-	-	-	-
% of adult males breeding	50	50	50	50	50
Starting population size	50	50	50	50	50
Habitat carrying capacity	70	70	70	70	70
S.D. of carrying capacity	5	5	5	5	5
Change in habitat	No	No	Yes	Yes	Yes
# of years of habitat loss	-	-	25	25	25
% habitat change per year	-	-	1	1	1
Will panthers be removed?	No	No	No	No	Yes
At what annual interval?	-	-	-	-	1 (annual)
For how many years?	-	-	-	-	3
# males removed/year	-	-	-	-	0
# females removed/year	-	-	-	-	2
Population augmentation?	Yes	No	Yes	No	No
If yes, at what interval?	10 y	-	10 y	-	-
For how many years?	100 y	-	100 y	-	-
# males added	0	-	0	-	-
# females added	2	-	2	-	-
Expected heterozygosity	0.759	0.690	0.719	0.672	0.603
Number of extant alleles	8.91	5.54	7.65	5.19	4.25
Prob. of surviving 100 years (500 iterations)	1.00	1.00	1.00	0.998	0.992
Mean final population	65.58	64.16	46.72	45.21	44.70

List of Figures

- Fig. 1. Comparison of persistence probabilities for seven population viability analyses for the Florida panther: 1989, the first PVA performed on the species in 1989; FWB, inputs provided by a federal wildlife biologist; SWB, inputs provided by a state wildlife biologist; NPE, inputs provided by a non-governmental organization population ecologist; ULE, inputs provided by a university landscape ecologist; UCB, inputs provided by a university conservation biologist.
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- Fig. 2. Probabilities of Florida panther extinction for PVAs conducted in 1989, 1992, and the consensus simulation from 1999.
- Fig. 3. Mean population sizes per 10-year time intervals for Florida panther PVAs conducted in 1989, 1992, and the consensus simulation from 1999.
- Fig. 4. Mean Florida panther population size projected for 500 years for the non-governmental population ecologist PVA.
- Fig. 5. Simulated population growth of the Florida panther based on inputs from the consensus 1999 model with a carrying capacity of 300.
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Independent, 1989, & "Ideal" Hybrid Inputs



