

ESTIMATION OF DEMOGRAPHIC PARAMETERS AND POPULATION VIABILITY
ANALYSIS FOR THE FLORIDA PANTHER

By

JEFFREY ALLAN HOSTETLER

A DISSERTATION PRESENTED TO THE GRADUATE SCHOOL
OF THE UNIVERSITY OF FLORIDA IN PARTIAL FULFILLMENT
OF THE REQUIREMENTS FOR THE DEGREE OF
DOCTOR OF PHILOSOPHY

UNIVERSITY OF FLORIDA

2010

© 2010 Jeffrey A. Hostetler

To my family and Jennifer Russell

ACKNOWLEDGMENTS

I thank my committee M. Oli, J. Nichols, M. Sunquist, B. Bolker, and D. Onorato for their tremendous help. I thank T. O'Meara, D. Land and C. Belden for valuable advice throughout the project. All genetic and ancestry analyses were performed at the National Cancer Institute by W. Johnson, M. Roelke, and S. O'Brien; I am greatly indebted to them. I thank S. Bass, J. Benson, M. Cunningham, D. Giardina, D. Jansen, A. Johnson, D. Land, M. Lotz, C. McBride, Rocky McBride, Rowdy McBride, Roy McBride, L. Oberhofer, S. Schulze, D. Shindle, staffs at Everglades National Park and Big Cypress National Preserve, and others for assistance with fieldwork. I also thank J. Benson, B. Bolker, M. Conroy, J. Hines, J. Laake, S. Mills, J. Nichols, M. Oli, D. Onorato, M. Sunquist, D. Valle, G. White, and J. White for advice and assistance regarding data analysis and panther biology. This work was funded through the Florida Panther Research and Management Trust Fund, National Park Service, University of Florida, and grant Agreement No. 401816G091 from the United States Fish and Wildlife Service.

TABLE OF CONTENTS

	<u>page</u>
ACKNOWLEDGMENTS.....	4
LIST OF TABLES.....	9
LIST OF FIGURES.....	12
ABSTRACT	14
CHAPTER	
1 INTRODUCTION	17
2 INTENTIONAL GENETIC INTROGRESSION IMPROVES SURVIVAL OF F ₁ ADULTS AND SUB-ADULTS IN A SMALL, INBRED FELID POPULATION	20
Introduction	20
Materials and Methods.....	22
Field Methods.....	22
The Introgression Program.....	23
Estimating Age Classes.....	23
Genetic Variables	24
Index of Abundance	27
Survival Analyses	27
Results.....	32
Age, Sex, Index of Abundance, and Year	32
Genetic Ancestry and Heterozygosity	32
Cause-Specific Mortality.....	34
Discussion	34
3 GENETIC INTROGRESSION AND THE SURVIVAL OF FLORIDA PANTHER KITTENS.....	46
Introduction	46
Materials and Methods.....	49
Field Methods.....	49
Heterozygosity and Genetic Ancestry	50
Index of Abundance	52
Data Preparation and Analysis.....	52
Three-Month Time Step Data Preparation and Analysis	57
Results.....	57
Discussion	59
4 DOES GENETIC INTROGRESSION IMPROVE REPRODUCTIVE PERFORMANCE? A TEST ON THE ENDANGERED FLORIDA PANTHER	71

Introduction	71
Materials and Methods.....	73
Study Area.....	73
Field Methods.....	73
Genetic Ancestry and Heterozygosity	74
Index of Abundance	75
Estimating Age Classes.....	76
Modeling Probability of Breeding.....	76
Modeling Litter Size	78
Modeling Approach	79
Results.....	81
Probability of Breeding	82
Litter Size	82
Discussion	83
5 THE EFFECT OF INTROGRESSION ON THE DYNAMICS AND PERSISTENCE OF THE FLORIDA PANTHER POPULATION.....	93
Introduction	93
Methods	95
Field and Genetic Methods.....	95
Model Structure	96
Parameter Values.....	98
Deterministic Demographic Analyses.....	100
Incorporating Parameter Uncertainty.....	100
Incorporating Model Selection Uncertainty	101
Incorporating Environmental Stochasticity.....	101
Estimating Stochastic Growth Parameters	104
Incorporating Density-Dependence	104
Incorporating Demographic Stochasticity	106
Estimating Extinction Parameters.....	108
What If the Introgression Never Happened?	108
Results.....	109
Density-Independent Growth Rate and Perturbation Analysis.....	109
Extinction Parameters	110
What If the Introgression Never Happened?	110
Discussion	112
6 SUMMARY AND CONCLUSIONS.....	131
APPENDIX	
A AGE ERROR ESTIMATION	135
Methods.....	135
Results and Discussion.....	136

B	FINE SCALE ANCESTRY EFFECTS ON SUB-ADULT AND ADULT SURVIVAL	139
	Methods	139
	Results.....	140
C	CAUSE-SPECIFIC MORTALITY ANALYSIS.....	146
	Materials and Methods.....	146
	Results.....	147
D	INFERENCE RESULTS FOR ANCESTRY AND HETEROZYGOSITY	150
	Materials and Methods.....	150
	Results.....	150
E	ANALYSIS OF FLORIDA PANTHER KITTEN SURVIVAL BASED ON 3 ANCESTRY CATEGORIES.....	154
	Materials and Methods.....	154
	Results and Discussion.....	155
F	DATA PREPARATION.....	159
G	ANALYSIS OF SURVIVAL OF FLORIDA PANTHER KITTENS USING DATA ORGANIZED IN 3-MONTH TIME STEPS	161
	Materials and Methods.....	161
	Results and Discussion.....	163
H	INCLUDING ANOTHER BASE MODEL	171
	Methods	171
	Results.....	171
I	ANALYSIS OF THE INFLUENCE OF ANCESTRY USING FINE-SCALE ANCESTRY TESTING.....	180
	Methods	180
	Results and Discussion.....	181
J	ANALYSIS OF REPRODUCTIVE PARAMETERS EXCLUDING OLDER-ADULTS (≥ 10 YEARS)	187
	Methods	187
	Results.....	187
K	ANNUAL BREEDING PARAMETERS FOR PVA	193
	Methods	193

Results.....	195
L DEMOGRAPHIC PARAMETERS FOR CANONICAL PANTHERS	201
Materials and Methods.....	201
Results.....	201
LIST OF REFERENCES	214
BIOGRAPHICAL SKETCH.....	228

LIST OF TABLES

<u>Table</u>	<u>page</u>
2-1	Model comparison results for the effects of sex, age class, abundance index, and year on Florida panther survival 41
2-2	Model-averaged annual survival rates (\hat{s}), standard errors ($S\hat{E}$), and number of Florida panthers tracked (n) in sex and age class categories..... 42
2-3	Model comparison results showing top-ranked models (difference in Akaike's Information Criterion [ΔAIC] < 4) for the effects of ancestry, heterozygosity, sex, and age class (sub-adults and prime-adults only) on Florida panther survival 43
2-4	Estimated annual survival rates (with $S\hat{E}$ and number of panthers) by ancestry, sex, and age-class 44
3-1	List of kitten survival models..... 65
3-2	Model comparison table to estimate annual kitten survival and select base model..... 66
3-3	Model selection table for effects of covariates on survival 67
4-1	Model selection table for probability of breeding (ρ) 88
4-2	Model selection table for litter size (μ) 89
5-1	Variable names used in this manuscript, with definitions..... 119
5-2	Models for sub-adult and adult survival 120
5-3	Models for kitten survival 121
5-4	Models for sub-adult and adult probability of breeding 122
5-5	Models for the average number of kittens produced by sub-adult and adult females (for females that bred in a year) 123
5-6	Summary statistics for extinction and quasi-extinction times (number of years until first dropping below critical thresholds) 124
A-1	Distribution of lengths of birthdate ranges (in months) 137
A-2	Resampling results examining error from using estimated age at capture to estimate survival by age class 138

B-1	Definitions of ancestry models, and the hypotheses they represent.....	142
B-2	Akaike's Information Criteria (AIC) model comparison results showing all models for the effects of ancestry, heterozygosity, sex, and age class on adult Florida panther survival.....	143
D-1	Full AIC table for ancestry and heterozygosity.	152
D-2	Genetic coefficients from all models including sex and age class and at least one genetic covariate	153
E-1	Definitions of simple ancestry models, and the hypotheses they represent	156
E-2	Model selection table for testing hypotheses regarding the effect of genetic ancestry on survival of kittens and older panthers based on 3 ancestry categories.....	157
G-1	A priori models used for the 3-month time step analysis	165
G-2	Kitten survival models to examine the effects of age (3-month time step).....	166
G-3	Estimates of annual sub-adult and adult survival from the 3-month kitten survival analysis and the adult analysis of Chapter 2	168
G-4	Model comparison table for examining the effects of season on kitten survival.	169
H-1	Model selection table for sex and litter size effects on kitten survival, using Base2 model.....	173
H-2	Model selection table for ancestry, heterozygosity, and abundance index effects on kitten survival, using Base2 model.....	174
H-3	Model selection table for three category ancestry effects on kitten and older survival, using the Base2 model.....	176
I-1	Definitions of complex ancestry models, and the hypotheses they represent. .	183
I-2	Model comparison table testing for the effects of complex ancestry (see Table I-1) on probability of breeding (p).....	184
I-3	Model comparison table testing for the effects of complex ancestry (see Table I-1) on litter size (μ).....	185
J-1	Model selection table evaluating the effects of factors on probability of breeding (p), excluding older-adults	188
J-2	Model selection table evaluating the effects of factors on litter size (μ), excluding older-adults.....	189

K-1	Model selection table evaluating the effects of factors on annual probability of breeding (q)	196
K-2	Model selection table evaluating the effects of factors on annual cumulative number of kittens (v).....	198
K-3	Model selection table testing for the random effect of year (rand(Year)), with and without abundance index as a covariate, on annual probability of breeding (q)	199
K-4	Model selection table testing for the random effect of year (rand(Year)) on annual cumulative number of kittens (v)	200
L-1	Models for canonical sub-adult and adult survival	203
L-2	Models for (density-dependent) canonical kitten survival	205
L-3	Models for density-independent canonical kitten survival	208
L-4	Models for sub-adult and adult canonical probability of breeding	211
L-5	Models for sub-adult and adult average number of kittens produced (for canonical females that bred in a year)	213

LIST OF FIGURES

<u>Figure</u>	<u>page</u>
2-1	Model-averaged effects of ancestry and heterozygosity on annual survival of female prime-adult Florida panthers from 1997-2006..... 45
3-1	The effect of genetic variables on model-averaged kitten survival estimates 68
3-2	The effect of a panther abundance index on model-averaged kitten survival estimates 69
3-3	Model-averaged kitten survival by 3-month age interval within the first year 70
4-1	Frequency distribution of litter sizes produced by radio-collared female panthers (1995 – 2008) 90
4-2	Model-averaged reproductive rates (\pm unconditional standard errors) by age class, season, and abundance index..... 91
4-3	Model-averaged reproductive rates (\pm unconditional standard errors) by ancestry category and heterozygosity 92
5-1	Pseudo-code for estimating probability of extinction..... 125
5-2	Perturbation analysis deterministic population growth rate (λ) to lower level parameters 126
5-3	Perturbation analysis results for stochastic population growth rate (λ_s) to lower level parameters 127
5-4	Simulated cumulative probabilities of extinction and quasi-extinction over 500 years..... 128
5-5	Contributions of lower level parameters (see Table 5-1) to differences between the deterministic population growth rates for the whole population (λ) and the canonical population ($\lambda^{(c)}$)..... 129
5-6	Results of simulations starting with conjectured 1995 population levels (total 15 females) and run for 500 years..... 130
B-1	Model averaged effects of complex ancestry and heterozygosity on annual survival of female prime-adult Florida panthers from 1997-2006..... 145
C-1	Cause specific mortality rates (with standard errors) 149
E-1	Model-averaged estimates of annual survival of Florida panther kittens based on 3 ancestry categories 158

G-1	Individual model estimates of annual kitten survival	170
H-1	The effect of genetic variables on model-averaged kitten survival estimates, including two different base models.....	177
H-2	The effect of a panther abundance index on model-averaged kitten survival estimates, including two different base models	178
H-3	Model-averaged estimates of annual survival of Florida panther kittens based on 3 ancestry categories, including two different base models.....	179
I-1	Model-averaged reproductive rates by complex ancestry category (\pm unconditional standard errors)	186
J-1	Model-averaged reproductive rates (\pm unconditional standard errors) by age class	190
J-2	Model-averaged reproductive rates (\pm unconditional standard errors) by season.....	191
J-3	Model-averaged reproductive rates (\pm unconditional standard errors) by ancestry category	192

Abstract of Dissertation Presented to the Graduate School
of the University of Florida in Partial Fulfillment of the
Requirements for the Degree of Doctor of Philosophy

ESTIMATION OF DEMOGRAPHIC PARAMETERS AND POPULATION VIABILITY
ANALYSIS FOR THE FLORIDA PANTHER

By

Jeffrey A. Hostetler

December 2010

Chair: Madan K. Oli
Major: Wildlife Ecology and Conservation

Inbreeding and low genetic diversity can cause reductions in individual fitness and increase extinction risk in animal populations. Introgression, achieved by releasing genetically diverse individuals into inbred populations, has been used as a conservation tool to improve demographic performance in endangered populations. By the 1980s, Florida panthers (*Puma concolor coryi*) had been reduced to a small, inbred population that appeared to be on the brink of extinction. In 1995, female pumas from Texas (*P. c. stanleyana*) were released in occupied panther range as part of an intentional introgression program to restore genetic variability and improve demographic performance of panthers. We used 25 years (1981-2006) of continuous radio-telemetry and genetic data to estimate and model sub-adult and adult panther survival and cause-specific mortality to provide rigorous sex and age class-specific survival estimates and evaluate the effect of the introgression program on these parameters. Genetic ancestry strongly influenced annual survival of sub-adults and adults after introgression, as F_1 generation admixed panthers ($\hat{s} = 0.98$) survived better than pre-introgression type panthers ($\hat{s} = 0.77$) and other admixed individuals ($\hat{s} = 0.82$). Furthermore,

heterozygosity was higher for admixed panthers relative to pre-introgression type panthers and positively influenced survival.

We used multiple sources of data collected during 1982-2008 and a live-recapture dead-recovery modeling framework to estimate and model survival of Florida panther kittens (age 0 – 1 year). Overall, annual survival of Florida panther kittens was 0.323 ± 0.065 (SE), which was lower than estimates used in previous population models. We found that kitten survival generally increased with degree of admixture: F_1 admixed and backcrossed to Texas kittens survived better than canonical Florida panther and backcrossed to canonical kittens. Average heterozygosity positively influenced kitten and older panther survival, whereas index of panther abundance negatively influenced kitten survival. Our approach to integrate data from multiple sources was effective at improving robustness as well as precision of estimates of Florida panther kitten survival.

We used long-term reproductive data (1995-2008) collected from 61 female Florida panthers to estimate and model breeding probability (probability of producing a litter) and litter size, and to investigate the influence of intentional introgression on these parameters. Overall, 6-month probability of breeding (± 1 SE) was 0.232 ± 0.021 and average litter size was 2.60 ± 0.09 . Although F_1 admixed females had lower breeding probability than females with other ancestries, this was most likely because kittens born to F_1 females survive better; consequently, these females are not available for breeding until kittens are independent. There was no evidence for the effect of ancestry on litter size, or of heterozygosity on probability of breeding or litter size.

Previous population viability analyses (PVA) for the Florida panthers have been critiqued for using unreliable inputs and for unrealistic model structures. The numbers

of Florida panthers have increased recently; this increase has been attributed to the genetic introgression, but this continues to be debated. We developed a female-only, birth-flow, age-structured matrix PVA for the Florida panther that incorporated robust parameter estimates, environmental and demographic stochasticity, density-dependence, and model and parameter uncertainty; this model was used to study the dynamics and persistence of the panther population and to explore what would have happened if there had been no genetic introgression. The stochastic estimate of the overall population growth was 1.05 (2.5 and 97.5 percentiles: 0.95 – 1.15), suggestive of a growing population. We estimated probability of extinction within the next 100 years at 3.7% (2.5 and 97.5 percentiles: 0 – 55%), but a probability of dropping below 30 females at some point within the next 100 years at 73.2% (2.5 and 97.5 percentiles: 1 – 100%). These estimates were largely based on data collected during a period of population increase (1995-2008), and do not consider the potential effects of catastrophic events or future changes in anthropogenic influences and habitat conditions; thus, the risk faced by the panther population is likely to be greater than those indicated by our results. The deterministic estimate for population growth without introgression was 0.95 (2.5 and 97.5 percentiles: 0.82 – 1.07), suggestive of a shrinking population, but effects of introgression on population persistence were mixed. We cannot conclude that observed population growth would not have happened without introgression. Nonetheless, our results along with those reporting improvements in biomedical indicators of inbreeding depression, do provide strong evidence that genetic introgression contributed substantially to the observed increases in Florida panther population.

CHAPTER 1 INTRODUCTION

The Florida panther (*Puma concolor coryi*), an endangered puma subspecies, is a textbook example of a small and isolated population facing a multitude of threats to its persistence. Once distributed across the southeastern United States, their number was reduced to ≤ 30 individuals by the 1980's (McBride et al., 2008). The population was thought to be severely inbred and was characterized by extremely low genetic diversity (Culver et al., 2000; Roelke et al., 1993b). Many phenotypic traits thought to be characteristics of inbreeding were reported from this population, including very low sperm quality, and high incidences of cryptorchidism, cowlicks, and kinked tails (Barone et al., 1994; Mansfield and Land, 2002; Roelke et al., 1993b). Due to concerns about inbreeding depression, 8 female Texas pumas (*P. c. stanleyana*) were brought into the Florida panther population in 1995. Since this genetic introgression, the population has increased (McBride et al., 2008), although the processes that have led to this increase continue to be debated (Creel, 2006; Maehr et al., 2006; Pimm et al., 2006b).

Coordinated research on Florida panther began in 1981 to learn more about their biology and to support conservation efforts. This body of works has not only improved our understanding of panther ecology and behavior (Belden et al., 1988; Maehr et al., 1990; Maehr et al., 1989; Roelke et al., 1993a), but also has contributed substantially to our understanding of the risks faced by small populations and challenges inherent in managing large carnivores in an increasingly human dominated landscape (Comiskey et al., 2002; Dees et al., 2001; Janis and Clark, 2002; Maehr et al., 2002b; O'Brien et al., 1990).

In 2003, the U.S. Fish and Wildlife Service (USFWS) and the Florida Fish and Wildlife Conservation Commission (FWC) convened the Scientific Review Team (SRT) to review the status of Florida panther science, and to make research and management recommendations. The SRT, composed of highly qualified scientists with expertise in carnivore ecology, population dynamics, and conservation biology, thoroughly reviewed existing scientific literature on the biology of the Florida panther, and found that rigorous estimates of several demographic parameters were not available. The SRT also noted that previously reported estimates of some demographic variables and those used in earlier population viability analyses (Maehr et al., 2002a) were unreasonable and led to unreliable inferences regarding the persistence of the panther population (Beier et al., 2003; Beier et al., 2006; Gross, 2005). The team recommended reanalysis of existing data to rigorously estimate age-specific demographic variables and to test hypotheses regarding factors influencing those variables (Beier et al., 2003). Furthermore, the SRT recommended development and analysis of population models that reflect biology of panthers and do not excessively rely on aspects of panther biology that are unknown.

In accordance with SRT recommendations (Beier et al., 2003), our goals were to provide rigorous estimates of demographic parameters of Florida panthers, and to evaluate the influences of various factors on those parameters. We analyzed long-term radio-telemetry (1981-2008) and passive integrated transponder (PIT)-tagging (1995-2008) data to estimate and model survival rates, and reproductive data to estimate and model probability of successful reproduction (breeding probability) and litter size.

One of the most important management actions undertaken for the conservation of Florida panthers was the genetic introgression. This was and remains a controversial

decision (Maehr and Caddick, 1995; Maehr et al., 2006; Pimm et al., 2006b). However, the potential influence of genetic introgression and resulting changes in the population's genetic structure on the demography of Florida panthers is not yet fully understood. Thus, we also evaluated the influence of genetic introgression on aforementioned demographic parameters. These results are expected to help guide future management efforts.

CHAPTER 2
INTENTIONAL GENETIC INTROGRESSION IMPROVES SURVIVAL OF F₁ ADULTS
AND SUB-ADULTS IN A SMALL, INBRED FELID POPULATION

Introduction

Hybridization, particularly between species, can have serious conservation implications if one of the parental types is rare or endangered because such populations may decline or become extinct due to hybridization (Allendorf et al., 2001; Levin et al., 1996; Rhymer and Simberloff, 1996; Wolf et al., 2001). However, intentional introgression, achieved by releasing individuals from different subspecies or populations into small, inbred populations, has been used as a conservation tool to restore genetic variability and improve demographic performance of endangered populations (Madsen et al., 1999; Westemeier et al., 1998). Despite the apparent success of some of these genetic manipulations (e.g., Westemeier et al., 1998), they remain controversial due to concerns regarding outbreeding depression (Edmands, 2007; Greig, 1979), potential loss of genetic integrity of endangered populations (Allendorf et al., 2001), and because few studies have convincingly quantified the effects of intentional introgression on demographic parameters (Beier et al., 2006).

When estimating the effect of hybridization on survival for populations that have experienced introgression, it is important to determine genetic ancestry of individuals because hybrid fitness may differ relative to parental types (Arnold and Hodges, 1995; Burke and Arnold, 2001). Hybrid superiority can be primarily due to exogenous selection, when hybrids are favored under specific environmental conditions that vary across time (Grant and Grant, 1992) or space (Good et al., 2000). Alternatively, hybrid superiority can be due to intrinsic qualities of outbred individuals as predicted by hybrid vigor theory (Crow, 1948; Shull, 1908). Hybrid vigor, or heterosis, is a phenomenon

whereby hybrids exhibit higher fitness relative to inbred parental types due to increased heterozygosity in the F₁ generation (Burke and Arnold, 2001).

Florida panthers (*Puma concolor coryi*) were once distributed across much of the southeastern United States, but currently exist only in 1 small (~100 individuals) breeding population in south Florida (McBride et al., 2008). This population represents the only breeding population of pumas east of the Mississippi River and is listed as endangered under the United States Endangered Species Act (Sullivan, 2004). By the late 1980s and early 1990s the population appeared to be at imminent risk of extinction as the population had declined to ≤30 individuals during this period (McBride et al., 2008) and was severely inbred and lacking in genetic diversity (Roelke et al., 1993b). In 1995, 8 female pumas from Texas (*P. c. stanleyana*) were released into south Florida as part of an intentional introgression program to restore genetic diversity (Johnson et al., 1997). The population has increased since the initiation of this program (McBride et al., 2008), but the effects of genetic introgression on specific demographic parameters, such as survival and sources of mortality, remain unclear. Rigorous evaluation of the effects of genetic admixture on survival rates following intentional introgression would have broad implications for the relevance of applied genetic management to the conservation of small, isolated populations (Beier et al., 2006).

We estimated survival and cause-specific mortality of radio-collared sub-adult and adult panthers from 1981-2006 and investigated the influence of multiple intrinsic variables with 2 main objectives. First, we sought to provide sex- and age class-specific estimates of annual survival and cause-specific mortality for panthers from 1981-2006 in order to provide a basic understanding of panther survival within which we could explore

the influence of intentional introgression on these parameters. Second, we investigated the influence of: a) genetic ancestry, with respect to hybridization with Texas pumas released during the introgression program, and b) genetic diversity, as quantified by individual heterozygosity, on survival and cause-specific mortality of sub-adult and adult panthers from 1997-2006. We hypothesized that survival rates of admixed panthers would be higher than for pre-introgression type panthers and that increased survival would be most evident in the F_1 generation, as predicted by hybrid vigor theory (Burke and Arnold, 2001).

Materials and Methods

Field Methods

Florida panthers and Texas pumas were captured and monitored by radio-telemetry from 1981-2006 across the range of the subspecies in south Florida, USA (Kautz et al., 2006) by biologists from the Florida Fish and Wildlife Conservation Commission (FWC) and National Park Service (NPS) using methods described by Belden et al. (1988) and Land et al. (2008). Kittens (<35 days old) were marked at natal dens with transponder chips (Benson et al., 2008; Land et al., 1998), which allowed us to more accurately estimate ages of marked kittens that were subsequently recaptured and radio-collared. Beginning in 1985, captured panthers were vaccinated against several diseases (for details see Cunningham et al., 2008), which potentially improved their survival.

When radio-collared panthers died, a cursory examination of the carcass and surrounding area was conducted in the field, and a suspected cause of death was assigned if evidence allowed. Eighty-four of 92 (91.3%) carcasses of radio-collared panthers were also necropsied by experienced veterinarians or pathologists who

attempted to determine cause of death. We estimated date of death from telemetry data and by assessing the condition of the carcasses found in the field.

The Introgression Program

Eight female pumas from west Texas were released into south Florida at 5 sites between 29 March and 26 July 1995 (Johnson et al., 1997). Two were released in Everglades National Park (ENP), 4 in Big Cypress National Preserve (BCNP), and 2 in Fakahatchee Strand Preserve State Park (FSPP). The introgression program was undertaken to restore genetic variability to the panther population by mimicking natural gene flow that occurred between Florida panthers and other puma populations before the extirpation of pumas from most of the southeastern United States. Five of the released Texas pumas reproduced and produced a total of 12 litters and ≥ 20 kittens.

Estimating Age Classes

We knew the ages (within a few days) for panthers that were handled as kittens at natal dens and subsequently recaptured and radio-collared ($n = 54$, 36.7% of total). For panthers not marked as kittens, their age was estimated in the field at time of first capture using tooth wear and pelage characteristics (Ashman and Greer, 1976). We examined potential error in survival estimates due to error in age estimates and found it to be small (Appendix A). Using both types of estimates, we separated panthers into 4 age classes: kittens (0-1 years old), sub-adults (1-2.5 and 1-3.5 years old for females and males, respectively), prime-adults (2.5-10 and 3.5-10 years old for females and males, respectively), and older-adults (≥ 10 years old for both sexes). We also combined prime-adults and older-adults into a single adult category for some of our analyses. Since panther kittens were not radio-collared until at least 4-6 months of age, and most mortality of puma kittens may occur ≤ 3 months after birth (Logan & Swenor

2001), a different analytical approach would be needed to properly estimate survival of kittens. Thus, we limited our current analyses to sub-adults and adults. The sub-adult age class was the period of a panther's life after independence from its mother until the approximate ages when females and males first establish home ranges. We estimated age of independence at just over 1 year (mean = 397 days, SD = 75 days, $n = 35$; FWC & NPS, unpublished data) from known-age kittens that were radio-tracked simultaneously with their mothers (before and after independence). We standardized the beginning of the sub-adult age class to 1 year for simplicity.

Genetic Variables

We extracted total genomic DNA from blood and tissue samples obtained from wild-caught panthers and captive pumas from south Florida and west Texas during 1981-2006. We amplified and scored 23 microsatellite loci (F37, F42, FCA43, FCA57, FCA75, FCA90, FCA91, FCA94, FCA95, FCA98, FCA124, FCA133, FCA161, FCA193, FCA 243, FCA249, FCA293, FCA310, FCA369, FCA441, FCA559, FCA566, FCA668) following previously described PCR amplification conditions (Menotti-Raymond et al., 1999; Menotti-Raymond et al., 1997).

A Bayesian procedure, implemented in the program STRUCTURE (Pritchard et al., 2000) was used to identify populations or genetic clusters and to estimate the genetic origin of individuals based on microsatellite allele frequencies. The STRUCTURE approach assumes departures from both Hardy-Weinberg and complete linkage equilibriums to be indications of population substructure (Pritchard et al., 2000). In addition to assigning individuals to various lineages based upon composite microsatellite genotype, the analysis also allows for estimation of proportion of genetic contribution from each group for individuals of mixed origin. We used results from the

STRUCTURE analysis, along with pedigree results and field evidence, to assign panthers to 3 groups that reflected the genetic makeup of the south Florida population (pre-introgression type panthers, F_1 admixed panthers, and other admixed panthers). Pre-introgression type panthers represent the genotypes present on the landscape prior to the introgression program and this group is composed mostly of non-admixed Florida panthers, which had no direct non-Florida relatives or < 10% non-Florida genetic contribution based on STRUCTURE analyses. Additionally, 1 pre-introgression type panther in the sample of individuals used to investigate the influence of genetic ancestry and heterozygosity on survival ($n = 98$) was a descendent of a panther from the Everglades genetic population with documented genetic links to Central America (Culver et al., 2000; Johnson et al., 2010; O'Brien et al., 1990; Roelke et al., 1993b). Admixed panthers were mostly the descendents of the introduced female Texas pumas released in 1995, except for 5 radio-collared individuals that shared genotypic similarities with pumas maintained in a large enclosure on the Seminole Indian Reservation (SIR) adjacent to BCNP. Radio-collared panthers were documented entering the enclosure and captive pumas were documented to have left the enclosure during our study. This captive population contained animals of unknown origins that had a genetic affinity with North American pumas (FWC, NPS, National Cancer Institute, unpublished data).

Differences in fitness between classes of hybrids are possible and hybrid vigor is predicted to be strongest in the F_1 generation (Arnold and Hodges, 1995; Burke and Arnold, 2001), so we included 2 classes of admixed panthers in our analyses: F_1 and other admixed. We defined F_1 admixed panthers as any offspring produced by matings

between a Texas female and a pre-introgression type male. As such, F_1 panthers in our sample were products of matings between Texas females and males that were either non-admixed Florida panthers or Everglades panthers. Of the 20 known kittens produced by Texas pumas, 15 were F_1 admixed panthers (the remaining 5 were sired by F_1 males). Ten of the 12 natal dens of the Texas pumas were visited shortly (<35 days) after parturition and all kittens were marked at these dens with transponder chips. Two F_1 kittens (1 from each litter) were captured from litters produced at the 2 dens not visited while they were still dependent offspring. Of the 15 known F_1 kittens, 8 were captured or recaptured and radio-collared, whereas the fates of the other 7 F_1 kittens are unknown.

In summary, all individuals in our radio-collared sample were placed into 1 of 3 categories for our survival analyses: pre-introgression type panthers ($n = 41$), F_1 admixed panthers ($n = 8$), and other admixed panthers ($n = 49$). We were also able to further classify most individuals from the other admixed category into 3 finer categories: backcrossed to Florida admixed panthers ($n = 16$), backcrossed to Everglades admixed panthers ($n = 4$), and backcrossed to Texas admixed panthers ($n = 14$). We considered potential differences in survival between pre-introgression type, F_1 admixed, and these finer admixture distinctions (Appendix B), but because admixed panthers beyond the F_1 generation did not differ substantially in their survival, we combined all non- F_1 admixed panthers into the other admixed category for our main analyses.

We estimated microsatellite-based average individual heterozygosity with the program MICROSAT (Minch et al., 1995) to investigate the influence of heterozygosity on survival during the same time period as the ancestry analysis. We also compared

the distribution of heterozygosity values between panthers of our 3 ancestry categories using permutation tests (Efron and Tibshirani, 1998).

Index of Abundance

To examine the potential effects of panther density on sub-adult and adult survival, we used minimum population counts as an index of abundance (McBride et al., 2008). These counts were based on radio-tracking and field evidence of sub-adult and adult panthers (tracks, scat, kills, and scrapes; McBride et al., 2008). The period 1981-1984 was characterized as a discovery period, when the researchers were still finding the panthers on the landscape. Because the counts from 1985-1995 were fairly constant, we applied the count from 1985 as the abundance index for 1981-1984. In 1994 and 2004, the panther surveys were incomplete, so complete counts were not possible. We followed McBride *et al.* (2008) and extrapolated these missing values by using the mid-point between counts from the years immediately prior to and after the years in question (1994 and 2004).

Survival Analyses

We estimated annual survival and examined the effects of covariates using a daily time scale and Cox proportional hazard regression (Cox, 1972; Therneau and Grambsch, 2000). We right-censored panthers that lost their collars or whose collars failed on the last day that an active signal was heard. An important assumption of survival analyses is that radio-failures are independent of mortality (Therneau and Grambsch, 2000). We are confident that this assumption was met in our study as we were able to confirm radio-failures by subsequent recapture or recovery in 22 of 32 cases.

We organized the data with records for each panther-year combination (Fieberg and DelGiudice, 2009). Time in the Cox model (the baseline) was defined as day within the year. When a panther changed age-class within a year, we created two records: one record with the younger age-class right-censored on the transition day and another record with the older age-class left-truncated (staggered entry) on the same day. To account for multiple records for the same animal existing at the same “time,” we estimated robust (“sandwich”) standard errors clustered by individual (except when including random effects; Fieberg and DelGiudice, 2009; Therneau and Grambsch, 2000), which were generally extremely close to uncorrected standard errors. We used the Fleming-Harrington method to generate survival estimates from the Cox analysis (Therneau and Grambsch, 2000). All survival analyses were performed in R version 2.8.1 (R Development Core Team, 2010), using the survival (version 2.34-1) and kinship (version 1.1.0-22) packages and additional code that we developed for our analyses (available on request).

For our survival analyses, we used an information-theoretic approach (Akaike’s Information Criterion; AIC) for model selection and statistical inference (Burnham and Anderson, 2002). Information-theoretic approaches allow comparison of non-nested models, selection of models that should best predict future data (from the same statistical population), and model-averaged estimates to address model selection uncertainty (Burnham and Anderson, 2002). We calculated AIC values, Akaike differences (ΔAIC_i , difference between AIC value of the i th model and the top-ranked model) and Akaike weights (w_i , the weight of evidence that the i th model is actually the best model of the models being considered given the data) as in Burnham and

Anderson (2002). Generally, we considered models with $\Delta AIC < 2$ to have substantial empirical support, models with ΔAIC of 2-4 to be plausible models with less empirical support, and models with $\Delta AIC > 4$ to have much less empirical support. In addition, the sum of the weights of models including a given variable can be interpreted as a measure of its importance, relative to other variables (Burnham and Anderson, 2002). We calculated model-averaged estimates of annual survival and unconditional variance for each level of categorical variables and across continuous covariates (Burnham and Anderson, 2002; Tinker et al., 2006). To generate these model-averaged estimates of survival we used all models included in the model selection process for a given analysis, weighted by their Akaike weights. Models with no effects of the covariates being presented were included in the averages (as having the same survival for all values of the covariate); therefore, the model averages represent unconditional estimates of survival (Burnham and Anderson, 2002). The unconditional standard errors estimated around the model averages are generally larger than standard errors estimated for parameters of single models and should not be interpreted as measures of statistical significance. We conducted 2 separate survival analyses: a main analysis to estimate survival from 1981-2006 with the entire dataset and a subset analysis using data from sub-adults and prime adults from 1997-2006 to investigate the effects of the introgression program on survival.

In the first set of analyses we investigated the influence of sex, age class, index of abundance, and year, and included 144 radio-collared sub-adults and adults from 1981 – 2006 (1 panther whose death was capture-related was excluded). We started by selecting the best model or set of models for sex and age (all models with $\Delta AIC < 2$).

Because the sub-adult and prime-adult age classes were defined differently for males and females, and because we had a priori reason to believe that the patterns of mortality would be different across ages for the two sexes, we only considered the interactive effect of sex and age for the difference between sub-adults and adults. We considered differences in survival between prime-adult and older-adult age classes both additively and interactively with sex, which resulted in 5 sex and age class models.

We used the best model or models (i.e. lowest AIC) from the preceding analysis as base models to test for the effect of abundance on panther survival. We also investigated potential temporal variation in survival using Gaussian shared frailty models with year as a random effect (Therneau and Grambsch, 2000). Each year was treated as a separate category, except for 1981 – 1986, which were combined as one category due to small sample sizes. We estimated temporal variance (variance of the random effect) for each model using a Laplace approximation under a maximum likelihood approach (Pankratz et al., 2005). Because our intent was to estimate the temporal variance rather than produce an estimate of survival for each year, we counted the random effect as a single parameter for purposes of model comparison (Vaida and Blanchard, 2005).

In a second set of analyses, we investigated potential effects of genetic introgression, in terms of genetic ancestry and genetic diversity, on survival rates. Given that the first offspring produced by a Texas female did not appear in our sample of sub-adults and adults until 1997, we conducted this subset analysis using data only from 1997 until the end of this study on December 31, 2006. Only 2 admixed panthers (born during 1995 and 1996) reached 10 years of age by the end of 2006, and both for

periods of <1 year; thus, we excluded older-adult panthers from these analyses to account for possible differences in survival for older animals. In addition to including an ancestry model where the 3 ancestry classes were separated (Ancest1), we included ancestry models where other admixed panthers were combined with either pre-introgression type (to test specifically for F_1 hybrid vigor; Ancest2) or F_1 panthers (to test for general hybrid superiority; Ancest3). We combined these 3 models with the effects of sex and age-class (sub-adult and prime-adult; Age3), and the effect of heterozygosity (Het).

Some radio-collared panthers were removed from the wild and held in captivity for various reasons, and some received medical treatment. We right-censored panthers that were permanently removed from the wild due to livestock depredation incidents ($n = 2$) on the date of removal. We also right-censored panthers that were temporarily removed for treatment and rehabilitation of injuries judged not to have been fatal ($n = 3$), capture-related injuries ($n = 3$), or for reproductive evaluation ($n = 1$) on date of removal and then re-entered them into the analyses upon release to the wild. Panthers removed for various reasons as kittens (<1 year old) and later released into the wild ($n = 7$) were entered into our analyses either on the day of release (if adults or sub-adults) or upon reaching the sub-adult age class after being released as kittens. Panthers removed from the wild due to injuries or illness judged to be fatal ($n = 4$) were treated as mortalities and the injury or illness was assigned as cause of death.

To estimate and model the importance of different mortality agents on rates and patterns of mortality for sub-adult and adult Florida panthers, we performed cause-

specific mortality analyses. Details of the methods used for these analyses can be found in Appendix C.

Results

Age, Sex, Index of Abundance, and Year

Models that incorporated the interactive effects of sex and age class (either 2 or 3 age classes per sex) had substantially higher empirical support than models with neither or only the effect of sex (Table 2-1). Survival rates were higher for females than for males, but these varied among age classes (Table 2-2). For males, prime-adults had the highest survival, whereas for females, sub-adults had the highest survival (Table 2-2). The highest ranked model included an additive effect of sex and old age, indicating that survival for this age class differed from other age classes, but there was no support for an interactive effect of sex and old age (Table 2-1). Survival estimates were lower for older-adults of both sexes (Table 2-2).

Models including the effect of abundance always had less empirical support than the equivalent models with no such effect (Table 2-1), indicating no evidence of density-dependence in sub-adult and adult survival. The models with a random effect of year had marginally lower support than the equivalent models with no random effect (Table 2-1), and the estimated temporal variance of the hazard rate for model 2 was small (0.115), suggesting that the temporal variance in survival rates was also small.

Genetic Ancestry and Heterozygosity

There was strong evidence that genetic ancestry influenced survival as all models with substantial empirical support ($\Delta AIC \leq 2$) included an ancestry variable, the ΔAIC of the top-ranked model containing neither ancestry nor heterozygosity was 7.61, and the sum of the weights of models including ancestry variables was 0.928 (Table 2-3).

Ancestry variables included in the top-ranked models were all in agreement that the survival of F_1 admixed panthers differed from that of other ancestry categories (sum of weights of such models was 0.890); however, evidence for a difference between other admixed panthers and pre-introgression type panthers was weaker (sum of weights = 0.315; Table 2-3). Model-specific and model-averaged survival was higher for F_1 admixed panthers than for other ancestry classes (Table 2-4; Figure 2-1).

There was also evidence that average heterozygosity influenced survival of sub-adult and prime-adult panthers after genetic introgression (1997-2006), as the sum of the weights of models including heterozygosity was 0.537 (Table 2-3) and model-averaged annual survival probability increased with heterozygosity (Figure 2-1). Average heterozygosity was highest for F_1 (mean = 0.337, SD = 0.035, $n = 8$), intermediate for other admixed (mean = 0.261, SD = 0.065, $n = 49$), and lowest for pre-introgression type panthers (mean = 0.161, SD = 0.063, $n = 41$). Each ancestry group differed significantly in average heterozygosity from both other groups in pairwise comparisons (all $p \leq 0.002$; permutation tests). There was also evidence that heterozygosity positively influenced survival even within ancestry groups, as the top-ranked model included both factors (Table 2-3). Although model-averaged survival was similar for pre-introgression type and other admixed panthers at a given level of heterozygosity, heterozygosity ranged higher for other admixed individuals, leading to an increased probability of survival (Figure 2-1; Table 2-4).

The full AIC table and selected Cox model coefficients for the genetic comparisons are presented in Appendix D. Robust z-tests on individual coefficients (in the context of sex and age class) also indicated that F_1 admixed panthers survived better than

panthers in other ancestry classes and that heterozygosity positively influenced survival (Appendix D).

Cause-Specific Mortality

The greatest cause of mortality for radio-collared Florida panthers was intraspecific aggression, followed by mortality from unknown causes, vehicles, and other (Appendix C). When sexes were combined, pre-introgression type panthers had a higher level of mortality due to intraspecific aggression than admixed panthers ($z = 2.404$, $p = 0.016$, risk ratio = 3.06). Increasing heterozygosity also significantly decreased the risk due to intraspecific aggression ($z = -2.943$, $p = 0.003$, risk ratio = 0.480). Additional details of the results of these analyses are available in Appendix C.

Discussion

We provide evidence of hybrid vigor in the panther population following intentional introgression, as genetic ancestry and heterozygosity strongly influenced survival of sub-adult and prime-adult panthers. Our findings correspond very closely to the outcomes of hybridization on an inbred population predicted by theory in that survival and heterozygosity were higher for F_1 admixed individuals compared with pre-introgression type Florida panthers, but evidence for higher survival in admixed generations beyond the F_1 was far weaker (Burke and Arnold, 2001; Crow, 1948). It should be noted that we did not compare survival between F_1 panthers and the released Texas females; thus, we investigated hybrid vigor by comparing survival between F_1 panthers and only 1 of the parental populations.

Hybrid vigor was first recognized by crossing divergent lines of agricultural plants and extensive research in agricultural genetics has confirmed the phenomenon (Birchler et al., 2003; Crow, 1948; Whitlock et al., 2000). Much less is known about the fitness

consequences of hybridization for plants and animals in nature (Campbell and Waser, 2001; Grant and Grant, 1992). For animals, hybrid vigor has been invoked by previous studies for a variety of species including insects (Ebert et al., 2002), fish (Rosenfield et al., 2004), salamanders (Fitzpatrick and Shaffer, 2007), and corals (Slattery et al., 2008). We are unaware of previous studies of free-ranging mammals demonstrating superior fitness of admixed individuals (or superiority of a component of fitness, as in our example) that was clearly due to intrinsic hybrid vigor rather than hybrids being favored under specific environmental conditions. Broadly speaking, hybrid fitness may be influenced by endogenous or exogenous selection, and hybrid superiority is often assumed to be primarily due to the latter (Burke and Arnold, 2001) as hybrids may be favored under environmental conditions that vary across time (Grant and Grant, 1992) or space (Good et al., 2000; Moore, 1977). Our demonstration of higher survival in F_1 admixed panthers relative to an inbred parental type is consistent with an intrinsic hybrid vigor effect (Burke and Arnold, 2001) and temporal variation in environmental conditions were minimized in our study by limiting the analysis to years during which admixed and pre-introgression type panthers co-existed on the south Florida landscape. However, environmental conditions could have varied spatially across the range of the panther and potentially contributed to the higher survival of F_1 admixed panthers in some instances. We suggest that variation in at least 2 extrinsic factors, panther density and habitat conditions, could have influenced panther survival across ancestry categories.

First, survey results and capture efforts suggested that adult males were at very low density in ENP and portions of BCNP (FWC & NPS, unpublished data). Low local density of adult males could have provided a survival advantage to sub-adult and adult

F₁ panthers in these areas ($n = 4$) by decreasing the risk of death by intraspecific aggression. This possibility is consistent with our results as pre-introgression type panthers were more frequently killed by intraspecific aggression than admixed panthers. Furthermore, ENP was likely devoid of females when the Texas females were released, which could have contributed to higher survival of female F₁ panthers in ENP ($n = 3$) through decreased competition and reducing the need for dispersal. However, half of the radio-collared F₁ panthers inhabited areas known to be occupied by both adult male and female panthers, so even if low density of adult panthers influenced our results in some portions of the range, it would only offer a partial potential explanation for the higher survival of F₁ panthers.

