Table 14.1 (*continued*)

	Originator of Variable Estimates for the VORTEX Simulation				
Model Inputs and Output	Population Ecologist (Lacy)	State Field Biologist (Land)	Federal Field Biologist (Bass)	University Landscape Ecologist (Hoctor)	University Conservation Biologist (Maehr)
Male mortality in adults	21.7	20	66	20	20
SD in male mortality, adults	5.425	3.0	6	5.0	10
Number of catastrophe types	0	0	0	2	1
Probability for catastrophe 1	—	—	—	0.05	0.02
Probability for catastrophe 2	—	—	—	0.01	—
Reproduction rate for catastrophe 1[a]	—	—	—	0.80	.98
Reproduction rate for catastrophe 2[a]	—	—	—	0.50	—
Survival for catastrophe 1[a]	—	—	—	0.80	0.95
Survival for catastrophe 2[a]	—	—	—	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
SD of above	0	5	2	10	5
Change in habitat	Lost	0	0	Lost	0
# of years of habitat loss	25	0	0	20	0
% habitat change per year	−1.0	0	0	−1.5	0
Will panthers be removed?	No	No	No	Yes	No
At what annual interval?	—	—	—	1	—
For how many years?	—	—	—	10	—
# males removed/year	—	—	—	1	—
# females 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	100	100	—	—
# males added per event	0	0	1	—	—
# females added per event	6	1	2	—	—
Outputs					
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
Probability of persistence to 100 years over 500 iterations	0.998	1.00	0.0689	.998	1.00
Mean final population	34.19	59.41	5.52	50.24	83.29
Median time to extinction	—	—	7.13 years	—	—

Note: SD = standard deviation.

[a] These values represent multipliers that reduce survival and reproduction due to catastrophe.

Table 14.2 Comparison of Variables Used in the PVA Models

Model Inputs and Outputs	1989 Panther PVA	1992 Panther PVA Consensus	1992 Panther PVA Optimistic	1999 Consensus Simulation
Inputs				
Inbreeding depression?	Yes	Yes	No	Yes
Lethal equivalents	3.4	3.0	0	3.14
% due to recessive lethals	0	0	0	50
Reproduction correlated with survival?	Yes	Yes	No	No
Polygynous mating system?	Yes	Yes	Yes	Yes
Age 1st female reproduction	3	2	2	2
Age 1st male reproduction	3	2	2	4
Maximum individual age	15	12	12	12
Reproduction density dependent?	No	No	No	No
Sex ratio at birth	50:50	50:50	50:50	50:50
Maximum litter size	5	3	3	4
% females with litter/year	50	50	50	50
SD of above	1	0	0	10
% litter of size 1	10	25	25	17.5
% litter of size 2	20	50	50	50.0
% litter of size 3	40	25	25	30.0
% litter of size 4	20	—	—	2.5
% litter of size 5	10	—	—	—
Female mortality in year 1	50	50	20	20
SD in female mortality, year 1	5	0	0	6
Female mortality in year 2	30	20	20	20
SD in female mortality, year 2	3	0	0	3
Female mortality in year 3	25	—	—	—
SD in female mortality, year 3	3	—	—	—
Female mortality in adults	25	20	20	17
SD in female mortality, adults	3	0	0	3
Male mortality in year 1	50	50	50	20
SD in male mortality, year 1	5	0	0	6
Male mortality in year 2	30	20	20	30
SD in male mortality, year 2	3	0	0	5
Male mortality in year 3	25	—	—	30
SD in male mortality, year 3	3	—	—	5
Male mortality in adults	25	20	20	15
SD in male mortality, adults	3	0	0	5
Number of catastrophes	2	0	0	1
Probability for catastrophe 1	0.01	—	—	0.5
Probability for catastrophe 2	0.02	—	—	—
Reproduction rate for catastrophe 1	—	—	—	0.95
Reproduction rate for catastrophe 2	—	—	—	—
Survival for catastrophe 1	—	—	—	0.95
Survival for catastrophe 2	—	—	—	—
% of adult males breeding	100	50	50	50
Starting population size	45	50	50	60
Habitat carrying capacity	45	50	50	70
SD of above	1	0	0	5

(*continued*)

Table 14.2 (*continued*)

Model Inputs and Outputs	1989 Panther PVA	1992 Panther PVA Consensus	1992 Panther PVA Optimistic	1999 Consensus Simulation
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	—	—	—
# males removed/year	1	—	—	—
# females removed/year	1	—	—	—
Population augmentation?	No	No	No	Yes
If yes, at what interval?	—	—	—	10 years
For how many years?	—	—	—	100
# males added per event	—	—	—	0
# females added per event	—	—	—	2
Outputs				
Expected heterozygosity	0	0	0.594	0.759
Number of extant alleles	0	0	4.02	8.91
Probability of persisting 100 years over 500 iterations	0	0	0.998	1.00
Mean final population	0	0	47.44	65.72
Median time to extinction	23.13	43.71	—	—