Time to First Extinction

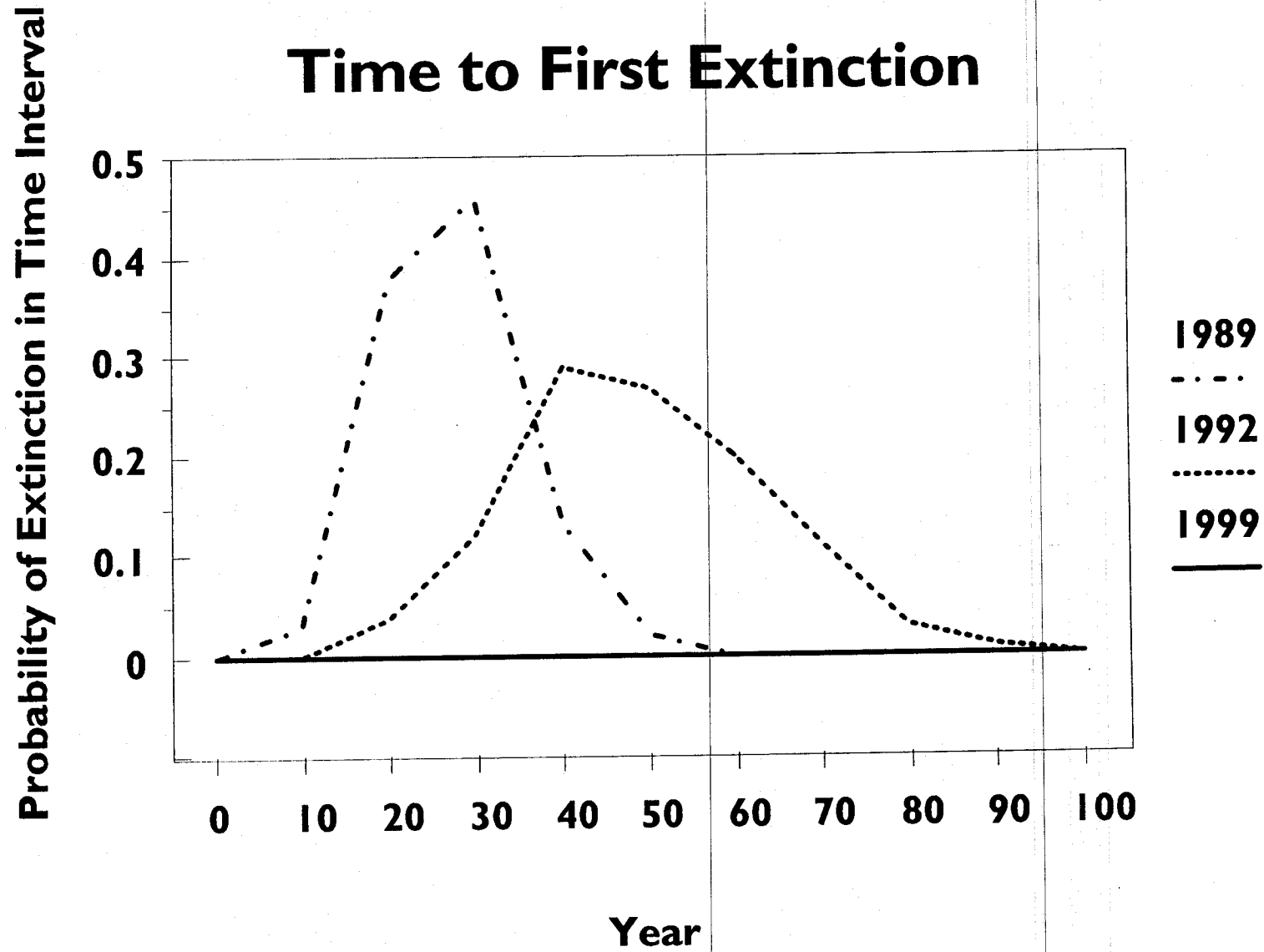


Fig. 2

Size of Extant Populations