A second extrinsic factor that may have influenced our results is variation in habitat conditions across the range of panthers, and we recognize the potential for interactions between habitat quality, genetic ancestry, and survival. Theoretical (Moore, 1977; Moore and Price, 1993) and empirical work (Good et al., 2000; Rand and Harrison, 1989) suggest that hybrids sometimes thrive in different habitat types than parental types, leading to the production of relatively fit hybrids and to the establishment and maintenance of hybrid zones. Novel phenotypes produced through hybridization can allow for niche differentiation between hybrid and parental types when some of the available habitat is not suitable for the parental types (Buerkle et al., 2000; Lewontin and Birch, 1966). It has been suggested that since introgression, panthers have moved into areas in south Florida that were not occupied during years of lower population size just prior to introgression (Pimm et al., 2006b), meaning that admixed individuals might have occupied and survived in areas that were not used by pre-introgression type

panthers. However, Creel (2006) pointed out that such an expansion into new areas could have simply been driven by demographics, as growing populations will often expand into new habitats. An intriguing possibility to consider with future analysis is whether admixed panthers (especially F_1 s) used different habitat types than pre-introgression type panthers and whether genotype-specific habitat selection patterns influenced survival (and other components of fitness).

An ideal test of the hybrid vigor theory would involve a carefully designed experiment with large sample sizes for robust statistical inferences. However, such experiments and sample sizes are rarely possible for elusive and highly endangered species of large carnivores that typically occur at low density. Populations small enough to experience inbreeding often result in smaller sample sizes than would be preferred for more robust statistical inferences. Nonetheless, analyzing these data is critically important in terms of increasing understanding of the dynamics of highly endangered populations. Although our sample of radio-collared F_1 individuals is numerically small ($n = 8$), it represents a substantial proportion of the total F_1 offspring produced by the introgression program (38–53%, depending on the range of possible litter sizes for the 2 dens not visited); therefore the survival of the F_1 individuals we studied should be representative.

Pimm et al. (2006) evaluated the effects of the introgression program on panther demographic parameters, including survival, but their results with respect to adult survival were equivocal (Creel 2006). Our dataset, analyses, and results differed from those of Pimm et al. (2006) in several important ways. Pimm et al. (2006) excluded 15 panthers because they did not know the genetic ancestry of these individuals, whereas

we determined ancestry for the entire dataset with updated genetic analyses completed in 2009. We also addressed aspects of the analysis by Pimm et al. (2006) following recommendations made by Creel (2006). First, we separated adults from sub-adults to consider possible differences in age structure between pre-introgression type and admixed categories, whereas Pimm et al. (2006) categorized all panthers independent from their mothers as adults. We also excluded older panthers (≥ 10 years) from our analysis because these individuals, which survived poorly relative to other age classes, were underrepresented in the admixed classes. Second, Pimm et al. (2006) compared demographic parameters of some panthers from years prior to introgression to those of admixed individuals following introgression, thus failing to control for potential temporal variation in panther demographic variables. We limited our comparison of survival between admixed and pre-introgression type genotypes to years when both co-existed on the landscape (i.e., 1997-2006). It should be noted that this restriction by itself has little effect on inference, except to weaken the evidence for an effect of heterozygosity (J. Hostetler, unpublished data). Perhaps the most important difference between our analysis and that of Pimm et al. (2006) is that we separated F_1 generation offspring from other admixed panthers, as recommended by previous researchers investigating fitness consequences of hybridization (reviewed by Arnold and Hodges, 1995; Burke and Arnold, 2001). Sub-adult and adult survival improved most dramatically for F_1 admixed panthers after introgression and this effect would be diluted by pooling all admixed panthers into a single category. Finally, we included data on heterozygosity to determine whether differences in survival across genotypes were associated with differences in genetic diversity. Thus, we believe our approach has provided additional

insight into the effect of the introgression program on sub-adult and adult panther survival and represents a well documented example of the utility of genetic introgression in improving a demographic parameter of an inbred population.

Age and sex influenced survival of panthers as survival rates for females were higher than for males in each age class. The sub-adult age class is the period when male panthers are dispersing and attempting to locate and establish home ranges (Maehr et al., 2002b) and our results indicate this is a dangerous period for male panthers. Conversely, female survival rates were highest for the sub-adult age class. Female pumas are often philopatric, dispersing less frequently and for shorter distances than males (Maehr et al., 2002b; Sweanor et al., 2000), consistent with most species of polygynous mammals (Greenwood, 1980). Our results also strongly suggest that older panthers (≥ 10 years) survived poorly compared with other age classes, despite the small sample size of older-adults and the potential bias against detecting survival senescence due to heterogeneity in individual survival (Cam et al., 2002).

Our results are an important first step to determining the demographic mechanisms that led to the numerical increase of panthers after introgression and indicate that intentional introgression can be a valuable tool for conserving small, inbred populations. However, potential variation in the response of populations to admixture, the possibility of outbreeding depression through loss of co-adapted gene combinations or adaptation to local environmental conditions (Edmands, 2007; Greig, 1979; Templeton, 1999), and the problem of losing genetically unique populations through swamping (Allendorf et al., 2001; Creel, 2006) suggest that intentional admixture of wild populations should be undertaken only when extinction appears imminent, as in the

panther example. Despite the success of the introgression program for panthers (at least in the short-term), the problems that led to a small population size and inbreeding, habitat loss and isolation from other populations, have not been corrected and will likely be exacerbated as development and human population growth are projected to increase in south Florida (Kautz et al., 2006). Therefore, investigating the influence of introgression on other demographic parameters (e.g., kitten survival and fecundity) and population growth and determining the longevity of any demographic benefits associated with intentional introgression will be important next steps for evaluating whether genetic augmentation will be an effective long-term management tool for panthers.

Table 2-1. Model comparison results for the effects of sex, age class, abundance index, and year on Florida panther survival. Abundance was included as a linear trend and year was included as a random effect using the top-ranked sex and age model as a base. For each model, we present the number of parameters, the difference in Akaike's Information Criterion (ΔAIC), and the Akaike weight (w_i). A) Model comparison results for the effects of sex and age class on survival. B) Model comparison results for the effects of abundance and year on survival.

Model	Parameters	ΔAIC	w_i
A. Sex and age class models			
1. Sex * Age1 ^a + Older ^b	4	0	0.658
2. Sex * Age2 ^c	5	1.98	0.245
3. Sex * Age1	3	4.69	0.063
4. Sex	1	5.95	0.034
5. Constant ^d	0	15.25	0.000
B. Additive effects of abundance (trend) and year (random)			
1. Sex * Age1 + Older	4	0.00	0.292
2. Sex * Age1 + Older + rand(Year) ^e	5	0.18	0.267
3. Sex * Age1 + Older + Abundance ^f	5	0.26	0.256
4. Sex * Age1 + Older + Abundance + rand(Year)	6	0.92	0.185

^a Age1 divides panthers into sub-adults (1-2.5 and 1-3.5 yrs for females and males respectively) and adults (≥ 2.5 and ≥ 3.5 yrs for females and males respectively).

^b Older refers to older-adults (≥ 10 yrs); model 1 therefore has the same older-adult effect for both sexes whereas model 2 allows for different older-adult effects between sexes.

^c Age2 divides the panthers into sub-adults (same as Age1), prime-adults (2.5-10 and 3.5-10 yrs for females and males respectively) and older-adults (≥ 10 yrs).

^d No predictor variables

^e rand(Year) refers to a random effect of year as a categorical variable, with 1981-1986 grouped together (temporal variance).

^f Abundance refers to a linear trend in survival by abundance index.

Table 2-2. Model-averaged annual survival rates (\hat{s}), standard errors ($S\hat{E}$), and number of Florida panthers tracked (n) in sex and age class categories. Models 1 – 5 (Table 2-1) were used for model averages.

Category	Females			Males		
	\hat{s}	$S\hat{E}$	n	\hat{s}	$S\hat{E}$	n
Sub-adult ^a	0.951	0.034	40	0.713	0.049	54
Prime-adult ^b	0.872	0.023	64	0.799	0.036	44
Older-adult ^c	0.760	0.056	12	0.635	0.083	11

^a 1-2.5 and 1-3.5 years old (estimated) for males and females, respectively

^b 2.5-10 and 3.5-10 years old (estimated) for males and females, respectively

^c ≥ 10 years old (estimated) for both males and females

Table 2-3. Model comparison results showing top-ranked models (difference in Akaike's Information Criterion [ΔAIC] < 4) for the effects of ancestry, heterozygosity, sex, and age class (sub-adults and prime-adults only) on Florida panther survival during 1997 – 2006. For each model, we present the number of parameters, ΔAIC , and the Akaike weight (w_i). The full table is presented in Appendix D.

Model	Parameters	ΔAIC	w_i
1. Sex * Age3 ^a + Ancest2 ^b + Het ^c	5	0.00	0.244
2. Sex * Age3 + Ancest2	4	0.23	0.217
3. Sex * Age3 + Ancest1 ^d	5	1.35	0.124
4. Sex * Age3 + Ancest1 + Het	6	1.98	0.090
5. Sex + Ancest2 + Het	3	2.77	0.061
6. Sex + Ancest2	2	2.98	0.055
7. Sex * Age3 + Het	4	3.09	0.052

^a Age3 differentiates sub-adult (age 1-2.5 for females and 1-3.5 for males) and prime-adult (ages 2.5-10 for females and 3.5-10 for males) panthers.

^b Ancest2 divides panthers into two ancestry categories: F₁ admixed, and other admixed and pre-introgression type combined.

^c Het refers to individual average heterozygosity.

^d Ancest1 divides panthers into three ancestry categories: F₁ admixed, other admixed, and pre-introgression type.

Table 2-4. Estimated annual survival rates (with \hat{SE} and number of panthers) by ancestry, sex, and age-class.

Group	Pre-Introgression Type	Other Admixed	F ₁ Admixed
All	0.775 (0.039; 41) ^a	0.821 (0.036; 49) ^a	0.978 (0.021; 8) ^a
Females	0.837 (0.041; 20) ^b	0.864 (0.035; 22) ^b	0.982 (0.018; 6) ^b
Males	0.713 (0.055; 21) ^b	0.758 (0.056; 27) ^b	0.967 (0.032; 2) ^b
Female Sub-Adults ^c	0.953 (0.049; 9) ^d	0.964 (0.036; 14) ^d	0.995 (0.007; 4) ^d
Female Prime-Adults ^e	0.803 (0.047; 19) ^d	0.848 (0.041; 22) ^d	0.977 (0.022; 6) ^d
Male Sub-Adults ^f	0.606 (0.088; 14) ^d	0.686 (0.073; 22) ^d	0.949 (0.050; 2) ^d
Male Prime-Adults ^g	0.789 (0.059; 12) ^d	0.836 (0.056; 13) ^d	0.976 (0.024; 2) ^d

^a Estimated using Ancest1 model (divides panthers into pre-introgression type, other admixed, and F₁ admixed).

^b Estimated using Sex + Ancest1 model.

^c Female sub-adults were 1-2.5 years old.

^d Estimated using Sex * Age3 (sub-adult vs. prime-adult) + Ancest1 model.

^e Female prime-adults were 2.5-10 years old.

^f Male sub-adults were 1-3.5 years old.

^g Male prime-adults were 3.5-10 years old.

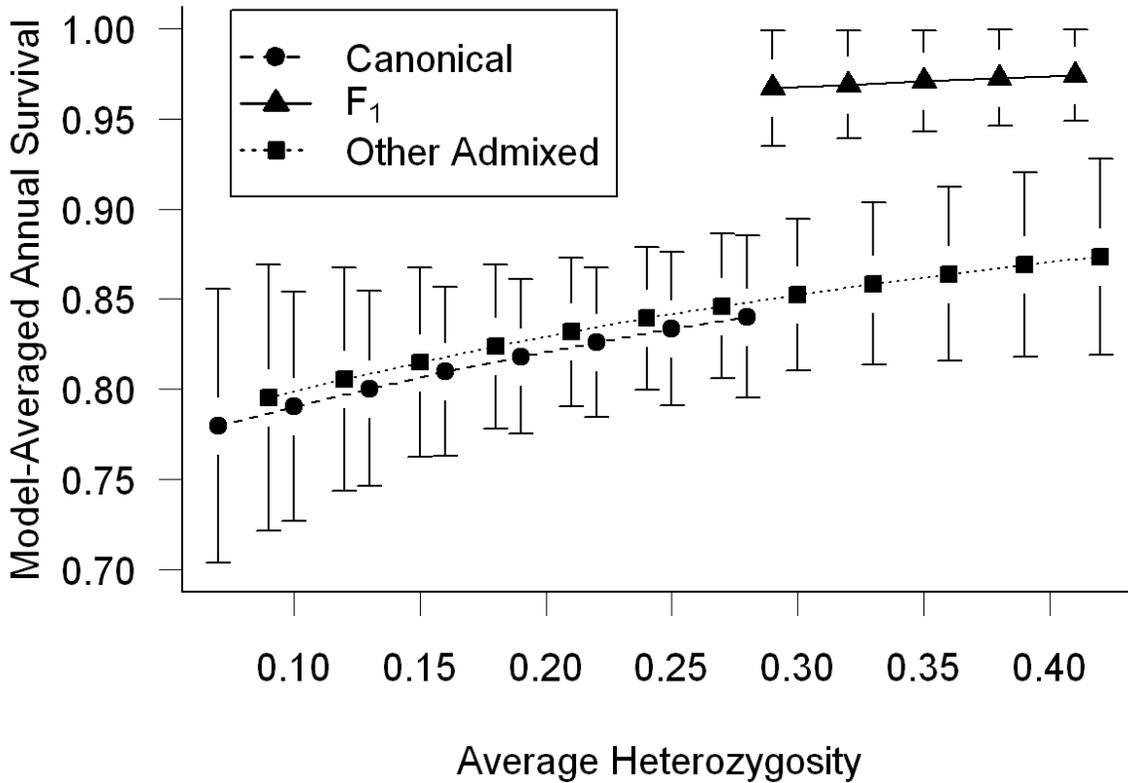


Figure 2-1. Model-averaged effects of ancestry and heterozygosity on annual survival of female prime-adult Florida panthers from 1997-2006. The range of heterozygosity values presented for each ancestry category approximately corresponds to those found in the dataset (all sub-adult and prime-adult panthers from 1997-2006 with that ancestry), except for one outlier with high heterozygosity excluded from the range for the pre-introgression-type. Error bars represent unconditional standard errors.

CHAPTER 3 GENETIC INTROGRESSION AND THE SURVIVAL OF FLORIDA PANTHER KITTENS

Introduction

Rigorous estimates of survival rates and understanding factors influencing those rates are critical for discerning proximate and ultimate causes of dynamics, regulation, and persistence of populations (Newton, 2004; Ozgul et al., 2006) and for devising and implementing management interventions for species conservation (Davis et al., 2007). Population dynamics of many vertebrate species are strongly influenced by changes in survival rates (Heppell et al., 2000; Oli and Dobson, 2003; Stahl and Oli, 2006). Estimates of survival also are necessary for the parameterization of population models, which are essential tools in conservation biology for evaluating population performance, diagnosing the causes of low numbers or population declines, developing solutions to those problems, and determining research priorities (Caswell, 2001; Caughley and Gunn, 1996; Fujiwara and Caswell, 2001). These population models can often be improved by including the estimated effects of factors such as population density or genetic diversity on survival.

The Florida panther (*Puma concolor coryi*) is a subspecies of puma that once ranged throughout the southeast United States. Florida panthers give birth to 1-4 kittens, which remain in the den for approximately 7-8 weeks (Maehr et al., 1990). Average age of independence is just over 1 year (mean = 397 days, SD = 74 days, $n = 32$; FWC & NPS, unpublished data). The Florida panther is now restricted to <5% of its historic range in south Florida (Maehr et al., 2002a), where it occurs in a single population with ca. 100 sub-adults and adults (McBride et al., 2008). It has been federally listed as endangered since 1967. Small population size, isolation, loss and

fragmentation of habitat, road-related mortalities, and other anthropogenic influences continue to threaten the long-term persistence of Florida panthers (Kautz et al., 2006).

Small populations are expected to suffer from inbreeding depression (Frankham et al., 2002); earlier studies of Florida panthers found evidence of inbreeding and recommended genetic introgression via the introduction of a subspecies of puma whose range historically abutted with the range of the Florida panther (Barone et al., 1994; Roelke et al., 1993b). Based on this recommendation, 8 female Texas pumas (*P. c. stanleyana*) were released into the Florida panther population in 1995. Although the panther population has experienced an almost fourfold increase since 1995 (McBride et al., 2008), the success of the introgression continues to be a topic of debate (Maehr et al., 2006; Onorato et al., 2010; Pimm et al., 2006a). There have also been non-management releases of captive pumas into south Florida; some of these (between 1957 and 1967) resulted in a genetic population with partial Central American ancestry in the Everglades (O'Brien et al., 1990).

In 2003, the U.S. Fish and Wildlife Service (USFWS) and the Florida Fish and Wildlife Conservation Commission (FWC) convened the Scientific Review Team (SRT) to review the status of Florida panther science, and to make research and management recommendations. The SRT thoroughly reviewed existing literature on demography and population ecology of the panther, and found that rigorous estimates of age- or stage-specific survival rates and cause-specific mortality rates were not available. Furthermore, SRT found that previously reported estimates of the survival rate of Florida panther kittens (Maehr and Caddick, 1995) and those used in population viability analyses (Maehr et al., 2002a) were not based on reliable inference methods and raised

doubt on predictions regarding the persistence of the panther population (Beier et al., 2003; Beier et al., 2006; Gross, 2005). The SRT recommended reanalysis of existing data to rigorously estimate age-specific survival rates and test hypotheses regarding factors influencing survival rates (Beier et al., 2003).

In accordance with SRT recommendations (Beier et al., 2003), our goals were to provide rigorous estimates of survival of Florida panther kittens (defined here as age 0 – 1 year), and to evaluate factors influencing kitten survival. We analyzed long-term radio-telemetry (1982-2008) and Passive Integrated Transponder (PIT)-tagging (1995-2008) data within a live-recapture, dead recovery modeling framework (Burnham, 1993; Williams et al., 2002). We tested the hypotheses that kitten survival: (1) would not differ between sexes, due to little or no sexual dimorphism during this stage of life; (2) would decrease with increasing litter size due to large litters potentially being more energetically demanding to dams and more difficult to protect from predators; (3) would be higher during the wet season (June – November) than during the dry season (December – May), due to potential higher prey availability during the wet season; and (4) would be negatively influenced by population abundance due to density-dependent effects. In many species of carnivores, survival of neonates is generally lower compared to older juveniles (Garrison et al., 2007; Logan and Swenor, 2001). Thus, we also hypothesized that kitten survival (5) would increase with age during their first year.

Results of rigorous analyses evaluating the effects of genetic introgression on kitten survival could assist in setting future management and research priorities. Thus, we tested these additional hypotheses: (6) kitten survival probability would increase with

average heterozygosity, because loss of genetic variation (especially due to inbreeding) has been shown to negatively influence fitness and its components (Crnokrak and Roff, 1999; Ralls and Ballou, 1983); and (7) survival probability would be higher for admixed kittens than for canonical (i.e., pure Florida panther) kittens as outcrossing has been shown to increase various measures of fitness for small, inbred populations (Heschel and Paige, 1995; Madsen et al., 1999; Vrijenhoek, 1994).

Materials and Methods

Field Methods

Florida panthers and Texas pumas were captured and monitored by radio-telemetry from 1982-2008 across the range of the subspecies in south Florida, USA (Kautz et al. 2006) by biologists from the FWC and National Park Service (NPS) using methods described by Belden et al. (1988) and Land et al. (2008). Age of captured panthers (if unknown) was estimated using a combination of toothwear, pelage characteristics, size, and developmental stage of teats and reproductive organs. Blood and tissue samples were collected for health assessment and genetic analysis. Radio collars were affixed on captured adults, sub-adults, and older kittens (occasionally as young as 5 months old; age and size qualifications for collaring varied over time).

Successive locations of females were continually assessed to determine the commencement of denning behavior; lack of movement between 3-4 fixes was taken as evidence of possible denning (Land et al., 1998). We visited dens 4-35 days post-partum (approximate median = 14 days). Kittens in dens were counted, sexed, sampled for genetic material, and implanted with passive integrated transponder (PIT) tags. Occasionally, dens were checked after dams vacated the area for evidence of dead kittens.

Females that denned ≤ 12 months after giving birth to a previous litter were classified as having lost that previous litter because 1) females are unlikely to copulate while they have dependent kittens, 2) the gestation period is about 3 months (Maehr, 1992), and 3) the minimum age of independence recorded is 9 months (D. Onorato, unpublished data). Similarly, litters whose dams died ≤ 9 months after denning were classified as having failed. These two types of litter failure data generally do not provide an estimated death date for individual kittens, only an upper limit on the date when litters could have failed.

Heterozygosity and Genetic Ancestry

We extracted total genomic DNA from blood and tissue samples obtained from wild-caught panthers and captive pumas from south Florida and west Texas during 1982-2007. We amplified and scored 23 microsatellite loci following previously described PCR amplification conditions (Menotti-Raymond et al., 1999; Menotti-Raymond et al., 1997). Derived genotypes were used to calculate average individual heterozygosity using the program MICROSAT (Minch et al., 1995).

A Bayesian procedure, implemented in the program STRUCTURE (Pritchard et al., 2000) was used to identify populations or genetic clusters (run without preset groups/ training individuals) and to estimate the genetic origin of individuals. The STRUCTURE approach assumes departures from both Hardy-Weinberg and complete linkage equilibriums to be indications of population substructure (Pritchard et al., 2000).

We used results from the STRUCTURE analysis along with pedigree information and field evidence to assign panthers to groups that reflect the genetic makeup of the southern Florida population: canonical panthers (92 total panthers; 50 kittens), backcrossed to canonical admixed panthers (92 total panthers; 80 kittens), backcrossed

to Everglades admixed panthers (19 total panthers; 18 kittens), backcrossed to Texas admixed panthers (42 total panthers; 38 kittens), and F_1 admixed panthers (15 total panthers; 13 kittens). Canonical Florida panthers showed no evidence of non-Florida genetic admixture (no direct non-Florida relatives or $< 10\%$ non-Florida genetic contribution based on STRUCTURE analyses). Admixed panthers were mostly the descendants of the introduced female Texas pumas released in 1995, except for 6 radio-collared individuals (0 kittens) that were genotypically similar to pumas maintained in a large enclosure on the Seminole Indian Reservation (SIR) adjacent to Big Cypress National Preserve. These SIR panthers, panthers of unknown ancestry (4 kittens), and admixed panthers whose ancestry could not be accurately determined (total = 54, of which 43 were kittens) were excluded from the survival analysis that incorporated ancestry.

Backcrossed to canonical panthers were admixed panthers with predominantly ($>50\%$) canonical heritage resulting from admixed panthers breeding with canonical panthers. Backcrossed to Everglades were admixed panthers with predominantly ($>50\%$) Everglades heritage resulting from breeding events between admixed and Everglades panthers. Backcrossed to Texas admixed panthers were admixed panthers of predominantly ($>50\%$) Texas heritage resulting from admixed panthers breeding with introduced Texas pumas. We defined F_1 admixed panthers as any offspring produced by matings between a Texas female and a pre-introgression type male (either canonical Florida panther or Everglades panther). In theory, Everglades panthers (with documented genetic links to Central American pumas) represent a sixth genetic

population; however, there were no recorded kittens of this group during the post-introgression study period (June 1995 – May 2008).

We also repeated our analyses based on a simpler ancestry classification (canonical, F_1 admixed, and other admixed) that allowed the inclusion of admixed panthers with unknown ancestry; results of these analyses are presented in Appendix E.

Index of Abundance

To examine the potential effects of panther density on kitten survival, we used minimum population counts as an index of abundance (McBride et al., 2008). These minimum counts were based on radio-tracking and field evidence of sub-adult and adult panthers (tracks, scat, kills, and scrapes) and collected for calendar years (e.g., total number of sub-adult and adult panthers known to have been alive in the wild over the period January 2005 – December 2005). In contrast, we analyzed annual kitten survival for periods extending from June – May. We applied the sub-adult/adult calendar year count for year x to the kitten June x – May $x + 1$ year, because puma kitten mortality is generally highest in the first three months of life (see Results), so adult abundance during that period seemed most likely to affect survival. In 2004, the panther survey was incomplete, so the minimum count is unknown. We followed McBride et al. (2008) and extrapolated it halfway between the 2003 and 2005 counts.

Data Preparation and Analysis

We used two datasets for the analysis of kitten survival. The first contained the capture (of live panthers) and recovery (of dead panthers) histories, observations of litter-failures (i.e., loss of entire litters), and radio-tracking data for panthers that were initially PIT-tagged in the den between June 1995 and May 2008 (13 years). The

second contained the capture, recovery, and radio-tracking histories of all other panthers between June 1982 and May 2008 (26 years). Details of data preparation can be found in Appendix F.

We analyzed data using the R (R Development Core Team, 2010) package RMark (Laake and Rexstad, 2010) as an interface for program MARK (White and Burnham, 1999) and Burnham's live-recapture dead-recovery modeling framework (Burnham, 1993; Williams et al., 2002). The Burnham model has four parameters: survival probability (S), recapture probability (p), recovery probability (r), and fidelity (F). For all models, we fixed $F=1$ for all panthers, as the recapture and recovery areas are the same and encompass the entire range of the Florida panther. We set p and r for radio-collared animals to 1, because we could count on knowing their status each year.

Although the focus of our study was kitten survival, we also used data from sub-adult and adult panthers to efficiently parameterize the likelihood functions. For example, the likelihood of a kitten being PIT-tagged in the den and then recaptured as a 2-year old panther depends on the probability of it surviving as a kitten, the probability of it surviving the first year of being a sub-adult, and the probability of recapture as a sub-adult. Thus, to estimate the kitten survival probability from data such as these, we also need to estimate the other aforementioned probabilities. We used a model with an interaction of sex and age class (sub-adult or adult), a reasonably well supported model (Benson et al., in revision) that could be applied to all individuals, to estimate the survival of sub-adults and adults. The boundary between sub-adult and adult panthers was originally defined at age 2.5 for females and age 3.5 for males (Benson et al., in revision). Transitions at these ages were impossible with a one-year time step;

therefore, we fitted survival models with those ages rounded up and down to the nearest integer (to 2 and 3 for females and 3 and 4 for males). We used an information-theoretic approach (Akaike's Information Criterion adjusted for overdispersion and small sample size; QAIC_c) for model selection and statistical inference (Burnham and Anderson, 2002). We calculated QAIC_c values, Akaike differences (ΔQAIC_{ci} , difference between QAIC_c value of the *i*th model and the top-ranked model) and Akaike weights (the weight of evidence that a model is the best model of the models being considered given the data) as in Burnham and Anderson (2002). We calculated model-averaged estimates of annual survival and unconditional variance for each level of categorical variables and across continuous covariates (Burnham and Anderson, 2002; Tinker et al., 2006). To generate these model-averaged estimates of survival we used all models included in the model selection process for a given analysis, with model-specific estimates weighted by their Akaike weights. Models with no effects of the covariates being presented were included in the averages.

We commenced by testing all *a priori* models for recapture and recovery combined with *a priori* models for survival of kittens, sub-adults, and adults with various divisions of age classes. Because kittens could only be recaptured as sub-adults the following year, there was no capture probability parameter for kittens (e.g., Pollock, 1981); for sub-adult and adult panthers we estimated a single capture probability. We used models that estimated separate recovery rate for kittens and older panthers as well as those that estimated a single recovery rate for all panthers.

We used a model that allowed kitten survival to vary between sexes and recapture probability to be different for kittens (the most parameterized model that applies to the

full dataset) to test for overdispersion of the data due to lack of independence within litters (\hat{c}) using the data bootstrap approach developed by Bishop et al. (2008); a $\hat{c} > 1$ indicates overdispersion. We estimated \hat{c} as the ratio of the replication-based estimate of the variance of bootstrapped survival estimates (this variance incorporates overdispersion associated with lack of independence) to the model-based estimate of variance of survival (estimated from the original dataset). For the bootstrap approach, we sampled litters from the dataset with replacement. Panthers first captured as sub-adults or adults were treated as litters of size 1 for the bootstrapping. If the model failed to estimate kitten survival parameters, the iteration was discarded. We repeated the resampling and estimation until we had 1,000 estimates of female and male kitten survival and estimated the mean \hat{c} as in Bishop et al. (2008). The estimate of overdispersion was 1.37 for females and 1.60 for males, with a mean \hat{c} of 1.48, indicating slight overdispersion of data. We used this value as a variance inflation factor and to calculate QAIC_c.

We selected the model with the lowest QAIC_c from preceding analyses as the base model to test hypotheses regarding factors affecting kitten survival (Table 3-1). The models for ancestry (Table 3-1A, models 3-6, Table 3-1B) and heterozygosity (Table 3-1A, models 7-10) were run on data collected between 1995 and 2008 only due to the absence of admixed panthers in Florida before 1995. We tested for the effect of ancestry and heterozygosity on survival of (1) kittens only; (2) sub-adult and adult panthers only; (3) kittens and older panthers considered separately; and (4) panthers of all ages. Based on previous results (Benson et al., in revision), however, we only considered 2 ancestry categories for sub-adult and adult panthers (F1Adv; Table 3-1B).

We tested for the effect of abundance on kitten survival (Table 3-1A, model 11) using data collected between 1995 and 2008. Data on kittens collected prior to 1995 were insufficient to test for the effect of abundance on kitten survival.

Finally, we estimated process variance (random effect of year; a critical parameter for stochastic population models) in kitten survival using the Markov Chain Monte Carlo (MCMC) option in MARK (Lukacs et al., 2009; White et al., 2009). We used the Bayesian MCMC approach instead of a method of moments approach because some missing kitten survival estimates for specific years (fixed effects categorical model used as an input for method of moments) made the method of moments approach unreliable (G. White personal communication). We estimated process standard deviation in logit survival from the mean and 95% credible interval of the posterior distribution. To estimate the temporal variation beyond that explained by abundance, we also estimated the temporal standard deviation associated with year in the model that included abundance index as a covariate. Temporal standard deviations were converted from the logit scale using the mean kitten survival (to $\hat{\sigma}$; without abundance index model) and the kitten survival computed for the mean abundance (to σ_{res} ; abundance index model). We estimated percentage of the temporal variance explained by abundance as $(\hat{\sigma}^2 - \sigma_{res}^2) / \hat{\sigma}^2$ (Loison et al., 2002).

We used the same non-informative priors as White et al. (2009); estimates from the fixed effects models were used as starting values where appropriate. We tested for lack of convergence using 10 Markov chains for each model (Gelman, 1996) and found no evidence of lack of convergence. For each chain we sampled the MCMC for 50,000 iterations, after 4,000 tuning samples and 1,000 burn-in samples.

Three-Month Time Step Data Preparation and Analysis

Using the data organized on an annual time scale, it was not possible to test for seasonal variation in kitten survival and age-specific variation in survival within the first year of life. Therefore, we recoded data into 3-month time intervals. This necessitated leaving out litter failure data, because information about the 3-month interval in which actual kitten deaths occurred was generally not available from these data. We also did not include the recapture/recovery histories of panthers not PIT tagged in the den (without working radio-collars), for computation efficiency (Appendix G).

Analysis of the data with a 3-month time step was similar to the annual time step analysis, except that there was now a possibility of recapture as a kitten. We commenced by testing all *a priori* models for recapture and recovery combined with *a priori* models for survival of kittens based on age (Appendix G). We report model-specific and model-averaged estimates of annual kitten survival probability and model-averaged estimates of 3-month kitten and annual sub-adult and adult survival probabilities (Burnham and Anderson, 2002).

Results

The most parsimonious model (model 1, Table 3-2) indicated that survival (S) and recapture (r) probabilities differed between kittens and older panthers, and that S differed between sex and age classes among older panthers, with the sub-adult to adult transition at the upper age limit for both sexes. The four models with lowest QAIC_c provided similar estimate of kitten survival (Table 3-2); the model-averaged estimate of annual kitten survival was 0.323 ± 0.065 (± 1 SE).

We selected the most parsimonious model from the initial model set (model 1, Table 3-2) as a base model for testing the effects of covariates on kitten survival. There

was no evidence of an effect of sex (Table 3-2) or litter size (ΔQAIC_c of litter size model = 2.04) on kitten survival.

Two of the ancestry models (base + k:CanDisF1Adv and base + k:F1Adv) failed to estimate a kitten survival parameter and were discarded. There was considerable evidence that ancestry influenced kitten survival; the 6 most parsimonious models all included ancestry effects on kitten survival (models 1-6, Table 3-3A). The top 2 models indicated that survival of kittens differed substantially between two ancestry categories: 1) canonical and backcrossed to canonical kittens and 2) F_1 , backcrossed to Texas, and backcrossed to Everglades kittens (Table 3-3A). Model-averaged kitten survival was lowest for canonical kittens and highest for F_1 kittens (Figure 3-1A).

The most parsimonious model including the effects of heterozygosity on survival indicated that survival of panthers of all ages (including survival of kittens) was positively affected by average heterozygosity (Table 3-3B, model 1). Although this model differed from the base model by $\Delta\text{QAIC}_c < 2$, the 95% confidence interval for the slope parameter did not include zero ($\beta = 2.89$; 95% CI: 0.16 – 5.63) suggesting a positive effect of average heterozygosity on panther survival. Model-averaged kitten survival increased with heterozygosity (Figure 3-1B).

There was considerable evidence that abundance negatively influenced kitten survival, with the model with no such effect having a ΔQAIC_c of 8.79 (Table 3-3C). Kitten survival declined with increasing population size (Figure 3-2; $\beta = -0.034$, 95% CI = -0.053 – -0.016).

We estimated temporal standard deviation of kitten survival (σ) at 0.228 (95% credible interval = 0.019 – 0.431) and 0.098 (95% credible interval = 0.004 – 0.286)

using models without and with the abundance index, respectively. Abundance index explained 81.5% of the temporal variation in kitten survival.

There was considerable uncertainty in the base model selection, with 8 models in Table 3-2 having $\Delta QAIC_c < 1$. We reran all covariate tests using model 5 from Table 3-2 as a base model (model 5 was the highest ranked model with a different estimate of kitten survival than model 1). Model selection and statistical inference were barely affected by the switch of base models, and model averaged estimates that included both sets of models were somewhat lower, but generally had similar precision (Appendix H).

There was strong evidence that kitten survival was lowest in the first 3 months of life (Figure 3-3). There was no evidence for seasonal variation in kitten survival (Appendix G). Details of results based on the analysis of data organized using 3-month time steps are presented in Appendix G.

Discussion

Models developed for population conservation and management have historically focused on either population dynamics (Morris and Doak, 2002) or threshold numbers required to avoid genetic problems (Franklin, 1980). The population ecology and population genetics of a species are frequently not integrated in these models. When they are, the demographic effects of inbreeding are often based on data from captive animals and/or program defaults (e.g., Brito, 2009; Maehr et al., 2002a; Nilsson, 2004). An important first step towards developing integrated models is determining the functional relationship between measures of inbreeding and juvenile survival in the wild, especially for managed populations.

Overall, the model-averaged estimate of annual survival probability of Florida panther kittens was 0.323 ± 0.065 ; this estimate is lower than those reported for western North American populations of pumas (range: 0.44 to 0.72; Lambert et al., 2006; Laundré et al., 2007; Logan and Swenor, 2001; Robinson et al., 2008). Our estimate of kitten survival also is substantially lower than those used in earlier demographic analyses of the Florida panther (Maehr and Caddick, 1995: 0.84 - 0.87; Maehr et al., 2002a: 0.735 - 1.0; Root, 2004: 0.62). Although our estimates of kitten survival varied slightly depending on the model (0.30 to 0.34; Table 3-2), they were consistently lower than those used in previous analyses. Furthermore, kittens were not tagged immediately after birth, and we could have missed kittens that had died before they were PIT-tagged at the den site; thus, true survival may be slightly lower. However, since most of our data on kitten survival came from a period of population growth (McBride et al., 2008), we have no reason to believe that the kitten survival rate for this population is unsustainable. Ongoing work developing updated population models for Florida panthers may shed additional light on the role of kitten survival in determining population dynamics.

Survival rates did not differ between male and female kittens. This result was as expected due to the lack of sexual dimorphism among kittens, although some authors have suggested sex-specific differences in survival of puma kittens (Logan and Swenor, 2001). There was no evidence that litter size influenced survival of kittens. This may reflect the possibility that females most able to successfully raise large litters are those most likely to produce them.

Perhaps the most dramatic panther conservation measure undertaken to date is the release of 8 female Texas pumas into the Florida panther population in 1995 (Seal 1994). Genetic introgression has been highly controversial (e.g., Maehr and Caddick, 1995; Maehr et al., 2006; Pimm et al., 2006b). Pimm et al. (2006) reviewed the arguments for and against genetic introgression in general, and in the Florida panther population in particular. They reported that admixed kittens are more than three times as likely to survive as purebred Florida panthers. Pimm et al.'s (2006) conclusions were based solely on the proportion of kittens PIT-tagged in the den that were subsequently captured and (generally) radio-collared. These kittens were recaptured at ages ranging from 6.5 months to 3.5 years and detection probability was not taken into account, so it is unclear how well these ratios represent differences in kitten survival.

In the present study, we used multiple sources of field data, a thorough determination of ancestry of nearly all kittens captured since genetic introgression occurred in 1995, and a statistically rigorous live-recapture dead-recovery modeling approach that takes detection probabilities into account to test for the effect of genetic introgression on the survival of Florida panther kittens. As recommended by Creel (2006), we limited this portion of the analysis to a period when both canonical and admixed kittens were on the landscape. We also were able to examine the effects of heterozygosity, which differed dramatically between canonical Florida panthers (0.161) and Texas pumas (0.318; Driscoll et al., 2002; Johnson et al., 2010). Furthermore, we were able to determine ancestry of panther kittens at a much finer scale than Pimm et al. (2006). We found that admixed kittens generally survived better than kittens born to canonical Florida panthers. Furthermore, F_1 admixed kittens had the highest survival,

followed by backcrossed to Texas kittens (Fig. 1A). Finally, we found that average heterozygosity positively influenced survival of Florida panther kittens (Fig. 1B). These results provide unambiguous evidence for the positive, population-level impact of genetic introgression.

Index of panther abundance negatively influenced kitten survival, which is suggestive of a density dependent effect. This could result from infanticide by sub-adult and adult males during territorial disputes or for mating opportunities (Garrison et al., 2007; Logan and Sweanor, 2001; Packer et al., 2009), from deaths of the dependent kittens' dams due to intraspecific aggression, or from competition for food or other resources. We note, however, that our results are based on an index of abundance, and thus may not be sufficient to conclusively demonstrate density-dependent influence on kitten survival. Interestingly, a substantial proportion of temporal variation in kitten survival was explained by temporal variance in index of abundance.

Analysis of data organized with 3-month time intervals revealed no evidence for seasonal (i.e., wet vs. dry) variation in survival of kittens. However, we found that survival was lowest during the first 3 months of life, which is consistent with other large carnivore populations (Garrison et al., 2007; Logan and Sweanor, 2001). These results point to the fact that young kittens are particularly vulnerable to various mortality factors.

Estimating survival of young can be challenging in elusive carnivores because they are rarely observed. Additionally, in the case of panthers, kittens are typically too small to be fitted with radio-transmitters when sampled at the den site – a method that would be effective for monitoring their fate during the first year of life. Furthermore, the small population size of endangered species and invariably small sample sizes may not

be adequate for rigorous estimates of survival of the young. For example, estimates of kitten survival that did not include litter failure data lacked robustness as well as precision; models that were similarly ranked based on QAIC_c provided very different estimates of kitten survival (Appendix G). We addressed this challenge by using a modeling framework that can utilize multiple data sources. Resulting estimates of kitten survival were more robust and precise, and also allowed us to test various hypotheses regarding factors influencing survival of Florida panther kittens. Similar approaches can be used to estimate survival of young in other elusive species that occur in low numbers.

Our study is the first to provide rigorous estimates of survival of Florida panther kittens. We found that kitten survival in our study population was lower than reported for western cougars, and substantially lower than values used in previous demographic analyses of Florida panthers. These results are consistent with an earlier suggestion that results of a previous PVA (Maehr et al., 2002a) that assumed kitten survival of up to 87% may be unreliable (Beier et al., 2003). Finally, we found strong evidence that survival of admixed (particularly, F₁) kittens was substantially higher than that of purebred kittens, and that heterozygosity positively influenced survival of Florida panther kittens. These results are consistent with hybrid vigor theory (Crow, 1948; Frankham et al., 2002), and suggest that genetic introgression had positive population-level effects in our study population. Although there are concerns that genetic introgression can have undesirable or even negative impacts on populations (Edmands, 2007; Maehr and Caddick, 1995; Shields, 1993), our analyses revealed beneficial results of deliberate introgression for this population. A combination of these results

with other recently published or on-going assessments of demography pre- and post-introgression should assist in directing management and research priorities that will ensure the continued persistence the critically endangered Florida panther.

Table 3-1. List of kitten survival models. A) All a priori models that were used to test hypotheses regarding the effect of covariates on kitten survival probability (S) and B) definitions of ancestry models. All models are based on the additive effects of covariates on survival of kittens (unless otherwise noted) from the base model(s) (base; see Table 3-2). s&a indicates an effect on sub-adult and adult survival and k indicates an effect on kitten survival.

A. All Models		
Model	Description	
1. S(base + k:sex)	Additive sex effect	
2. S(base + k:LS)	Additive linear litter size effect	
3. S(base + k:Ancestry)	Additive ancestry effect (see below) on kitten survival	
4. S(base + Ancestry)	Additive ancestry effect (see below) on survival of panthers of all ages	
5. S(base + s&a:F1Adv)	Additive F_1 ancestry effect (see below) on survival of sub-adult and adult panthers only	
6. S(base + k:Ancestry + s&a:F1Adv)	Separate additive ancestry effects (see below) on kitten survival and sub-adult and adult survival (F_1 only)	
7. S(base + k:Het)	Additive linear heterozygosity effect on kitten survival	
8. S(base + Het)	Additive linear heterozygosity effect on survival of panthers of all ages	
9. S(base + s&a:Het)	Additive linear heterozygosity effect on survival of sub-adults and adults only	
10. S(base + k:Het + s&a:Het)	Separate additive linear heterozygosity effects on survival of kittens and survival of sub-adults and adults	
11. S(base + k:Abundance)	Additive linear effect of abundance index	
B. Ancestry Models		
Term	Definition	Hypothesis
IntAdv	2 ancestry categories: 1) canonical; 2) backcrossed to canonical, backcrossed to Everglades, backcrossed to Texas, and F_1 .	General introgression advantage (or disadvantage).
AdmAdv	2 ancestry categories: 1) canonical and backcrossed to canonical; 2) backcrossed to Everglades, backcrossed to Texas, and F_1 .	General admixture advantage (or disadvantage), but with backcrossed to canonical reverting to canonical.
50TexAdv	2 ancestry categories: 1) canonical, backcrossed to canonical, and backcrossed to Everglades; 2) backcrossed to Texas, and F_1 .	Survival advantage (or disadvantage) for those \geq 50% Texas.
CanDisF1Adv	3 ancestry categories: 1) canonical; 2) backcrossed to canonical, backcrossed to Everglades, and backcrossed to Texas; and 3) F_1 .	Differences in survival between pre-introgression types, backcrosses, and F_1 's.
CanDis50TexAdv	3 ancestry categories: 1) canonical; 2) backcrossed to canonical and backcrossed to Everglades; 3) backcrossed to Texas and F_1 .	Differences in survival between pre-introgression types, \geq 50% Texas, and intermediate types.
F1Adv	2 ancestry categories: 1) canonical, backcrossed to canonical, backcrossed to Everglades, and backcrossed to Texas; and 2) F_1 .	Survival advantage (or disadvantage) for F_1 's.