Note: SD = standard deviation.

supplementation and included a 25% loss in habitat. Scenario 3 combined the changes in scenarios 1 and 2 (no supplementation; 25% habitat loss), and scenario 4 combined no supplementation, 25% habitat loss, and the removal of six females over a three-year period (table 14.3). A fifth set of simulations used the consensus model to examine the effect of a growing population on heterozygosity (table 14.4). In this scenario, carrying capacity was increased gradually from 70 to 500. The sixth scenario allowed the population to grow beyond the constraints of south Florida and simulated a population that had the capacity to colonize vacant range. This was done by increasing *K* to 300 and leaving the other variables constant. The final scenario divided existing and potential range into a metapopulation of three subpopulations: the Everglades sink, the Big Cypress Swamp source, and the region north of the Caloosahatchee River. Dispersers were two- to four-year-old panthers of either sex with a 1% likelihood of leaving either extant population.

Table 14.3 Consensus Model Simulation Compared to Four Variations in Management Trajectory over 100 Years

Model Inputs and Outputs	Consensus Simulation	No Cats Added	25% Habitat Loss	25% Loss, No Cats Added	25% Loss, No Cats Added, Cats Removed
Inputs					
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
For how many years?	—	—	—	—	3
# males removed/year	—	—	—	—	0
# females removed/year	—	—	—	—	2
Population augmentation?	Yes	No	Yes	Noy	No
If yes, at what interval?	10 years	—	10 years	—	—
For how many years?	100	—	100	—	—
# males added per event	0	—	0	—	—
# females added per event	2	—	2	—	—
Outputs					
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
Probability of persisting 100 years over 500 iterations	1.00	1.00	1.00	0.998	0.992
Median final population	65.58	64.16	46.72	45.21	44.70

Notes: Only those variables that diverge from the consensus model are displayed. All others are identical to column 4 of table 14.2.

Table 14.4 Effects of Increasing Carrying Capacity on Genetic Heterozygosity after 100 Years, Using the Consensus VORTEX Simulation

Carrying Capacity	Predicted Heterozygosity (%)[a]
70	72.2
100	80.6
150	84.1
200	86.5
250	87.5
300	89.6
400	90.7
500	92.4

[a] As percentage of initial value of *H*.

RESULTS AND DISCUSSION

Independent Simulations

Four out of the five independent models resulted in projections of the south Florida panther population that maintained a >99% probability of persisting for 100 years (table 14.1). Mean ending population size ranged from 34 to 83 individuals. The only model that had a very low probability of persistence (<7%) reflected only the demographics of the Everglades subpopulation. The Everglades represents a large proportion (>50%) of occupied panther range, but it supports only a small portion (<10%) of the total population in south Florida. Compared to the original PVA conducted in 1989 (table 14.2), only the Everglades model (federal wildlife biologist) and the 1992 PVA consensus model (table 14.2) follow similar trajectories to extinction in less than 50 years (figs. 14.1–14.3).

Inasmuch as the ultimate results were 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. Without the possibility of immigration from a nearby population (which is behaviorally and demographically possible and was excluded in this particular model), there is no opportunity for recolonization after an initial extinction. The other four 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

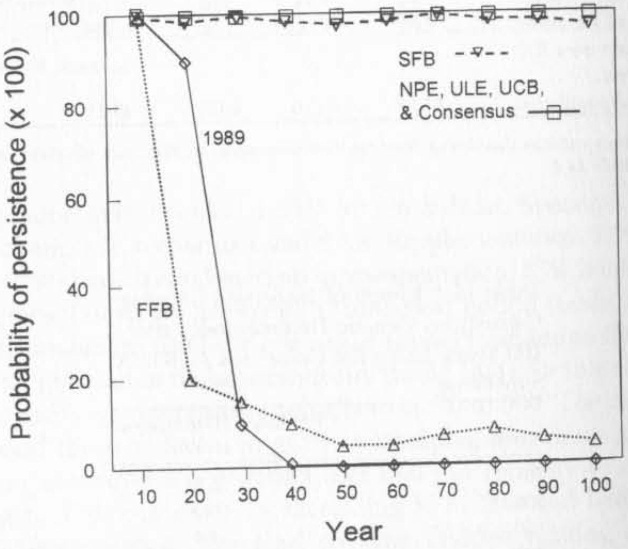

Fig. 14.1 Comparison of persistence probabilities for seven PVAs for the Florida panther: *1989*, the first PVA performed on the subspecies; *FFB*, inputs provided by a federal field biologist; *SFB*, inputs provided by a state field biologist; *NPE*, inputs provided by a non-governmental-organization population ecologist; *ULE*, inputs provided by a university landscape ecologist; *UCB*, inputs provided by a university conservation biologist; and *Consensus*, inputs resulting from the agreement among the authors.