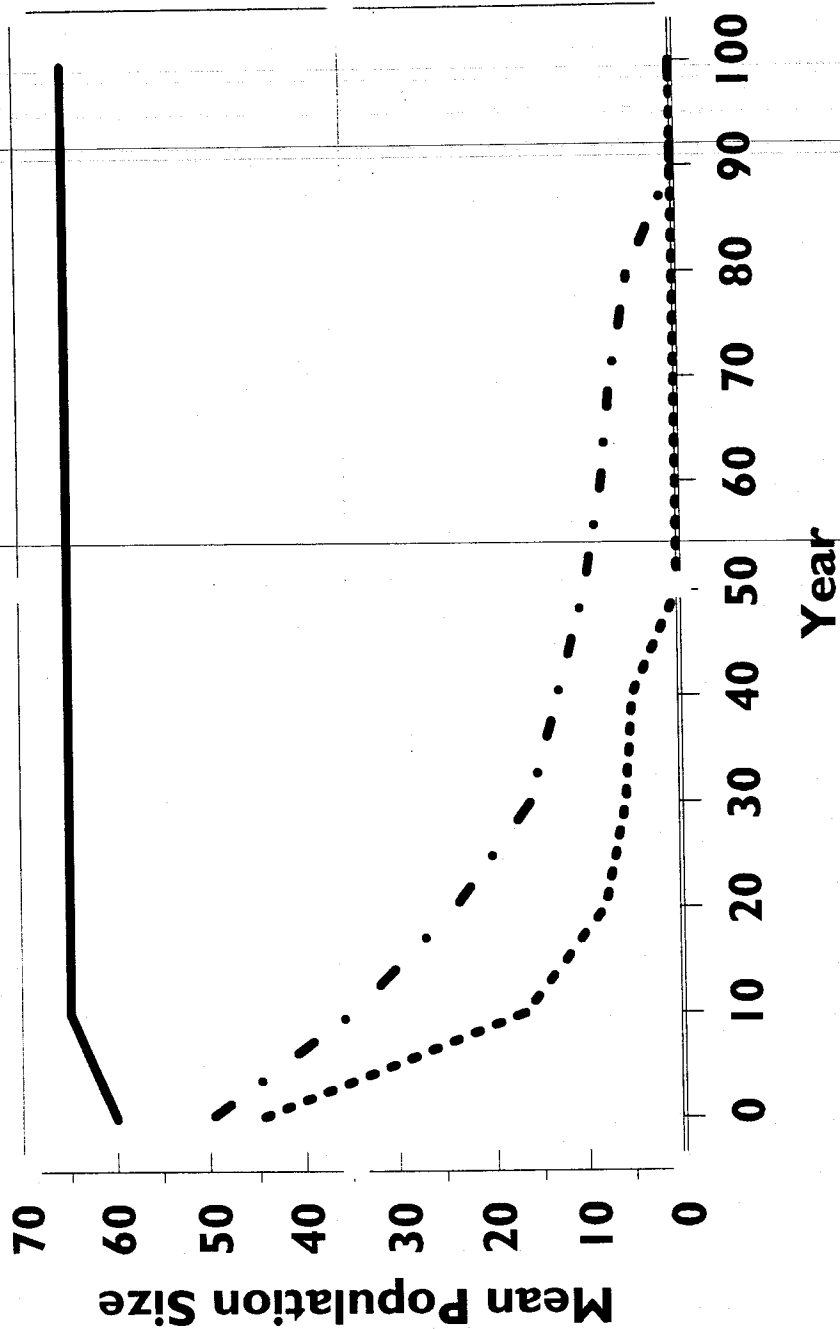
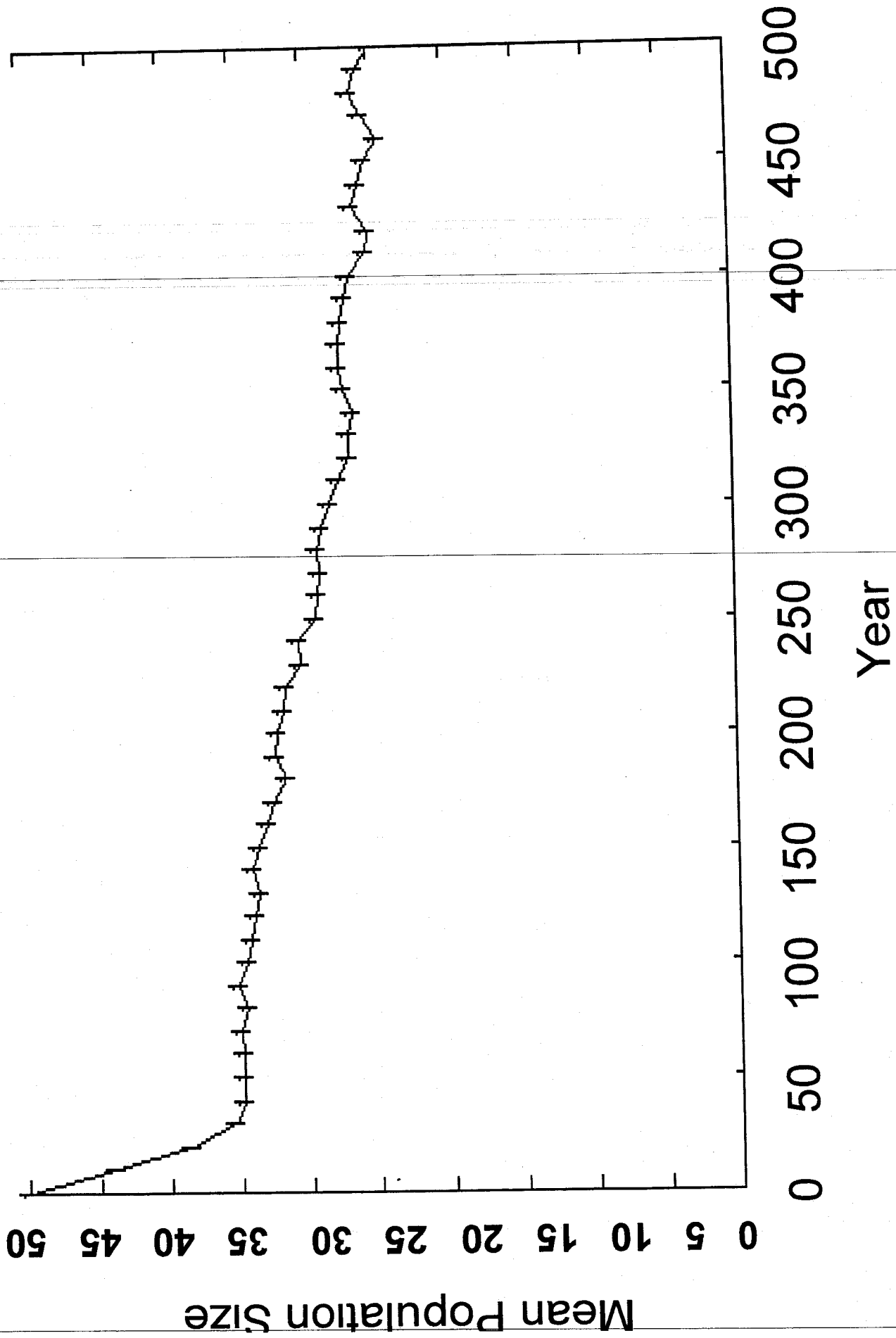