Table 3-2. Model comparison table to estimate annual kitten survival and select base model. For each model, we present the number of parameters (K), the difference from the top model in Akaike's Information Criterion adjusted for overdispersion and small sample size ($\Delta QAIC_c$), the model $QAIC_c$ weight, and the estimate of annual kitten survival with standard error. The base model selected is in the first row (representing survival differing between kittens, females age 1 and 2, females 3 and older, males age 1-3, and males 4 and older; recapture the same for all uncollared panthers; and recovery differing between uncollared kittens and uncollared older panthers).

Model	K	$\Delta QAIC_c$	Weight	Annual Kitten Survival Estimate (SE)
1. S(k, 1≤f<3, f≥3, 1≤m<4, m≥4)p(.)r(k, s&a)	8	0.00	0.147	0.343 (0.070)
2. S(k, 1≤f<3, f≥3, 1≤m<3, m≥3)p(.)r(k, s&a)	8	0.19	0.134	0.342 (0.070)
3. S(k, 1≤f<2, f≥2, 1≤m<4, m≥4)p(.)r(k, s&a)	8	0.24	0.130	0.345 (0.071)
4. S(k, 1≤f<2, f≥2, 1≤m<3, m≥3)p(.)r(k, s&a)	8	0.43	0.119	0.344 (0.070)
5. S(k, 1≤f<3, f≥3, 1≤m<4, m≥4)p(.)r(.)	7	0.47	0.116	0.296 (0.049)
6. S(k, 1≤f<3, f≥3, 1≤m<3, m≥3)p(.)r(.)	7	0.62	0.108	0.296 (0.049)
7. S(k, 1≤f<2, f≥2, 1≤m<4, m≥4)p(.)r(.)	7	0.76	0.100	0.297 (0.049)
8. S(k, 1≤f<2, f≥2, 1≤m<3, m≥3)p(.)r(.)	7	0.92	0.093	0.297 (0.049)
9. S(k + sex, 1≤f<3, f≥3, 1≤m<4, m≥4)p(.)r(k, s&a)	9	2.02	0.053	0.349 (0.084) ^a 0.335 (0.089) ^b

^a Female kitten survival.

^b Male kitten survival.

Table 3-3. Model selection table for effects of covariates on survival. A) Ancestry effects. B) Heterozygosity effects. C) Abundance index effects. These analyses were performed on subsets of the data (excluding panthers before 1995 for all analyses and panthers of unknown ancestry for A, and panthers before their heterozygosity was sampled for B). For each model, we present the number of parameters (K), the difference from the top model in Akaike's Information Criterion adjusted for overdispersion and sample size (ΔQAIC_c), and the weight. See Table 3-1 for descriptions of the covariate models and Table 3-2 for the base model. All models estimate constant recapture rates and recovery rates that differ between kittens and older panthers.

A. Ancestry models				
Survival Model	K	ΔQAIC_c	Weight	
1. base + k:AdmAdv + s&a:F1Adv	10	0.00	0.242	
2. base + AdmAdv	9	1.34	0.124	
3. base + F1Adv	9	1.44	0.118	
4. base + CanDisF1Adv	10	1.99	0.090	
5. base + k:50TexAdv + s&a:F1Adv	10	2.38	0.074	
6. base + k:AdmAdv	9	3.27	0.047	
7. base + s&a:F1Adv	9	3.35	0.045	
8. base + 50TexAdv	9	3.43	0.044	
9. base + k:F1Adv + s&a:F1Adv	10	3.46	0.043	
10. base + k:IntAdv + s&a:F1Adv	10	3.49	0.042	
11. base + k:CanDis50TexAdv + s&a:F1Adv	11	3.98	0.033	
12. base + k:CanDisF1Adv + s&a:F1Adv	11	4.22	0.029	
13. base + CanDis50TexAdv	10	4.92	0.021	
14. base + IntAdv	9	5.56	0.015	
15. base + k:50TexAdv	9	5.80	0.013	
16. base + k:IntAdv	9	7.34	0.006	
17. base + k:CanDis50TexAdv	10	7.36	0.006	
18. base	8	7.43	0.006	
B. Heterozygosity models				
Survival Model	K	ΔQAIC_c	Weight	
1. base + Het	9	0.00	0.325	
2. base + s&a:Het	9	0.75	0.223	
3. base	8	0.91	0.206	
4. base + k:Het	9	1.88	0.127	
5. base + k:Het + s&a:Het	10	2.00	0.119	
C. Abundance index models				
Survival Model	K	ΔQAIC_c	Weight	
1. base + k:Abundance	9	0.00	0.988	
2. base	8	8.79	0.012	

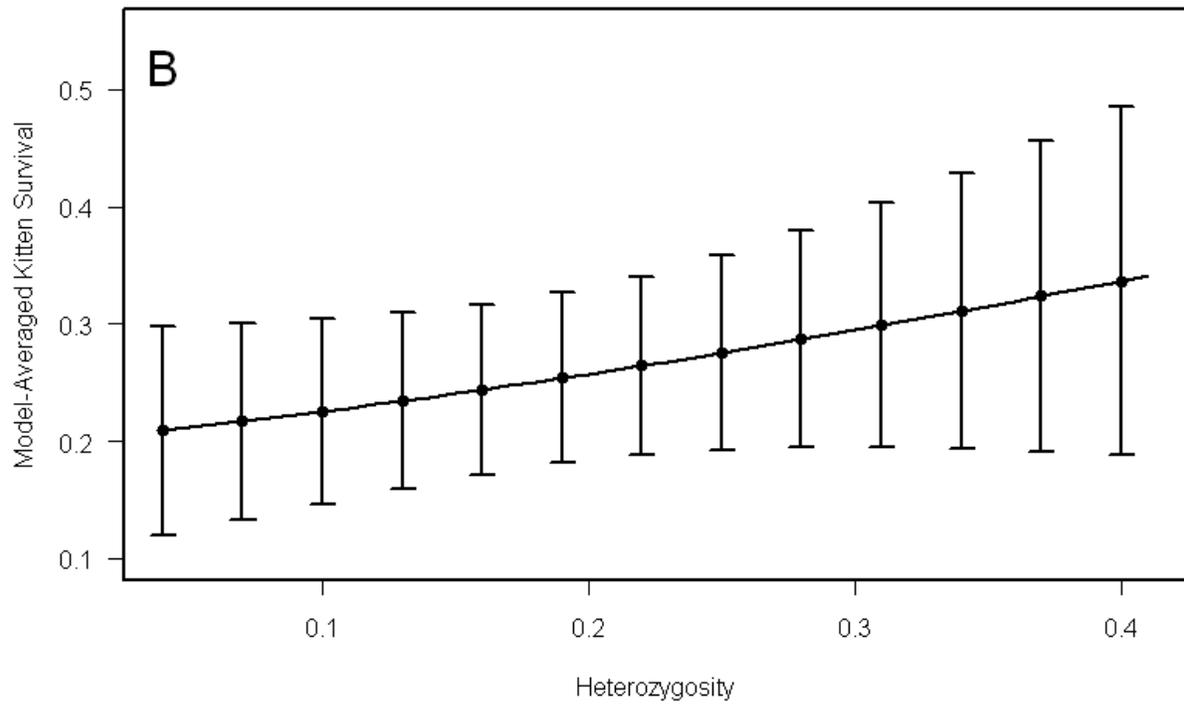
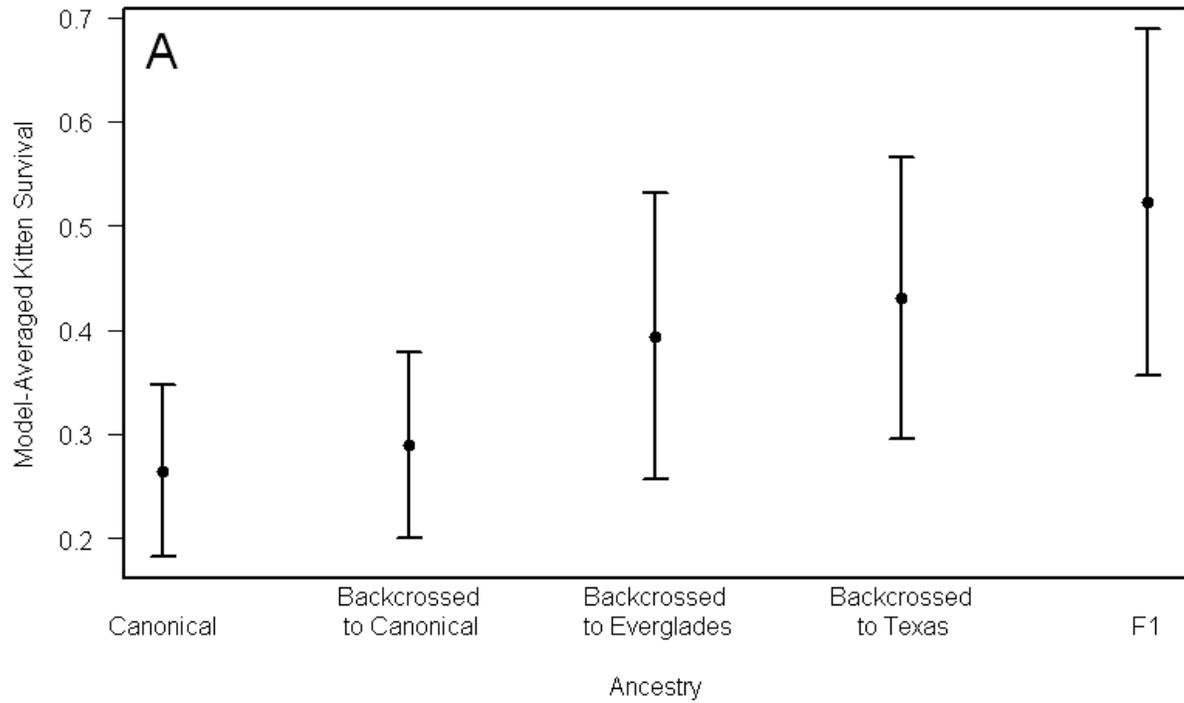


Figure 3-1. The effect of genetic variables on model-averaged kitten survival estimates. A) Annual survival plotted against ancestry category. B) Annual survival plotted against heterozygosity. Error bars represent unconditional standard errors.

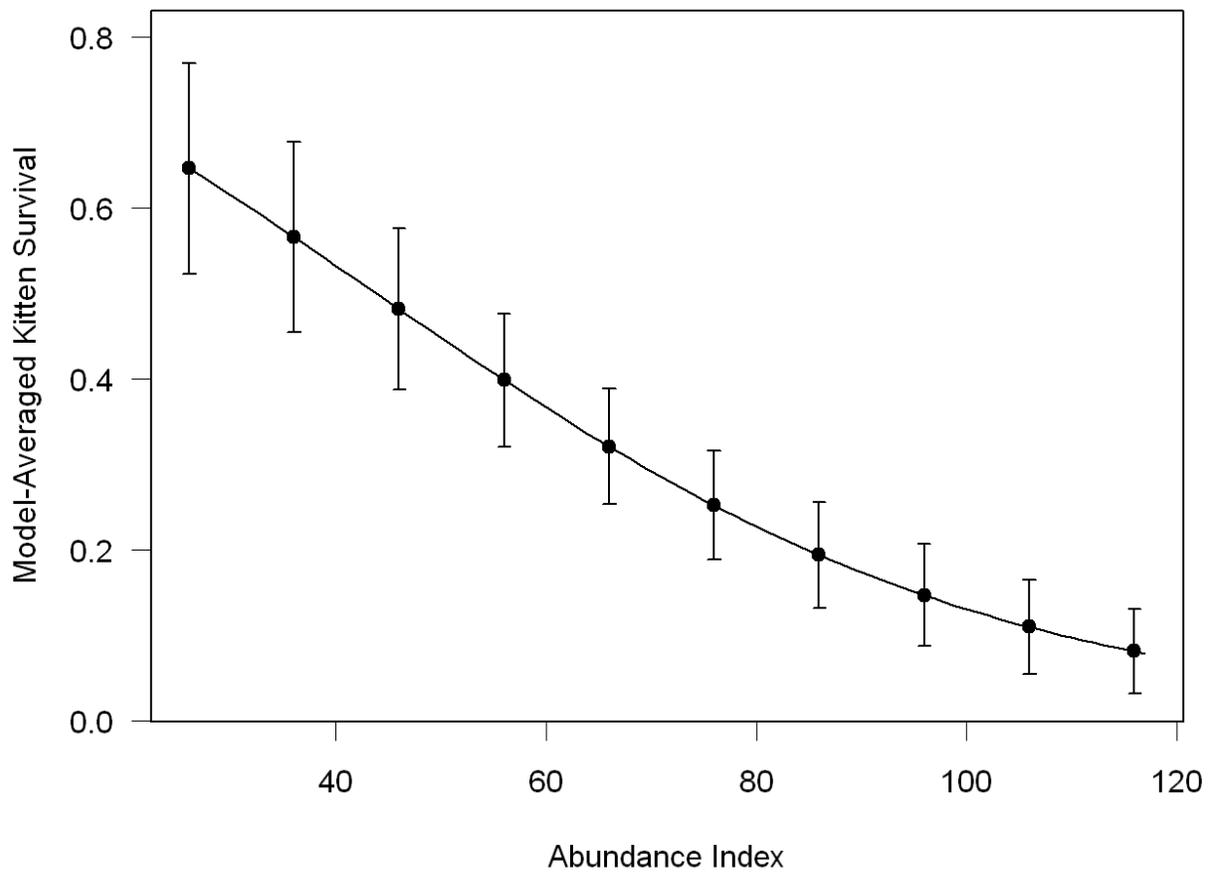


Figure 3-2. The effect of a panther abundance index on model-averaged kitten survival estimates. Error bars represent unconditional standard errors.

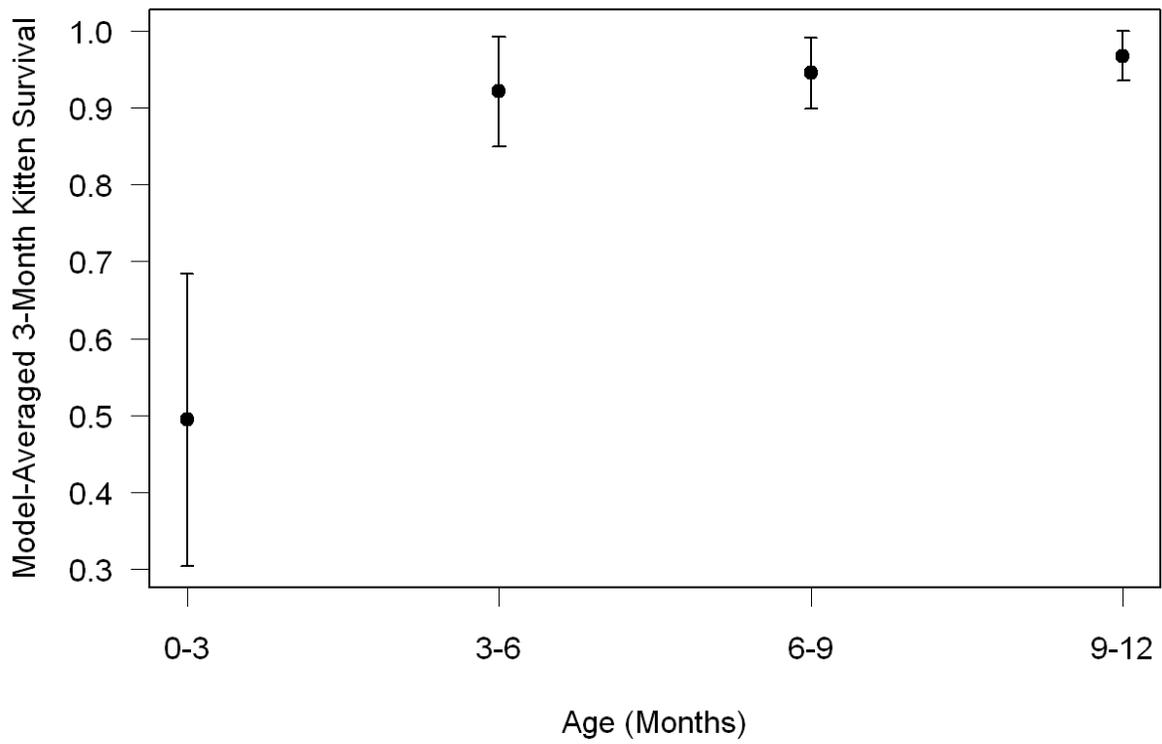


Figure 3-3. Model-averaged kitten survival by 3-month age interval within the first year. Error bars represent unconditional standard errors.

CHAPTER 4 DOES GENETIC INTROGRESSION IMPROVE REPRODUCTIVE PERFORMANCE? A TEST ON THE ENDANGERED FLORIDA PANTHER

Introduction

The small population paradigm of conservation biology postulates that inbreeding (mating between close relatives) is inevitable in small, isolated populations, and that inbred individuals have reduced fitness (Caughley, 1994; Slate et al., 2000). This phenomenon, commonly referred to as inbreeding depression, is thought to be a major challenge in managing such imperiled populations. Inbreeding and loss of genetic diversity have been shown to influence many fitness traits, including age of first reproduction (Charpentier et al., 2008), litter or clutch size (Ortego et al., 2007), survival (Hostetler et al., 2010; Keller et al., 1994), lifetime reproductive success and other measures of individual fitness (Ferreira and Amos, 2006; Slate et al., 2000), and population persistence (Brook et al., 2002b; Ebert et al., 2002). However, outbreeding depression (reduction in fitness due to the mating of individuals that are genetically too dissimilar) is also a risk when intentional hybridization is undertaken to mitigate the effects of inbreeding depression (Edmands, 2007).

The Florida panther (*Puma concolor coryi*), an endangered puma subspecies, is a textbook example of a small and isolated population. Once distributed across the southeastern United States, their number was reduced to ≤ 30 individuals by the 1980s (McBride et al., 2008). The population was thought to be severely inbred and characterized by extremely low genetic diversity (Culver et al., 2000; Johnson et al., 2010; Roelke et al., 1993b). Many phenotypic traits thought to be characteristics of inbreeding were reported from this population, including very low sperm quality, and high incidences of cryptorchidism, cowlicks, and kinked tails (Barone et al., 1994;

Mansfield and Land, 2002; Roelke et al., 1993b). Due to concerns about inbreeding depression, 8 female Texas pumas (*P. c. stanleyana*) were brought into the Florida panther population in 1995. Since this genetic introgression, the population has increased (McBride et al., 2008), although the processes that have led to this increase continues to be debated (Creel, 2006; Maehr et al., 2006; Pimm et al., 2006b). The influence of genetic introgression on age-specific survival of Florida panthers has been explored (Benson et al., in revision; Hostetler et al., 2010; Pimm et al., 2006b), but the potential effect of introgression on the panther's reproductive parameters remains unknown (but see Pimm et al., 2006b for a qualitative comparison). Furthermore, the Scientific Review Team (SRT), commissioned by the U.S. Fish and Wildlife Service (USFWS) and the Florida Fish and Wildlife Conservation Commission (FWC) partly in order to make recommendations for continuing Florida panther research, recommended reanalysis of existing data to rigorously estimate reproductive parameters, and to evaluate the potential influence of introgression on demographic parameters of Florida panthers (Beier et al., 2003).

We used long-term field and genetic data (1995-2008) to address the following questions: (1) Do probability of breeding or litter size differ among age classes? (2) Do probability of breeding or litter size vary seasonally? (3) Are probability of breeding or litter size affected by population size (through negative or positive density-dependent effects)? (4) Are probability of breeding or litter size affected by genetic diversity (as measured by heterozygosity)? (5) Are reproductive parameters positively influenced by genetic introgression as predicted by the hybrid vigor theory?

Materials and Methods

Study Area

Our study area was the entire current breeding range of the Florida panther, and encompassed Big Cypress National Preserve, Everglades National Park, Florida Panther National Wildlife Refuge, Okaloacoochee Slough Wildlife Management Area and State Forest, Fakahatchee Strand Preserve State Park, Picayune Strand State Forest, Big Cypress Seminole Indian Reservation, and adjoining private lands in south Florida. Although transient males tend to roam widely, no females have been verified north of Caloosahatchee River since 1972 (Land et al., 2008). The climate of south Florida is tropical (Henry et al., 1994) with a wet season extending roughly from June to November and a dry season from December to May.

Field Methods

We located and treed Florida panthers using trained hounds and houndsmen (supplied by Livestock Protection Company, Alpine, Texas). Immobilization and capture protocols are described in detail elsewhere (FWC, 2008; Land et al., 2008; McCown et al., 1990; Taylor et al., 2002). Age of captured panthers (if unknown) was estimated using a combination of toothwear, pelage characteristics, size, and developmental stage of teats and reproductive organs. Blood and tissue samples were collected for health assessment and genetic analysis.

We affixed radio collars on captured adults, sub-adults, and older kittens. Collars contained mortality switches that altered the pulse rate of transmitters when a panther did not move for a period of time. We located radio-collared panthers using aerial telemetry, generally three times per week. When mortality signals were detected, the locations were investigated on the ground to confirm the death of the panther.

Successive locations of females were continually assessed to determine the commencement of denning behavior; lack of movement between 3-4 fixes was taken as evidence of possible denning (Land et al., 1998). We visited dens 4-35 days post-partum (approximate median = 14 days). Kittens in dens were counted, sexed, sampled for genetic material, and implanted with passive integrated transponder (PIT) tags. Florida panther gestation length averages at 3 months and litter sizes range from 1 to 4 (Maehr, 1992).

Genetic Ancestry and Heterozygosity

We estimated the heterozygosity and genetic origins of individuals from genetic samples using techniques detailed elsewhere (Benson et al., in revision; Hostetler et al., 2010; Johnson et al., 2010). We used results from the genetic origins analysis along with pedigree information and field evidence to assign panthers to 3 groups that reflect the genetic makeup of the southern Florida population (pre-introgression type panthers, F1 admixed panthers, and other admixed panthers; Benson et al., in revision).

Pre-introgression type panthers represent the genotypes present on the landscape prior to the introgression program and this group is composed mostly of canonical Florida panthers, which showed no evidence of non-Florida genetic admixture (no direct non-Florida relatives or < 10% non-Florida genetic contribution). Additionally, 2 pre-introgression type panthers in the sample of individuals used to investigate the influence of genetic ancestry on reproductive rates ($n = 58$) were descendents of panthers from the Everglades genetic population with documented genetic links to Central America (Culver et al., 2000; O'Brien et al., 1990). Admixed panthers were mostly the descendents of the introduced female Texas pumas released in 1995 (Benson et al., in revision; Johnson et al., 2010).

Differences in fitness between classes of admixed panthers are possible and hybrid vigor is predicted to be strongest in the F_1 generation (Arnold and Hodges, 1995; Burke and Arnold, 2001), so we included 2 classes of admixed panthers in our analyses: F_1 and other admixed. We defined F_1 admixed panthers as any offspring produced by matings between a Texas female and a pre-introgression type male.

In summary, all individuals in our radio-collared sample were placed into 1 of 3 categories: pre-introgression type panthers ($n = 24$), F_1 admixed panthers ($n = 6$), and other admixed panthers ($n = 28$). We were also able to further classify most individuals from the other admixed category into 3 finer categories: backcrossed to Florida admixed panthers ($n = 6$), backcrossed to Everglades admixed panthers ($n = 3$), and backcrossed to Texas admixed panthers ($n = 11$). We considered potential differences in reproductive rates between pre-introgression type, F_1 admixed, and these finer admixture distinctions (results available in Appendix I).

Index of Abundance

To examine the potential effects of panther density on reproductive rates, we used the minimum population counts as an index of abundance (McBride et al., 2008). These minimum counts were based on radio-tracking and field evidence of sub-adult and adult panthers (tracks, scat, kills, and scrapes) collected for calendar years. In contrast, we analyzed reproductive rates based on years from June – May. We applied the calendar year count for year t to the June t – May $t + 1$ year. In 2004, the panther survey was incomplete, so the minimum count is unknown. We followed McBride et al. (2008) and extrapolated it halfway between the 2003 and 2005 counts.

Estimating Age Classes

We knew the ages (to within a few days) for panthers that were handled as kittens at natal dens and then subsequently recaptured and radio-collared ($n = 29$, 46.8% of total). These kittens were handled <35 days after birth as estimated by the date when the mother was first located at the den site and by the physical characteristics of the kittens. Age of panthers not marked as kittens was estimated in the field at time of first capture using tooth wear and pelage characteristics. We separated female panthers into 4 age classes: kittens (0-1 years old), sub-adults (1-2.5 years old), prime-adults (2.5-10 years old), and older-adults (≥ 10 years old). Since panther kittens do not reproduce, we limited analyses to sub-adults, prime-adults, and older-adults. The sub-adult age class was the period of a panther's life after independence from its mother until the approximate ages when females and males first establish home ranges. We estimated age of independence at just over 1 year (mean = 397 days, SD = 74 days, $n = 32$; FWC and NPS, unpublished data) from known-age kittens that were radio-tracked simultaneously with their mothers (before and after independence). We standardized the beginning of the sub-adult age class to 1 year for simplicity.

Modeling Probability of Breeding

We used radio-tracking and reproductive histories of female panthers monitored between June 1995 and May 2008 (13 years) in the present analyses. We organized the data into 6 month intervals (June – November and December – May). We recorded the following information for each panther in each 6 month interval: number of months tracked, number of kittens produced, number of kittens produced that survived to be PIT-tagged in the den, age class, heterozygosity, and ancestry category. If a female

advanced to an older age class within a 6 month interval, two records were created, each with one of the age classes and the appropriate number of months tracked.

We modeled probability of a female panther giving birth at least once during a season (p) using binomial regression. Since no female panther was recorded giving birth twice within 1 season, p can also be interpreted as the probability that a panther gives birth once during a season. The parameter p can be modeled as a function of covariates. We modeled p using a complementary log-log link:

$$p_i = 1 - \exp[-\exp(\mathbf{Z}_i\boldsymbol{\gamma})] \quad (4-1)$$

where \mathbf{Z}_i is the matrix of covariates for panther i and $\boldsymbol{\gamma}$ is the vector of binomial model's coefficients.

Often, panthers were not tracked for entire seasons (e.g., due to radio failure before the end of a season or radio-collaring after the start of a season). To account for the effect of the number of months a panther was tracked in a season on the probability that it gives birth while being tracked, we used $\log(m)$ as an offset, where m is the number of months a panther was tracked during a season. The combination of this offset and the complementary log-log link for p were chosen to generate the property:

$$\Pr(b = 0 | M = m) = \Pr(b = 0 | M = 1)^m \quad (4-2)$$

where b is a binary variable indicating whether a panther bred or not in an interval. In other words, the probability that a panther does not breed in m months is the same as the probability that a panther does not breed in 1 month, taken to the m power. We used the `glm` function in the `stats` library in R (version 2.11.1; R Development Core Team, 2010) to fit the model.

Modeling Litter Size

We estimated and modeled litter sizes of female panthers, conditional on their giving birth, using cumulative logit regression. Although this model is traditionally used for ordered categorical data (Agresti, 2007), it can also be used for count data (Min and Agresti, 2005). The model includes J categories for number of offspring, with N_j being the number of offspring represented by category j (because panthers can have 1 to 4 offspring, $J = 4$ and $N_j = j$ in our case). The probability that the litter size will be at most N_j for individual i (Y_i) is represented by δ_{ij}

$$P(Y_i \leq N_j) = \delta_{ij} = \begin{cases} \frac{1}{1 + \exp(-\theta_j + \boldsymbol{\beta}\mathbf{X}_i)} & j = 1, 2, \dots, J-1 \\ 1 & j = J \end{cases} \quad (4-3)$$

where θ_j is the intercept for litter size being at most N_j , \mathbf{X}_i is the matrix of covariates for panther i , and $\boldsymbol{\beta}$ is the vector of the model's coefficients. In Equation 4-3, θ has a subscript for j but $\boldsymbol{\beta}$ does not. This model therefore represents the underlying structure of the data in a flexible fashion but assumes the effects of \mathbf{X} are identical for all $J-1$ cumulative logits. When $\beta > 0$, the covariate positively influences the probability of a larger litter size. The probability that Y_i will be exactly N_j is

$$P(Y_i = j) = \pi_{ij} = \begin{cases} \delta_{i1} & j = 1 \\ \delta_{ij} - \delta_{i(j-1)} & j = 2, \dots, J \end{cases} \quad (4-4)$$

The expected average litter size for individual i is

$$\mu_i = \sum_{j=1,2,\dots,J} N_j \pi_{ij} \quad (4-5)$$

We implemented the cumulative logit model using the `clm` function in the ordinal library in R (version 2.10.1).

Modeling Approach

We used an information-theoretic approach (Akaike's Information Criterion; AIC) for model selection and statistical inference (Burnham and Anderson, 2002). We calculated AIC values, Akaike differences (ΔAIC_i , difference between AIC value of the i th model and the top-ranked model) and Akaike weights (w_i , the weight of evidence that the i th model is actually the best model of the models being considered given the data) as in Burnham and Anderson (2002). Generally, we considered models with $\Delta AIC < 2$ to have substantial empirical support, models with ΔAIC of 2-4 to be plausible models with less empirical support, and models with $\Delta AIC > 4$ to have much less empirical support. In addition, the sum of the weights of models including a given variable can be interpreted as a measure of its importance, relative to other variables (Burnham and Anderson 2002). We calculated model-averaged estimates of reproductive rates and unconditional variances for each level of categorical variables and across continuous covariates (Burnham and Anderson 2002). To generate these model-averaged estimates we used all models included in the model selection process for a given analysis, weighted by their Akaike weights. Models with no effects of the covariates being presented were included in the averages (as having the same reproductive parameter values for all values of the covariate), the model averages therefore represent unconditional estimates of reproductive parameters (Burnham & Anderson 2002).

We used a step-wise approach to test for the effects of various covariates on reproductive parameters. First, we examined the effects of age class on reproductive parameters (i.e., breeding probability and litter size). We considered 3 age-structures: Age1, which separates female panthers into 3 age classes (sub-adults, prime-adults,

and older-adults); Age2, which separates females into 2 age classes: older-adult and young-adult (sub-adults and prime-adults combined) panthers; and Age3, which also divides female panthers into 2 age classes: sub-adult and adult (prime-adults and older-adults combined) age classes (note that these model labels differ from those used in Chapter 2). We tested for the effect of all 3 age-structures on p , but did not test for the effect of Age1 or Age2 on μ , because those separate out older-adults and sample size was not adequate for a separate analysis of litters produced by older-adult panthers. We chose the minimum AIC model from each age class analysis as a base model to test for the additive effect of season (wet: June – November vs. dry: December – May) on p and μ . The most parsimonious models from these analyses were used as base models for all subsequent analyses.

We next tested for the effects of age class and season on reproductive rates, excluding older-adults. We did this to check the robustness of our estimates of reproductive parameters for sub-adults and prime-adults. Excluding the older-adults had very little effect on estimates (Appendix J).

We used the minimum AIC models from the seasonal analyses as base models, and tested for linear and quadratic effect of abundance index on reproductive parameters; the quadratic term was used to test for the possibility of both negative and positive density-dependence in components of reproduction. Effect of abundance on both p and μ were tested additively with the base models.

Next, we tested for the additive effect of ancestry on p and μ . We excluded 1 panther with unknown ancestry from these analyses. We tested three models of ancestry: Ancest1, which divides females into 3 ancestry categories: pre-introgression

type, other admixed, and F1 admixed; Ancest2, which combines the other admixed with the pre-introgression type females; and Ancest3, which combines the other admixed with the F1 admixed females. There were no older-adult female admixed panthers in our dataset, so we wanted to check the robustness of our ancestry statistical inference and estimates to the inclusion of the pre-introgression type older-adults. Excluding the older-adults had very little effect on estimates or inference (Appendix J). Finally, we tested for the effects of heterozygosity on reproductive parameters. We excluded 1 panther with unknown heterozygosity from these analyses. We tested for the additive effect of heterozygosity on both p and μ .

Appendix K contains results of analyses performed on an annual time scale, rather than 6-month, for comparison with other studies and for use in population models. For these models, kittens were only counted (included as breeding events and in litter counts) if they received PIT tags in the den, and estimates of temporal variance in reproductive parameters were generated (Appendix K).

Results

We tracked 61 female panthers for a total of 2,414 panther-months, and recorded 94 litters. Estimated ages of dams when they produced litters ranged from 21 months to 11.45 years. There was only one recorded litter produced by 9 older-adult (≥ 10 years) females, which were tracked for a total of 313 months. Mean litter size was 2.60 and the modal litter size was 3 (Figure 4-1). A naïve estimate of probability of breeding during a 6-month period for all female panthers (number of litters/number of months tracked * 6) was 0.234. These correspond closely to the model-based estimates for all female panthers (mean \pm 1SE litter size = 2.60 ± 0.09 , probability of breeding = 0.232 ± 0.021).

Probability of Breeding

There was strong evidence that breeding probability varied among age classes; the Δ AIC of the constant model was about 20 (Table 4-1A). Older-adults had a lower probability of breeding than younger females, but there was no evidence that breeding probabilities differed between sub-adult and prime-adult females (Figure 4-2A). Furthermore, there was evidence that probability of breeding varied seasonally (Model 1, Table 4-1B), with model averaged probability of breeding being higher during the dry season (Figure 4-2B). Index of abundance positively influenced breeding probability (Model 1, Table 4-1C; Figure 4-2C).

The most parsimonious model evaluating the effect of ancestry on reproductive parameters revealed that probability of breeding differed between F_1 panthers and those with other ancestry (Model 1, Table 4-1D). Model-averaged probability of breeding was lower for F_1 's than pre-introgression type and marginally higher for other admixed than pre-introgression type (Figure 4-3A). The most parsimonious heterozygosity model suggested that heterozygosity had no effect on probability of breeding (Model 1, Table 4-1E). Model-averaged probability of breeding declined somewhat with increasing heterozygosity (Figure 4-3B).

Litter Size

Sub-adult females produced somewhat larger litters than females of other age classes; there was evidence for age-specific variation in litter size (Table 4-2A; Figure 4-2D). Older adult females produced only 1 litter during this study, and we were unable to test for differences in litter size between older-adults and younger females. There was some evidence for seasonal variation in litter size (Model 1, Table 4-2B), with larger

litters during the dry season (Figure 4-2E). However, there was no evidence that litter size was affected by abundance (Model 1, Table 4-2C; Figure 4-2F).

The most parsimonious model evaluating the effect of ancestry showed no effect on litter size (Model 1, Table 4-2D); admixed females produced slightly larger litters than pre-introgression type females (Figure 4-3C). The most parsimonious heterozygosity model suggested that heterozygosity had no effect on litter size (Model 1, Table 4-2E; Figure 4-3F).

Discussion

The case of the Florida panther demonstrates how loss and degradation of habitat, persecution, rapid urbanization and other anthropogenic influences can threaten biodiversity. Indeed, the plight of the panther has attracted the attention of ecologists, conservation organizations, state and Federal agencies, and various interest groups (<http://www.floridapanther.net.org/>, Fergus, 1998; Gross, 2005). Various conservation measures have been undertaken to ensure long-term persistence of this population; perhaps the most drastic among these was the genetic project implemented in 1995 (Seal, 1994). Although the prevalence of phenotypic traits indicative of inbreeding (e.g., heart defects, susceptibility to heavy parasite loads, poor sperm quality and cryptorchidism) have declined (Mansfield and Land, 2002; Onorato et al., 2010) and the panther population has increased (McBride et al., 2008), the role of the introgression in the panther population increase continues to be debated (Gross, 2005; Maehr and Caddick, 1995; Maehr et al., 2006; Pimm et al., 2006b). Also, some aspects of the reproductive ecology of panthers remain poorly understood, especially the effect of genetic introgression.

The overall 6-month probability of breeding was 0.232 ± 0.021 , which translates into annual cumulative probability of breeding of 0.410 ± 0.034 (Appendix K). This annual estimate is within the range reported for western North America puma populations (0.24-0.45; Cooley et al., 2009; Stoner et al., 2006). However, our annual estimate of breeding probability was lower than that used by previous demographic analyses of Florida panthers (0.5; Maehr et al., 2002a; Root, 2004). Breeding probability varied substantially among age classes; older females (≥ 10 years) had a lower probability of breeding compared to younger females but the breeding probability of sub-adult females (1 – 2.5 years) did not differ from that of prime adults (2.5 – 10 years). We expected probability of breeding to be higher for prime-adults than for the other two age classes because they should have a defined home range that allows them to maximize their energetic allocations towards reproduction. Our results provide strong evidence of reproductive senescence (manifested as a lower probability of breeding) in older Florida panthers, but suggest that age-specific differences in reproduction prior to senescence are minor.

The overall average litter size was 2.60 ± 0.09 ; this estimate, although slightly higher than previous estimates for Florida panthers (Lotz et al., 2005: 2.4; Maehr and Caddick, 1995: 2.25), is within the range of litter size estimates reported for western populations of pumas (1.7-3.0; Cooley et al., 2009; Lambert et al., 2006; Laundré et al., 2007; Logan and Swenor, 2001; Robinson et al., 2008; Stoner et al., 2006). Sub-adult females produced somewhat larger litters. This result was to some extent surprising because we expected prime-aged females to produce larger litters than sub-adult or older females. Effects of age and/or breeding experience on litter size have previously

been shown for other large carnivores (Garrison et al., 2007; Zedrosser et al., 2009), although not for pumas (Logan and Sweanor, 2001).

Probability of breeding was higher in the dry season than in the wet, but litter sizes were similar. Previous examinations of raw number of litters per month suggest that the actual birth peak is March – June (Lotz et al., 2005), which is supported by our results. Dry season coincides with the peak white-tailed deer (*Odocoileus virginianus*) fawning season in south Florida (Fleming, 1994; February - March; Richter and Labisky, 1985; Schortemeyer et al., 1991) and peak feral hog (*Sus scrofa*) farrowing (parturition) season (Belden and Frankenberger, 1990), which may allow females to make caloric gains necessary to achieve a successful pregnancy by preying on vulnerable fawns and piglets during their first months of life.

We found that abundance index positively influenced breeding probability. This may be due to a mate-finding Allee effect (Gascoigne et al., 2009). However, there was also a decrease in kitten survival observed with increasing abundance index, possibly due to infanticide by male panthers (Hostetler et al., 2010). Panther females are unlikely to copulate while they have dependent offspring, and, in fact, a female panther giving birth soon after the birth of a previous litter (≤ 12 months) is indicative of the fact that the first litter failed (Hostetler et al., 2010). Therefore, one possibility is that the increase in probability of breeding is caused by the decrease in kitten survival. Abundance index also increased fairly steadily over time during our study period (1995-2008; McBride et al., 2008). It is possible that there was an increase in probability of breeding over time that was due to something besides, or in addition to, population size. One intriguing (although speculative) possibility is that reproductive vigor of the male

panthers has increased since 1995, possibly due to the reduction in inbreeding depression in male reproductive traits (Johnson et al., 2010).

In earlier studies, we found that F_1 admixed panthers of all ages survived substantially better than panthers in ancestry categories (Benson et al., in revision; Hostetler et al., 2010). Based on these results and predictions of hybrid vigor theory (Crow, 1948), we expected higher probability of breeding (and litter size) for F_1 female panthers. Thus, our results that breeding probabilities were lower for F_1 (and backcrossed to Texas; Appendix I) female panthers than for other admixed and pre-introgression type female panthers were unexpected. This may be a sign of outbreeding depression in female reproduction, due to loss of local adaptations and/or co-adapted gene sequences (Edmands, 2007; Hallerman, 2003). Although outbreeding depression cannot be ruled out as a possibility, the relative lack of genetic differentiation within North American pumas (Culver et al., 2000) and the former adjacency and presumed interbreeding between *P. c. coryi* and *P. c. stanleyana* make outbreeding depression less likely. An alternative, and perhaps a more plausible, explanation is that the F_1 panthers were breeding less often because their offspring were more likely to survive to independence (Hostetler et al., 2010). Finally, the sample of radio-collared F_1 female Florida panthers was small ($n = 6$), and it is possible that these individuals bred less often than other panthers due to chance alone (or for reasons other than genetic ancestry). Thus, although our results provide strong evidence that that genetic introgression did not positively influence probability of breeding for Florida panthers, we cannot conclude that introgression negatively affected panthers' reproductive parameters.

Interestingly, litter size did not vary among females with various ancestry categories. Additionally, we found no evidence that heterozygosity influenced breeding probability or litter size. These results were surprising because heterozygosity has been shown to influence litter or clutch size (Ortego et al., 2007), lifetime reproductive success and other measures of individual fitness (Ferreira and Amos, 2006; Slate et al., 2000), and also because heterozygosity positively influenced age-specific survival probabilities of Florida panthers (Benson et al., in revision; Hostetler et al., 2010). Our study extends the work of Pimm et al. (2006b), who graphically examined the lifetime kitten production of 24 female panthers and found no evidence of a difference between pre-introgression type and admixed panthers. We used a larger sample size, more detailed ancestry categories, and separated two components of reproduction (breeding probability and litter size) using robust statistical methods.

These results clearly demonstrate that one intrinsic or extrinsic environmental factor can differentially influence demographic rates or fitness components. For example, prior to this study we had concluded that genetic introgression positively influences demographic traits, whereas population density can negatively influence them (Benson et al., in revision; Hostetler et al., 2010); neither of these conclusions is supported by the present study. These contrasts highlight the importance of simultaneously examining the effect of management actions on all components of fitness.

Table 4-1. Model selection table for probability of breeding (p). A) Age class effects. B) Season effects. C) Abundance index effects. D) Ancestry effects. E) Heterozygosity effects. The top ranked model for age class (part A, model 1, in bold) was used as a base model to test for the effects of season; the top ranked model for season (part B, model 1, in bold) was used as a base model to test for the effects of abundance, ancestry, and heterozygosity. For each model, we present the number of parameters (K), the difference in Akaike's Information Criterion (ΔAIC), and the Akaike weight (w_i). The ancestry and heterozygosity analyses were performed on a subset of the data (excluding 1 panther with unknown heterozygosity).

Model	p	K	ΔAIC	w_i
A) Age Models				
1	Age2^a	2	0.00	0.562
2	Age1 ^b	3	0.50	0.438
3	Constant ^c	1	19.94	0.000
4	Age3 ^d	2	21.58	0.000
B) Season Models				
1	Age2 + Season	3	0.00	0.743
2	Age2	2	2.12	0.257
C) Abundance Index Models				
1	Age2 + Season + Abundance	4	0.00	0.433
2	Age2 + Season + Abundance + Abundance ²	5	0.78	0.293
3	Age2 + Season	3	0.91	0.274
D) Ancestry Models				
1	Age2 + Season + Ancest2^e	4	0.00	0.627
2	Age2 + Season + Ancest1 ^f	5	1.58	0.284
3	Age2 + Season	3	4.54	0.065
4	Age2 + Season + Ancest3 ^g	4	6.48	0.025
E) Heterozygosity Models				
1	Age2 + Season	3	0.00	0.610
2	Age2 + Season + Het ^h	4	0.89	0.390

^a Age2 divides panthers into young-adults and older-adults.

^b Age1 divides panthers into sub-adults, prime-adults, and older-adults.

^c No predictor variables.

^d Age3 divides panthers into sub-adults and adults.

^e Ancest2 divides panthers into 2 ancestry categories: F₁ admixed, and other admixed and pre-introgression type combined.

^f Ancest1 divides panthers into 3 ancestry categories: pre-introgression type, other admixed, and F₁ admixed.

^g Ancest3 divides panthers into 2 ancestry categories: pre-introgression type and admixed. Heterozygosity.

Table 4-2. Model selection table for litter size (μ). A) Age class effects. B) Season effects. C) Abundance index effects. D) Ancestry effects. E) Heterozygosity effects. The top ranked model for age class (part A, model 1, in bold) was used as a base model to test for the effects of season; the top ranked model for season (part B, model 1, in bold) was used as a base model to test for the effects of abundance, ancestry, and heterozygosity. For each model, we present the number of parameters (K), the difference in Akaike's Information Criterion (Δ AIC), and the Akaike weight (w_i). The ancestry and heterozygosity analyses were performed on a subset of the data (excluding 1 panther with unknown heterozygosity).