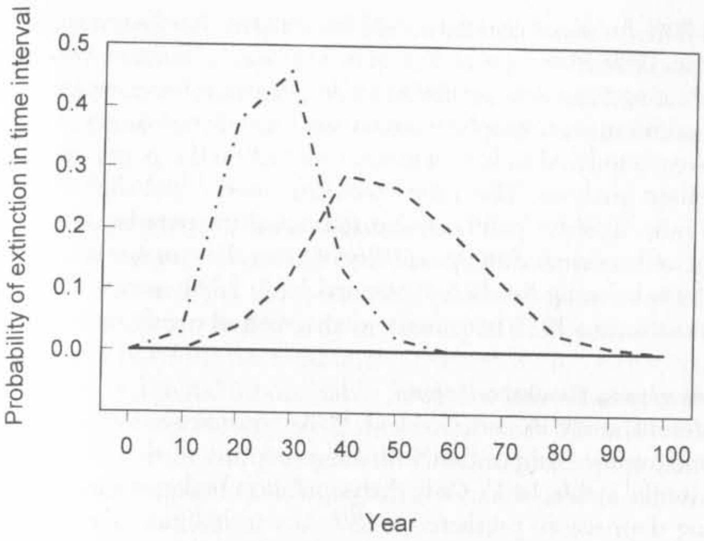

Fig. 14.2 Probabilities of Florida panther extinction for PVAs conducted in 1989 and 1992, and the consensus simulation from 1999.

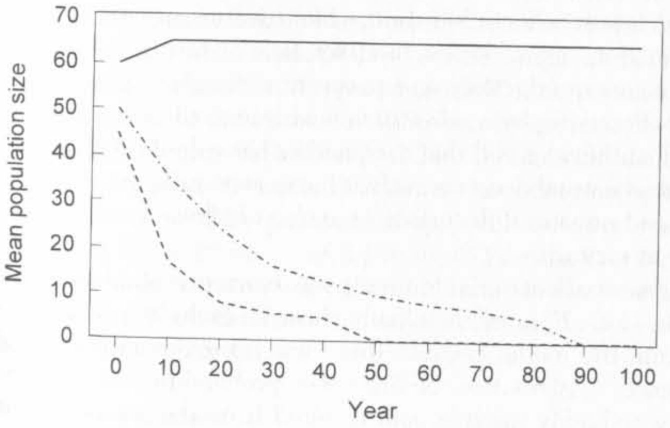

Fig. 14.3 Mean extant population sizes per ten-year intervals for Florida panther PVAs conducted in 1989 and 1992, and the consensus simulation from 1999.

and 25 to 30% for older age classes. Although litter sizes were relatively large in the 1989 PVA, age at first reproduction in females was three years, and habitat loss was predicted to be 1% a year for 50 years (table 14.2). In addition, catastrophes, which were predicted to occur infrequently, were modeled to have a greater impact on the population than in 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 litter size greater than three. Data collected during the late 1980s and early 1990s was not used in the 1992 consensus PVA because it was viewed as overly optimistic.

Agreement among Simulation Inputs

In the present study all independent PVAs were very similar in their basic demographic composition with the exception of the federal field biologist model (table 14.1). Only the population biologist incorporated inbreeding depression, predicted a 25% loss in habitat over 25 years, and suggested that litter sizes were somewhat skewed toward one. These factors were insufficient to drive the model to extinction, although population size declined to a mean of 34 (table 14.1). General agreement among models was reflected in similar biological inputs, such as age at first reproduction, age of senescence, sex ratio at birth, lack of density dependence in reproduction, and proportion of adults breeding. The probability of catastrophe was low or nonexistent in all independent simulations. All authors agreed that the panther has exhibited a virtual immunity against natural disasters such as hurricanes and periodic drought and flood, and unnatural disturbances such as highways and accidental mortalities at captures.

Disagreement about variable inputs was more prevalent than agreement (table 14.1). Four of us initially chose to exclude inbreeding depression from the model because there was no 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. Variation in most of the inputs, either demographic- or habitat-related, were within reasonable limits, given the relatively small population of panthers in south Florida and the uncertainty in some variables. For example, the high mortality estimates provided by the university conservation biologist for males aged two to three years stemmed from the disappearance of uncollared animals in an age and sex cohort that experienced the highest mortality in the collared population (Maehr et al. 1991a). The greatest 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. 1991b) 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 five authors was relatively straightforward. For variables that have received research attention since earlier publications, we relied heavily on the input from active field biologists (Land and Bass) for the most current information. Despite the discrepancy between initial inputs (table 14.1), the state and federal biologists were able to resolve opposing views of a south Florida–wide panther population versus the Everglades. Thus, model inputs based on observed demography in the Everglades were not used in subsequent iterations of the model.