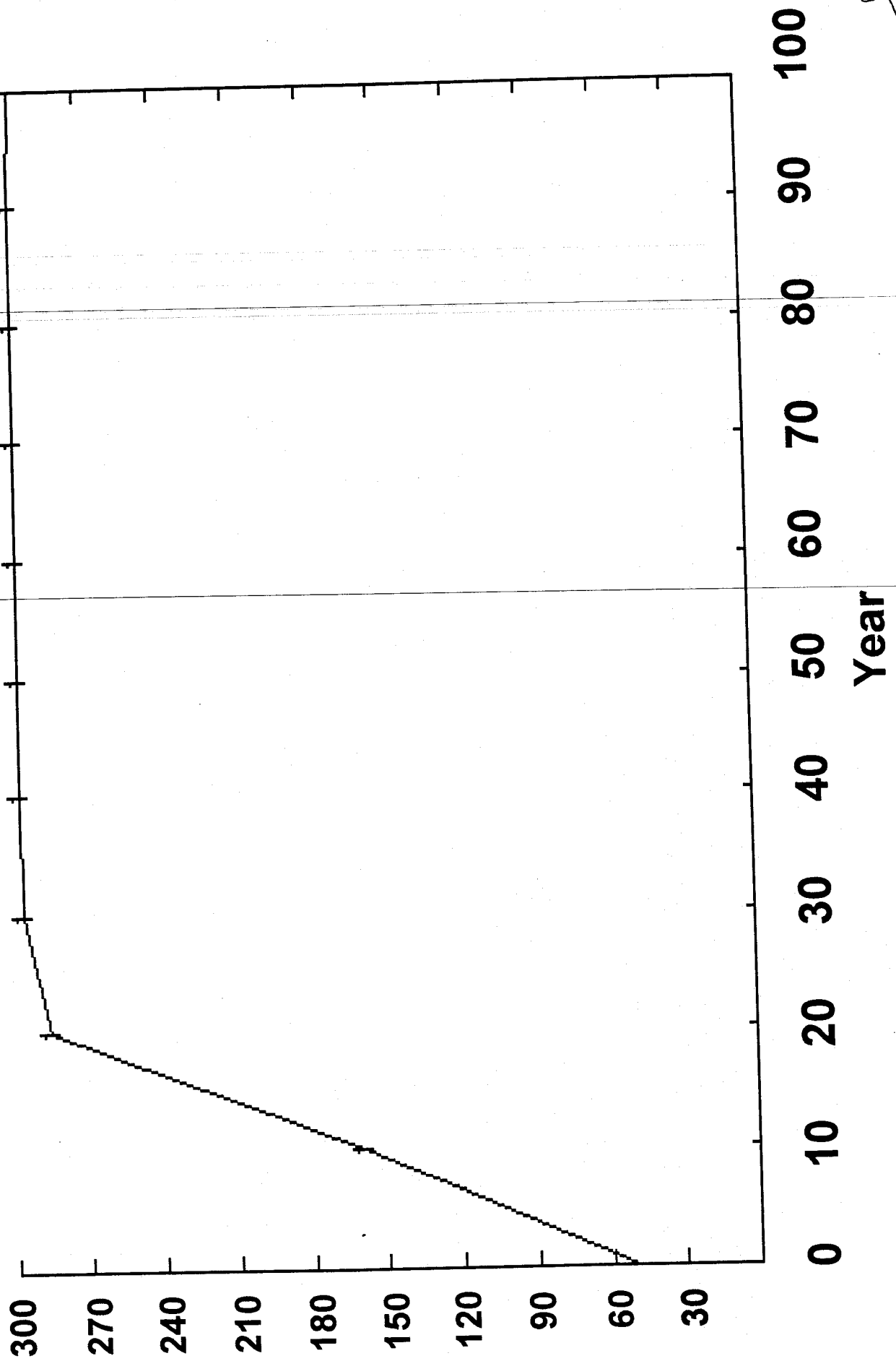


Fig 3





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