Model μ	K	Δ AIC	w_i
A) Age Models			
1 Age3^a	4	0.00	0.794
2 Constant ^b	3	2.70	0.206
B) Season Models			
1 Age3 + Season	5	0.00	0.551
2 Age3	4	0.41	0.449
C) Abundance Index Models			
1 Age3 + Season	5	0.00	0.619
2 Age3 + Season + Abundance	6	1.74	0.260
3 Age3 + Season + Abundance + Abundance ²	7	3.26	0.121
D) Ancestry Models			
1 Age3 + Season	5	0.00	0.443
2 Age3 + Season + Ancest3 ^c	6	0.87	0.286
3 Age3 + Season + Ancest2 ^d	6	1.98	0.165
4 Age3 + Season + Ancest1 ^e	7	2.86	0.106
E) Heterozygosity Models			
1 Age3 + Season	5	0.00	0.729
2 Age3 + Season + Het ^f	6	1.98	0.271

^a Age3 divides panthers into sub-adults and adults.

^b No predictor variables.

^c Ancest3 divides panthers into 2 ancestry categories: pre-introgression type and admixed.

^d Ancest2 divides panthers into 2 ancestry categories: F₁ admixed, and other admixed and pre-introgression type combined.

^e Ancest1 divides panthers into 3 ancestry categories: pre-introgression type, other admixed, and F₁ admixed.

^f Heterozygosity.

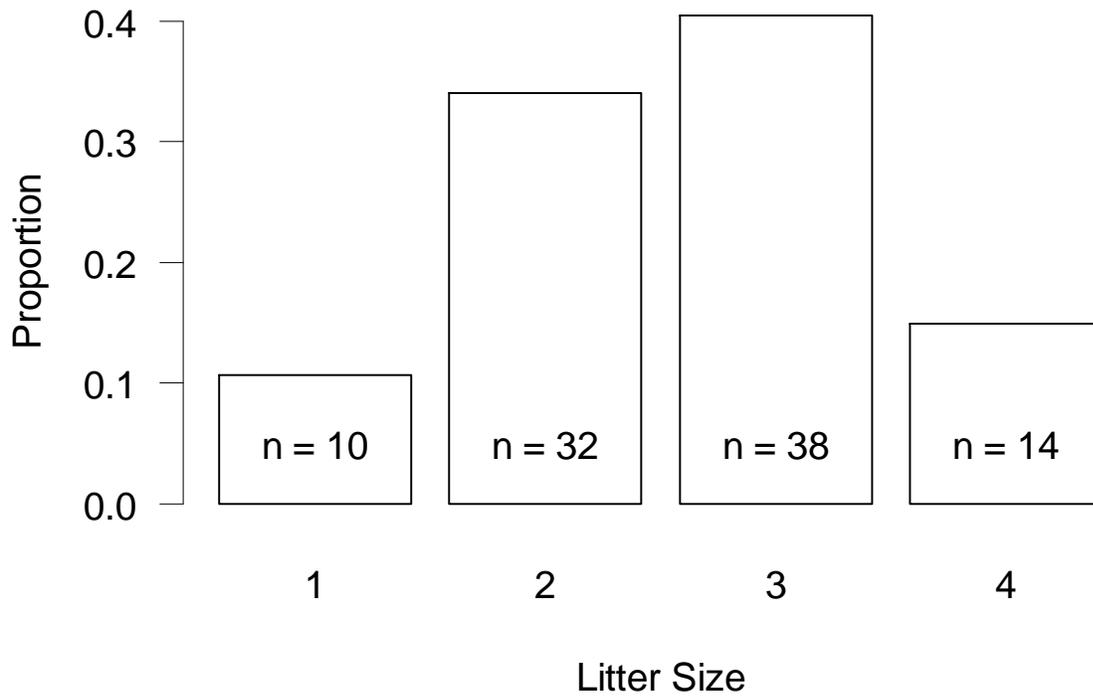


Figure 4-1. Frequency distribution of litter sizes produced by radio-collared female panthers (1995 – 2008). Numbers inside bars indicate number of litters of that size.

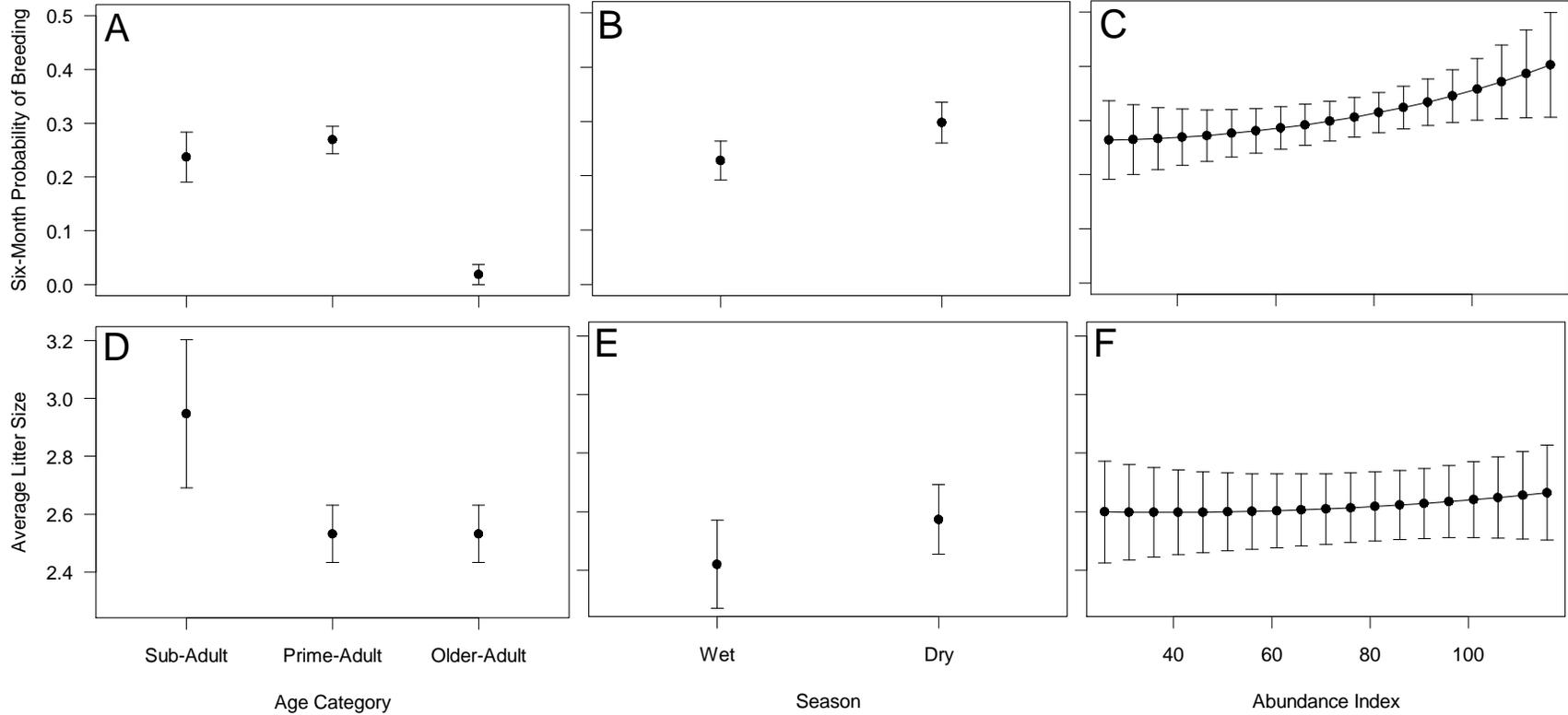


Figure 4-2. Model-averaged reproductive rates (\pm unconditional standard errors) by age class, season, and abundance index. A) Six-month probability of breeding by age class. B) Same by season, for young-adult panthers (<10 years old). C) Same by abundance index, for young-adult panthers in the dry season. D) Average litter size by age class. E) Same by season, for adult panthers (≥ 2.5 years old). F) Same by abundance index, for adult panthers in the dry season. Sub-adults are defined as ages 1-2.5, prime-adults ages 2.5-10, and older-adults ages 10 and older.

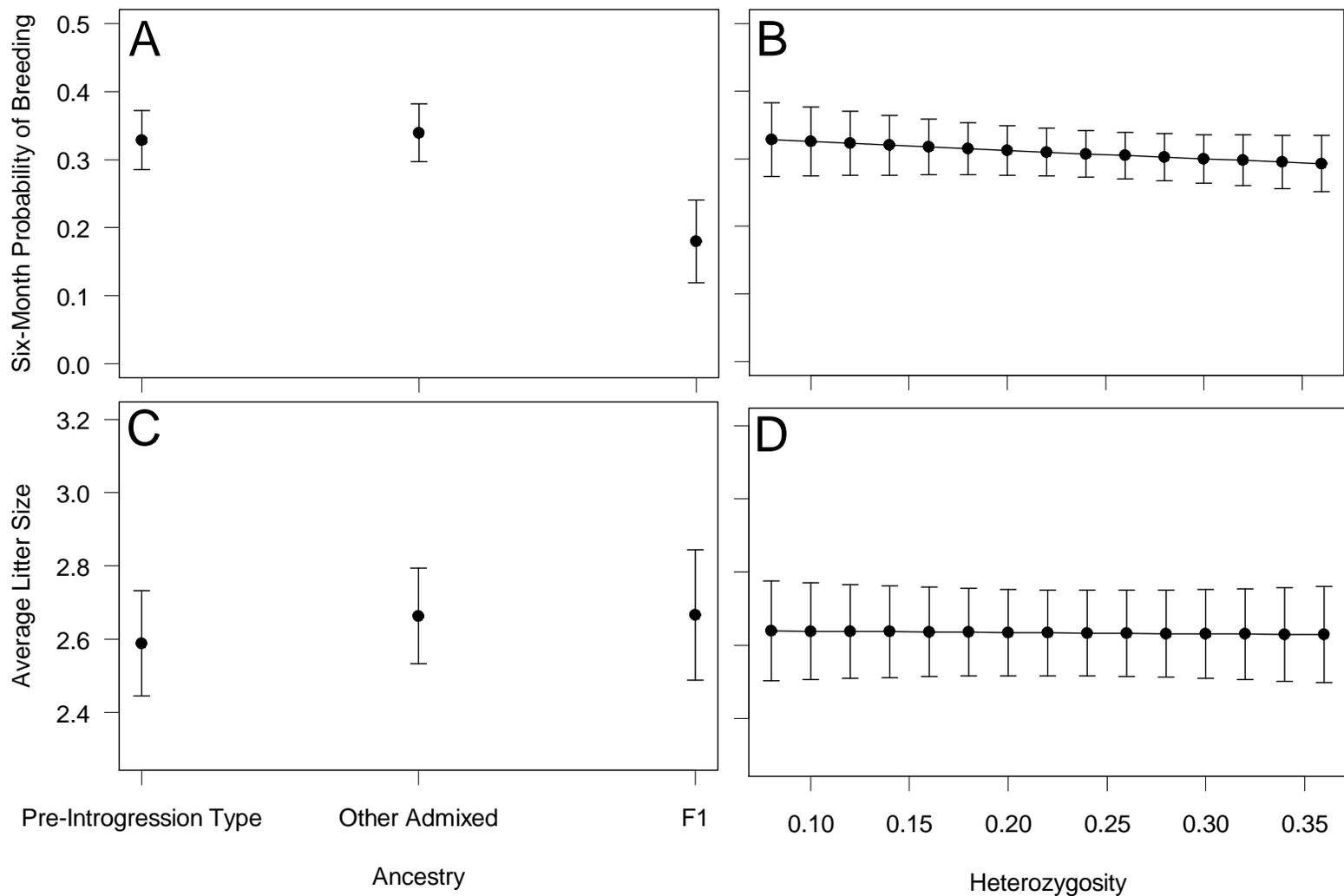


Figure 4-3. Model-averaged reproductive rates (\pm unconditional standard errors) by ancestry category and heterozygosity. A) Six-month probability of breeding for young-adult panthers (<10 years old) in the dry season by ancestry. B) Same by heterozygosity. C) Average litter size, for adult panthers (≥ 2.5 years old) in the dry season, by ancestry. D) Same by heterozygosity.

CHAPTER 5 THE EFFECT OF INTROGRESSION ON THE DYNAMICS AND PERSISTENCE OF THE FLORIDA PANTHER POPULATION

Introduction

Population viability analyses (PVA) are a widely used set of tools in conservation ecology, but have been critiqued for often ignoring uncertainty in their inputs, outputs, and model structure (Ellner et al., 2002; Reed et al., 2002). Recent studies have highlighted the need to incorporate parametric uncertainty as well as model selection uncertainty to quantify uncertainty in PVA predictions (Bakker et al., 2009; Ellner and Fieberg, 2003; White, 2000). Despite these uncertainties, PVAs can help understand the dynamics and persistence of biological populations, especially when adequate data are available to parameterize biologically meaningful models (Brook et al., 2002a; Brook et al., 2000; Lindenmayer et al., 2003).

Population projection models in general and PVA in particular tend to be forward looking. However, there can be advantages to using them to look backwards. These advantages include model validation (Ball et al., 2003; Brook et al., 2000; Lindenmayer et al., 2003) and evaluating the impacts of past management actions (Kauffman et al., 2003). Asking “what would have happened” if management actions had been different can be at least as bedeviled by known and unknown biases and uncertainties as trying to forecast the future. However, if we acknowledge these biases and uncertainties, both processes can be valuable: evaluating the effects of past management actions on population dynamics and modeling potential future population changes and risks are critical tools for choosing current and future management actions.

The Florida panther (*Puma concolor coryi*) is an endangered large carnivore found in a single small population in south Florida (McBride et al. 2008). Monitoring, research

and management actions implemented to prevent the extinction of the panther have been extensive (Beier et al. 2003). Perhaps the most important (and controversial) management action has been the release of 8 female Texas pumas (*P. c. stanleyana*) into south Florida in 1995. This genetic introgression was undertaken to reduce apparent inbreeding depression and mimic historic gene flow between these subspecies. Since 1995, the number of panthers has grown dramatically (McBride et al. 2008). Previous analyses have shown that admixed panthers resulting from genetic introgression have higher survival than canonical or pre-introgression type panthers (Benson et al., in revision; Hostetler et al., 2010). Additionally, admixed panthers have a lower breeding probability than pre-introgression type panthers; litter sizes were not different between these groups (Chapter 4). How this combination of demographic responses to genetic introgression contributed to the observed population growth remains unanswered.

Concern about the future of the panther population has led to the development of several population viability analyses (PVA) since the 1980s (Maehr et al. 2002, Root 2004). The Scientific Review Team (SRT), commissioned by the Florida Fish and Wildlife Conservation Commission and US Fish and Wildlife Service to review the scientific literature on the panther and to make recommendations for future research, reviewed results of these PVA and other demographic studies. The SRT noted that previous PVA were based on unreliable estimates of demographic parameters, required too many arbitrary assumptions, performed insufficient sensitivity analysis, and also used “consensus” approaches to determine parameter values and model structure (Beier et al., 2003; Beier et al., 2006; Gross, 2005). The team recommended rigorous

analyses of available data to estimate demographic parameters, and to perform demographic analyses using those empirically estimated parameters. Now that statistically rigorous estimates of demographic parameters for the Florida panther are available (Chapters 2-4), the time is appropriate for revisiting the dynamics and persistence of the panther population.

In accordance with SRT recommendations, our objectives for this study were to: 1) estimate deterministic and stochastic population growth rates for Florida panthers, 2) perform sensitivity analyses to explore the sensitivity and elasticity of deterministic and stochastic population growth rates to model parameters, 3) estimate probabilities of extinction and distribution of extinction time under various stochastic models, 4) estimate deterministic population growth rate, probability of extinction, and effects of vital rates on the population growth rate for a hypothetical population of pre-introgression type panthers, and 5) to adequately address the uncertainty in all of the model inputs and outputs.

Methods

Field and Genetic Methods

Florida panthers were treed, captured, radio-collared, and tracked starting in 1981 by biologists from the Florida Fish and Wildlife Conservation Commission (FWC) and National Park Service (NPS) using methods described in Chapter 2, by Belden et al. (1988), and by Land et al. (2008). Litters of Florida panther kittens were detected, counted, PIT tagged, recaptured, and recovered starting in 1995 as described in Chapters 3 and 4 and by Land et al. (1998).

We divided female panthers into four age categories: kittens (age 0-1 years), sub-adults (age 1 – 2.5 years), prime-adults (age 2.5 – 10 years), and older-adults (age

≥ 10 years). Male age categories were the same except the shift from sub-adult to prime-adult occurred at age 3.5 years. Age of captured panthers was known or estimated from time since previous capture, tooth wear, and pelage characteristics (Chapter 2; Ashman and Greer, 1976) and error in parameter estimates due to age estimation error was found (for sub-adult and adult survival) or suspected (for other parameters) to be small (Chapter 2).

Genetic samples were collected and analyzed as described in Johnson et al. (2010). For the purposes of estimating parameters for canonical panthers (see below), we followed Benson et al. (in revision) and Chapter 4 and assigned panthers to three ancestry categories for the analysis of sub-adult and adult survival and reproductive parameters (pre-introgression type, other admixed, and F_1 admixed). We followed Hostetler et al. (2010), and assigned panthers to five ancestry categories for the analysis of kitten survival (canonical, backcrossed to canonical, backcrossed to Everglades, backcrossed to Texas, and F_1 admixed). Since the pre-introgression type panthers in these analyses were mostly canonical individuals (with a few Everglades individuals; Johnson et al., 2010), the pre-introgression type and canonical categories were treated as equivalent (and hereafter referred to as canonical).

Model Structure

We modeled population dynamics of the Florida panther using age-structured, birth-flow matrix models focusing on the female segment of the population (Caswell 2001). We used birth-flow approximations to age-specific survival and fertility rates (Caswell, 2001) because panthers can give birth in any month of the year (Lotz et al. 2005, Chapter 4 of this dissertation). We assumed that female panthers can live and reproduce until age 18.5, which corresponds to the age of the oldest radio-collared

female in our study (18.6 years). Therefore, the population projection matrix has dimensions 19x19. Each annual population projection matrix was of the form:

$$\mathbf{A}^t = \begin{bmatrix} F_1^t & F_2^t & \cdots & \cdots & F_{19}^t \\ P_1^t & 0 & \cdots & \cdots & 0 \\ 0 & P_2^t & \ddots & \ddots & \vdots \\ \vdots & \ddots & \ddots & \ddots & \vdots \\ 0 & 0 & \cdots & P_{18}^t & 0 \end{bmatrix} \quad (5-1)$$

where F and P indicate survival and fertility rates, respectively; subscripts indicate age-classes and t stands for time-specificity (the superscript does not apply to deterministic demographic analyses; Table 5-1). In a birth-flow population, individuals within an age class can have a range of ages. We approximated age-specific survival rate as:

$$P_i^t = \sqrt{S_i^t S_{i+1}^t} \quad (5-2)$$

where S_i^t is the survival rate from age $i-1$ to age i between time steps t and $t + 1$ (equivalent to equation 2.25 in Caswell 2001). Because the boundary between the sub-adult and prime-adult age categories was at age 2.5 (and there was no estimated survival rate between ages 2 and 3), we simplified the equations for two of the age-specific survival rates:

$$P_2^t = S_{sa}^t \cdot P_3^t = S_{pa}^t \quad (5-3)$$

where S_{sa}^t is the survival rate of sub-adults between time steps t and $t + 1$ and S_{pa}^t is the survival rate of prime-adults between time steps t and $t + 1$ (Table 5-1). We approximated age-specific fertility rate as:

$$F_i^t = \sqrt{S_k^t \left(\frac{m_i^t + P_i^t m_{i+1}^t}{2} \right)} \quad (5-4)$$

where S_k^t is the survival rate of kittens between time steps t and $t + 1$ and m_i^t is the fecundity (expected number of female offspring produced per surviving female of age class i) for individuals of age i during time step t (Caswell 2001). Similar to age-specific survival, we simplified the equations for two of the age-specific fertility rates:

$$F_2^t = \sqrt{S_k^t} \frac{m_{sa}^t + P_2^t m_{sa}^t}{2}; \quad F_3^t = \sqrt{S_k^t} \frac{m_{pa}^t + P_3^t m_{pa}^t}{2} \quad (5-5)$$

where m_{sa}^t and m_{pa}^t are the age-specific fecundity rates for sub-adult and prime-adult female panthers during time step t . The age-specific fecundity rate was estimated as a function of 3 underlying parameters as:

$$m_i^t = q_i^t v_i^t f_k \quad (5-6)$$

where q_i^t is the probability of breeding for a female in age class i during time step t , v_i^t is the cumulative number of kittens produced by a panther that does breed in age class i during time step t (cumulative because panthers can give birth more than once in a year), and f_k is the proportion of kittens that are female (Table 5-1). Using logistic regression, we found no evidence that f_k deviated from 0.5 (observed proportion = 0.46, $p = 0.22$); thus, we used 0.5 for f_k in all cases.

Parameter Values

We estimated survival probabilities of sub-adult, prime-adult, and older-adult females (S_{sa} , S_{pa} , and S_{oa}) using Cox proportional-hazard models as described in Benson et al. (in revision). We ran models evaluating the effects of sex, age class, and abundance on survival. Survival models with $\Delta AIC < 10$, Akaike weights (Burnham and Anderson, 2002), and estimates of S_{sa} , S_{pa} , S_{oa} (at abundance 0), and effects of abundance on log-hazard, based on each of these models are presented in Table 5-2.

We estimated kitten survival probability (S_k) using Burnham's mark-recapture-recovery modeling techniques (Burnham, 1993) described in Hostetler et al. (2010). We ran models with different recovery (r) probabilities for kittens and older panthers, and evaluated effects of sex and abundance on kitten survival, using the "base" model presented in Hostetler et al. (2010). Survival models with $\Delta\text{QAIC}_c < 10$ (compared to the top model and/or the top density-independent model), Akaike weights, and estimates of S_k (at abundance 0) and the effect of abundance on logit kitten survival, based on each of these models are presented in Table 5-3.

We estimated annual breeding probabilities (probabilities of successful reproduction) of sub-adult, prime-adult, and older-adult females (q_{sa} , q_{pa} , and q_{oa}) using complementary log-log regression as described in Chapter 4. We ran models evaluating the effects of age class and abundance in all combinations on probability of breeding. Probability of breeding models with $\Delta\text{AIC} < 10$, Akaike weights, and estimates of q_{sa} , q_{pa} , q_{oa} , and the effects of abundance and abundance² on complementary log-log monthly probability of breeding, based on each of these models are presented in Table 5-4.

We estimated the number of kittens produced by sub-adult and adult females (v_{sa} and v_a , respectively) using the cumulative logit methods described in Chapter 4. We ran models evaluating the effects of age class of the dam and panther abundance on annual kitten production. Models with $\Delta\text{AIC} < 10$ (all of them), their Akaike weights, and estimates of v_{sa} and v_a and the effect of abundance on cumulative logit number of kittens, based on each of these models are presented in Table 5-5.

Deterministic Demographic Analyses

The asymptotic deterministic annual population growth rate (λ) was estimated as the dominant eigenvalue of **A** (Caswell 2001). Sensitivity and elasticity of λ to lower-level parameters (Table 5-1) were calculated following Caswell (2001).

Incorporating Parameter Uncertainty

We incorporated parameter or sampling uncertainty into model outputs via a parametric bootstrap method (Efron and Tibshirani, 1998). We estimated a variance-covariance matrix for each set of parameters: 1) kitten survival (on logit scale), 2) sub-adult and adult survival (baseline survival converted to logit scale and log-hazard effect sizes), 3) probability of breeding (on complementary log-log scale), and 4) number of kittens produced in the year from female panthers that did breed (on cumulative logit scale). We assumed no overall covariance between the four categories but used the estimated covariance within categories. We ran multiple parametric bootstraps (50,000 for deterministic analyses), selecting random multivariate normal values using the parameter means (on the appropriate scales) and variance-covariance matrices, and then converting the results to the real scale, for each bootstrap run. In this way, we selected random values from the empirical distributions of the demographic parameters.

For deterministic λ , sensitivities, and elasticities, we present the results obtained from the point estimates of parameters as the parameter values. If the mean and/or median of the bootstrap outputs differ substantially from the deterministic output based on point estimates, we present those as well. We also report the 2.5 and 97.5 percentiles of bootstrap outputs as a measure of uncertainty (these should not be interpreted as 95% confidence intervals when the point estimate differs substantially from the median; Efron and Tibshirani, 1998).

Incorporating Model Selection Uncertainty

Another source of statistical uncertainty is model selection uncertainty – uncertainty about whether the minimum AIC (or QAIC_c) model for a parameter is actually the best model in the model set (Burnham and Anderson, 2002). We incorporated this form of uncertainty by randomly selecting statistical models for each set of parameters, based on their AIC (or QAIC_c) weights (Bakker et al., 2009). For deterministic and stochastic demographic analyses, we restricted model sets to density independent models only (Tables 2-5). In all cases, we did not include models with ΔAIC (or ΔQAIC_c) > 10. When one or more models were excluded, model weights were recalculated to sum to 1.

For each analysis for which model selection uncertainty was incorporated (we ran deterministic demographic analyses with and without model uncertainty, and did not include model uncertainty in stochastic demographic analyses), parameter uncertainty was also incorporated by selecting parameter values from their distributions (as discussed in Incorporating Parameter Uncertainty) for the model selected, and then estimating the output parameters (such as deterministic λ , sensitivities, and elasticities). This process was repeated multiple times (50,000 for the deterministic demographic analyses). As there is no single point estimate for λ or other outputs from multiple models, the means of these outputs were reported (if the median differed substantially from the mean, both were reported). Again, we report the 2.5 and 97.5 percentiles (Efron and Tibshirani, 1998).

Incorporating Environmental Stochasticity

Our estimate of temporal variance (random effect of year) for v was essentially 0 (chapter 4); therefore, we only considered environmental stochasticity in sub-adult and

adult survival, kitten survival, and probability of breeding, where there was evidence for environmental stochasticity (Benson et al., in revision; Hostetler et al., 2010; chapter 4). Because factors such as abundance can affect estimates of temporal variance, we estimated temporal variance in those probabilities for each statistical model, and present those estimates in Tables 2-4. For all stochastic analyses, we used the temporal variances from the selected models. However, we assumed that the fixed effect model weights and the fixed effect estimates and covariances were unchanged by the inclusion of random effects.

We assumed that temporal correlation between S and q was 0 because we know of no reasonable method for estimating this correlation. Our method of estimating a single temporal variance for S_{sa} , S_{pa} , and S_{oa} implicitly assumes that the temporal correlation between those rates is 1 (as did the estimate of a single temporal variance for q_{sa} , q_{pa} , and q_{oa}). To estimate the temporal correlation between S_k and other survival parameters, we used the Markov Chain Monte Carlo (MCMC) option in MARK (as we did for estimating temporal variance in kitten survival; Lukacs et al., 2009; White et al., 2009). Because the kitten survival model also estimates sub-adult and adult survival for both sexes (Hostetler et al., 2010; it does not distinguish between prime-adult and older-adult survival) the MCMC option can be used with it to estimate temporal variance in logit sub-adult and adult survivals and correlation of these survivals with logit kitten survival. We used the same non-informative priors as White et al. (2009); estimates from the fixed effects models were used as starting values where appropriate. We sampled the MCMC for 50,000 iterations, after 4,000 tuning samples and 1,000 burn-in samples.

Estimates of the temporal correlation between S_k and other survival parameters were consistently around 0.341 in models where neither kitten survival nor sub-adult and adult survival depended on abundance. In models where kitten survival and/or sub-adult and adult survival depended on abundance, the estimates of correlation were close to 0. Therefore, we assumed that the correlation between logit S_k and logit of other survival parameters was 0.341 in model sets where all survival parameters were density-independent and 0 otherwise. Although temporal variance in S_{sa} , S_{pa} , and S_{oa} was estimated and applied on the log-hazard rather than the logit scale (Benson et al., in revision; Therneau and Grambsch, 2000), we found that simply reversing the sign (to -0.341) for correlation between logit kitten survival and sub-adult and adult log-hazard generated the correct correlation between logit survivals.

When incorporating environmental stochasticity into a simulation, we selected three random numbers from multivariate normal distributions each time step, using means of 0 and the temporal variances (and correlations) described above. We added the first random number to the intercept for kitten survival (on the logit scale) and the third to the intercept for probability of breeding (on the complementary log-log scale). These could then be converted to S_k , q_{sa} , q_{pa} , and q_{oa} (on the probability scale). The second random number (t_2) represented temporal change in log-hazard for sub-adults and adults, and was applied to S_{sa} , S_{pa} , and S_{oa} as:

$$S_i^t = (S_i)^{\exp(t_2)} \quad (5-7)$$

In this way, we generated random values for survival and breeding probabilities based on the estimated temporal variances in the same ways in which they were estimated.

Estimating Stochastic Growth Parameters

We estimated the stochastic version of instantaneous growth rate ($\log(\lambda_s)$) via simulation as the arithmetic mean of the log ratio of population sizes in successive years (Caswell, 2001; Morris and Doak, 2002). We exponentiated this to obtain estimates of finite stochastic growth rate (λ_s). We applied parametric uncertainty but limited inference to the minimum AIC (and QAIC_c) density-independent models (we did not include model selection uncertainty in this analysis). We ran 10,000 parametric bootstraps, each for 50,000 years. We included environmental stochasticity (see above) but not demographic stochasticity (see below).

Which parameters impact the stochastic growth rate the most, and whether this is primarily due to the sensitivity of λ_s to their means or their standard deviations is often of considerable interest for determining research and management priorities. We estimated overall stochastic sensitivities, overall stochastic elasticities, stochastic elasticities to the parameter means, and stochastic elasticities to the parameter standard deviations of λ_s to lower-level parameters (Caswell, 2005; Tuljapurkar et al., 2003).

Incorporating Density-Dependence

There was strong evidence for negative density-dependence in kitten survival, moderate evidence for positive density-dependence in probability of breeding (with weak evidence for a quadratic trend), weak evidence for negative density-dependence in sub-adult and adult survival, and weak evidence for positive density-dependence in number of kittens produced by females (Benson et al., in revision; Hostetler et al., 2010; chapter 4). The presence and form of density-dependence in population models can affect the estimated probability of extinction (Henle et al., 2004). Therefore, we included

models that did and did not include the effect of panther abundance on vital rates in our simulations.

The annual index of abundance (Benson et al., in revision; Hostetler et al., 2010; chapter 4) was the minimum count of older kittens (out of the den but still dependent on their dams), sub-adult and adult panthers of both sexes. Since age class 1 in our birth-flow model can be roughly viewed as representing ages 0.5 – 1.5 years, we included all modeled age classes in computing abundance. Because our model was female only but the index of abundance was based on both sexes, we had to convert modeled female population size into total population size. We used the following formulae to estimate the proportion of females (Miller and Lacy, 2005):

$$w_i^f = \frac{l_i^f \lambda^{-i}}{\sum l_i^f \lambda^{-i} + \sum l_i^m \lambda^{-i}} \quad w_i^m = \frac{l_i^m \lambda^{-i}}{\sum l_i^f \lambda^{-i} + \sum l_i^m \lambda^{-i}} \quad (5-8)$$

$$f = \sum w_i^f \quad (5-9)$$

where w_i^f is the proportion of total panthers that are females in age class i , w_i^m is the proportion of total panthers that are males in age class i , l_i^f is the female survivorship to age class i , l_i^m is the male survivorship to age class i , and f is the proportion of females (Table 5-1). This formula was parameterized using demographic parameters obtained from the top density independent models (Tables 2-5; male sub-adult, prime-adult, and older-adult survivals were 0.712, 0.802, and 0.624, respectively). Using this approach, we estimated f at 0.609. Preliminary simulations showed that total equilibrium population size of both sexes (back-computed from the same f used for density-dependence) varied less than one panther across the range of possible f values (although the equilibrium population size in terms of number of females did vary),

suggesting that model outputs are generally robust to violations of the assumption of constant f .

At each time step of a density-dependent simulation (after applying environmental stochasticity but before applying demographic stochasticity; see Box 1 below) the abundance index was computed by dividing total female population size by f . We recomputed the vital rates affected by abundance using this index. These vital rates could be used to compute \mathbf{A}^t or for individual panthers under demographic stochasticity (see below).

Not all model sets included negative density-dependence, and simulations with those that did not could experience extremely large populations. For biological plausibility and computational efficiency, we imposed a ceiling density limit of 1000 female panthers for all simulations. When the population exceeded 1000 females, we removed panthers proportionally from all age classes to reach a total population size of 1000.

Incorporating Demographic Stochasticity

At small population sizes demographic stochasticity (fluctuations in population growth caused by the random fates of individuals) can increase probability of extinction and otherwise influence population dynamics. We simulated demographic stochasticity by applying the time specific vital rates (influenced by environmental stochasticity and/or density-dependence) to the fates of individual female panthers. The number of females that survived a year in each age class was determined by drawing a binomial random sample using the matrix-entry survival probabilities (P_i^t).

The birth flow model complicated determining how many females reproduced in a year. We constructed a birth-flow breeding probability from equations 5.4 and 5.6:

$$PB_i^t = \frac{q_i^t + P_i^t q_{i+1}^t}{2} \quad (5-10)$$

We could then determine the number of females that bred in a year by drawing binomial random samples using PB_i^t . We thus modeled P_i^t into breeding probability separate from its effect on number of survivors.

We used the cumulative logit formula to randomly determine the number of offspring for each female that bred in a year:

$$n_r = \begin{cases} 1 & \text{if } \kappa_r \leq \delta_{r1} \\ 6 & \text{if } \kappa_r > \delta_{r4} \\ s & \text{if } \delta_{r(s-1)} < \kappa_r \leq \delta_{rs} \text{ for } s = 2, 3, 4 \end{cases} \quad (5-11)$$

where n_r is the number of offspring for individual r , κ_r is a uniform random number generated for individual r , and δ_{rs} is the probability that individual r will have at most s offspring (chapter 4; Table 5-1). We drew random binomial samples to determine the number of these kittens that were female (using f_k) and survived the first year (using $\sqrt{S_k^t}$). When large numbers of individuals were simulated for one time step using this algorithm, the numbers in each age class the next year closely matched the results from matrix multiplication, as they should.

When number of females in every age class exceeded 20, we used matrix multiplication instead of demographic stochasticity to project the population forward, but rounded the results so they could be used with demographic stochasticity (which operates on individuals) the next year (Morris and Doak, 2002). This was done to reduce computational burden, and because demographic stochasticity's effects are reduced as population size increases (Morris and Doak, 2002).

Estimating Extinction Parameters

We simulated populations starting with the current estimate of population size (100 total panthers). We determined number of females in each age class by multiplying 100 by each w_i^f (see density-dependence section and Table 5-1), and then rounding (so demographic stochasticity could be applied). After rounding, the estimated total number of females was 59.

We simulated the population forward 500 years. If a simulated population fell below a critical threshold (set at 1, 10, 20 and 30 females) it was considered extinct or quasi-extinct from that point forward. In addition to probabilities of extinction and quasi-extinction, we were interested in the timing of these events. Therefore we also kept track of the year each simulation first fell below each critical threshold (extinction and quasi-extinction times).

We ran simulations with the equivalent of four nested loops (Bakker et al., 2009; Ellner and Fieberg, 2003; White, 2000). The process used is detailed in Figure 5-1.

We present mean, median, and 2.5 and 97.5 percentiles of extinction and quasi-extinction probabilities at each time step, and minimum, maximum, mean, median, and 2.5 and 97.5 percentiles of extinction and quasi-extinction times.

What If the Introgression Never Happened?

An interesting question in the management of the Florida panther is: what might have happened to the panther population if genetic introgression had not occurred? To address this question, we estimated demographic parameter for canonical panthers only (Appendix L). However, we used estimates of σ_t from the overall population as described previously. We assumed that demographic parameters based on canonical panthers after introgression were representative of a hypothetical post-1995 canonical

panther population. Using these estimates, we parameterized a projection matrix and estimated population growth rate for a canonical population ($\lambda^{(c)}$), as well as error in $\lambda^{(c)}$. To determine how lower level parameters drove differences between λ and $\lambda^{(c)}$, we performed a fixed effect, one way life-table response experiment analysis (LTRE; Caswell, 2001).

In addition to population growth, we wanted to investigate how introgression affected probability of extinction. We ran the overall population and canonical population models both starting at the abundance index for 1995 (26, or 15 females; McBride et al., 2008). We ran 1000 runs of 1000 simulations, each for 500 years using procedures described previously. Since the starting female population size was <20 , we only estimated probability of quasi-(extinction) and extinction times for critical thresholds of 1 and 10 panthers.

Results

Density-Independent Growth Rate and Perturbation Analysis

The estimate of deterministic λ from the top set of statistical models was 1.06 (2.5 and 97.5 percentiles: 0.95 – 1.18). When model selection uncertainty was incorporated, λ dropped to 1.04 (both mean and median; 2.5 and 97.5 percentiles: 0.94 – 1.16). The λ had the highest sensitivity to kitten survival and the highest elasticity to prime-adult survival; model selection uncertainty had little effect on sensitivity or elasticity (Figure 5-2).

The estimate of λ_s was 1.05 (mean and median = 1.04; 2.5 and 97.5 percentiles: 0.95 – 1.15). Stochastic overall sensitivities and elasticities were similar to deterministic ones, with λ_s having the highest sensitivity to kitten survival and the highest elasticity to prime-adult survival (Figure 5-3A & B). Most of the overall stochastic elasticity was

contributed by elasticity to the means of parameters, not their temporal standard deviations (Figure 5-3C & D); λ_s had much higher magnitude elasticity to the standard deviation of S_k than those of other vital rates (Figure 5-3D; v_{sa} and v_a had temporal standard deviation of 0).

Extinction Parameters

We estimated probability of extinction within the next 100 years at 0.037 (median = 0, 2.5 and 97.5 percentiles: 0 – 0.55; Figure 5-4A). The probabilities of quasi-extinction within the next 100 years were 0.083 (median = 0, 2.5 and 97.5 percentiles: 0 – 0.88), 0.280 (median = 0.12, 2.5 and 97.5 percentiles: 0 - 1), and 0.732 (median = 0.92, 2.5 and 97.5 percentiles: 0.01 – 1) for critical thresholds of 10, 20, and 30 females, respectively (Figure 5-4B-D). At 500 years, 2.5 and 97.5 percentiles stretched from 0 to 1 for all critical limits except 30 females, for which they were 0.05 – 1.

Distributions of extinction and quasi-extinction times are shown in Table 5-6. The median time to extinction (among populations that went extinct within 500 years) was 128 years. Median time to (quasi-)extinction dropped with increasing critical numbers, and mean times of extinction and quasi-extinction were higher than the medians (Table 5-6).

What If the Introgression Never Happened?

The estimate of $\lambda^{(c)}$ for the hypothetical canonical population based on the top set of statistical models was 0.95 (mean and median = 0.94; 2.5 and 97.5 percentiles: 0.82 – 1.07). When model selection uncertainty was included, the estimate of $\lambda^{(c)}$ was still 0.95 (mean and median; 2.5 and 97.5 percentiles: 0.80 – 1.12). Patterns of sensitivities and elasticities (not shown) were similar to those for the overall population (Figure 5-2).

The largest contributor to the difference between λ and $\lambda^{(c)}$ was kitten survival probability (Figure 5-5). This was due to both a large difference in kitten survival probabilities (0.133; Table 5-3, Appendix L) and a large sensitivity of λ and $\lambda^{(c)}$ to S_k (Figure 5-2A). Prime-adult survival probability also contributed to the lower λ for the canonical population, while prime-adult probability of breeding, sub-adult probability of breeding, and sub-adult survival probability had slightly compensatory effects on λ for the canonical population (Figure 5-5). Although canonical panthers in general had lower survival than the overall panther population, the estimate for $S_{sa}^{(c)}$ was slightly higher in the top models (Appendix L and Table 5-2), because the canonical estimates came from a subset of the data (1997 – 2006) from which female sub-adult survival estimates were higher in general. The predicted $\lambda^{(c)}$ from the LTRE (calculated as the sum of the contributions from all vital rates) was also 0.95, indicating that the LTRE approximation was reasonable.

A sampling of density-dependent simulations run from 1995 population levels (whole population vital rates and canonical population vital rates scenarios) showed both scenarios tended to increase towards some equilibrium density but that equilibrium densities were, on average, higher for the whole population and the fluctuations greater (Figure 5-6A and B). This may be due to an average stronger estimated density-dependent effect on kitten survival for the canonical population than for the whole population and/or lower average σ_t for q and S_{sa-oa} parameters for the canonical population than for the whole population (Tables 2-4 and Appendix L). In turn, this could have lead to the higher estimated probability of extinction for the whole population (Figure 5-6C; at 100 years = 0.074, median = 0, 2.5 and 97.5 percentiles: 0 - 0.963)

than for the canonical population (Figure 5-6D; at 100 years = 0.039, median = 0, 2.5 and 97.5 percentiles: 0 - 0.513), but a somewhat lower probability of dropping below 10 females for the whole population (Figure 5-6E; at 100 years = 0.136, median = 0.015, 2.5 and 97.5 percentiles: 0 - 0.989) than for the canonical population (Figure 5-6F; at 100 years = 0.154; median = 0.009, 2.5 and 97.5 percentiles: 0 - 0.994). Both extinction and quasi-extinction times were lower, on average, for the whole population (Table 5-6).

Discussion

The situation for the Florida panther has undoubtedly improved since the early 1990's. Population size, genetic diversity and survival rates have increased, and morphological abnormalities and other biomedical conditions indicative of inbreeding depression have decreased (Benson et al., in revision; Hostetler et al., 2010; Johnson et al., 2010; McBride et al., 2008; Onorato et al., 2010). However, the population still faces numerous threats, including isolation, habitat loss and fragmentation, road kills, other interactions with humans, disease, and the potential future loss of genetic diversity (Onorato et al., 2010). In this context, a quantitative assessment of risk faced by the Florida panther and an objective evaluation of the role of genetic introgression on observed increases in population performance is of paramount importance.

The stochastic growth rate was 1.05 (2.5 and 97.5 percentiles: 0.95 – 1.15). This is consistent with the evidence for a growing population between 1995 and 2007 (McBride et al., 2008), the period over which the bulk of the data used to estimate parameters was collected. Both λ and λ_s showed highest elasticity to survival parameters. This is consistent with other studies for long-lived species (especially for lower-level elasticities; Heppell et al., 2000; Morris and Doak, 2005; Stahl and Oli, 2006). Although fewer studies have examined elasticity patterns for birth-flow

populations, the same patterns seem to hold there (e.g., Alberts and Altmann, 2003; Federico and Canziani, 2005; Fisher et al., 2000). The lower elasticities to sub-adult vital rates than to prime-adult vital rates is probably an artifact of age-class duration (1.5 and 7.5 years, respectively), as matrix-entry elasticities (not shown) generally declined with age.

Our estimate of probability of extinction within 100 years (baseline scenario) was 3.7% (2.5 and 97.5 percentiles: 0 – 55%). Earlier PVA for the Florida panther had, under their baseline scenarios, estimates for this of 0% (Maehr et al., 2002a) and 2%, 5%, or 78.5% (depending on parameter values used; Root, 2004). Root (2004) estimated the probability of dropping from 40 to 20 females within 100 years at 9%, 20%, or 94.1% (depending on parameter values used); our estimate of the probability that the population falls below 20 and 30 females (approximately by half) within 100 years were 28.0% (2.5 and 97.5 percentiles: 0 - 100%) and 73.2% (2.5 and 97.5 percentiles: 1 - 100%), respectively. We believe our PVA results are more robust than those from earlier PVA efforts, because our results are based on robust estimates of demographic parameters, and a more realistic birth-flow population model, and also because we have appropriately incorporated the potential effects of environmental and demographic stochasticities. Furthermore, we have considered the influence of parametric and model selection uncertainty. Fieberg and Ellner (2001) and Ellner et al. (2002) demonstrated that long-term estimates of extinction risk can be highly imprecise, even with considerable quantities of data. Our results for Florida panthers support these predictions. Despite this, we disagree with the notion that the apparently inherent imprecision of PVA results makes them useless to science or management.