Demographic Parameters

Compromises on the distributions of litter sizes, survival probabilities, and age at first reproduction were quickly achieved. Starting population size was the arithmetic mean of the three different values (two of which were identical) offered for the entire south Florida population. A carrying capacity 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 was a decreasing trend in the area of habitat used by panthers, 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 be resumed reflects the facts that augmentation has occurred and that captive breeding has not.

Genetic Considerations

Inbreeding depression was the most difficult variable to reconcile. We agreed that, despite the apparent lack of demographic declines in the panther, genetic erosion is predicted by theory, and prudence dictated that we accept this potential as a default position. Without immigration or rapid population growth, some form of depression is theoretically predicted, and the population may be otherwise doomed to extinction (Diamond 1978; Allendorf and Ryman, chap. 4 in this volume; Lande, chap. 2 in this volume). Several of us were uncomfortable with this compromise inasmuch as genetic introgression has the potential to alter the Florida panther genome sufficiently to alter important local adaptations

(Maehr and Caddick 1995). Furthermore, because the population has always existed at a distributional extreme on a large peninsula that has effectively become an island, deleterious alleles may have been purged if the decline was not too rapid. Although we recognized 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 outlined by Caughley (1994).

Despite the low rates of extinction, all of the simulations presented in tables 14.1 through 14.3, including those that did not incorporate inbreeding depression, projected considerable loss 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 some 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), so theoretically, the much smaller panther population should be 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. However, more than a decade's worth of intense monitoring has not verified that either kittens or adults suffer increased mortality. Like the cheetah, the Florida panther exhibits genetic impoverishment without clear impacts on demographics (Caughley 1994).

However, there may be long-term consequences of inbreeding. In some species, inbreeding depression does not appear until inbreeding has accumulated to higher levels, after which rapid fitness declines can lead to extinction (Frankham 1995; Lacy and Ballou 1998). Although the Florida panther population is projected to remain demographically viable through 100 years, the consensus population model declined over longer time periods, presumably because of a decline in survival due to inbreeding. If allowed to run for 500 years, the consensus model declines steadily with an increasing probability of extinction beyond 100 years (fig. 14.4). Even if the Florida panther is one of the few mammalian populations that is relatively unaffected by inbreeding, lack of genetic diversity would reduce 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 that was present when recovery efforts began. Of course, this presumes that environmental conditions will not change, or that the population will not be challenged with disease or other stresses.

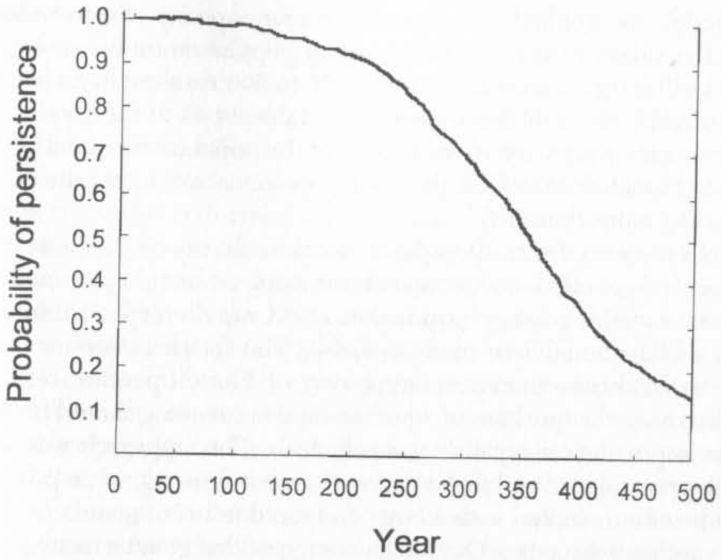

Fig. 14.4 Probability of persistence of the Florida panther based on the consensus simulation run for 500 years.

At workshops held in 1991 and 1992, it was recommended that some pumas from Texas be released in south Florida to restore genetic variability to reverse existing inbreeding (Seal and Lacy 1992). The subsequent releases of female Texas cougars in Florida will partly accomplish this. However, even in the simulations that included continued releases of unrelated females (two per decade, or about one per generation), the population lost 24% to 28% of its heterozygosity over 100 years. These models suggest that the population in south Florida is too small to avoid considerable losses of genetic variation unless there is a steady inflow of unrelated animals. If the population was allowed to grow dramatically, these individuals would, of necessity, come from a different subspecies.

To prevent significant future losses of the remaining genetic diversity in the Florida panther, the population would have to be expanded severalfold. Franklin's rule of thumb (1980) for keeping inbreeding below 1% per generation would require an effective population size of at least 50 and a doubling of panther carrying capacity. Using our consen-