PVA are generally the best tools science has to offer for assessing extinction risk, and it is better to make use of what science has to tell us (taking into account the uncertainty) than to ignore it in favor of subjective assessments (Brook et al., 2002a). An estimate for probability of extinction with wide confidence intervals still represents the most likely value for that probability (under the modeling assumptions that lead to it).

Our inclusion of density-dependent effects undoubtedly had a significant impact on our estimated probabilities of extinction and quasi-extinction, and may have had different effects at different quasi-extinction thresholds (Henle et al., 2004). There are reasons that these results should be interpreted carefully. The abundance index we used (McBride et al., 2008) was not a true estimate of population size and may be biased low in some years. We used different functional forms for each set of vital rates (Benson et al., in revision; Hostetler et al., 2010; Chapter 4), but these functional forms were chosen more for convenience than from biological intuition. We only tested quadratic effects for reproductive parameters (and could not fit those effects for v) and did not test for lagged/delayed density-dependence. The abundance index may have stabilized at around 100 panthers in recent years (D. Land, personal communication), but most of our density-dependent models (when run deterministically; not shown) lead to an equilibrium population size (converted to total panthers) lower than that. This may result from error in the abundance index or how we modeled density-dependence.

We note that the estimated growth and extinction parameters were based on demographic data mostly collected during a period of rapid population growth. Field data suggest that the population growth may have ceased. Current and future conditions may therefore make long term population growth lower and probability of

extinction higher than reported here. Genetic stochasticity (not modeled) may also increase overall probability of extinction.

The estimated deterministic growth rate for a canonical population was $\lambda^{(c)} = 0.95$ (2.5 and 97.5 percentiles: 0.82 – 1.07). Although percentile ranges for λ and $\lambda^{(c)}$ overlapped, a 10% difference in population growth rate is biologically meaningful. The most important demographic cause of this difference was the lower survival rate for canonical panther kittens. Given the evidence that a canonical population would have declined (or continued to not increase), the concerns of conservationists and managers about the demographic health of the panther population in the early 1990's seem quite warranted (Fergus, 1991; Roelke et al., 1993b; Seal, 1994). However, these growth rates were estimated from models without stochasticity or density-dependence. When these were included, the canonical population actually had a lower probability of extinction, but a higher probability of dropping below 10 females. As pointed out in the results, this is probably due to stronger estimated density-dependence and/or lower assigned stochasticity for the models including ancestry. Because all of our statistical models had additive effects of abundance and ancestry (when both were included) we did not specifically look at how canonical vital rates tracked abundance, but assumed that vital rates of all panthers were affected by abundance similarly. Density-dependent effects may also have little effect on population dynamics at 1995 population levels. Future analyses could estimate temporal standard deviation separately for ancestry models, simulate short-term extinction probabilities without density-dependence, estimate demographic parameters for the canonical subset of the data separately

(instead of using ancestry models), and/or examine interactive effects between abundance index and ancestry.

Our models also did not include genetic stochasticity; potential further loss of genetic diversity could have further increased the probability of extinction for a canonical population after 1995. On the other hand, all vital rates for canonical panthers were estimated over a period when they were sharing the landscape with admixed panthers. Without the increased competition and intraspecific aggression from these panthers, survival of canonical panthers (and $\lambda^{(c)}$) might have been higher. Although our results are suggestive, we cannot therefore state with certainty that the observed increase in panther numbers would not have happened without the genetic introgression (Creel, 2006).

Currently we make no allowances for potential catastrophes such as disease outbreaks, which can have large impacts on population viability but which may require guesses as to the frequency and severity of catastrophes to implement (Coulson et al., 2001; de Castro and Bolker, 2005; Gerber et al., 2005). We could expand perturbation analysis for population growth to probability of extinction, using methods such as squared semi-partial correlation coefficients (Bakker et al., 2009). We could take into account the impact of random effects on the model weights or fixed effect estimates, or develop true confidence interval ranges based on bias-correction techniques for bootstrap percentiles (Caswell, 2001; Efron and Tibshirani, 1998; Ellner and Fieberg, 2003). Finally, a spatially-explicit, individual-based PVA for the Florida panther would be very useful for answering questions about the effects of habitat changes and behavioral interactions on panther population growth and persistence.

Nonetheless, the PVA we developed can be used to ask several further management questions, and we plan to do so in the near future. Road mortality is one of the leading causes of mortality for the Florida panther (Benson et al., in revision), and 2009 had the largest number of reported panther road kills. Management agencies are curious to know the effect of road mortality (and changes in it) affects population viability. There is no estimate of the effect of road kills on kitten survival; analyses would have to make some assumptions about how kitten survival changes with changes in sub-adult and adult road kill mortality.

Although young male Florida panthers frequently roam out of south Florida, no female panthers have been recorded north of the Caloosahatchee River since 1972 (McBride, 2002). Starting a breeding population of Florida panthers in central Florida or elsewhere within their former range might be important for the long-term recovery of the subspecies (Thatcher et al., 2009; USFWS, 2006). Against this, managers must weigh the impacts of removing female panthers from south Florida on the viability of the source population. We can predict the impacts of different numbers, ages, and timing of female panther removals on south Florida panther viability quite easily with the current model. In addition, we could model the viability of the new population or the joint viability of the two populations, although this would require making several (possibly unwarranted) assumptions about vital rates and stochasticity in the new location. The ideal age class to remove for behavioral reasons might be the sub-adult females that have not yet set up home ranges. This age class also has the highest reproductive value (at least for the top deterministic density-independent model; J. Hostetler,

unpublished results) and so might also be ideal for contributing to population growth of the new population (Maguire and Servheen, 1992).

The panther population size was at best stable (at low numbers) before 1995 but grew rapidly afterwards (McBride et al., 2008). We found evidence that the difference in survival probabilities between canonical and admixed panthers (particularly for kittens; Benson et al., in revision; Hostetler et al., 2010) contributed to this difference in population growth rates. If the Florida panther continues to exist in one small population in south Florida in the future, inbreeding depression may again lead to a population decline. Our results suggest that continued genetic introgressions may be a useful strategy for combating this risk.

Table 5-1. Variable names used in this manuscript, with definitions.

Variable	Definition
$\beta_{abundance}$	Modeled effects of abundance index on vital rates
$\beta_{abundance2}$	Modeled effects of squared abundance index on vital rates
δ_{rs}	Probability that individual r will have at most s offspring (given that she breeds)
I_2	(Multivariate) random normal number generated for sub-adult and adult log-hazard
K_r	Uniform random number generated for individual r
λ	Deterministic asymptotic population growth rate
λ_s	Stochastic asymptotic population growth rate
V_a	Average number of kittens produced by an adult female in a year, given that she breeds
V_{sa}	Average number of kittens produced by an sub-adult female in a year, given that she breeds
σ_t	Temporal standard deviation in a group of vital rates
\mathbf{A}^t	Time-specific population projection matrix
(c)	Parameter estimated for canonical panthers
$f.$	(Stable) proportion of entire population that is female
f_k	Proportion of newborn kittens that are female
F_i^t	Fertility (number of female kittens produced each year per female) for female of age class i in year t
l_i^f	Survivorship of a female to age i
l_i^m	Survivorship of a male to age i
m_i^t	Fecundity (number of female kittens produced each year per surviving female) for female of age class i in year t
n_r	Number of kittens produced by individual r in a year, given that she breeds
P_i^t	Survival probability for female of age class i in year t
PB_i^t	Probability that a female of age class i breeds in year t
q_{oa}	Probability that an older-adult female breeds in a year, given that she survives
q_{pa}	Probability that an prime-adult female breeds in a year, given that she survives
q_{sa}	Probability that an sub-adult female breeds in a year, given that she survives
S_k	Annual survival probability for kittens (age 0-1 years)
S_{oa}	Annual survival probability for older-adults (age 10 years and up)
S_{pa}	Annual survival probability for prime-adults (ages 2.5-10 years)
S_{sa}	Annual survival probability for sub-adults (ages 1-2.5 years)
w_i^f	Stable proportion of total panthers that are females in age class i
w_i^m	Stable proportion of total panthers that are males in age class i

Table 5-2. Models for sub-adult and adult survival, with Akaike model weights, estimates of sub-adult female survival (S_{sa}), prime-adult female survival (S_{pa}), older-adult female survival (S_{oa}), the effect of abundance index on log-hazard ($\beta_{abundance}$), and temporal standard deviation (σ_t). Survival estimates for density-dependent models are for abundance index 0. Age category model names are different than in Benson et al. (in revision).

Model	Weight	S_{sa}	S_{pa}	S_{oa}	$\beta_{abundance}$	σ_t
Sex * Age3 ^a + Older ^b	0.357	0.954 ± 0.032	0.873 ± 0.022	0.748 ± 0.048	0	0.34
Sex * Age3 + Older + Abundance ^c	0.313	0.966 ± 0.025	0.906 ± 0.029	0.795 ± 0.057	0.005 ± 0.004	0.31
Sex * Age1 ^d	0.133	0.954 ± 0.032	0.872 ± 0.024	0.754 ± 0.055	0	0.34
Sex * Age1 + Abundance	0.118	0.966 ± 0.025	0.905 ± 0.030	0.803 ± 0.061	0.005 ± 0.004	0.30
Sex * Age3	0.034	0.954 ± 0.032	0.852 ± 0.022	0.852 ± 0.022	0	0.25
Sex	0.018	0.868 ± 0.019	0.868 ± 0.019	0.868 ± 0.019	0	0.22
Sex * Age3 + Abundance	0.018	0.961 ± 0.028	0.875 ± 0.034	0.875 ± 0.034	0.003 ± 0.004	0.24
Sex + Abundance	0.010	0.889 ± 0.030	0.889 ± 0.030	0.889 ± 0.030	0.003 ± 0.004	0.21

^a Age3 divides panthers into sub-adults (1-2.5 and 1-3.5 years old for females and males respectively) and adults (≥2.5 and ≥3.5 yrs for females and males respectively).

^b Older refers to older-adults (≥10 years old).

^c Abundance refers to a linear trend in log-hazard by abundance index.

^d Age1 divides the panthers into sub-adults (same as Age3), prime-adults (2.5-10 and 3.5-10 years old for females and males respectively), and older-adults (≥10 years old).

Table 5-3. Models for kitten survival, with Akaike model weights, estimates of female kitten survival (S_k), the effect of abundance index on logit kitten survival ($\beta_{abundance}$), and temporal standard deviation (σ_t). Survival estimates for density-dependent models are for abundance index 0. For more details, see Hostetler et al. (2010).

Model	Weight	S_k	$\beta_{abundance}$	σ_t
$S(\text{Base}^a + k:\text{Abundance}^b)r(.)^c$	0.379	0.806 ± 0.119	-0.034 ± 0.011	0.37
$S(\text{Base} + k:\text{Abundance})r(k, s\&a)^d$	0.337	0.829 ± 0.115	-0.034 ± 0.011	0.46
$S(\text{Base} + k:\text{Abundance} + k:\text{sex}^e)r(.)$	0.148	0.824 ± 0.119	-0.035 ± 0.011	0.36
$S(\text{Base} + k:\text{Abundance} + k:\text{sex})r(k, s\&a)$	0.126	0.843 ± 0.116	-0.034 ± 0.012	0.36
$S(\text{Base})r(k, s\&a)$	0.004	0.345 ± 0.076	0	1.03
$S(\text{Base})r(.)$	0.003	0.291 ± 0.050	0	1.01
* $S(\text{Base} + k:\text{sex})r(k, s\&a)$	0.001	0.350 ± 0.090	0	-
* $S(\text{Base} + k:\text{sex})r(.)$	0.001	0.305 ± 0.069	0	-

^a The base survival model represents survival differing between kittens, females age 1 and 2, females 3 and older, males age 1-3, and males 4 and older (Hostetler et al., 2010).

^b $k:\text{Abundance}$ refers to a linear trend in logit kitten survival by abundance index.

^c The same recovery probability for all panthers.

^d Recovery probabilities differing between kittens and older panthers.

^e Kitten survival differing by sex.

* These models are $> 10 \text{QAIC}_c$ units from the top model, but are $< 10 \text{QAIC}_c$ units from the top density-independent model, and were therefore included in estimation of λ but not in estimation of probability of extinction.

Table 5-4. Models for sub-adult and adult probability of breeding, with Akaike model weights, estimates of sub-adult probability of breeding (q_{sa}), prime-adult probability of breeding (q_{pa}), older-adult probability of breeding (q_{oa}), the effects of abundance index and abundance index squared on monthly complementary log-log probability of breeding ($\beta_{abundance}$ and $\beta_{abundance2}$, respectively), and temporal standard deviation (σ_t). Probability of breeding estimates for density-dependent models are for abundance index 0.

Model	Weight	q_{sa}	q_{pa}	q_{oa}	$\beta_{abundance}$	$\beta_{abundance2}$	σ_t
Age2 ^a + Abundance ^b	0.304	0.278 ± 0.095	0.278 ± 0.095	0.024 ± 0.025	0.009 ± 0.005	0	0.38
Age2	0.209	0.459 ± 0.037	0.459 ± 0.037	0.038 ± 0.037	0	0	0.42
Age2 + Abundance + Abundance ²	0.152	0.462 ± 0.293	0.462 ± 0.293	0.044 ± 0.055	-0.011 ± 0.025	0.0001 ± 0.0002	0.38
Age1 ^c + Abundance	0.141	0.252 ± 0.096	0.301 ± 0.105	0.025 ± 0.026	0.008 ± 0.005	0	0.37
Age1	0.128	0.382 ± 0.083	0.477 ± 0.041	0.038 ± 0.037	0	0	0.41
Age1 + Abundance + Abundance ²	0.066	0.407 ± 0.287	0.465 ± 0.292	0.043 ± 0.054	-0.009 ± 0.025	0.0001 ± 0.0002	0.37

^a Age2 divides panthers into young-adults (1-10 years old) and older-adults (≥10 years old).

^b Abundance refers to a linear trend in monthly complementary log-log probability of breeding by abundance index.

^c Age1 divides the female panthers into sub-adults (1-2.5 years old), prime-adults (2.5-10 years old) and older-adults (≥10 years old).

Table 5-5. Models for the average number of kittens produced by sub-adult and adult females (for females that bred in a year), with Akaike model weights, estimates of sub-adult kittens (v_{sa}), adult kittens (v_a), and the effects of abundance index on cumulative logit number of kittens ($\beta_{abundance}$). Number of kittens estimates for density-dependent models are for abundance index 0. Estimated temporal standard deviation (σ_t) was 0.

Model	Weight	v_{sa}	v_a	$\beta_{abundance}$
Age3 ^a	0.368	3.13 ± 0.28	2.69 ± 0.12	0
Constant ^b	0.318	2.76 ± 0.12	2.76 ± 0.12	0
Age3 + Abundance ^c	0.177	2.87 ± 0.44	2.41 ± 0.38	0.006 ± 0.009
Abundance	0.137	2.55 ± 0.39	2.55 ± 0.39	0.005 ± 0.009

^a Age3 divides female panthers into sub-adults (1-2.5 years old) and adults (≥ 2.5 years old).

^b No predictor variables.

^c Abundance refers to a linear effect of abundance index on cumulative logit number of kittens produced by female panthers.

Table 5-6. Summary statistics for extinction and quasi-extinction times (number of years until first dropping below critical thresholds). The starting size refers to the total number of females at the beginning of each simulation and the population refers to the group of panthers parameters were estimated for. Therefore, the first four rows are for the baseline scenario, the next two rows are for the baseline parameter values but starting at 1995 population levels scenario, and the bottom two rows are for the “what would have happened without introgression” scenario. The maximum (quasi-)extinction time was always 500, the number of years all simulations were run.

Population	Starting Size	Critical Threshold	Minimum	Mean	Median	2.5 and 97.5 Percentiles
Whole	59	1	12	171.1	128	29 – 468
Whole	59	10	6	155.5	108	16 – 465
Whole	59	20	2	132.2	80	10 – 456
Whole	59	30	1	62.2	25	5 – 358
Whole	15	1	5	120.4	60	15 – 450
Whole	15	10	1	104.6	36	2 – 454
Canonical	15	1	6	167.6	123	20 – 471
Canonical	15	10	1	137.4	86	4 – 461

```
PARAMETRIC BOOTSTRAP LOOP (runs; 10,000 times)
  Select models randomly by AIC weights
  Select parameters from the distributions for those models
  SIMULATION LOOP (simulations; 100 times)
    TIME STEP LOOP (years; 500 years)
      INDIVIDUAL LOOP (number of individuals)
        Determine fate of individual using demographic stochasticity
      END INDIVIDUAL LOOP
      Determine number of individuals the next year
    END TIME STEP LOOP
  END SIMULATION LOOP
  Estimate probabilities of extinction and quasi-extinction as the proportion of simulations that
  go extinct/quasi-extinct
END PARAMETRIC BOOTSTRAP LOOP
Summarize distributions of (quasi-)extinction times and probabilities
```

Figure 5-1. Pseudo-code for estimating probability of extinction.

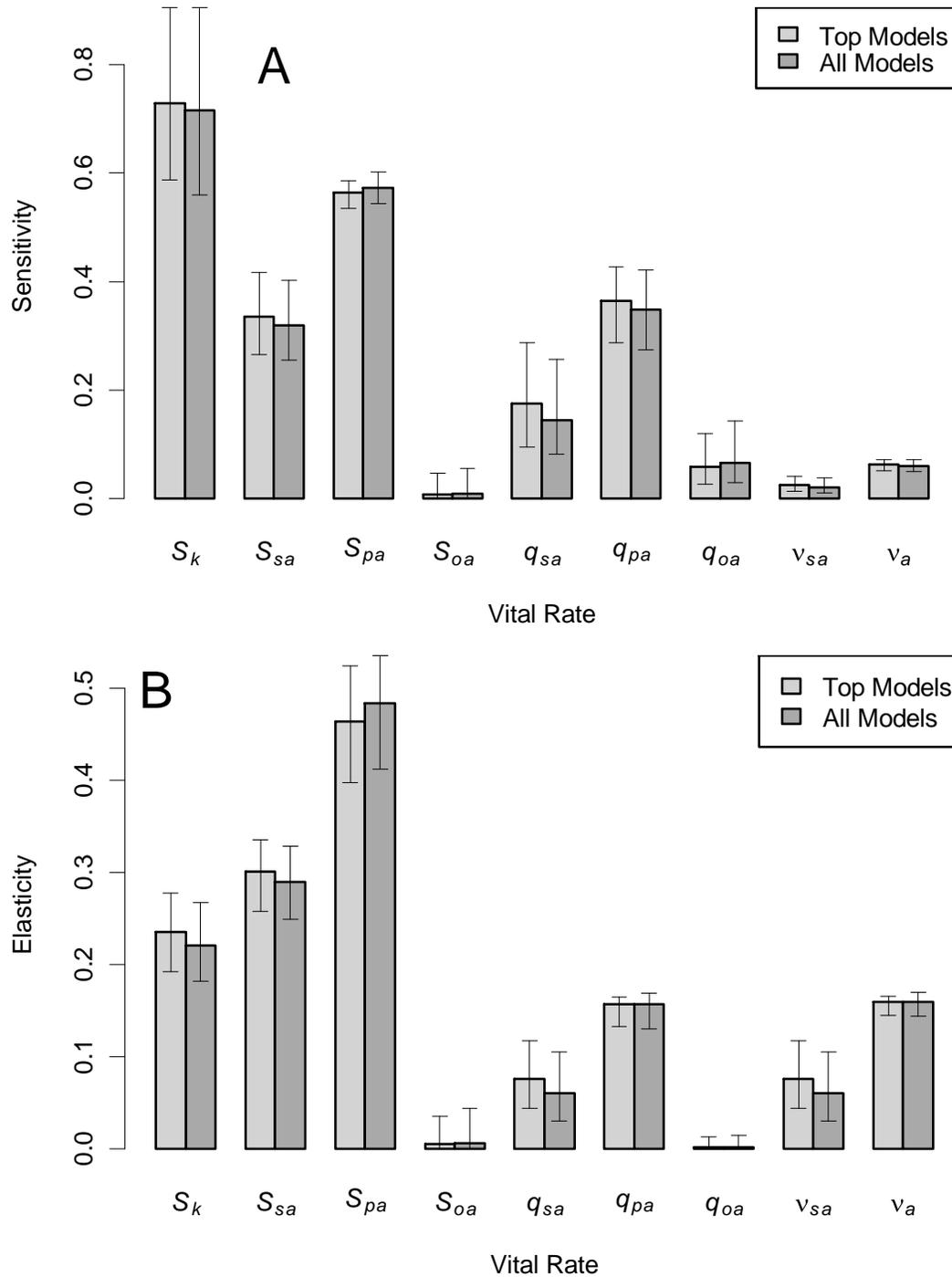


Figure 5-2. Perturbation analysis deterministic population growth rate (λ) to lower level parameters (see Table 5-1). A) Sensitivity for the set of top-ranked density-independent statistical models and for all density-independent statistical models. B) Proportional sensitivity (elasticity) for the same. Solid bars represent point estimates for top models (means and median of parametric bootstraps were very similar) and medians of parametric bootstraps for all models (means were very similar). Error bars represent 2.5 and 97.5 percentiles of parametric bootstrap runs in both cases.

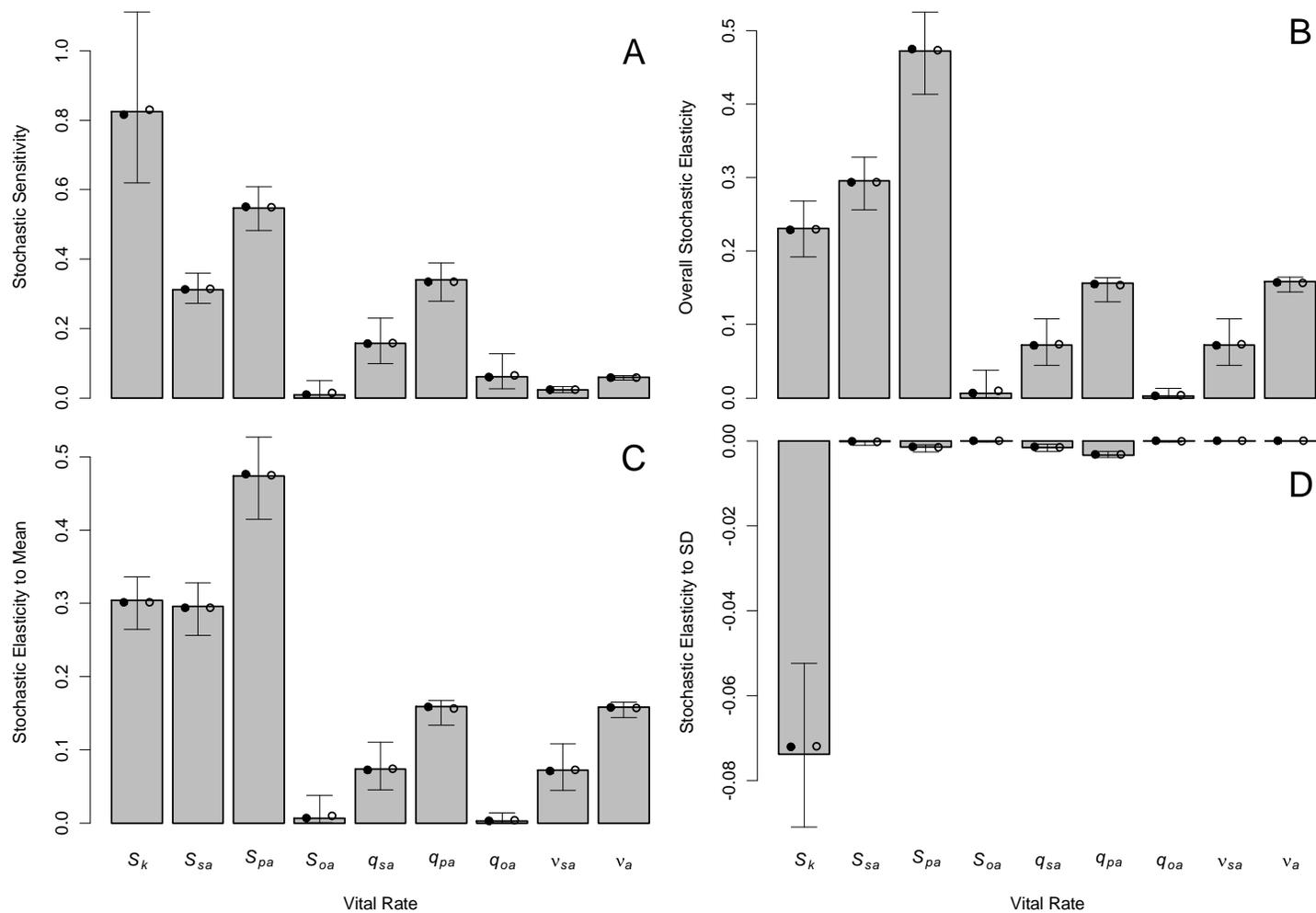


Figure 5-3. Perturbation analysis results for stochastic population growth rate (λ_s) to lower level parameters (see Table 5-1) for the set of top-ranked density-independent statistical models. A) Stochastic sensitivities. B) Overall stochastic elasticities. C) Stochastic elasticities to means. D) Stochastic elasticities to standard deviations. Solid bars represent point estimates, solid circles represent medians of parametric bootstrap runs, and open circles represent means. Error bars represent 2.5 and 97.5 percentiles of parametric bootstrap runs.

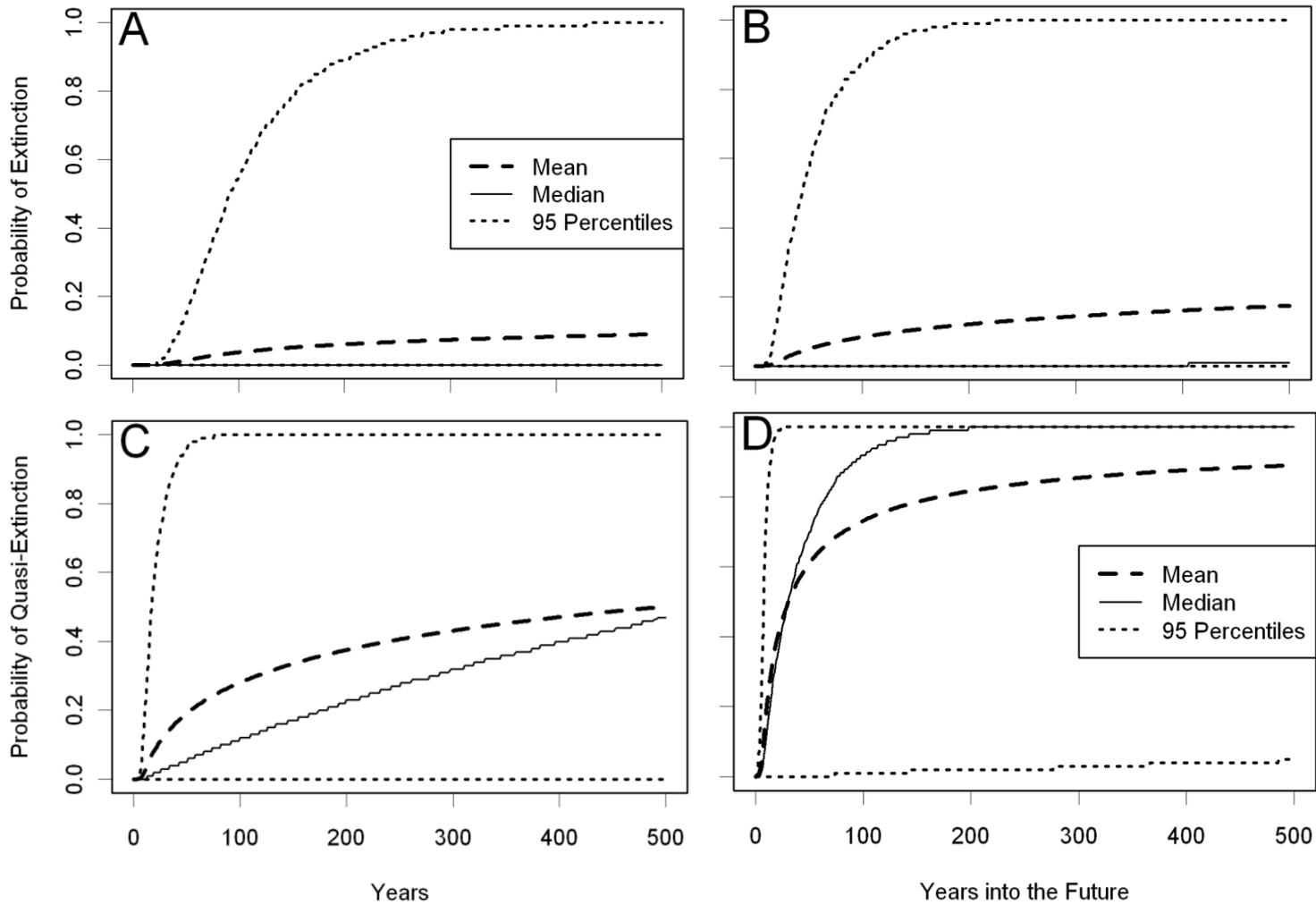


Figure 5-4. Simulated cumulative probabilities of extinction and quasi-extinction over 500 years. Panels depict estimated probabilities of reaching A) <1 female, B) <10 females, C) <20 females, and D) <30 females. The thick dashed lines represent simulation means, the solid lines simulation medians, and the dotted lines 2.5 and 97.5 simulation percentiles.

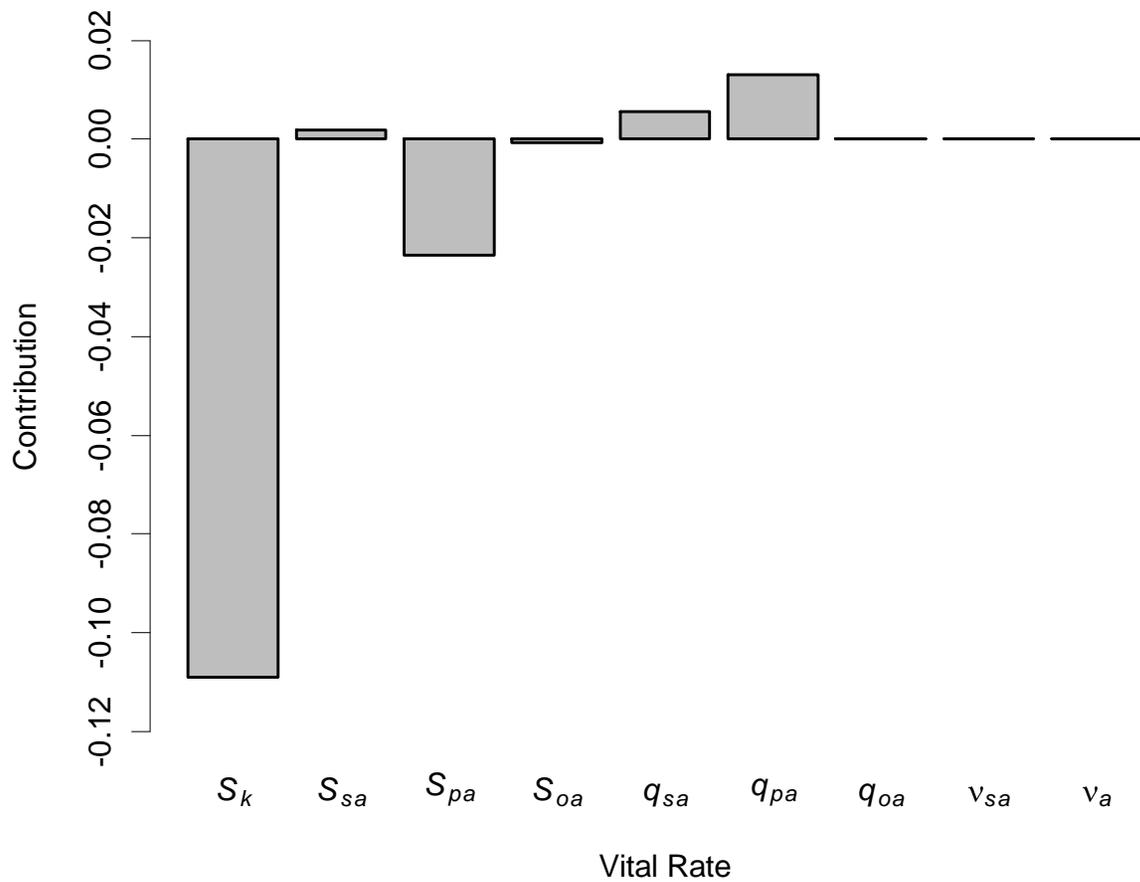


Figure 5-5. Contributions of lower level parameters (see Table 5-1) to differences between the deterministic population growth rates for the whole population (λ) and the canonical population ($\lambda^{(c)}$). Negative contributions lead to $\lambda^{(c)}$ being lower than λ .

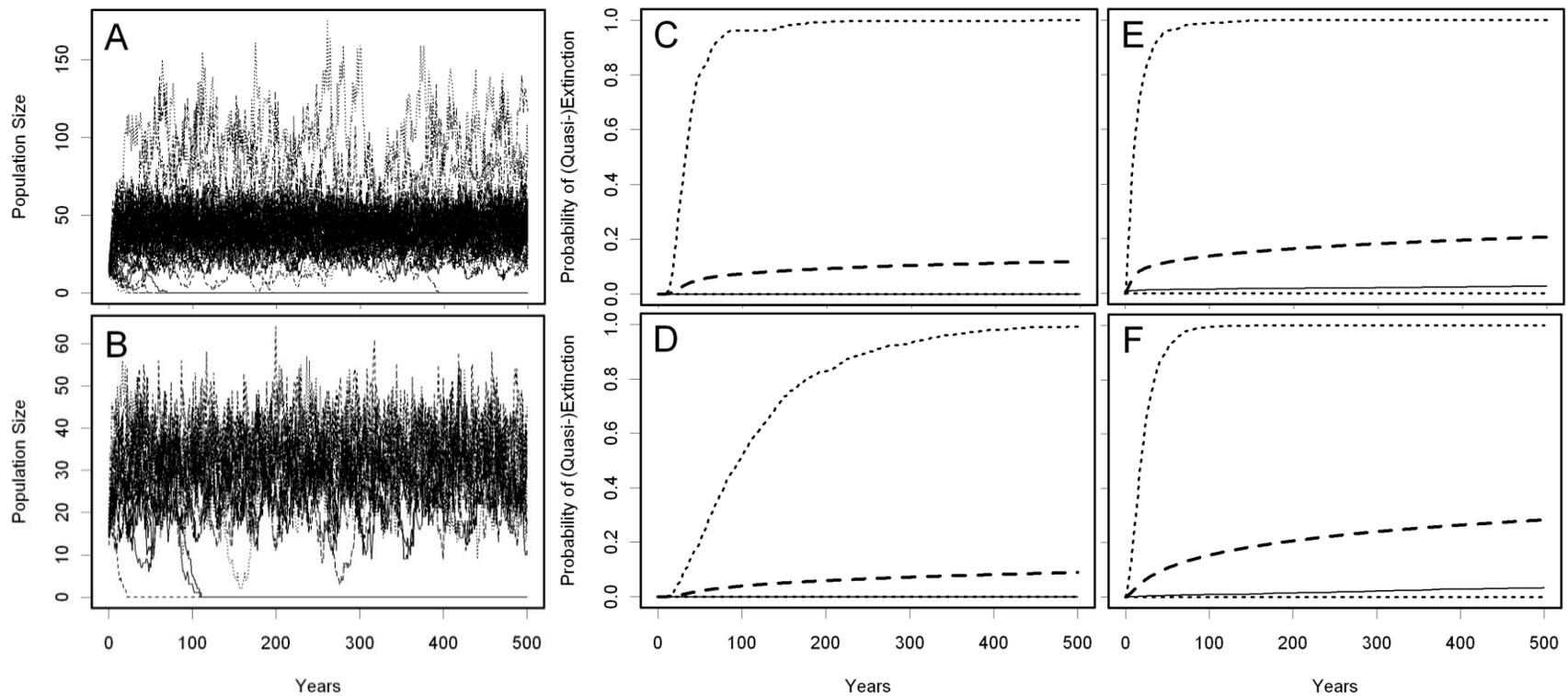


Figure 5-6. Results of simulations starting with conjectured 1995 population levels (total 15 females) and run for 500 years. Panels A and B) depict random selections of population sizes for different scenario runs; C and D) depict cumulative probabilities of reaching <1 female; and E and F) depict cumulative probabilities of reaching <10 females. A, C, and E) are for the whole population and B, D, and F) are for a canonical population. The thick dashed lines represent simulation means, the solid lines simulation medians, and the dotted lines 2.5 and 97.5 simulation percentiles.

CHAPTER 6 SUMMARY AND CONCLUSIONS

Our study achieved 3 major objectives. First, we have used all appropriate data and robust statistical methods to provide rigorous estimates of demographic parameters for Florida panthers. Second, we have provided estimates of population growth and persistence parameters for our study population. Finally, we have objectively tested for the potential influence of genetic introgression, one of the most important and controversial management actions undertaken for the conservation of the panther, on demographic parameters and population growth.

We estimated overall annual kitten (age 0-1 year) survival at 0.328 ± 0.065 (SE) and sub-adult and adult panther survivals ranging from 0.951 ± 0.034 for female sub-adults (1 – 2.5 years) to 0.635 ± 0.083 for male older-adults (≥ 10 years). The estimate of kitten survival is lower than previously reported. There was evidence that sub-adult and adult females had higher survival than male sub-adults and adults, but no evidence of a difference in survival by sex for kittens. Survival within the first year increases with age, whereas female survival declines from sub-adults to prime-adults (2.5 – 10 years) to older-adults (≥ 10 years). Male survival peaks in the prime-adult stage, which was defined as 3.5 – 10 years.

Overall female 6-month probability of breeding was 0.232 ± 0.021 and average litter size was 2.60 ± 0.09 . Sub-adult dams had larger litters on average than adult (ages 2.5 – 10 years) dams, but we were unable to detect a difference in probability of breeding between sub-adult and prime-adult female panthers. However, older-adult females did have a lower probability of breeding (0.019 ± 0.019). Females were more

likely to give birth in the dry season (December – May) than in the wet season (June – November), and also had larger litters in the dry season.

We used annual minimum panther population counts (McBride et al., 2008) as an index of abundance to estimate the effects of density on vital rates. We found that abundance negatively affected the probability of survival for kittens and positively affected the female probability of breeding (which may have been an artifact of its effect on kitten survival). However, we found little evidence for an effect of abundance on litter size or sub-adult and adult survival.

Deterministic annual population growth rate (λ) for the overall population was 1.06 (2.5 and 97.5 percentiles: 0.95 – 1.18) and stochastic annual growth rate (λ_s) was 1.05 (2.5 and 97.5 percentiles: 0.95 – 1.15), which suggest that the population has been growing and corroborates recent trends in minimum population counts. Elasticity analyses showed that λ_s was proportionately most sensitive to changes in survival, particularly of prime-adult and sub-adult females. Our stochastic simulations incorporating demographic and environmental stochasticity, parameter and model selection uncertainty, and density-dependence provided an estimate of the probability of extinction within 100 years of 3.7% (2.5 and 97.5 percentiles: 0 – 55%). We estimated the probability of dropping below 30 females at some point within the next 100 years at 73.2% (2.5 and 97.5 percentiles: 1 – 100%). Among populations that went extinct within 500 years, the median time to extinction was 128 years (2.5 and 97.5 percentiles: 29 – 468). These estimates may be optimistic, as most of the data used for our models were collected during a period of population increase, and our model did not include

catastrophic events, genetic stochasticity, or potential future changes in habitat or anthropogenic influences.

We found considerable evidence that the genetic introgression in 1995 had effects on both demographic rates and population dynamics. Florida panther survival was higher for F_1 admixed (0.494 ± 0.156) and backcrossed to Texas (0.400 ± 0.124) kittens than for backcrossed to canonical (0.267 ± 0.078) and canonical Florida panther (0.245 ± 0.073) kittens. For sub-adults and adults, survival was higher for F_1 admixed (0.978 ± 0.021) panthers than for other admixed (0.821 ± 0.036) or pre-introgression type (canonical and Everglades) panthers (0.775 ± 0.039). Conversely, 6-month probability of breeding was lower for F_1 admixed sub-adult and adult female panthers than for other admixed or pre-introgression type female panthers (although this may have been an artifact of higher kitten survival), and there was no evidence that ancestry affected litter size. A population matrix model parameterized for a hypothetical population of all canonical panthers yielded a λ of 0.95 (2.5 and 97.5 percentiles: 0.82 – 1.07), suggestive of a shrinking population. A life table response experiment (LTRE) demonstrated that the vital rate with the largest effect on the difference between λ for the overall population and for the canonical population was kitten survival.

These results cannot conclusively prove that the observed post-introgression increase in the panther population would not have occurred without genetic introgression or that factors other than introgression did not contribute to the observed population increase. Proof in such “what would have happened” scenarios may be outside the reach of science. They do, however, strongly support the hypothesis that

genetic introgression had a positive population-level effect on Florida panthers, primarily via improved survival of admixed panthers.

APPENDIX A AGE ERROR ESTIMATION

Methods

To examine the error in survival estimates associated with using the estimated age at capture to estimate the age category and age category changes of each animal, we created a range of plausible birthdates for each panther, centered at the estimated birthdate. When the field estimate of age included a range (e.g., 3-4 years old), we used that range. Otherwise, we used a range of 1 year (6 months on either side of the estimated birthdate). Birthdates were known (within a few days) for 54 panthers; birthdate ranges for other panthers were as low as 1 month or as high as 2 years (Table A-1).

We used a resampling approach, randomly selecting (from a uniform distribution) a birthdate for each panther whose age was unknown within its birthdate range. We then assigned age category and age category changes for each panther based on the new birthdates. We ran the survival analysis for the top-ranked age and sex category model (Sex * Age1 + Older). We repeated these steps 1000 times, and recorded the mean and standard deviations of the survival estimates. We used the standard deviation as a measure of the error due to choosing the midpoint of the range. This assumes that the true birthdates were somewhere within the ranges. We also assumed that these errors and the standard errors of the original survival estimates were independent, and estimated the total error as:

$$TE(\hat{s}_i) = \sqrt{SE(\hat{s}_i)^2 + SD(\bar{s}_i)^2}$$

where \hat{s}_i is the survival rate estimated for category i using the Cox proportional-hazard method and the midpoints of the birthdate ranges, $SE(\hat{s}_i)$ is the standard error of that estimate, \bar{s}_i is the mean of the resampling survival estimates for category i , and $SD(\bar{s}_i)$ is the standard deviation of the resampling survival estimates for category i .

Results and Discussion

The mean survival estimates from the resampling analysis were generally quite close to the original survival estimates (Table A-2). The errors due to birthdate selection were smaller than the errors due to other causes. The total errors were very similar to the errors due to other causes. The relatively high difference between \hat{s}_i and \bar{s}_i and relatively high $SD(\bar{s}_i)$ for female sub-adults are probably due to a single female panther that died a few days less than a year after her estimated birthdate. This panther was not included as a sub-adult in the survival analyses in the body of the paper (i.e., because she was classified as a kitten) but was included in some resampling runs, bringing down the female sub-adult survival estimates in those runs. We did not test the effects of birthdate error on model selection or multi-model inference, but suspect that those effects would be quite small as well.

Table A-1. Distribution of lengths of birthdate ranges (in months). A birthdate range of 0 indicates that the birthdate of the panther was known within a few days. The default birthdate range length used (when only a point estimate for birthdate was given in the field) was 12 months.

Length of Birthdate Range (Months)	Number of Panthers
0	55
1	5
2	15
3	1
6	7
12	58
24	5

Table A-2. Resampling results examining error from using estimated age at capture to estimate survival by age class. For each sex and age class, we present estimated survival (\hat{s}), standard error of that estimate (SE (\hat{s})), mean survival from the resampling approach (\bar{s}), standard deviation of that mean (SD(\bar{s})), and the total error from both sources (TE(\hat{s})). All results are using the top-ranked sex and age model (Sex * Age1 + Older).

Sex	Age Class	\hat{s}	SE (\hat{s})	\bar{s}	SD(\bar{s})	TE(\hat{s})
Female	Sub-Adult	0.954	0.032	0.937	0.017	0.036
Female	Prime-Adult	0.873	0.022	0.875	0.003	0.022
Female	Older-Adult	0.748	0.048	0.747	0.011	0.049
Male	Sub-Adult	0.712	0.049	0.714	0.011	0.050
Male	Prime-Adult	0.802	0.034	0.802	0.008	0.034
Male	Older-Adult	0.624	0.073	0.617	0.015	0.074

APPENDIX B
FINE SCALE ANCESTRY EFFECTS ON SUB-ADULT AND ADULT SURVIVAL

Methods

In order to investigate potential variation in survival across ancestry categories based on finer-scale genotypic distinctions than those used in the body of the paper, we placed individuals from our radio-collared sample into 7 categories: canonical Florida panthers ($n = 40$), Everglades panther ($n = 1$), F_1 admixed panthers ($n = 8$), backcrossed to canonical admixed panthers ($n = 16$), backcrossed to Everglades admixed panthers ($n = 4$), backcrossed to Texas admixed panthers ($n = 14$), and unknown admixed panthers ($n = 15$). We assigned individuals to these categories using pedigree analysis and results of Structure analysis of microsatellite allele distributions. Canonical Florida panthers showed no evidence of non-Florida genetic admixture (no direct non-canonical relatives or $< 10\%$ non-canonical genetic contribution based on Structure analyses). Everglades panthers were mostly captured within or adjacent to ENP and had documented genetic links to Central America (O'Brien et al. 1990, Culver et al. 2000). Note that canonical and Everglades panthers were combined into 1 category (pre-introgression type panthers) for the ancestry analysis in body of the paper which represents the known genotypes present on the south Florida landscape prior to the introgression program. F_1 admixed panthers were defined previously in body of the paper. Backcrossed to Texas admixed panthers were admixed panthers of predominantly ($>50\%$) Texas heritage resulting from admixed panthers breeding with introduced Texas cougars. Backcrossed to canonical panthers were admixed panthers with predominantly ($>50\%$) canonical heritage. Backcrossed to Everglades were admixed panthers with predominantly ($>50\%$) Everglades heritage resulting from

breeding events between Texas admixed and Everglades panthers. Unknown admixed panthers were excluded because we were missing information that precluded placing them into the finer admixture categories (e.g., 1 or both parents were not identified). Note that backcrossed to Texas, backcrossed to canonical, backcrossed to Everglades, and unknown admixed were all combined into the other admixed category in the ancestry analysis in the body of the paper.

We used ancestry models (GenAnc1 – GenAnc6; Table B-1) with different combinations of ancestry categories to test specific hypotheses. We combined these 6 models with the effects of sex, age-class (sub-adult and prime-adult; Age3), and heterozygosity. Other than the unknown admixed exclusions and the different ancestry models, this analysis was identical to the second analysis described in the methods of the main text.

Results

There was again strong evidence that genetic ancestry influenced survival as the top 3 models ($\Delta AIC \leq 0.94$) included an ancestry variable, and the sum of the weights of models including ancestry variables was 0.854 (Table B-2). As in our main ancestry analysis, the evidence indicated that ancestry influenced survival through higher F_1 survival (ancestry models GenAnc4 and GenAnc6; sum of weights = 0.653), whereas models suggesting differences between survival of canonical and backcrossed panthers (GenAnc1-5) or between different classes of backcrossed panthers (GenAnc2, GenAnc3, and GenAnc5) had less empirical support (sum of weights = 0.394 and 0.113, respectively; Table B-2; Figure B-1). The evidence that higher heterozygosity positively influenced sub-adult and prime-adult survival remained strong (Table B-2; Figure B-1). Although model-averaged survival was similar for canonical, backcrossed to canonical,

and backcrossed to Texas panthers at a given level of heterozygosity, mean heterozygosity was highest for backcrossed to Texas individuals, leading to an increased probability of survival, and lowest for canonical panthers, leading to a decreased probability of survival (Figure B-1).

Table B-1. Definitions of ancestry models, and the hypotheses they represent.

Term	Definition	Hypothesis
GenAnc1	2 ancestry categories: 1) Canonical and Everglades; 2) Backcrossed to Canonical, Backcrossed to Everglades, Backcrossed to Texas, and F_1 .	General introgression advantage (or disadvantage).
GenAnc2	2 ancestry categories: 1) Canonical and Backcrossed to Canonical; 2) Everglades, Backcrossed to Everglades, Backcrossed to Texas, and F_1 .	General admixture advantage (or disadvantage), but with Backcrossed to Canonical reverting to Canonical.
GenAnc3	2 ancestry categories: 1) Canonical, Everglades, Backcrossed to Canonical, and Backcrossed to Everglades; 2) Backcrossed to Texas, and F_1 .	Survival advantage (or disadvantage) for those $\geq 50\%$ Texas.
GenAnc4	3 ancestry categories: 1) Canonical and Everglades; 2) Backcrossed to Canonical, Backcrossed to Everglades, and Backcrossed to Texas; and 3) F_1 .	Differences in survival between pre-introgression types, backcrosses, and F_1 's.
GenAnc5	3 ancestry categories: 1) Canonical and Everglades; 2) Backcrossed to Canonical and Backcrossed to Everglades; 3) Backcrossed to Texas and F_1 .	Differences in survival between pre-introgression types, $\geq 50\%$ Texas, and intermediate types.
GenAnc6	2 ancestry categories: 1) Canonical, Everglades, Backcrossed to Canonical, Backcrossed to Everglades, and Backcrossed to Texas; and 2) F_1 .	Survival advantage (or disadvantage) for F_1 's.

Table B-2. Akaike's Information Criteria (AIC) model comparison results showing all models for the effects of ancestry, heterozygosity, sex, and age class on adult Florida panther survival. For each model, we show the number of parameters, Akaike differences (ΔAIC), and the Akaike weight (w_i). The ancestry categories (GenAnc1 – GenAnc6) are defined in Table B-1. This analysis was restricted to sub-adults and prime-adults that were of known ancestry and to the years 1997 - 2006.

Model	Parameters	ΔAIC	w_i
Sex * Age3 ^a + GenAnc6 + Het ^b	5	0.00	0.148
Sex + GenAnc6 + Het	3	0.54	0.113
GenAnc6 + Het	2	0.94	0.093
Sex * Age3 + Het	4	1.77	0.061
Sex * Age3 + GenAnc4 + Het	6	2.00	0.055
Sex * Age3 + GenAnc6	4	2.01	0.054
Sex + Het	2	2.42	0.044
Sex + GenAnc4 + Het	4	2.49	0.043
Het	1	2.68	0.039
Sex + GenAnc6	2	2.75	0.037
GenAnc4 + Het	3	2.93	0.034
Sex * Age3 + GenAnc4	5	3.05	0.032
Sex * Age3 + GenAnc3 + Het	5	3.73	0.023
Sex * Age3 + GenAnc1 + Het	5	3.74	0.023
Sex * Age3 + GenAnc2 + Het	5	3.77	0.023
Sex + GenAnc4	3	4.01	0.020
Sex + GenAnc3 + Het	3	4.39	0.016
Sex + GenAnc2 + Het	3	4.42	0.016
Sex + GenAnc1 + Het	3	4.42	0.016
GenAnc3 + Het	2	4.66	0.014
GenAnc1 + Het	2	4.66	0.014
GenAnc2 + Het	2	4.68	0.014
GenAnc6	1	4.80	0.013
GenAnc4	2	5.53	0.009
Sex * Age3 + GenAnc5 + Het	6	5.65	0.009
Sex + GenAnc5 + Het	4	6.39	0.006
GenAnc5 + Het	3	6.61	0.005
Sex * Age3 + GenAnc2	4	7.13	0.004
Sex * Age3 + GenAnc1	4	7.33	0.004
Sex + GenAnc2	2	8.43	0.002
Sex * Age3 + GenAnc3	4	8.67	0.002
Sex + GenAnc1	2	9.07	0.002
Sex * Age3 + GenAnc5	5	9.12	0.002
GenAnc2	1	9.43	0.001
Sex * Age3	3	9.54	0.001

Sex + GenAnc3	2	9.59	0.001
Sex + GenAnc5	3	10.58	0.001
GenAnc1	1	10.81	0.001
Sex	1	10.97	0.001
GenAnc3	1	11.38	0.001
GenAnc5	2	12.12	0.000
Constant	0	14.09	0.000

^a Age3 differentiates sub-adult and prime-adult panthers.

^b The predictor variable Het refers to heterozygosity.

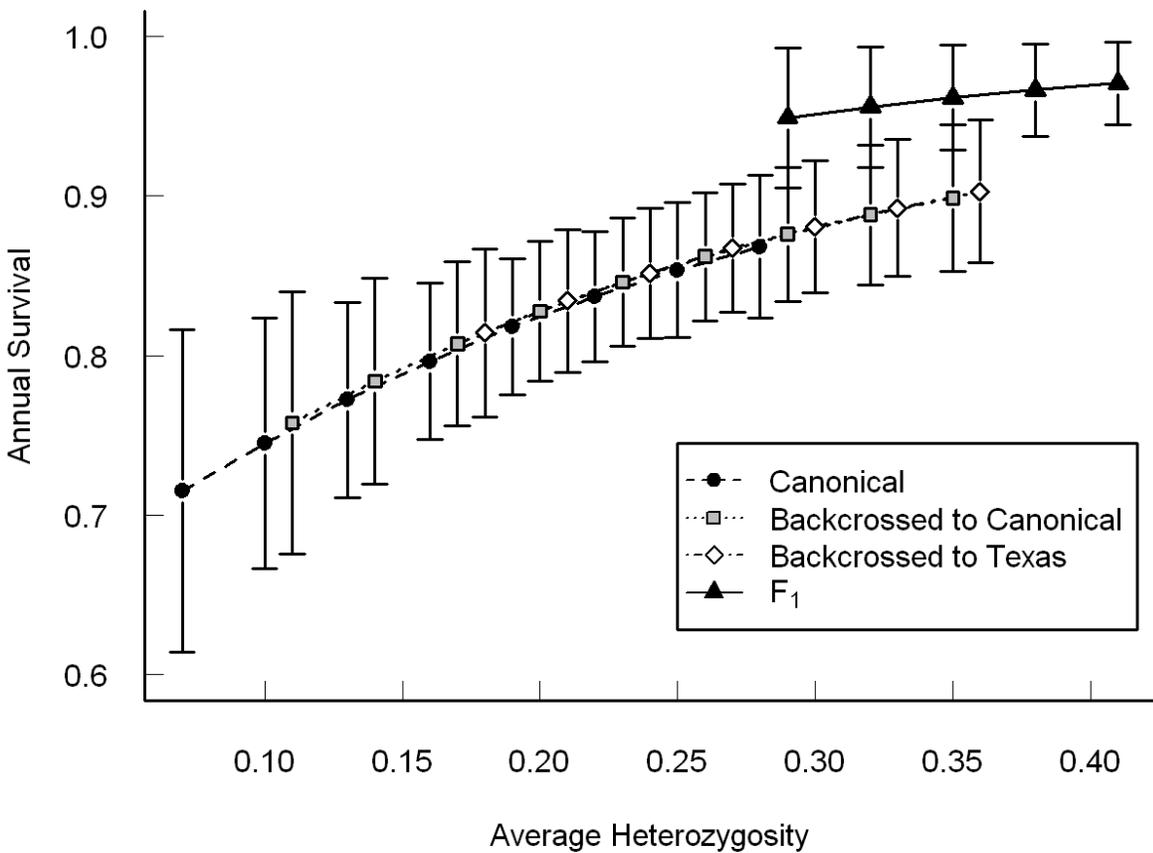


Figure B-1. Model averaged effects of complex ancestry and heterozygosity on annual survival of female prime-adult Florida panthers from 1997-2006. Panthers with Everglades and backcrossed to Everglades ancestries were included in the analysis but are not presented here; unknown admixed panthers were excluded from this analysis. The range of heterozygosity values presented for each ancestry category roughly corresponds to those found in the dataset (all panthers with that ancestry in the genetics analysis). Error bars represent unconditional standard errors.

APPENDIX C CAUSE-SPECIFIC MORTALITY ANALYSIS

Materials and Methods

We attributed mortality of radio-collared panthers to 1 of 4 causes: 1) hit by vehicle, 2) intraspecific aggression, 3) other (included known causes of death such as disease, heart failure, and infections unrelated to intraspecific aggression), and 4) unknown (mortalities for which evidence from field and necropsy examinations was insufficient to assign cause of death). We estimated cause-specific annual mortality rates for Florida panthers overall and within categories (sex, age class within sex, and ancestry within sex), using the nonparametric cumulative incidence function estimator (NPCIFE; Heisey and Patterson 2006). The NPCIFE is a generalization of the staggered-entry Kaplan-Meier method of survival estimation (Pollock et al., 1989). All cause-specific mortality analyses were performed using SPLUS code from Heisey and Patterson (2006) which we modified for use in R.

We tested for effects of covariates (sex, age-class, ancestry, and average heterozygosity) on cause-specific mortality rates, using the same subsets of the data used for survival analyses. We ran a Cox proportional-hazard regression for each covariate, stratified by the cause of death (Heisey and Patterson, 2006). We identified covariates that had significant (at $\alpha = 0.05$) and marginally significant (at $\alpha = 0.10$) effects on cause-specific mortality rates. We compared cause-specific mortality of sub-adults to that of prime-adults and cause-specific mortality of older-adults to that of prime-adults for each sex, as well as older-adults to prime-adults for the sexes combined. For ancestry, we compared cause-specific mortality of all admixed panthers (F_1 and other admixed were combined due to small sample sizes) to that of pre-

introgression types within each sex and for the sexes combined. We also present risk ratios for significant effects of covariates where cause-specific mortality rates were not estimated. For heterozygosity (the only continuous covariate), these were scaled as the proportional increases in instantaneous hazard from a cause with an increase of 0.1 in the covariate level (e.g., a change from heterozygosity of 0.2 to 0.3).

Results

The greatest cause of mortality for radio-collared Florida panthers was intraspecific aggression (0.078, SE = 0.013, 39 deaths), followed by mortality from unknown causes (0.043, SE = 0.010, 22 deaths), vehicles (0.036, SE = 0.008, 18 deaths), and other (0.027, SE = 0.008, 14 deaths). Mortality was higher from all causes for males than for females (Figure C-1A), but only significantly so for intraspecific aggression ($z = -2.823$, $p = 0.005$). We were unable to compare mortality rates for sub-adult and prime-adult females due to the low number of deaths in the former. Older-adult males had significantly higher ($z = 2.867$, $p = 0.004$) and sub-adult males had marginally higher ($z = 1.866$, $p = 0.062$) mortality due to intraspecific aggression than prime-adult males (Figure C-1C). Older-adult males had no recorded deaths from “other”; this difference was highly significant ($z = -25.430$, $p < 2e-16$). Other differences in mortality rates among age classes within sexes were not significant (Figure C-1B and C). When sexes were combined, older-adults had higher mortality due to intraspecific aggression than prime-adults ($z = 2.990$, $p = 0.003$, risk ratio = 2.99).

Female pre-introgression type panthers had a higher level of mortality due to all causes compared to female admixed panthers, but not significantly for any cause (Figure C-1D). Male pre-introgression type panthers had no mortality due to other, which was highly significant ($z = -21.861$, $p < 2e-16$, Figure C-1E). When sexes were

combined, pre-introgression type panthers had a higher level of mortality due to intraspecific aggression than admixed panthers ($z = 2.404$, $p = 0.016$, risk ratio = 3.06). The effect of heterozygosity was significant for intraspecific aggression ($z = -2.943$, $p = 0.003$, risk ratio = 0.480), with the risk declining with increased heterozygosity.

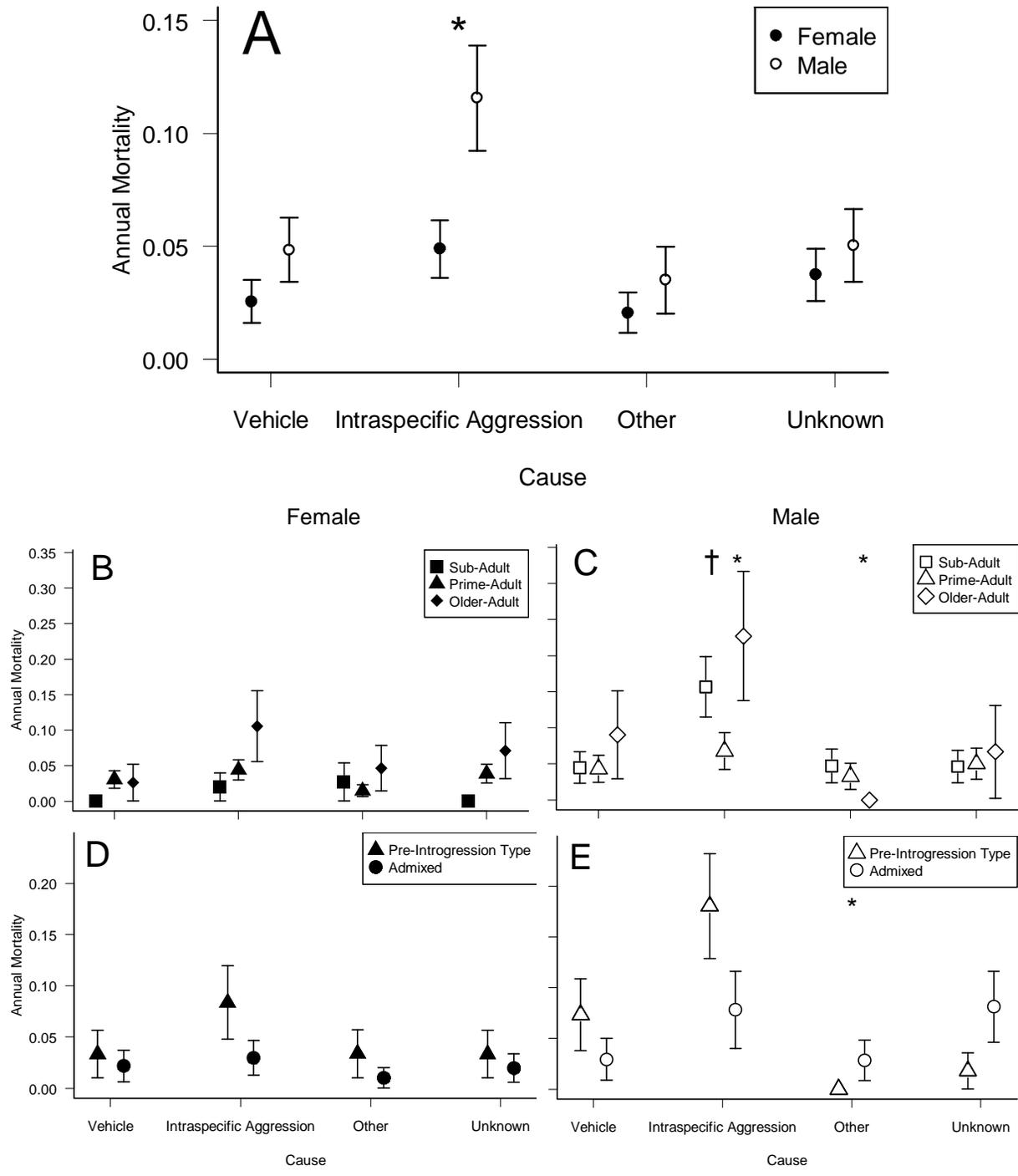


Figure C-1. Cause specific mortality rates (with standard errors). A) By sex. B) By age class within females. C) By age class within males. D) By ancestry within females. E) By ancestry with males. For age class within each sex, older-adult mortality rates for each cause were compared against prime-adult rates. In addition, sub-adult male rates were compared against prime-adult male rates. For ancestry within each sex, pre-introgression panthers were compared with all admixed panthers. Significant comparison results at $\alpha = 0.10$ are indicated by †, and at $\alpha = 0.05$ by an asterisk (*).

Appendix D
INFERENCE RESULTS FOR ANCESTRY AND HETEROZYGOSITY

Materials and Methods

We present the full AIC table for ancestry and heterozygosity (this was limited to top models in the main text due to space limitations) and selected Cox model coefficients for the genetic comparisons. Along with the Cox model coefficient estimates, we present uncorrected and robust standard error estimates, test results for differences between the coefficients and 0 (Wald/Z-tests calculated using the robust standard errors), and the associated p-values. Testing whether a categorical covariate's coefficient (for log hazard) is different from 0 is mostly equivalent to testing whether the survival rates for the two categories are different from each other, but allows a single test of that covariate in a model that contains other covariates (e.g., sex and age).

Results

The full AIC table for the genetic comparisons is found in Table D-1. Cox model genetic coefficients for all models containing the sex and age class interaction and at least one genetic covariate are found in Table D-2. The F_1 effect was statistically significant when considered in isolation of heterozygosity ($p = 0.048$ for Sex * Age3 + Ancest1 model [difference between F_1 and other admixed panthers] and $p = 0.031$ for Sex * Age3 + Ancest2 model [difference between F_1 and all other panthers]). The heterozygosity effect was statistically significant when considered in isolation of ancestry ($p = 0.022$ for Sex * Age3 + Het model). In contrast, the pre-introgression type effect was not significant (when compared with either other admixed panthers or all other panthers). These results indicate that F_1 admixed panthers survived significantly

better than either pre-introgression type or other admixed panthers, but that there were not significant differences in survival between pre-introgression type and other admixed panthers. When sex, age class, ancestry, and heterozygosity were included in the same model, neither ancestry nor heterozygosity was significant, likely due to these 2 factors confounding one another (Table D-2).

Table D-1. Full AIC table for ancestry and heterozygosity. Model comparison results showing all models for the effects of ancestry, heterozygosity, sex, and age class (sub-adults and prime-adults only) on Florida panther survival during 1997 – 2006. For each model, we present the number of parameters, Δ AIC (difference in Akaike’s Information Criterion), and the Akaike weight (w_i).

Model	Parameters	Δ AIC	w_i
1. Sex * Age3 ^a + Ancest2 ^b + Het ^c	5	0.00	0.244
2. Sex * Age3 + Ancest2	4	0.23	0.217
3. Sex * Age3 + Ancest1 ^d	5	1.35	0.124
4. Sex * Age3 + Ancest1 + Het	6	1.98	0.090
5. Sex + Ancest2 + Het	3	2.77	0.061
6. Sex + Ancest2	2	2.98	0.055
7. Sex * Age3 + Het	4	3.09	0.052
8. Sex + Ancest1	3	4.54	0.025
9. Ancest2 + Het	2	4.69	0.023
10. Sex + Ancest1 + Het	4	4.73	0.023
11. Sex * Age3 + Ancest3 ^e + Het	5	4.99	0.020
12. Ancest2	1	5.99	0.012
13. Sex * Age3 + Ancest3	4	6.13	0.011
14. Sex + Het	2	6.38	0.010
15. Ancest1 + Het	3	6.68	0.009
16. Ancest1	2	7.23	0.007
17. Sex * Age3	3	7.61	0.005
18. Het	1	8.36	0.004
19. Sex + Ancest3 + Het	3	8.38	0.004
20. Ancest3 + Het	2	10.35	0.001
21. Sex + Ancest3	2	10.72	0.001
22. Sex	1	11.50	0.001
23. Ancest3	1	14.03	0.000
24. Constant	0	15.84	0.000

^a Age3 differentiates sub-adult (age 1-2.5 for females and 1-3.5 for males) and prime-adult (ages 2.5-10 for females and 3.5-10 for males) panthers.

^b Ancest2 divides panthers into two ancestry categories: F₁ admixed, and other admixed and pre-introgression type combined.

^c Het refers to individual average heterozygosity.

^d Ancest1 divides panthers into three ancestry categories: F₁ admixed, other admixed, and pre-introgression type.

^e Ancest3 divides panthers into two ancestry categories: F₁ admixed and other admixed combined, and pre-introgression type.

Table D-2. Genetic coefficients from all models including sex and age class and at least one genetic covariate. We present the survival model, the genetic covariate, the regression coefficient associated with that covariate (β), the uncorrected and robust (or “sandwich”) standard errors for the coefficient, the z-score, and the associated p value. β values are on the log-hazard scale; a negative β indicates a reduction in hazard (and increase in survival) for an increase in a continuous covariate or the given level of a categorical covariate.

Model	Covariate	β	Uncorr . SE	Robust SE	z	p
Sex * Age3 ^a + Ancest1 ^b	Ancest1: PIT ^c	0.28	0.30	0.29	0.96	0.337
Sex * Age3 + Ancest1	Ancest1: F1 ^d	-1.98	1.03	1.00	-1.98	0.048
Sex * Age3 + Ancest2 ^e	Ancest2: F1	-2.14	1.01	0.99	-2.16	0.031
Sex * Age3 + Ancest3 ^f	Ancest3: PIT	0.55	0.30	0.30	1.84	0.065
Sex * Age3 + Het ^g	Het	-4.40	1.74	1.92	-2.29	0.022
Sex * Age3 + Ancest1 + Het	Ancest1: PIT	0.04	0.37	0.34	0.13	0.895
Sex * Age3 + Ancest1 + Het	Ancest1: F1	-1.80	1.04	1.01	-1.78	0.075
Sex * Age3 + Ancest1 + Het	Het	-2.61	2.25	2.33	-1.12	0.263
Sex * Age3 + Ancest2 + Het	Ancest2: F1	-1.81	1.04	1.01	-1.79	0.074
Sex * Age3 + Ancest2 + Het	Het	-2.76	1.86	2.01	-1.38	0.168
Sex * Age3 + Ancest3 + Het	Ancest3: PIT	0.12	0.38	0.36	0.33	0.740
Sex * Age3 + Ancest3 + Het	Het	-3.96	2.25	2.34	-1.69	0.091

^a Age3 differentiates sub-adult (age 1-2.5 for females and 1-3.5 for males) and prime-adult (ages 2.5-10 for females and 3.5-10 for males) panthers.

^b Ancest1 divides panthers into three ancestry categories: F₁ admixed, other admixed, and pre-introgression type.

^c The covariate PIT indicates a difference in log hazard for pre-introgression type panthers, compared with other admixed (Ancest1) or all other panthers (Ancest3).

^d The covariate F1 indicates a difference in log hazard for F₁ admixed panthers, compared with other admixed (Ancest1) or all other panthers (Ancest2).

^e Ancest2 divides panthers into two ancestry categories: F₁ admixed, and other admixed and pre-introgression type combined.

^f Ancest3 divides panthers into two ancestry categories: F₁ admixed and other admixed combined, and pre-introgression type.

^g Het refers to individual average heterozygosity.

Appendix E
ANALYSIS OF FLORIDA PANTHER KITTEN SURVIVAL BASED ON 3 ANCESTRY
CATEGORIES

Materials and Methods

We used results from the STRUCTURE analysis along with pedigree results and field evidence to assign panthers to 3 groups that reflect the genetic makeup of the southern Florida population (canonical panthers, F_1 admixed panthers, and other admixed panthers). Canonical and F_1 admixed ancestry categories are defined in the main text. The other admixed category includes: backcrossed to canonical (admixed panthers with predominantly (>50%) canonical heritage); backcrossed to Everglades (admixed panthers with predominantly (>50%) Everglades heritage resulting from breeding events between Texas admixed and Everglades panthers); backcrossed to Texas (admixed panthers of predominantly (>50%) Texas heritage resulting from admixed panthers breeding with introduced Texas cougars); unknown admixed; and Seminole admixed panthers (these last two categories were not included in the analyses presented in the text). Based on these 3 ancestry categories, we formulated alternative hypotheses regarding the effect of ancestry on kitten survival (Table E-1).

We selected model 1 in Table 4 as the base model because this model had the lowest QAIC_c among candidate models (Table 4), and used model selection to draw inferences for hypotheses about the effects of ancestry on kitten survival (Table E-1). For these analyses, we used a subset of data collected between 1995 and 2008, due to the absence of admixed panthers in Florida before 1995. We tested for the effect of ancestry on survival of (1) kittens only; (2) sub-adult and adult panthers only; (3) kittens and older panthers considered separately; and (4) panthers of all ages. Based on previous results (Benson et al., in revision), however, we only considered 2 ancestry

categories for sub-adult and adult panthers (Ancest2; Table E-1). We report model-averaged annual estimates of kitten survival probability (Burnham and Anderson, 2002).

Results and Discussion

Three models (Base + k :Ancest1, Base + k :Ancest1 + $s&a$:Ancest2, and Base + k :Ancest2) failed to estimate a kitten survival parameter and were discarded. The most parsimonious model testing for the effect of simple ancestry on survival indicated that survival of panthers of all ages (including survival of kittens) was higher for F_1 admixed (Table E-2, model 1). Although this model differed from the model where ancestry only affects the survival of sub-adults and adults (model 3) by $\Delta QAIC_c < 2$, the 95% confidence interval for the slope parameter did not include zero ($\beta = 1.55$; 95% CI: 0.46 – 2.65) providing strong evidence of a difference between the survival of F_1 admixed and other panthers. Model-averaged estimated kitten survival increased from canonical to other admixed to F_1 admixed panthers (Figure E-1).

These results suggest that although there are subtle differences in survival of kittens with various genetic ancestries, the main difference is that between F_1 admixed kittens and those of all other ancestry categories. F_1 admixed kittens survived substantially better than kittens with other ancestry categories. This F_1 admixed kitten survival advantage was also found in the ancestry analysis presented in the text. One difference in that analysis is that we found that some of the other admixed categories (specifically backcrossed to Texas and possibly backcrossed to Everglades) also had higher survivals than the canonical kittens. We believe that those results represent real differences within the other admixed category, and are not an artifact of the exclusions required for that analysis.

Table E-1. Definitions of simple ancestry models, and the hypotheses they represent.

Term	Definition	Hypothesis
Ancest1	3 ancestry categories: 1) Canonical; 2) Other Admixed; and 3) F ₁ Admixed.	Different survival probability for each ancestry group.
Ancest2	2 ancestry categories: 1) Canonical and Other Admixed; and 2) F ₁ Admixed.	First generation survival advantage (or disadvantage).
Ancest3	2 ancestry categories: 1) Canonical; and 2) Other Admixed and F ₁ Admixed.	General admixed survival advantage (or disadvantage).

Table E-2. Model selection table for testing hypotheses regarding the effect of genetic ancestry on survival of kittens and older panthers based on 3 ancestry categories. These analyses were performed on a subset of the data (excluding panthers before 1995 and panthers of unknown ancestry). For each model, we present the number of parameters (K), the difference from the top model in Akaike's Information Criterion adjusted for small sample size and overdispersion (ΔQAIC_c), and the model QAIC_c weight. All models estimate constant recapture rates and recovery rates that differ between kittens and older panthers ($p(\cdot)r(k, s\&a)$). Model 1 in Table 2 was used as the base model for these analyses. Ancestry categories are defined in Table E-1.

Survival Model	K	ΔQAIC_c	Weight
1. Base + Ancest2	9	0.00	0.367
2. Base + Ancest1	10	1.15	0.207
3. Base + s&a:Ancest2	9	1.86	0.145
4. Base + k:Ancest2 + s&a:Ancest2	10	2.04	0.132
5. Base + k:Ancest3 + s&a:Ancest2	10	2.52	0.104
6. Base + Ancest3	9	5.81	0.020
7. Base	8	6.46	0.015
8. Base + k:Ancest3	9	6.91	0.012

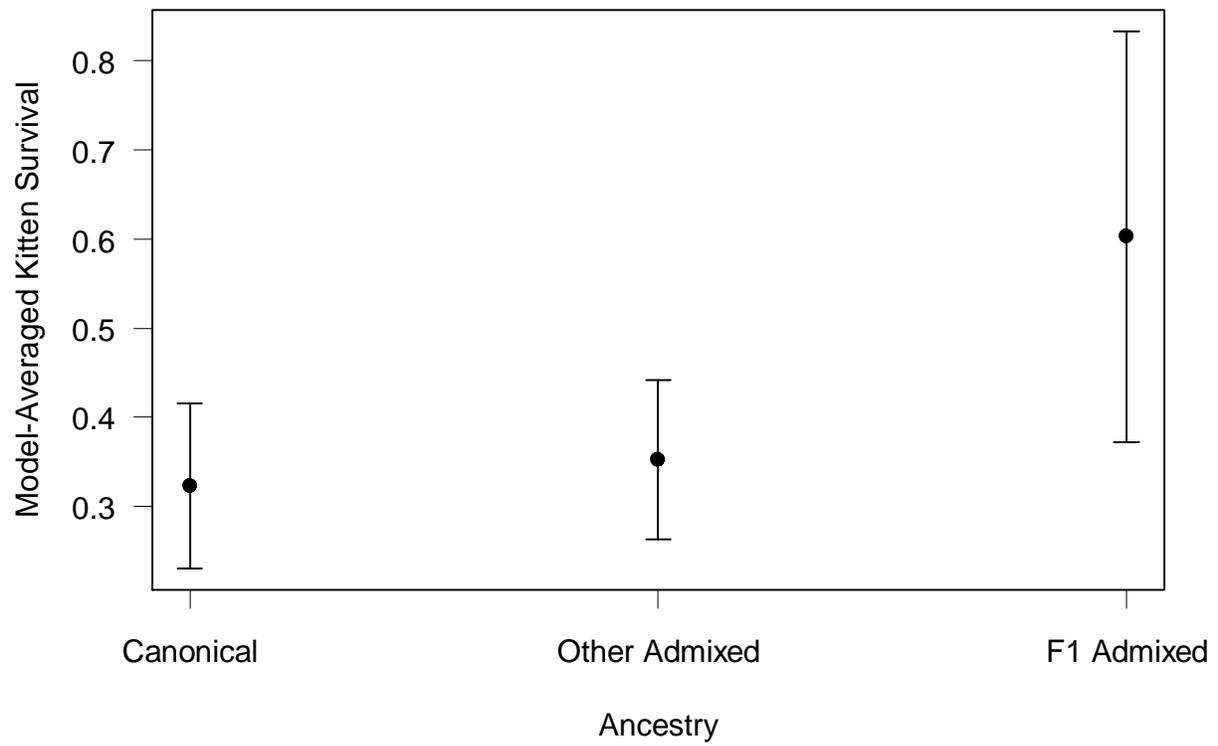


Figure E-1. Model-averaged estimates of annual survival of Florida panther kittens based on 3 ancestry categories (Table E-1). Error bars represent unconditional estimated standard errors.

APPENDIX F DATA PREPARATION

We used two datasets for the analysis of kitten survival. The first contained the capture (of live panthers) and recovery (of dead panthers) histories, observations of litter-failures (i.e., loss of entire litters), and radio-tracking data for panthers that were initially PIT-tagged in the den between June 1995 and May 2008 (13 years). The second contained the capture, recovery, and radio-tracking histories of all other panthers between June 1982 and May 2008 (26 years). We used a live-dead data input format (Cooch and White, 2008).

We coded the data with a 1-year time step. All litter failures were treated as recoveries within the first year, because all known litter failures occurred within the first year of kittens' lives (after which the kittens' fates were considered to be independent of their dams'). For panthers that were not PIT-tagged in the den, captures and radio-failures were coded as occurring on the closest June 1, and known deaths were coded as occurring in the June-May interval in which they occurred. PIT-tagging events of kittens in the den were also coded as occurring on the closest June 1. Subsequent captures, radio-failures, and known deaths of that group were coded to happen at the correct age, rather than the correct year, on the occasions when those were in conflict.

Panthers that would have died if we had not removed them to captivity were treated as having died on the date of removal. One exception was a panther whose injuries were apparently capture related; it was right-censored on the capture date and added again to the analysis on the date it was returned to the wild. Kittens that were found dead during the initial den visit ($n=7$) were not included in the survival analysis, but were included in the litter size counts of PIT-tagged kittens in their litters.

The ages of 91 radio-collared panthers not handled as kittens in the den were estimated as previously described; 11 were estimated to be < 1 year of age. When ages were estimated as a range in the field (e.g., 5-6 years old), we used the average of the range for assigning age class transitions. The influence of estimated age on the estimates of survival of adult panthers was insubstantial (Appendix A); this effect is likely even smaller for survival of kittens.

The sex of two kittens from a single litter was not recorded in the field; since their fates were the same and the overall numbers of kittens PIT-tagged for each sex were similar (119 females and 131 males), we randomly assigned one as a female and the other male. We did not have covariate data for all panthers included in the analyses. Thus, we tested for the effect of litter size and ancestry on survival separately after excluding kittens or all panthers, respectively, with missing values. For average heterozygosity, we ran a separate analysis excluding panthers that had not been genotyped, as well as captures of panthers that occurred before they were successfully genotyped. This approach removed the potential bias in survival estimates by heterozygosity that would be caused by only excluding those that were never genotyped (Nichols et al., 2004).

APPENDIX G
ANALYSIS OF SURVIVAL OF FLORIDA PANTHER KITTENS USING DATA
ORGANIZED IN 3-MONTH TIME STEPS

Materials and Methods

Using the data organized on an annual time scale, it was not possible to test for seasonal variation in kitten survival and changes in survival within the first year of life. Therefore, we recoded the data with 3-month time steps. This necessitated leaving out litter failure data, because the 3-month interval in which actual kitten deaths occurred was generally not available from these data. The large number of capture occasions ($26 \times 4 = 104$) made it computationally necessary to divide the sampling period in half. All data from panthers PIT tagged in the den were in the second half and could be handled normally, but all other panthers were only followed while radio-collared to accommodate the half transition. The analyses of data organized in 3-month time step also allowed us to compare sub-adult and adult survival with the results of Benson et al. (in revision), because we were now able to put the transition from sub-adult to adult at the same age as in their analyses (2.5 years old for females and 3.5 years old for males).

Analysis of the data with a 3-month time step was similar to the annual time step analysis, except that there was now a possibility of recapture as a kitten. We set recapture probability (p) and recovery probability (r) for radio-collared animals to 1, and p for 3-month old panthers to 0, because none of the few panthers captured and radio-collared at <6 months of age were PIT-tagged first. The FWC and National Park Service (NPS) instituted a policy in November 2001 restricting the capturing and radio-collaring of kittens < 12 months in age. Therefore we fixed p at 0 for 6-month old kittens starting at that date.

Data analysis proceeded as described in the text. We commenced by testing all *a priori* models for recapture and recovery combined with *a priori* models for survival of kittens based on age (Table G-1). The kittens of Texas cougars may have been more likely to be captured than other kittens, due to greater efforts expended to capture those kittens (model 1, Table G-1A). The justification for the separate recovery rate for kittens ≤ 3 months of age (models 4 and 5, Table G-1B) is that a different series of events leads to recovery of kittens in the den (approximately the first 7-8 weeks, Maehr et al., 1990) compared to older panthers. For a kitten in the den to be recovered, it has to be PIT-tagged, die, and then be found in a subsequent visit to the den. For an older (non-radio-collared) panther that was handled and marked with a PIT tag as a kitten to be recovered, it has to die (most likely due to a vehicle collision), and subsequently be reported to panther researchers. A cause-specific mortality analysis of radio-collared sub-adult and adult panthers suggests that the probability of a panther's death being due to vehicular collision is independent of sex or age class (Benson et al., in revision).

We tested all combinations of survival, recapture, and recovery models from Table G-1 and selected the most general model that converged successfully (if there was a tie, we selected the model with the lowest AIC_c). We used that model to test for overdispersion of the data due to lack of independence within litters using a data bootstrap (Bishop et al., 2008). We sampled litters from the dataset with replacement. Panthers first captured as sub-adults or adults were treated as litters of size 1 for the bootstrapping. We estimated annual survival of kittens as a derived parameter of the model. If the model failed to estimate any parameters, the iteration was discarded. We repeated the resampling and estimation until we had 1,000 estimates of kitten survival.

We calculated the mean and standard deviation of the estimates, and estimated the overdispersion parameter (\hat{c}) as [(bootstrap standard deviation of estimates of kitten survival) / (standard error of kitten survival obtained from the original model run)]². An estimated $\hat{c} > 1$ indicates overdispersion. We used the estimated \hat{c} to calculate the QAICc for each model and as a variance inflation factor.

We selected the model or set of models with the lowest QAIC_c as the base model(s) to test our hypothesis that kitten survival varies seasonally. We report model-specific and model-averaged 3-month and annual estimates of kitten survival probability and model-averaged estimates of recapture, recovery, and sub-adult and adult survival probabilities (Burnham and Anderson, 2002).

Results and Discussion

Of the 72 models run (all permutations from Table G-1), 14 failed to estimate all parameters and were discarded, including all models using survival model 7 (Table G-1C). From the most general models remaining (with 13 parameters), the model $S(k<3, 3\leq k<9, k\geq 9) p(k:DO, s\&a) r(k<3, k\geq 3, s\&a)$ had the lowest AIC_c and was used in the litter bootstrap to estimate \hat{c} . We estimated \hat{c} at 2.20, which is only slightly less than the average litter size of PIT tagged kittens used in the analysis (mean litter size = 2.47).

There was strong support for kitten survival being lowest in the first 3 months of life (Table G-2; main text Figure 1). Several closely ranked models yielded very different estimates of annual kitten survival, and variances of most estimates were substantial (Table G-2, Figure G-1). These results suggest that estimates of kitten survival obtained from data organized in 3 month-time steps lacked precision and robustness, most likely due to sample size limitations. Among the top models, the main

factor that affected estimated kitten survival was whether recovery of dead panthers differed between kittens in the first 3 months of life and other panthers (low estimates of survival, about 0.33) or not (high estimates of survival, about 0.50). The model-averaged estimate of annual kitten survival from the 3-month analysis was 0.404 (95% CI: 0.169 – 0.693). The uncertainty of this estimate was high due to 1) small sample sizes and uncertainty about the fates of individual kittens leading to large standard errors for estimates from individual models; 2) further increase of these standard errors by the variance inflation factor, to account for overdispersion; and 3) different models often producing very different estimates of kitten survival, and the unconditional confidence interval presented here incorporates that uncertainty.

Estimated annual survival rates of sub-adults and adults were fairly consistent among models and the model-averaged estimates were similar to those from the corresponding model in Benson et al. (in revision; Table G-3). The slightly lower estimate of sub-adult female survival may be in part due to a death of a female panther near her estimated 1st birthday that was categorized as a sub-adult in the kitten analysis and as a kitten in the adult analysis.

We selected two highly ranked models with differing estimates of kitten survival (models 1 & 2, Table G-2) as base models for testing the effects of season on kitten survival. There was no evidence of an effect of season on kitten survival (Table G-4).

Table G-1. A priori models used for the 3-month time step analysis. A) Models for recapture probability (p). B) Models for recovery probability (r). C) Models for survival probability (age models only; S). All combinations of p , r , and S models in this table were run. We also tested for the effect of season (wet vs. dry) on S , using the top model(s) from this analysis. For all models, p and r were fixed at 1 for radio-collared panthers. We fixed p at 0 for kittens younger than 6 months old and for kittens younger than 9 months old after November 2001 for all models. All models estimated non-kitten survival as the interaction of sex and age-class (sub-adult or adult); therefore, we only describe how kitten survival was modeled.

A) Model for p	Description
1. $p(k:DO, s\&a)$	Recapture probability differs between kittens and older panthers, and between kittens with dam origin of Florida and Texas.
2. $p(k, s\&a)$	Recapture probability differs between kittens and older panthers.
3. $p(.)$	Recapture probability is the same for all panthers.
B) Model for r	Description
4. $r(k<3, k\geq 3, s\&a)$	Recovery probability differs between kittens in their first three months, older kittens, and non-kittens.
5. $r(k<3, \geq 3)$	Recovery probability differs between kittens in their first three months and older panthers.
6. $r(.)$	Recovery probability the same for all panthers.
C) Model for S	Description
7. $S(k<3, 3\leq k<6, 6\leq k<9, k\geq 9)$	Age effect (survival differs between each of 4 3-month age intervals)
8. $S(k<6, 6\leq k<9, k\geq 9)$	Age effect (survival same for first two age intervals)
9. $S(k<3, 3\leq k<9, k\geq 9)$	Age effect (survival same for second two age intervals)
10. $S(k<6, k\geq 6)$	Age effect (survival same for first two age intervals, same for second two age intervals)
11. $S(k<3, k\geq 3)$	Age effect (survival same for last three age intervals)
12. $S(AT)$	Age trend (survival over the first 4 3-month intervals as a linear trend)
13. $S(.)$	Survival same for all kittens

Table G-2. Kitten survival models to examine the effects of age (3-month time step). For each model, we present the number of parameters (K), the difference from the top model in second-order Quasi-Akaike's Information Criterion (ΔQAIC_c), the model QAIC_c weight, and the estimate of annual kitten survival with standard error. See Table G-1 for descriptions of models. The base models selected are in bold.

Model	K	ΔQAIC_c	Weight	Annual Kitten Survival Estimate (SE)
1. $S(k<3, k\geq 3)p(k, s\&a)r(k<3, \geq 3)$	10	0	0.170	0.323 (0.090)
2. $S(k<3, k\geq 3)p(k, s\&a)r(.)$	9	1.170	0.095	0.508 (0.136)
3. $S(k<3, 3\leq k<9, k\geq 9)p(k, s\&a)r(k<3, \geq 3)$	11	1.361	0.086	0.326 (0.091)
4. $S(k<3, k\geq 3)p(k, s\&a)r(k<3, k\geq 3, s\&a)$	11	1.518	0.079	0.326 (0.092)
5. $S(\text{AT})p(k, s\&a)r(.)$	9	1.914	0.065	0.484 (0.133)
6. $S(k<3, k\geq 3)p(k:\text{DO}, s\&a)r(k<3, \geq 3)$	11	1.991	0.063	0.326 (0.093)
7. $S(k<3, 3\leq k<9, k\geq 9)p(k, s\&a)r(.)$	10	2.057	0.061	0.487 (0.133)
8. $S(k<3, k\geq 3)p(k:\text{DO}, s\&a)r(.)$	10	2.935	0.039	0.517 (0.136)
9. $S(k<3, 3\leq k<9, k\geq 9)p(k, s\&a)r(k<3, k\geq 3, s\&a)$	12	3.188	0.034	0.327 (0.093)
10. $S(k<3, 3\leq k<9, k\geq 9)p(k:\text{DO}, s\&a)r(k<3, \geq 3)$	12	3.354	0.032	0.329 (0.095)
11. $S(\text{AT})p(k, s\&a)r(k<3, \geq 3)$	10	3.454	0.030	0.399 (0.137)
12. $S(k<3, k\geq 3)p(k:\text{DO}, s\&a)r(k<3, k\geq 3, s\&a)$	12	3.512	0.029	0.329 (0.096)
13. $S(\text{AT})p(k:\text{DO}, s\&a)r(.)$	10	3.717	0.026	0.493 (0.134)
14. $S(k<3, 3\leq k<9, k\geq 9)p(k:\text{DO}, s\&a)r(.)$	11	3.863	0.025	0.496 (0.134)
15. $S(.)p(k, s\&a)r(k<3, \geq 3)$	9	4.42	0.019	0.770 (0.137)
16. $S(\text{AT})p(k, s\&a)r(k<3, k\geq 3, s\&a)$	11	4.58	0.018	0.355 (0.111)
17. $S(k<3, 3\leq k<9, k\geq 9)p(k:\text{DO}, s\&a)r(k<3, k\geq 3, s\&a)$	13	5.18	0.013	0.330 (0.097)
18. $S(\text{AT})p(k:\text{DO}, s\&a)r(k<3, \geq 3)$	11	5.36	0.012	0.411 (0.148)
19. $S(k<6, k\geq 6)p(k, s\&a)r(.)$	9	5.63	0.010	0.498 (0.138)
20. $S(k<6, 6\leq k<9, k\geq 9)p(k, s\&a)r(.)$	10	5.67	0.010	0.481 (0.133)
21. $S(.)p(k:\text{DO}, s\&a)r(k<3, \geq 3)$	10	5.98	0.009	0.775 (0.135)
22. $S(.)p(k, s\&a)r(k<3, k\geq 3, s\&a)$	10	6.43	0.007	0.781 (0.267)
23. $S(\text{AT})p(k:\text{DO}, s\&a)r(k<3, k\geq 3, s\&a)$	12	6.54	0.007	0.361 (0.118)
24. $S(.)p(k, s\&a)r(.)$	8	7.12	0.005	0.590 (0.129)
25. $S(k<6, 6\leq k<9, k\geq 9)p(k, s\&a)r(k<3, k\geq 3, s\&a)$	12	7.22	0.005	0.400 (0.154)
26. $S(k<6, k\geq 6)p(k:\text{DO}, s\&a)r(.)$	10	7.40	0.004	0.507 (0.139)
27. $S(k<6, 6\leq k<9, k\geq 9)p(k:\text{DO}, s\&a)r(.)$	11	7.49	0.004	0.490 (0.135)
28. $S(k<6, k\geq 6)p(k, s\&a)r(k<3, k\geq 3, s\&a)$	11	7.74	0.004	0.404 (0.163)
29. $S(k<3, k\geq 3)p(.)r(k<3, \geq 3)$	9	8.13	0.003	0.307 (0.076)
30. $S(.)p(k:\text{DO}, s\&a)r(.)$	9	8.79	0.002	0.595 (0.128)
31. $S(k<6, 6\leq k<9, k\geq 9)p(k:\text{DO}, s\&a)r(k<3, k\geq 3, s\&a)$	13	9.13	0.002	0.414 (0.172)
32. $S(k<3, 3\leq k<9, k\geq 9)p(.)r(k<3, \geq 3)$	10	9.62	0.001	0.308 (0.077)

33. $S(k < 6, k \geq 6)p(k:DO, s \& a)r(k < 3, k \geq 3, s \& a)$	12	9.62	0.001	0.422 (0.189)
34. $S(k < 3, k \geq 3)p(.)r(.)$	8	9.91	0.001	0.437 (0.118)
35. $S(k < 3, k \geq 3)p(.)r(k < 3, k \geq 3, s \& a)$	10	9.95	0.001	0.308 (0.077)
36. $S(AT)p(.)r(.)$	8	10.77	0.001	0.420 (0.113)
37. $S(k < 3, 3 \leq k < 9, k \geq 9)p(.)r(.)$	9	10.98	0.001	0.423 (0.113)
38. $S(k < 3, 3 \leq k < 9, k \geq 9)p(.)r(k < 3, k \geq 3, s \& a)$	11	11.57	0.001	0.308 (0.077)
39. $S(AT)p(.)r(k < 3, \geq 3)$	9	11.97	0.000	0.355 (0.101)
40. $S(AT)p(.)r(k < 3, k \geq 3, s \& a)$	10	12.59	0.000	0.326 (0.086)
41. $S(k < 6, k \geq 6)p(.)r(.)$	8	14.13	0.000	0.428 (0.117)
42. $S(.)p(.)r(k < 3, \geq 3)$	8	14.18	0.000	0.640 (0.184)
43. $S(k < 6, 6 \leq k < 9, k \geq 9)p(.)r(.)$	9	14.39	0.000	0.417 (0.112)
44. $S(.)p(.)r(k < 3, k \geq 3, s \& a)$	9	14.57	0.000	0.426 (0.144)
45. $S(k < 6, 6 \leq k < 9, k \geq 9)p(.)r(k < 3, k \geq 3, s \& a)$	11	14.99	0.000	0.350 (0.099)
46. $S(.)p(.)r(.)$	7	15.09	0.000	0.487 (0.125)
47. $S(k < 6, k \geq 6)p(.)r(k < 3, k \geq 3, s \& a)$	10	15.21	0.000	0.350 (0.101)
48. $S(k < 6, k \geq 6)p(.)r(k < 3, \geq 3)$	9	15.87	0.000	0.491 (0.218)
49. $S(k < 6, 6 \leq k < 9, k \geq 9)p(.)r(k < 3, \geq 3)$	10	16.01	0.000	0.488 (0.211)

Table G-3. Estimates of annual sub-adult and adult survival from the 3-month kitten survival analysis and the adult analysis of Chapter 2. Sub-adult is defined as ages 1-2.5 for females and 1-3.5 for males; adult is defined as ages 2.5 and up for females and 3.5 and up for males. The results from the kitten analysis are the model-averaged survivals from all models in the 3-month analysis; the results from the adult analysis are from the Sex * Age1 model (Chapter 2).

Sex	Age Class	Annual Survival Estimates (SE)	
		Kitten Analysis	Adult Analysis
Female	Sub-Adult	0.929 (0.051)	0.954 (0.032)
Female	Adult	0.858 (0.03)	0.852 (0.023)
Male	Sub-Adult	0.723 (0.066)	0.712 (0.05)
Male	Adult	0.774 (0.049)	0.782 (0.035)

Table G-4. Model comparison table for examining the effects of season on kitten survival. For each model, we present the number of parameters (K), the difference from the top model in second-order Quasi-Akaike's Information Criterion (ΔQAIC_c), the model QAIC_c weight, and the estimate of seasonal kitten survival with standard error. The same recapture model ($p(k, s\&a)$) was used in all models. See Table G-1 for descriptions of models.

Model	K	ΔQAIC_c	Weight	6-Month Kitten Survival	
				Wet Season	Dry Season
1. $S(k<3, k\geq 3)r(k<3, \geq 3)$	10	0.00	0.469		0.568 (0.079)
2. $S(k<3, k\geq 3)r(.)$	9	1.17	0.261		0.713 (0.096)
15. $S(k<3, k\geq 3 + \text{season})r(k<3, \geq 3)$	11	2.01	0.172	0.564 (0.102)	0.572 (0.093)
16. $S(k<3, k\geq 3 + \text{season})r(.)$	10	3.14	0.098	0.736 (0.144)	0.703 (0.107)

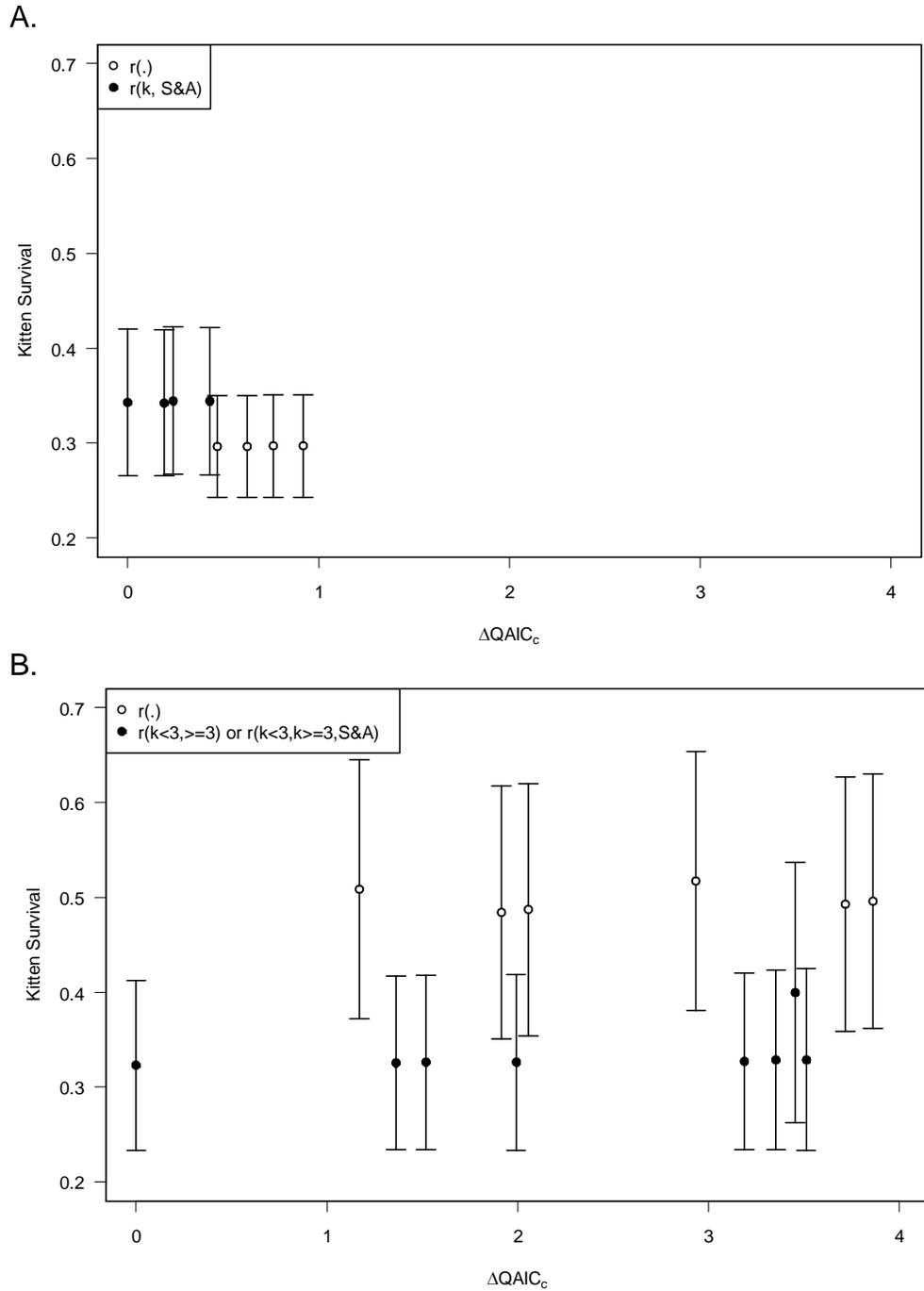


Figure G-1. Individual model estimates of annual kitten survival. A) Estimates from the 1-year time step analysis. B) Estimates from the 3-month time step analysis. All models are shown in A, whereas only top models (the difference from the top model in second-order Quasi-Akaike's Information Criterion or $\Delta QAIC_c < 4$) are plotted in B. Models are aligned by their $\Delta QAIC_c$ value on the x-axis. Error bars represent standard errors (adjusted by the variance inflation factor).

APPENDIX H INCLUDING ANOTHER BASE MODEL

Methods

To examine the effects of base model uncertainty on covariate testing, we ran all covariates with the highest ranked model from Table 3-2 that had a different estimate of kitten survival than the base model (this was model 5). This model (hereafter called Base2) modeled survival identically to the base model but estimated one recovery rate for all panthers instead of dividing it between kittens and older panthers. All covariate analyses were performed the same way as in the main text. We report full model average estimates based on all models run with both base models.

Results

All covariate models using Base2 could estimate all parameters. There was still no evidence that sex or litter size affected kitten survival (Table H-1). There was still considerable evidence that ancestry influenced kitten survival; the 7 most parsimonious models all included ancestry effects on kitten survival (models 1-7, Table H-2A). The top 2 models indicated that survival of kittens differed substantially between two ancestry categories: 1) canonical and backcrossed to canonical kittens and 2) F_1 , backcrossed to Texas, and backcrossed to Everglades kittens (Table H-2A). Full model-averaged kitten survival was lowest for canonical kittens and highest for F_1 kittens (Figure H-1A), and were slightly lower for all ancestry classes than model averages from the base model alone (Figure 3-1A).

The most parsimonious model testing for the effect of heterozygosity on survival indicated that survival of panthers of all ages (including survival of kittens) was

positively affected by average heterozygosity (Table H-2B, model 1). Full model-averaged estimated kitten survival increased with heterozygosity (Figure H-1B).

The evidence for the effect of abundance index on kitten survival was even stronger using Base2 (Table H-2C). Full model-averaged estimated kitten survival declined with abundance index (Figure H-2). We estimated temporal standard deviation of kitten survival (σ) at 0.199 (95% credible interval = 0.011 – 0.380) and 0.077 (95% credible interval = 0.003 – 0.234) using models without and with abundance index, respectively.

The most parsimonious model testing for the effect of simple ancestry on survival indicated that survival of panthers of all ages (including survival of kittens) was higher for F_1 admixed (Table H-3, model 1). Full model-averaged estimated kitten survivals increased from canonical to other admixed to F_1 admixed (Figure H-3), and were slightly lower for all ancestry classes than model averages from the base model alone (Figure E-1).

Interestingly, unconditional standard errors estimated for the full model set tended to be lower than those estimated for the base model set alone, even when the full model-averaged estimate was closer to 0.5.

Table H-1. Model selection table for sex and litter size effects on kitten survival, using Base2 model. A) Sex models. B) Litter size models. For each model, we present the number of parameters (K), the difference from the top model in Akaike's Information Criterion adjusted for overdispersion and small sample size (ΔQAIC_c), the model QAIC_c weight, and the estimates of annual kitten survival with standard error (for both sexes and the highest and lowest litter sizes). The QAIC_c values of the top models are 857.23 and 845.66, respectively (compare to QAIC_c values for the base models run with the same datasets of 856.76 and 845.64, respectively). See Table 3-1 for descriptions of the covariate models and Table 3-2 (model 5) for the Base2 model. The litter size analysis was performed on a subset of the data (excluding kittens from litters of unknown size). All models estimate constant recapture and recovery rates ($p(.)r(.)$).

A. Sex models				Annual Kitten Survival Estimate (SE)	
Survival Model	K	ΔQAIC_c	Weight	Female	Male
1. Base2	7	0.00	0.725	0.296 (0.054)	
2. Base2 + $k:\text{sex}$	8	1.94	0.275	0.311 (0.068)	0.282 (0.065)
B. Litter size models				Annual Kitten Survival Estimate (SE)	
Survival Model	K	ΔQAIC_c	Weight	1 kitten	4 kittens
1. Base2	7	0.00	0.735	0.280 (0.050)	
2. Base2 + $k:\text{LS}$	8	2.04	0.265	0.279 (0.109)	0.280 (0.081)

Table H-2. Model selection table for ancestry, heterozygosity, and abundance index effects on kitten survival, using Base2 model. A) Ancestry effects on kitten and older survival. B) Heterozygosity effects on kitten and older survival. C) Abundance index effects on kitten survival. These analyses were performed on subsets of the data (excluding panthers before 1995 for all analyses and panthers of unknown ancestry for A, and panthers before their heterozygosity was successfully sampled for B). For each model, we present the number of parameters (K), the difference from the top model in Akaike's Information Criterion adjusted for overdispersion and small sample size (ΔQAIC_c), and the model QAIC_c weight. The QAIC_c values of the top models are 623.98, 577.80, and 716.22, respectively (compare to QAIC_c values for the top models of Table 3 of 624.41, 577.37, and 716.46, respectively). See Table 1 for descriptions of the covariate models and Table 2 (model 5) for the Base2 model. All models estimate constant recapture and recovery rates ($p(\cdot)r(\cdot)$).

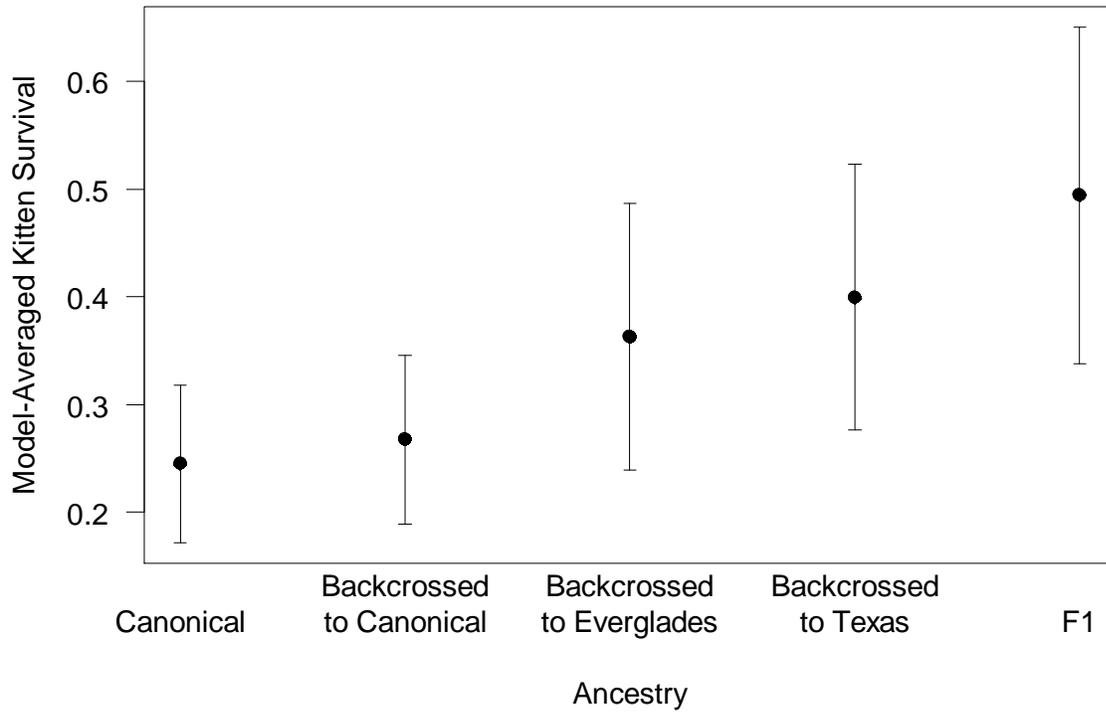
A. Ancestry models			
Survival Model	K	ΔQAIC_c	Weight
1. Base2 + $k:\text{GenAnc2}$ + $s\&a:\text{GenAnc6}$	9	0.00	0.232
2. Base2 + GenAnc2	8	1.18	0.128
3. Base2 + GenAnc6	8	1.35	0.118
4. Base2 + GenAnc4	9	1.83	0.093
5. Base2 + $k:\text{GenAnc3}$ + $s\&a:\text{GenAnc6}$	9	2.07	0.082
6. Base2 + $k:\text{GenAnc6}$ + $s\&a:\text{GenAnc6}$	9	3.20	0.047
7. Base2 + GenAnc3	8	3.21	0.047
8. Base2 + $s\&a:\text{GenAnc6}$	8	3.23	0.046
9. Base2 + $k:\text{GenAnc1}$ + $s\&a:\text{GenAnc6}$	9	3.71	0.036
10. Base2 + $k:\text{GenAnc5}$ + $s\&a:\text{GenAnc6}$	10	3.84	0.034
11. Base2 + $k:\text{GenAnc2}$	8	3.85	0.034
12. Base2 + $k:\text{GenAnc4}$ + $s\&a:\text{GenAnc6}$	10	4.29	0.027
13. Base2 + GenAnc5	9	4.69	0.022
14. Base2 + GenAnc1	8	5.55	0.014
15. Base2 + $k:\text{GenAnc3}$	8	5.94	0.012
16. Base2 + $k:\text{GenAnc6}$	8	6.44	0.009
17. Base2 + $k:\text{GenAnc4}$	9	7.53	0.005
18. Base2	7	7.54	0.005
19. Base2 + $k:\text{GenAnc5}$	9	7.72	0.005
20. Base2 + $k:\text{GenAnc1}$	8	7.93	0.004
B. Heterozygosity models			
Survival Model	K	ΔQAIC_c	Weight
1. Base2 + Het	8	0.00	0.320
2. Base2 + $s\&a:\text{Het}$	8	0.53	0.245
3. Base2	7	0.78	0.216
4. Base2 + $k:\text{Het}$ + $s\&a:\text{Het}$	9	2.07	0.114

5. Base2 + <i>k</i> :Het	8	2.22	0.105
C. Abundance index models			
Survival Model	K	Δ QAICc	Weight
1. Base2 + <i>k</i> :Abundance	8	0.00	0.992
2. Base2	7	9.65	0.008

Table H-3. Model selection table for three category ancestry effects on kitten and older survival, using the Base2 model. These analyses were performed on subsets of the data (excluding panthers before 1995 and panthers of unknown ancestry). For each model, we present the number of parameters (K), the difference from the top model in Akaike's Information Criterion adjusted for overdispersion and small sample size (ΔQAIC_c), and the model QAIC_c weight. The QAIC_c value of the top model is 716.21 (compare to QAIC_c value for the top model of Table A2 of 715.74). See Table A1 for descriptions of the covariate models and Table 2 (model 5) for the Base2 model. All models estimate constant recapture and recovery rates ($p(\cdot)r(\cdot)$).

Survival Model	K	ΔQAIC_c	Weight
1. Base2 + Ancest2	8	0.00	0.321
2. Base2 + Ancest1	9	1.04	0.191
3. Base2 + s&a:Ancest2	8	1.68	0.138
4. Base2 + k:Ancest2 + s&a:Ancest2	9	1.77	0.133
5. Base2 + k:Ancest3 + s&a:Ancest2	9	2.68	0.084
6. Base2 + k:Ancest1 + s&a:Ancest2	10	3.19	0.065
7. Base2 + k:Ancest2	8	5.50	0.020
8. Base2 + Ancest3	8	5.74	0.018
9. Base2	7	6.58	0.012
10. Base2 + k:Ancest1	9	6.92	0.010
11. Base2 + k:Ancest3	8	7.50	0.008

A.



B.

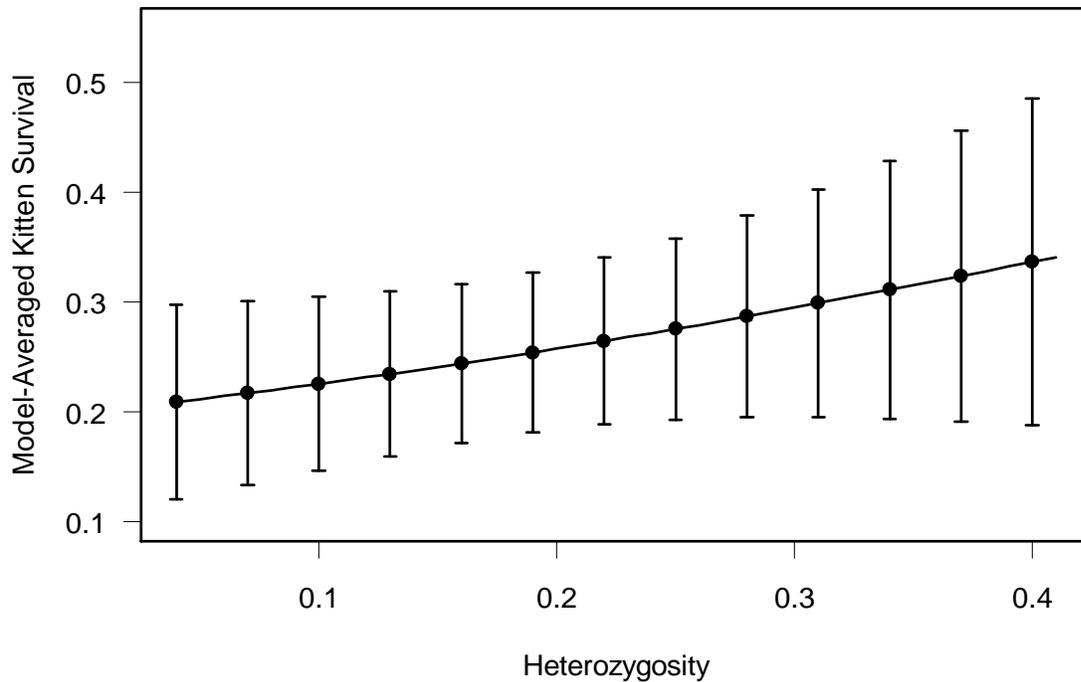


Figure H-1. The effect of genetic variables on model-averaged kitten survival estimates, including two different base models (Base and Base2). A) Annual survival plotted against ancestry category. B) Annual survival plotted against heterozygosity. Error bars represent unconditional estimated standard errors.

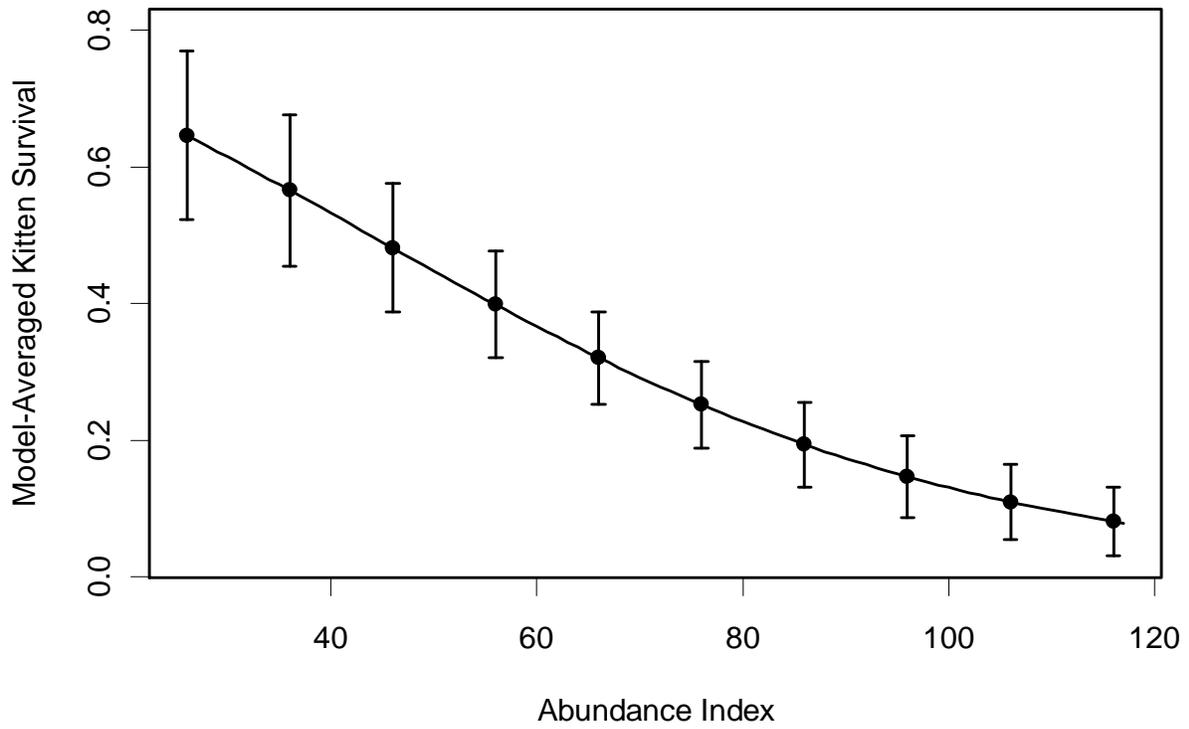


Figure H-2. The effect of a panther abundance index on model-averaged kitten survival estimates, including two different base models (Base and Base2). Error bars represent unconditional estimated standard errors.

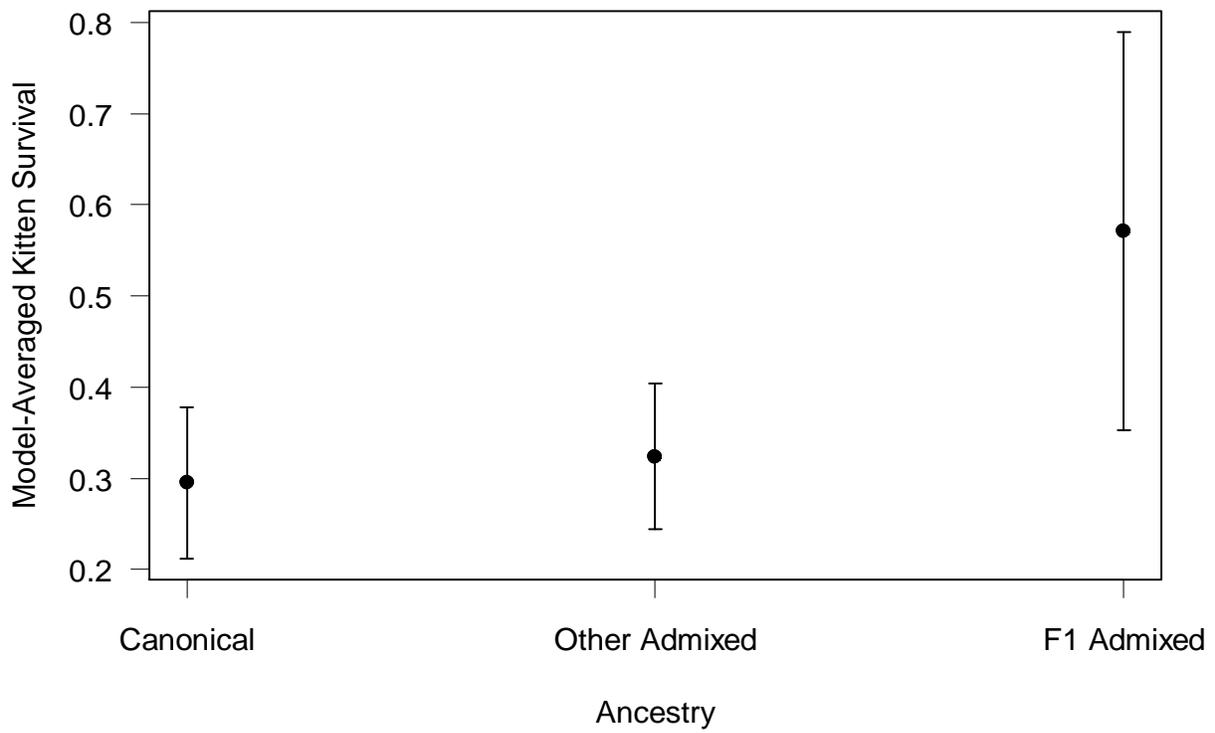


Figure H-3. Model-averaged estimates of annual survival of Florida panther kittens based on 3 ancestry categories, including two different base models (Base and Base2). Error bars represent unconditional estimated standard errors.

APPENDIX I
ANALYSIS OF THE INFLUENCE OF ANCESTRY USING FINE-SCALE ANCESTRY
TESTING

Methods

In order to investigate potential variation in reproductive rates across ancestry categories based on finer-scale genotypic distinctions than those used in the body of the paper, we placed females from our radio-collared sample into 7 categories: canonical Florida panthers ($n = 22$), Everglades panthers ($n = 2$), F₁ admixed panthers ($n = 6$), backcrossed to canonical admixed panthers ($n = 6$), backcrossed to Everglades admixed panthers ($n = 3$), backcrossed to Texas admixed panthers ($n = 11$), and unknown admixed panthers ($n = 8$). Canonical Florida panthers showed no evidence of non-Florida genetic admixture (no direct non-canonical relatives or < 10% non-canonical genetic contribution based on Structure analyses). Everglades panthers were mostly captured within or adjacent to Everglades National Park and had documented genetic links to Central America (Culver et al., 2000; O'Brien et al., 1990). Note that canonical and Everglades panthers were combined into 1 category (pre-introgression type panthers) for the ancestry analysis in the body of the paper which represents the known genotypes present on the south Florida landscape prior to the introgression program. We defined F₁ admixed panthers (as before) as any offspring produced by a mating between a Texas female and a pre-introgression type male. Backcrossed to Texas admixed panthers were admixed panthers whose admixture proportions from the Structure analysis were >50% Texas. Backcrossed to canonical panthers were admixed panthers whose admixture proportions were >50% but <90% canonical. Backcrossed to Everglades were admixed panthers were panthers with documented Texas admixture and admixture proportions of >50% Everglades. Unknown admixed

panthers were excluded (in addition to 1 unknown ancestry panther) because we were missing information needed to place them into the finer admixture categories (e.g., 1 or both parents were not identified). Note that backcrossed to Texas, backcrossed to Canonical, backcrossed to Everglades, and unknown admixed were all combined into the other admixed category in the ancestry analysis in the body of the paper.

We used ancestry models (GenAnc1 – GenAnc6; Table I-1) with different combinations of ancestry categories to test specific hypotheses. We used the minimum AIC model from the age and season analysis as a base model to test for the effects of ancestry on reproductive rates. We tested for the effects of ancestry on both p and μ , additively with the base models. Although panthers in six ancestry categories were used in the analysis, the sample sizes for Everglades and backcrossed to Everglades were quite small, so we only present model-averaged estimates for the other four ancestry categories.

Results and Discussion

The most parsimonious models for ancestry separated F_1 and backcrossed to Texas panthers from others for both probability of breeding and litter size (Model 1, Table I-2; Model 1, Table I-3). Model-averaged probability of breeding was highest for backcrossed to canonical panthers, intermediate for canonical panthers, and lowest for backcrossed to Texas and F_1 panthers (Figure I-1A). Model-averaged litter size was lowest for canonical panthers and highest for backcrossed to Texas and F_1 panthers, although these differences are less dramatic (Figure I-1B).

These results corroborate and extend the ancestry results from the main text. In addition to F_1 panthers, backcrossed to Texas panthers have lower probabilities of reproduction than canonical panthers. Two of the proposed explanations in the main

text discussion (outbreeding depression and increased kitten survival) are compatible with these results as well. The other explanation (chance) seems less likely, as the combined F_1 and backcrossed to Texas sample size ($n = 17$ panthers) is more substantial than the F_1 sample size alone ($n = 6$ panthers).

Table I-1. Definitions of complex ancestry models, and the hypotheses they represent.

Term	Definition	Hypothesis
GenAnc1	2 ancestry categories: 1) Canonical and Everglades; 2) Backcrossed to Canonical, Backcrossed to Everglades, Backcrossed to Texas, and F_1 .	General introgression advantage (or disadvantage).
GenAnc2	2 ancestry categories: 1) Canonical and Backcrossed to Canonical; 2) Everglades, Backcrossed to Everglades, Backcrossed to Texas, and F_1 .	General admixture advantage (or disadvantage), but with Backcrossed to Canonical reverting to Canonical.
GenAnc3	2 ancestry categories: 1) Canonical, Everglades, Backcrossed to Canonical, and Backcrossed to Everglades; 2) Backcrossed to Texas, and F_1 .	Reproduction advantage (or disadvantage) for those $\geq 50\%$ Texas.
GenAnc4	3 ancestry categories: 1) Canonical and Everglades; 2) Backcrossed to Canonical, Backcrossed to Everglades, and Backcrossed to Texas; and 3) F_1 .	Differences in reproduction between pre-introgression types, backcrosses, and F_1 's.
GenAnc5	3 ancestry categories: 1) Canonical and Everglades; 2) Backcrossed to Canonical and Backcrossed to Everglades; 3) Backcrossed to Texas and F_1 .	Differences in reproduction between pre-introgression types, $\geq 50\%$ Texas, and intermediate types.
GenAnc6	2 ancestry categories: 1) Canonical, Everglades, Backcrossed to Canonical, Backcrossed to Everglades, and Backcrossed to Texas; and 2) F_1 .	Reproduction advantage (or disadvantage) for F_1 's.

Table I-2. Model comparison table testing for the effects of complex ancestry (see Table I-1) on probability of breeding (p). The base model used was $p(\text{Age2} + \text{Season})$ (Age2 distinguishes between young adults and older-adults). For each model, we present the number of parameters (K), the difference in Akaike's Information Criterion (ΔAIC), and the Akaike weight (w_i). This analysis was performed on a subset of the data (excluding 1 panther with unknown ancestry and unknown admixed panthers).

Model	p	K	ΔAIC	w_i
1	Age2 + Season + GenAnc3	4	0.00	0.308
2	Age2 + Season + GenAnc5	5	0.51	0.239
3	Age2 + Season + GenAnc6	4	1.03	0.185
4	Age2 + Season + GenAnc2	4	1.43	0.151
5	Age2 + Season + GenAnc4	5	2.98	0.070
6	Age2 + Season	3	4.50	0.032
7	Age2 + Season + GenAnc1	4	6.05	0.015

Table I-3. Model comparison table testing for the effects of complex ancestry (see Table I-1) on litter size (μ). The base model used was $\mu(\text{Age3} + \text{Season})$ (Age3 divides panthers into sub-adults and adults). For each model, we present the number of parameters (K), the difference in Akaike's Information Criterion (ΔAIC), and the Akaike weight (w_i). This analysis was performed on a subset of the data (excluding unknown admixed panthers).

Model	μ	K	ΔAIC	w_i
1	Age3 + Season + GenAnc3	6	0.00	0.252
2	Age3 + Season	5	0.29	0.218
3	Age3 + Season + GenAnc1	6	0.60	0.187
4	Age3 + Season + GenAnc5	7	1.66	0.110
5	Age3 + Season + GenAnc6	6	2.29	0.080
6	Age3 + Season + GenAnc2	6	2.29	0.080
7	Age3 + Season + GenAnc4	7	2.50	0.072

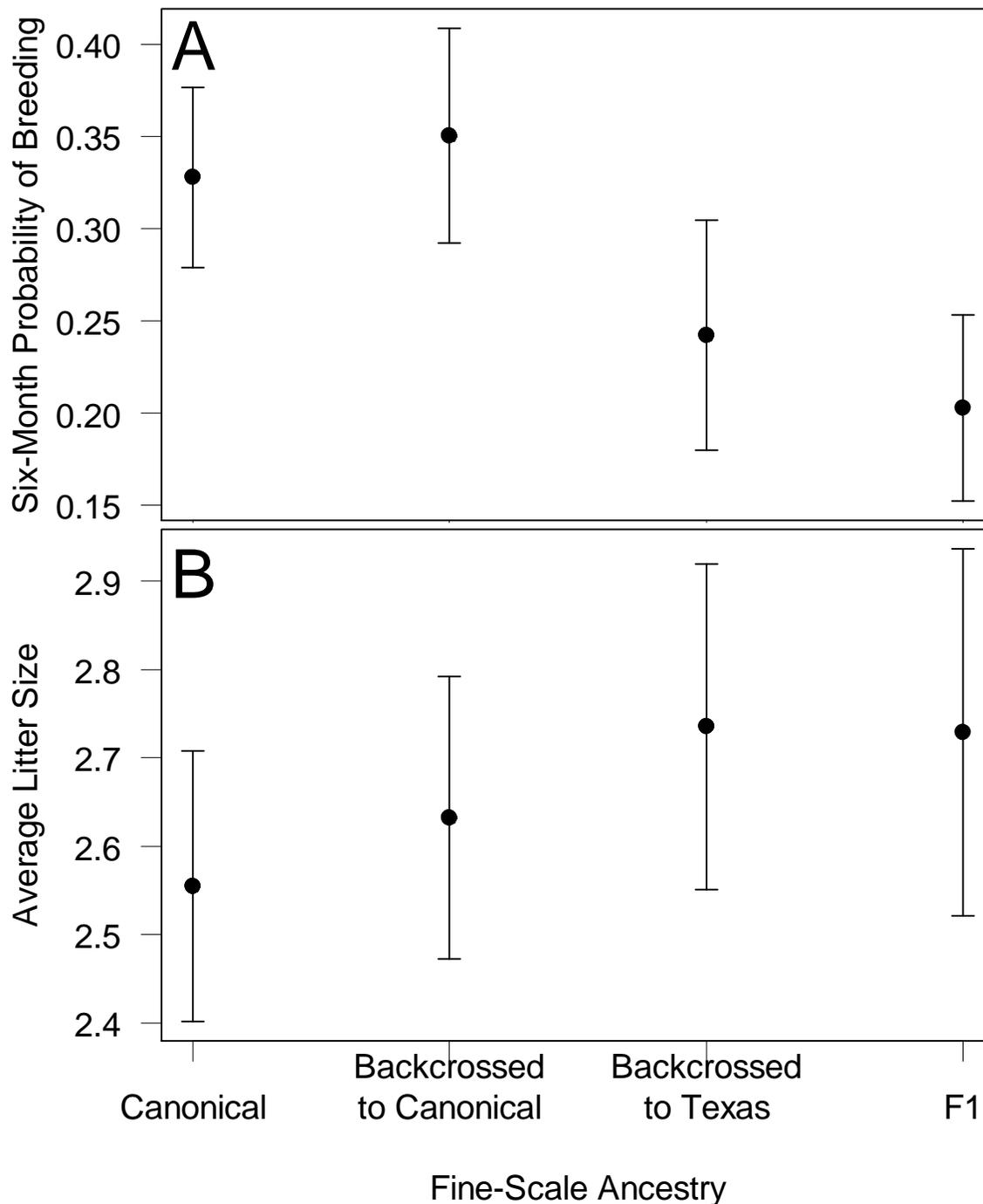


Figure I-1. Model-averaged reproductive rates by complex ancestry category (\pm unconditional standard errors). A) Probability of a young-adult female panther giving birth within the 6-month dry season and B) average litter size for an adult female panther during the dry season. Although panthers in six ancestry categories were used in the analysis, the sample sizes for Everglades and backcrossed to Everglades were quite small, so we only present model-averaged estimates for the other four ancestry categories

APPENDIX J
ANALYSIS OF REPRODUCTIVE PARAMETERS EXCLUDING OLDER-ADULTS (≥ 10
YEARS)

Methods

We tested for the effects of age class and season on reproductive rates, excluding older-adults. We did this to check the robustness of our estimates of reproductive parameters for sub-adults and prime-adults to distortion from older-adults, which only bred once (with a litter size of 1). There were no older-adult female admixed panthers in our dataset, so we also wanted to check the robustness of our ancestry statistical inference and estimates to the inclusion of the pre-introgression type older-adults. To consider the effects of age class on p and μ , we created a new age class model: Age4, which divides sub-adult (ages 1 – 2.5) and prime-adult (ages 2.5 – 10) panthers. Otherwise, analyses proceeded as in the main text.

Results

Excluding older-adults had little effect on inference (Table J-1) or model-averaged estimates (Figures J-1A, J-2A, and J-3A) for breeding probability of sub-adults and prime-adults. Excluding the one older-adult that bred (instead of combining her with prime-adults in the adult category) had some small effects on inference (Table J-2) and model-averaged estimates (Figures J-1B, J-2B, and J-3B) for μ , including moving season from a marginally supported model (Table 4-2B) to a marginally unsupported model (Table J-2B).

Table J-1. Model selection table evaluating the effects of factors on probability of breeding (p), excluding older-adults. A) Age class effects. B) Season effects. C) Ancestry effects. The top ranked model for age class (part A, model 1, in bold) was used as a base model to test for the effects of season; the top ranked model for season (part B, model 1, in bold) was used as a base model to test for the effects of ancestry. For each model, we present the number of parameters (K), the difference in Akaike's Information Criterion (ΔAIC), and the Akaike weight (w_i). These analyses were performed on subsets of the data (excluding older-adults for all analyses and 1 panther with unknown ancestry for ancestry analysis).

Model	p	K	ΔAIC	w_i
A) Age Models				
1	Constant^a	1	0.00	0.562
2	Age4 ^b	3	0.50	0.438
B) Season Models				
1	Season	2	0.00	0.785
2	Constant	1	2.59	0.215
C) Ancestry Models				
1	Season + Ancest2^c	3	0.00	0.628
2	Season + Ancest1 ^d	4	1.59	0.284
3	Season	2	4.56	0.064
4	Season + Ancest3 ^e	3	6.49	0.024

Table J-2. Model selection table evaluating the effects of factors on litter size (μ), excluding older-adults. A) Age class effects. B) Season effects. C) Ancestry effects. The top ranked model for age class (part A, model 1, in bold) was used as a base model to test for the effects of season; the top ranked model for season (part B, model 1, in bold) was used as a base model to test for the effects of ancestry. For each model, we present the number of parameters (K), the difference in Akaike's Information Criterion (Δ AIC), and the Akaike weight (w_i). These analyses were performed on subsets of the data (excluding older-adults for all analyses and 1 panther with unknown ancestry for ancestry).

Model	μ	K	Δ AIC	w_i
A) Age Models				
1	Age4^a	4	0.00	0.777
2	Constant ^b	3	2.50	0.223
B) Season Models				
1	Age4	4	0.00	0.519
2	Age4 + Season	5	0.16	0.481
C) Ancestry Models				
1	Age4	4	0.00	0.478
2	Age4 + Ancest3 ^c	5	1.29	0.251
3	Age4 + Ancest2 ^d	5	2.00	0.176
4	Age4 + Ancest1 ^e	6	3.24	0.095

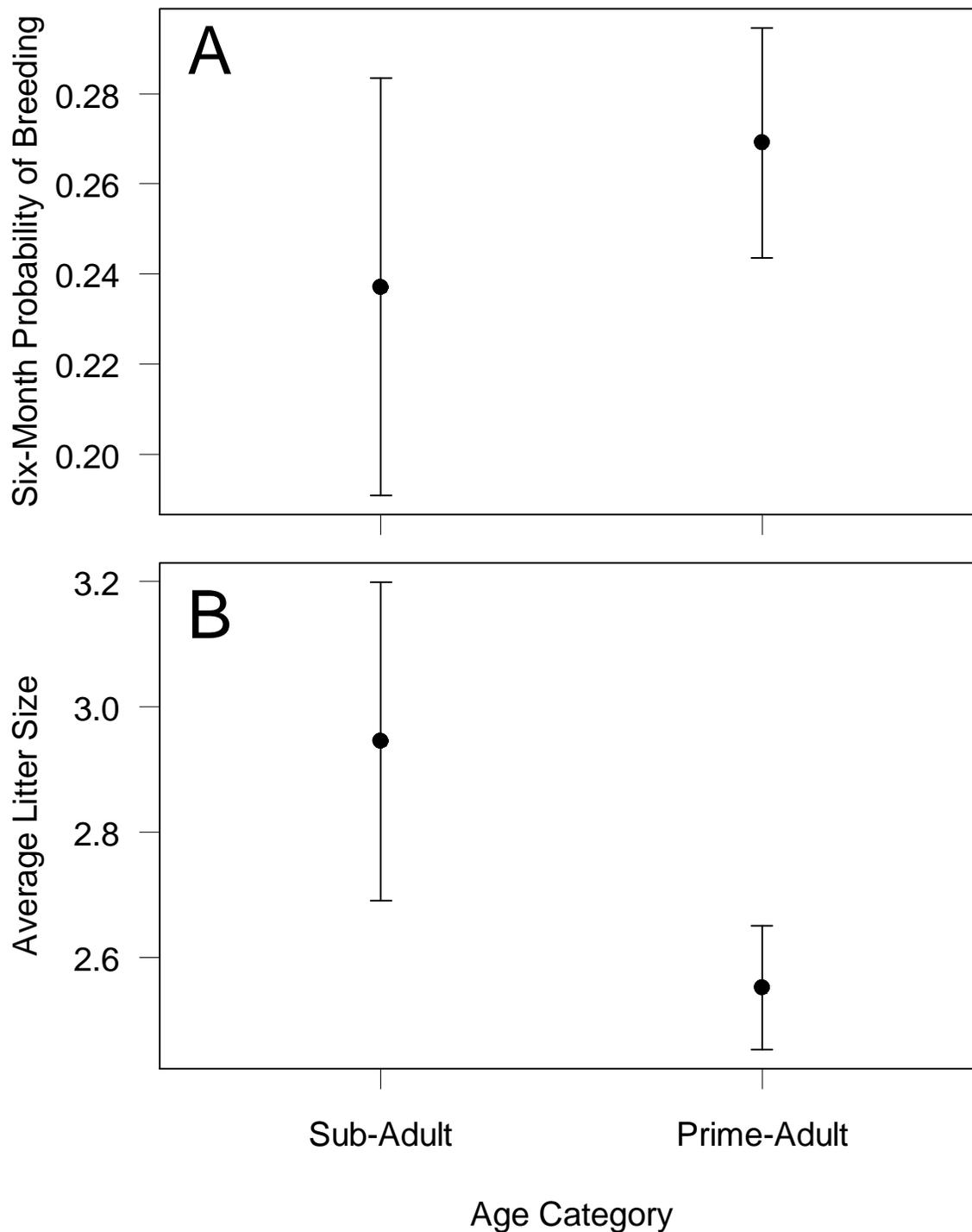


Figure J-1. Model-averaged reproductive rates (\pm unconditional standard errors) by age class. Sub-adults are defined as ages 1-2.5 and prime-adults ages 2.5-10. We present A) six-month probability of breeding and B) average litter size. The estimates are from an analysis excluding older-adult (age \geq 10 years) panthers.

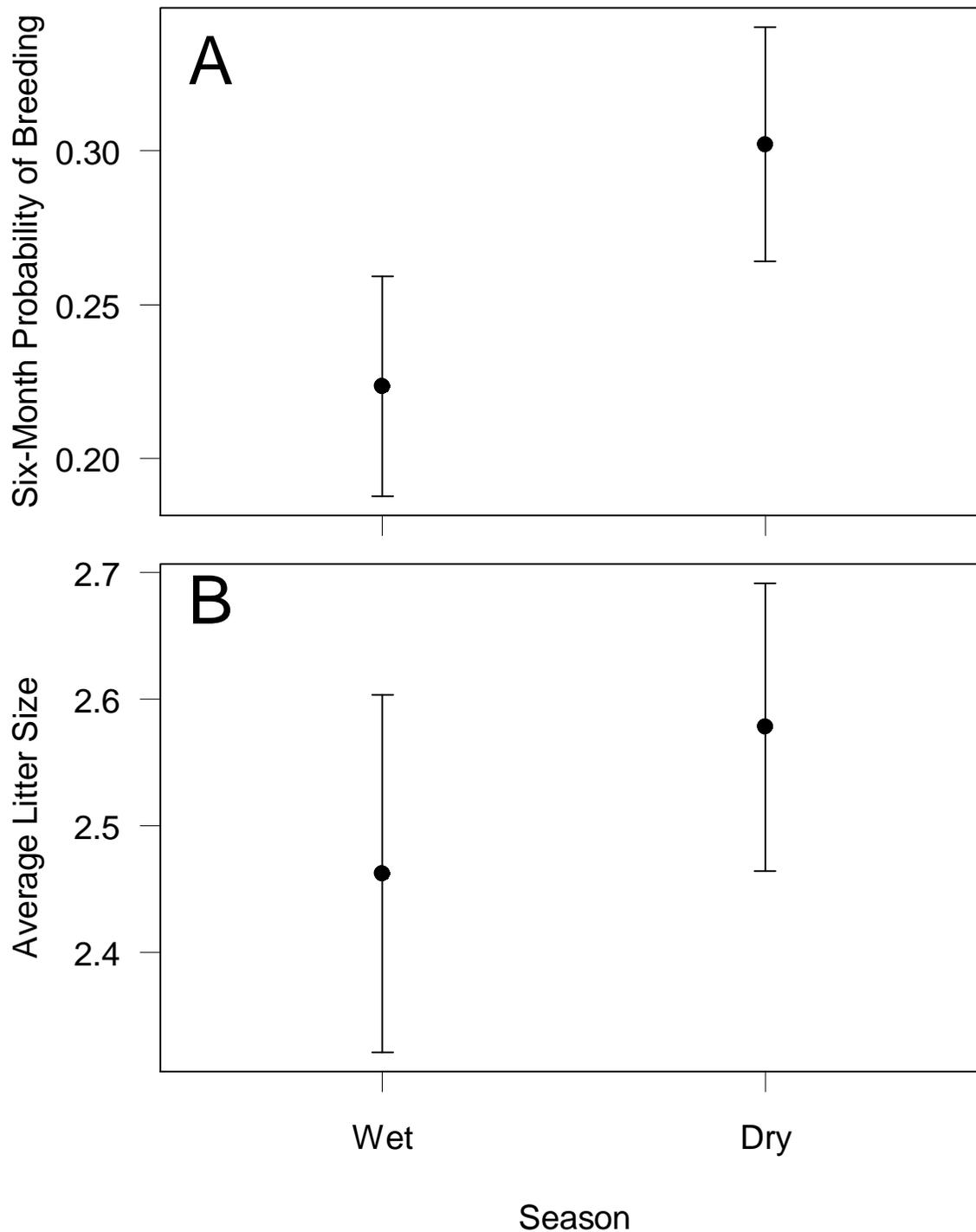


Figure J-2. Model-averaged reproductive rates (\pm unconditional standard errors) by season. We present A) six-month probability of breeding for young-adult panthers (<10 years old) and B) average litter size for prime-adult panthers (ages 2.5-10). The estimates are from an analysis excluding older-adult (age \geq 10 years) panthers.

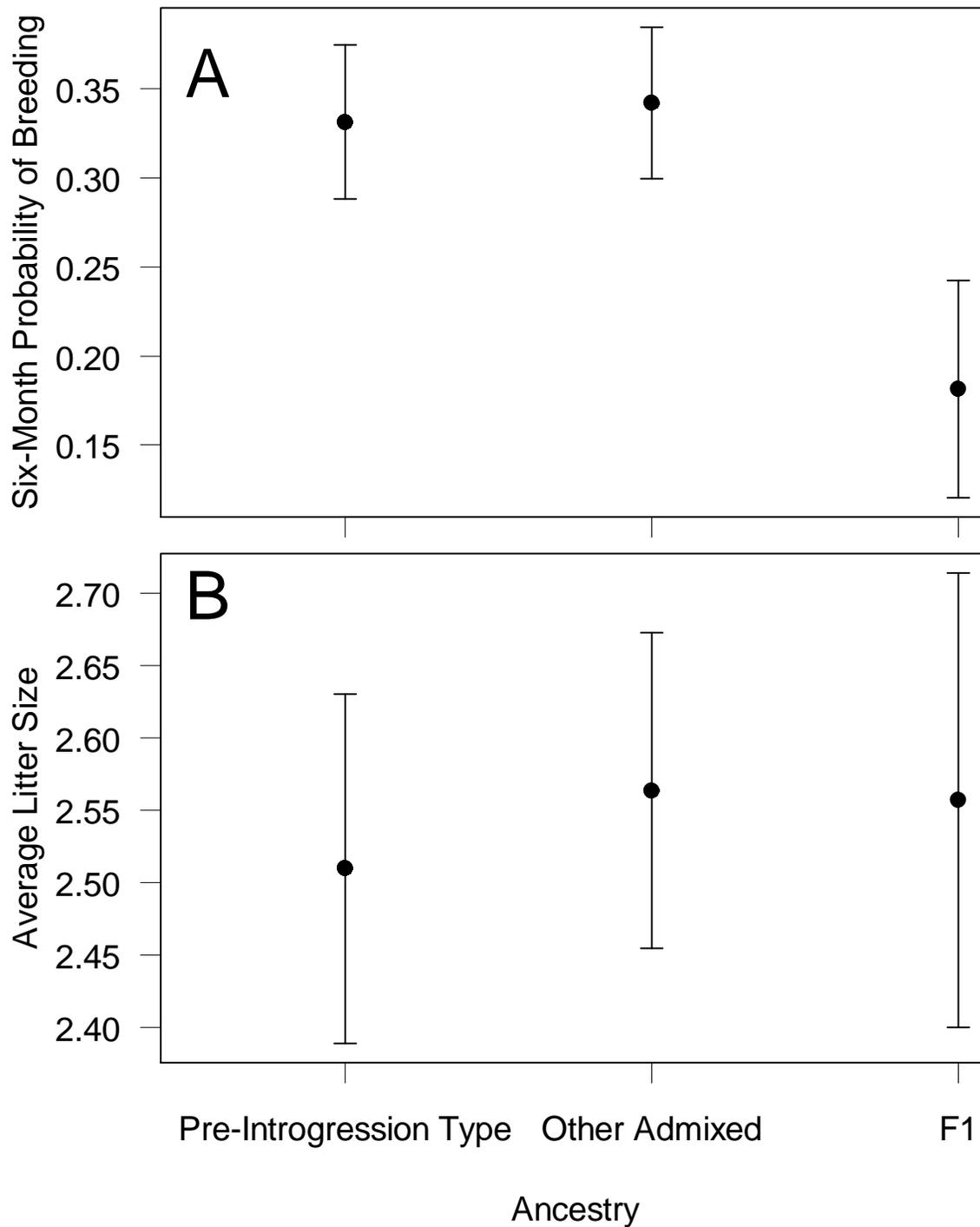


Figure J-3. Model-averaged reproductive rates (\pm unconditional standard errors) by ancestry category. We present A) six-month probability of breeding for young-adult panthers (<10 years old) in the dry season and B) average litter size, for prime-adult panthers (ages 2.5-10). The estimates are from an analysis excluding older-adult (age \geq 10 years) panthers.

APPENDIX K ANNUAL BREEDING PARAMETERS FOR PVA

Methods

For use in population viability analyses (PVA) we estimated and modeled reproductive parameters similar to the methods detailed in the main text, with five key differences: 1) we organized data with an annual time step and estimated annual reproductive rates; 2) we did not include kittens that were not PIT tagged in the den in reproductive counts; 3) we used all age models for examining the effects of abundance index, ancestry, and heterozygosity on reproductive parameters instead of choosing base models; and 4) we estimated random effects of year on reproductive rates as measures of temporal variance (environmental stochasticity).

For use in PVA with annual time steps, we estimated and modeled annual probability of breeding (q) and annual cumulative number of kittens (v ; see below). We organized the data with years extending from June – May. This precluded examining the effects of season on reproductive rates. Because there were instances of female panthers giving birth more than once in a year, q is the probability of giving birth at least once during a year and v is the total predicted number of kittens produced from all breeding attempts within a year. The range of observed v was 1 – 6, but $v = 5$ was not observed. We therefore modeled v with $J = 5$ categories, with $N_j = j$ for $j = 1 - 4$ and $N_5 = 6$. Otherwise, q was modeled similarly to p , and v was modeled similarly to μ .

Most kittens included in the reproductive analyses in the main text were found and PIT tagged during den visits soon after parturition. However, some were found dead during den checks and a few were missed in initial den checks and documented later. Florida panther kitten survival estimates for use in PVA were made conditional on

kittens being PIT tagged in the den (Hostetler et al., 2010). To avoid bias in population growth rates from PVA, we defined reproduction as giving birth to kittens that were PIT tagged in the den and excluded kittens from analyses in this appendix that were not PIT tagged in the den. However, we also present overall annual reproductive rates without this exclusion, for comparison with other studies.

Stepwise model selection (choosing a base model from testing one covariate to test the next covariate, as used in the main text) can be a useful technique for reducing the size of model sets used with information-theoretic inference. However, there are trade-offs involved with this approach. When there are two or more closely ranked models in a model set and only one of these is chosen as a base model, subsequent model averages will not include this (possibly important) source of uncertainty. To incorporate uncertainty about the effects of age category on q and v in model-averaged estimates that also included abundance index, ancestry, or heterozygosity, we included all age models in these model sets (in all combinations with the other models).

Finally, we examined the random effects of year (June – May, 1-13) on q and v , as a measure of environmental stochasticity. The minimum AIC models from the age analysis for each parameter were used as base models, with and without abundance index as a covariate. We modeled temporal variance in q by using the logistic model including random effects for year, which is a type of generalized linear mixed model (GLMM; Bolker et al., 2009). Again, we used the complementary log-log link (equation 1.4) and $\log(m)$ as an offset. We implemented the mixed logistic model using the R function `lmer` in the package `lme4`. We modeled temporal variance by using the cumulative logit including random effects (Min and Agresti, 2005). We implemented the

mixed cumulative logistic model using the R function `clmm` in the package `ordinal`. Because our intent was to estimate the temporal variance rather than produce an estimate of probability of breeding for each year, we counted the random effect as a single parameter for model comparison (Vaida and Blanchard, 2005).

Results

The overall annual probability of breeding was 0.406 ± 0.034 , or 0.410 ± 0.034 including reproduction that did not lead to kittens being PIT tagged in the den. The overall annual cumulative number of kittens was 2.76 ± 0.12 , or 2.84 ± 0.11 including kittens not PIT tagged in the den.

The model selection results (Tables K1 and K2) were similar to those in the main text. Model averaged annual probabilities of breeding were 0.430 ± 0.066 for sub-adults, 0.466 ± 0.039 for prime-adults, and 0.038 ± 0.037 for older-adults. Model averaged annual cumulative numbers of kittens were 2.96 ± 0.28 for sub-adults and 2.72 ± 0.13 for adults. Models including the quadratic effect of abundance on v failed to converge and were discarded.

There was strong evidence for temporal variance in annual breeding probability, with or without abundance index (estimated at 0.123 and 0.138, respectively; Table K-3). There was no evidence for temporal variance in annual cumulative number of kittens (without abundance index) (Table K-4). The model with both temporal variance and abundance index effects on annual cumulative number of kittens failed to converge and was discarded.

Table K-1. Model selection table evaluating the effects of factors on annual probability of breeding (q). A) Age class effects. B) Abundance index effects. C) Ancestry effects. D) Heterozygosity effects. For each model, we present the number of parameters (K), the difference in Akaike's Information Criterion (Δ AIC), and the Akaike weight (w_i). The ancestry and heterozygosity analyses were performed on subsets of the data (excluding one panther with unknown heterozygosity).

Model	q	K	Δ AIC	w_i
A) Age Models				
1	Age2^a	2	0.00	0.620
2	Age1 ^b	3	0.98	0.380
3	Constant ^c	1	19.77	0.000
4	Age3 ^d	2	21.67	0.000
B) Abundance Index Models				
1	Age2 + Abundance	3	0.00	0.304
2	Age2	2	0.75	0.209
3	Age2 + Abundance + Abundance ²	4	1.39	0.152
4	Age1 + Abundance	4	1.53	0.141
5	Age1	3	1.73	0.128
6	Age1 + Abundance + Abundance ²	5	3.06	0.066
7	Abundance	2	14.22	0.000
8	Abundance + Abundance ²	3	16.09	0.000
9	Age3 + Abundance	3	16.22	0.000
10	Age3 + Abundance + Abundance ²	4	18.08	0.000
11	Constant	1	20.53	0.000
12	Age3	2	22.43	0.000
C) Ancestry Models				
1	Age2 + Ancest2^e	3	0.00	0.295
2	Age2 + Ancest1 ^f	4	0.48	0.232
3	Age1 + Ancest2	4	0.92	0.186
4	Age1 + Ancest1	5	1.13	0.168
5	Age2	2	3.44	0.053
6	Age1	3	4.40	0.033
7	Age2 + Ancest3 ^g	3	5.32	0.021
8	Age1 + Ancest3	4	6.22	0.013
9	Ancest1	3	16.21	0.000
10	Age3 + Ancest1	4	17.61	0.000
11	Ancest3	2	21.05	0.000
12	Ancest2	2	22.51	0.000
13	Age3 + Ancest3	3	22.62	0.000
14	Constant	1	23.26	0.000

15	Age3 + Ancest2	3	24.43	0.000
16	Age3	2	25.15	0.000

D) Heterozygosity Models

1	Age2 + Het^h	3	0.00	0.315
2	Age2	2	0.03	0.310
3	Age1	3	1.00	0.192
4	Age1 + Het	4	1.09	0.183
5	Constant	1	19.85	0.000
6	Age3	2	21.75	0.000
7	Het	2	21.82	0.000
8	Age3 + Het	3	23.73	0.000

a. Age2 divides panthers into young-adults and older-adults.

b. Age1 divides panthers into sub-adults, prime-adults, and older-adults.

c. No predictor variables.

d. Age3 divides panthers into sub-adults and adults.

e. Ancest2 divides panthers into 2 ancestry categories: F₁ admixed, and other admixed and pre-introgression type combined.

f. Ancest1 divides panthers into 3 ancestry categories: pre-introgression type, other admixed, and F₁ admixed.

g. Ancest3 divides panthers into 2 ancestry categories: pre-introgression type and admixed.

h. Heterozygosity.

Table K-2. Model selection table evaluating the effects of factors on annual cumulative number of kittens (ν). A) Age class effects. B) Abundance index effects. C) Ancestry effects. D) Heterozygosity effects. For each model, we present the number of parameters (K), the difference in Akaike's Information Criterion (Δ AIC), and the Akaike weight (w_i).

Model	ν	K	Δ AIC	w_i
A) Age Class Models				
1	Age3^a	5	0.00	0.537
2	Constant ^b	4	0.30	0.463
B) Abundance Index Models				
1	Age3	5	0.00	0.368
2	Constant	4	0.30	0.318
3	Age3 + Abundance	6	1.46	0.177
4	Abundance	5	1.98	0.137
C) Ancestry Models				
1	Age3	5	0.00	0.270
2	Constant	4	0.30	0.233
3	Age3 + Ancest2 ^c	6	1.64	0.119
4	Ancest2	5	1.92	0.103
5	Age3 + Ancest3 ^d	6	1.98	0.100
6	Ancest3	5	2.23	0.089
7	Age3 + Ancest1 ^e	7	3.55	0.046
8	Ancest1	6	3.74	0.042
D) Heterozygosity Models				
1	Age3	5	0.00	0.374
2	Constant	4	0.30	0.323
3	Age3 + Het ^f	6	1.75	0.156
4	Het	5	1.88	0.146

^a Age3 divides panthers into sub-adults and adults.

^b No predictor variables.

^c Ancest2 divides panthers into 2 ancestry categories: F₁ admixed, and other admixed and pre-introgression type combined.

^d Ancest3 divides panthers into 2 ancestry categories: pre-introgression type and admixed.

^e Ancest1 divides panthers into 3 ancestry categories: pre-introgression type, other admixed, and F₁ admixed.

^f Heterozygosity.

Table K-3. Model selection table testing for the random effect of year (rand(Year)), with and without abundance index as a covariate, on annual probability of breeding (q). Age2 divides panthers into young-adults and older-adults. The top ranked model for age (Table K-1A, model 1, in bold) was used as a base model. For each model, we present the number of parameters (K), the difference in Akaike's Information Criterion (ΔAIC), the Akaike weight (w_i), and temporal standard deviation on the complementary log-log scale and real scale. Standard deviation was converted to the real scale for young-adults (model 1), and young-adults with mean abundance (model 2).

Model p	K	ΔAIC	w_i	Temporal SD	
				Complementary Log-Log Scale	Real Scale
1	3	0.00	0.449	0.420	0.138
2	4	0.63	0.328	0.378	0.123
3	3	2.45	0.132	-	-
4	2	3.21	0.090	-	-

Table K-4. Model selection table testing for the random effect of year (rand(Year)) on annual cumulative number of kittens (ν). Age3 divides panthers into sub-adults and adults. The top ranked model for age (Table K-2A, model 1, in bold) was used as a base model. For each model, we present the number of parameters (K), the difference in Akaike's Information Criterion (ΔAIC), the Akaike weight (w_i), and temporal standard deviation on the cumulative logit scale and real scale. Standard deviation was converted to the real scale for adults (model 2).

Model	ν	K	ΔAIC	w_i	Temporal SD	
					Cumulative Logit Scale	Real Scale
1	Age3	5	0.00	0.731	-	-
2	Age3 + rand(Year)	6	2.00	0.269	0.0006	0.0004

APPENDIX L
DEMOGRAPHIC PARAMETERS FOR CANONICAL PANTHERS

Materials and Methods

To address questions regarding the dynamics and persistence of a hypothetical post-1995 canonical population, we needed estimates of demographic parameters for canonical panthers. Model fitting procedures followed those from the original ancestry analyses with a few differences. We ran additional ancestry models for each parameter to account for factors left out of the ancestry analyses (Benson et al., in revision; Hostetler et al., 2010; chapter 4), such as abundance index. In addition, we included older-adults in the new sub-adult and adult survival analyses (unlike in Benson et al., in revision). Originally, they were left out because there were few older-adult admixed panthers in the period covered (1997-2006). For this analysis, we needed model specific estimates, variances, and covariances for older-adult survival, so we included them, but applied ancestry effects to young-adults only.

From each of these models, we obtained estimates of parameter values for canonical panthers. However, we used estimates of σ_t from the equivalent non-ancestry models. We present models with ΔAIC (or ΔQAIC_c) < 10 . Only density-independent models were used in estimation of $\lambda^{(c)}$, but all models with ΔAIC (or ΔQAIC_c) < 10 were used in estimation of extinction parameters.

Results

The top ancestry model for sub-adult and adult survival contained terms for Ancest1 (survival varying by three ancestry categories) and abundance (Table L-1), even though the original top ancestry model contained Ancest2 instead (the equivalent was the second ranked model here) and the top model from the original abundance

analysis did not contain abundance (Benson et al., in revision). Similarly, the inclusion of abundance index changed the top kitten survival model from having the AdmAdv model (backcrossed to canonical and canonical have lower survivals; Hostetler et al., 2010) to having the IntAdv model (only canonical kittens have lower survival; Table L-2). Because no density-independent kitten survival models were within 10 QAIC_c of the top model, we present those models separately (for estimation of $\lambda^{(c)}$; Table L-3).

The top model for probability of breeding included Ancest2 and abundance (Table L-4). The top model for annual kitten production contained neither ancestry nor abundance effects (Table L-5).

Table L-1. Models for canonical sub-adult and adult survival, with Akaike model weights (w_i), estimates of sub-adult female canonical survival ($S_{sa}^{(c)}$), prime-adult female canonical survival ($S_{pa}^{(c)}$), older-adult female canonical survival ($S_{oa}^{(c)}$), the effect of abundance index on log-hazard ($\beta_{abundance}$), and temporal standard deviation (σ_t). Density-independent models are in bold. Survival estimates for density-dependent models are for abundance index 0. Age category model names are different than in Benson et al. (in revision).

Model	w_i	$S_{sa}^{(c)}$	$S_{pa}^{(c)}$	$S_{oa}^{(c)}$	$\beta_{abundance}$	σ_t
Sex * Age3 ^a + Older ^b + Young ^c :Ancest1 ^d + Abundance ^e	0.195	0.983 ± 0.018	0.937 ± 0.039	0.868 ± 0.076	0.017 ± 0.008	0.306
Sex * Age3 + Older + Young:Ancest2^f	0.155	0.960 ± 0.040	0.832 ± 0.035	0.668 ± 0.067	0	0.340
Sex * Age3 + Older + Young:Ancest2 + Abundance	0.105	0.978 ± 0.024	0.909 ± 0.054	0.786 ± 0.100	0.009 ± 0.007	0.306
Sex * Age1 ^g + Young:Ancest1 + Abundance	0.091	0.983 ± 0.018	0.934 ± 0.041	0.880 ± 0.072	0.017 ± 0.009	0.305
Sex * Age3 + Older + Young:Ancest1	0.085	0.953 ± 0.048	0.812 ± 0.044	0.666 ± 0.068	0	0.340
Sex * Age1 + Young:Ancest2	0.069	0.960 ± 0.040	0.825 ± 0.037	0.691 ± 0.067	0	0.339
Sex * Age3 + Young:Ancest2	0.052	0.960 ± 0.040	0.798 ± 0.034	0.798 ± 0.034	0	0.253
Sex * Age1 + Young:Ancest2 + Abundance	0.046	0.978 ± 0.024	0.905 ± 0.057	0.801 ± 0.096	0.008 ± 0.008	0.305
Sex * Age3 + Older + Young:Ancest3 ^h + Abundance	0.044	0.986 ± 0.015	0.951 ± 0.029	0.891 ± 0.062	0.021 ± 0.008	0.306
Sex * Age1 + Young:Ancest1	0.039	0.953 ± 0.049	0.803 ± 0.047	0.691 ± 0.068	0	0.339
Sex * Age3 + Young:Ancest2 + Abundance	0.021	0.968 ± 0.034	0.837 ± 0.079	0.837 ± 0.079	0.003 ± 0.007	0.239
Sex * Age1 + Young:Ancest3 + Abundance	0.021	0.986 ± 0.015	0.949 ± 0.031	0.901 ± 0.058	0.020 ± 0.008	0.305
Sex * Age3 + Young:Ancest1	0.019	0.959 ± 0.042	0.795 ± 0.045	0.799 ± 0.039	0	0.253
Sex + Young:Ancest2	0.011	0.824 ± 0.030	0.824 ± 0.030	0.824 ± 0.03	0	0.224
Sex * Age3 + Young:Ancest1 + Abundance	0.008	0.969 ± 0.033	0.842 ± 0.078	0.856 ± 0.085	0.005 ± 0.008	0.239
Sex * Age3 + Older + Young:Ancest3	0.008	0.954 ± 0.048	0.818 ± 0.045	0.665 ± 0.068	0	0.340
Sex + Young:Ancest2 + Abundance	0.005	0.865 ± 0.067	0.865 ± 0.067	0.865 ± 0.067	0.004 ± 0.007	0.210
Sex + Young:Ancest1	0.004	0.826 ± 0.040	0.826 ± 0.040	0.822 ± 0.035	0	0.224
Sex * Age3 + Older	0.004	0.967 ± 0.033	0.861 ± 0.029	0.669 ± 0.067	0	0.340
Young:Ancest2	0.004	0.780 ± 0.026	0.780 ± 0.026	0.780 ± 0.026	0	0.177
Sex * Age1 + Young:Ancest3	0.004	0.953 ± 0.048	0.810 ± 0.048	0.691 ± 0.068	0	0.339
Sex * Age3 + Older + Abundance	0.003	0.982 ± 0.019	0.928 ± 0.043	0.792 ± 0.099	0.009 ± 0.008	0.306
Sex + Young:Ancest1 + Abundance	0.002	0.866 ± 0.067	0.866 ± 0.067	0.872 ± 0.077	0.005 ± 0.008	0.210
Sex * Age1	0.002	0.967 ± 0.033	0.855 ± 0.031	0.691 ± 0.067	0	0.339
Young:Ancest2 + Abundance	0.002	0.831 ± 0.085	0.831 ± 0.085	0.831 ± 0.085	0.004 ± 0.007	0.167
Young:Ancest1	0.002	0.774 ± 0.040	0.774 ± 0.040	0.784 ± 0.035	0	0.177

- ^a Age3 divides panthers into sub-adults (1-2.5 and 1-3.5 years old for females and males respectively) and adults (≥ 2.5 and ≥ 3.5 yrs for females and males respectively).
- ^b Older refers to older-adults (≥ 10 years old).
- ^c Young refers to young-adults (1-10 years old).
- ^d Ancest1 divides panthers into three ancestry categories: F_1 admixed, other admixed, and pre-introgression type.
- ^e Abundance refers to a linear trend in log-hazard by abundance index.
- ^f Ancest2 divides panthers into two ancestry categories: F_1 admixed, and other admixed and pre-introgression type combined.
- ^g Age1 divides the panthers into sub-adults (same as Age3), prime-adults (2.5-10 and 3.5-10 years old for females and males respectively), and older-adults (≥ 10 years old).
- ^h Ancest3 divides panthers into two ancestry categories: pre-introgression type, and other admixed and F_1 admixed combined.

Table L-2. Models for (density-dependent) canonical kitten survival, with Akaike model weights (w_i), estimates of female canonical kitten survival ($S_k^{(c)}$), the effect of abundance index on logit kitten survival ($\beta_{abundance}$), and temporal standard deviation (σ_t). All models shown here are density-dependent; survival estimates are for abundance index 0. For more details, see Hostetler et al. (2010).

Model	w_i	$S_k^{(c)}$	$\beta_{abundance}$	σ_t
S(Base ^a + k:IntAdv ^b + s&a:F1Adv ^c + k:Abundance ^d)r(.) ^e	0.149	0.782 ± 0.145	-0.055 ± 0.016	0.368
S(Base + k:IntAdv + s&a:F1Adv + k:Abundance)r(k,s&a) ^f	0.080	0.796 ± 0.145	-0.055 ± 0.016	0.457
S(Base + k:CanDisF1Adv ^g + s&a:F1Adv + k:Abundance)r(.)	0.067	0.814 ± 0.136	-0.06 ± 0.018	0.368
S(Base + k:IntAdv + s&a:F1Adv + k:Abundance + k:Sex ^h)r(.)	0.057	0.803 ± 0.146	-0.055 ± 0.016	0.357
S(Base + k:CanDis50TexAdv ⁱ + s&a:F1Adv + k:Abundance)r(.)	0.053	0.779 ± 0.15	-0.055 ± 0.016	0.368
S(Base + k:CanDisF1Adv + s&a:F1Adv + k:Abundance)r(k,s&a)	0.035	0.822 ± 0.135	-0.06 ± 0.018	0.457
S(Base + k:(IntAdv + Abundance))r(.)	0.034	0.805 ± 0.137	-0.059 ± 0.017	0.368
S(Base + k:IntAdv + s&a:F1Adv + k:Abundance + k:Sex)r(k,s&a)	0.030	0.813 ± 0.147	-0.055 ± 0.017	0.363
S(Base + k:CanDis50TexAdv + s&a:F1Adv + k:Abundance)r(k,s&a)	0.028	0.794 ± 0.148	-0.055 ± 0.017	0.457
S(Base + k:CanDisF1Adv + s&a:F1Adv + k:Abundance + k:Sex)r(.)	0.026	0.834 ± 0.134	-0.06 ± 0.018	0.357
S(Base + k:(IntAdv + Abundance))r(k,s&a)	0.024	0.824 ± 0.133	-0.06 ± 0.017	0.457
S(Base + k:AdmAdv ^j + s&a:F1Adv + k:Abundance)r(.)	0.023	0.743 ± 0.16	-0.037 ± 0.013	0.368
S(Base + IntAdv + k:Abundance)r(.)	0.020	0.814 ± 0.124	-0.046 ± 0.013	0.368
S(Base + k:CanDis50TexAdv + s&a:F1Adv + k:Abundance + k:Sex)r(.)	0.020	0.801 ± 0.151	-0.055 ± 0.016	0.357
S(Base + CanDisF1Adv + k:Abundance)r(.)	0.018	0.779 ± 0.146	-0.042 ± 0.013	0.368
S(Base + AdmAdv + k:Abundance)r(.)	0.017	0.771 ± 0.146	-0.038 ± 0.013	0.368
S(Base + k:CanDisF1Adv + s&a:F1Adv + k:Abundance + k:Sex)r(k,s&a)	0.013	0.839 ± 0.135	-0.06 ± 0.018	0.363
S(Base + k:(IntAdv + Abundance) + k:Sex)r(.)	0.013	0.825 ± 0.137	-0.059 ± 0.017	0.357
S(Base + k:CanDis50TexAdv + k:Abundance)r(.)	0.013	0.799 ± 0.143	-0.058 ± 0.017	0.368
S(Base + k:AdmAdv + s&a:F1Adv + k:Abundance)r(k,s&a)	0.012	0.757 ± 0.16	-0.037 ± 0.013	0.457
S(Base + k:CanDisF1Adv + k:Abundance)r(.)	0.012	0.813 ± 0.137	-0.061 ± 0.018	0.368
S(Base + CanDis50TexAdv + k:Abundance)r(.)	0.011	0.796 ± 0.135	-0.044 ± 0.013	0.368
S(Base + IntAdv + k:Abundance)r(k,s&a)	0.011	0.829 ± 0.122	-0.046 ± 0.013	0.457
S(Base + k:50TexAdv ^k + s&a:F1Adv + k:Abundance)r(.)	0.010	0.771 ± 0.146	-0.037 ± 0.012	0.368
S(Base + k:CanDis50TexAdv + s&a:F1Adv + k:Abundance + k:Sex)r(k,s&a)	0.010	0.811 ± 0.151	-0.055 ± 0.017	0.363
S(Base + CanDisF1Adv + k:Abundance)r(k,s&a)	0.010	0.799 ± 0.143	-0.041 ± 0.014	0.457
S(Base + AdmAdv + k:Abundance)r(k,s&a)	0.010	0.791 ± 0.144	-0.038 ± 0.013	0.457
S(Base + s&a:F1Adv + k:Abundance)r(.)	0.009	0.825 ± 0.116	-0.038 ± 0.012	0.368
S(Base + IntAdv + k:Abundance + k:Sex)r(.)	0.009	0.845 ± 0.118	-0.046 ± 0.013	0.357
S(Base + k:AdmAdv + s&a:F1Adv + k:Abundance + k:Sex)r(.)	0.009	0.77 ± 0.162	-0.038 ± 0.013	0.357
S(Base + k:CanDis50TexAdv + k:Abundance)r(k,s&a)	0.009	0.819 ± 0.138	-0.059 ± 0.018	0.457

S(Base + $k:(\text{IntAdv} + \text{Abundance}) + k:\text{Sex}$) $r(k, s\&a)$	0.009	0.839 ± 0.135	-0.06 ± 0.017	0.363
S(Base + $k:\text{CanDisF1Adv} + k:\text{Abundance}$) $r(k, s\&a)$	0.008	0.824 ± 0.136	-0.06 ± 0.018	0.457
S(Base + $\text{CanDisF1Adv} + k:\text{Abundance} + k:\text{Sex}$) $r(.)$	0.008	0.813 ± 0.141	-0.042 ± 0.014	0.357
S(Base + $50\text{TexAdv} + k:\text{Abundance}$) $r(.)$	0.008	0.788 ± 0.138	-0.038 ± 0.013	0.368
S(Base + $\text{AdmAdv} + k:\text{Abundance} + k:\text{Sex}$) $r(.)$	0.007	0.802 ± 0.144	-0.039 ± 0.013	0.357
S(Base + $\text{F1Adv} + k:\text{Abundance}$) $r(.)$	0.006	0.774 ± 0.147	-0.035 ± 0.013	0.368
S(Base + $\text{CanDis50TexAdv} + k:\text{Abundance}$) $r(k, s\&a)$	0.006	0.813 ± 0.132	-0.044 ± 0.013	0.457
S(Base + $k:50\text{TexAdv} + s\&a:\text{F1Adv} + k:\text{Abundance}$) $r(k, s\&a)$	0.005	0.786 ± 0.145	-0.037 ± 0.013	0.457
S(Base + $s\&a:\text{F1Adv} + k:\text{Abundance}$) $r(k, s\&a)$	0.005	0.837 ± 0.114	-0.038 ± 0.013	0.457
S(Base + $s\&a:\text{F1Adv} + k:\text{Abundance} + k:\text{Sex}$) $r(.)$	0.005	0.858 ± 0.107	-0.039 ± 0.013	0.357
S(Base + $k:\text{CanDisF1Adv} + k:\text{Abundance} + k:\text{Sex}$) $r(.)$	0.005	0.833 ± 0.136	-0.06 ± 0.018	0.357
S(Base + $k:\text{CanDis50TexAdv} + k:\text{Abundance} + k:\text{Sex}$) $r(.)$	0.005	0.819 ± 0.144	-0.058 ± 0.017	0.357
S(Base + $\text{CanDis50TexAdv} + k:\text{Abundance} + k:\text{Sex}$) $r(.)$	0.005	0.827 ± 0.131	-0.044 ± 0.013	0.357
S(Base + $\text{IntAdv} + k:\text{Abundance} + k:\text{Sex}$) $r(k, s\&a)$	0.005	0.858 ± 0.115	-0.046 ± 0.014	0.363
S(Base + $k:(\text{AdmAdv} + \text{Abundance})$) $r(.)$	0.005	0.756 ± 0.156	-0.039 ± 0.013	0.368
S(Base + $k:\text{AdmAdv} + s\&a:\text{F1Adv} + k:\text{Abundance} + k:\text{Sex}$) $r(k, s\&a)$	0.005	0.779 ± 0.164	-0.037 ± 0.013	0.363
S(Base + $k:50\text{TexAdv} + s\&a:\text{F1Adv} + k:\text{Abundance} + k:\text{Sex}$) $r(.)$	0.004	0.804 ± 0.143	-0.038 ± 0.013	0.357
S(Base + $50\text{TexAdv} + k:\text{Abundance}$) $r(k, s\&a)$	0.004	0.808 ± 0.135	-0.039 ± 0.013	0.457
S(Base + $\text{CanDisF1Adv} + k:\text{Abundance} + k:\text{Sex}$) $r(k, s\&a)$	0.004	0.831 ± 0.138	-0.042 ± 0.014	0.363
S(Base + $\text{AdmAdv} + k:\text{Abundance} + k:\text{Sex}$) $r(k, s\&a)$	0.004	0.819 ± 0.142	-0.039 ± 0.013	0.363
S(Base + $k:\text{F1Adv} + s\&a:\text{F1Adv} + k:\text{Abundance}$) $r(.)$	0.004	0.805 ± 0.135	-0.037 ± 0.013	0.368
S(Base + $\text{F1Adv} + k:\text{Abundance}$) $r(k, s\&a)$	0.004	0.798 ± 0.144	-0.035 ± 0.013	0.457
S(Base + $50\text{TexAdv} + k:\text{Abundance} + k:\text{Sex}$) $r(.)$	0.003	0.82 ± 0.134	-0.039 ± 0.013	0.357
S(Base + $k:\text{CanDis50TexAdv} + k:\text{Abundance} + k:\text{Sex}$) $r(k, s\&a)$	0.003	0.833 ± 0.141	-0.059 ± 0.018	0.363
S(Base + $k:(\text{AdmAdv} + \text{Abundance})$) $r(k, s\&a)$	0.003	0.776 ± 0.154	-0.039 ± 0.013	0.457
S(Base + $k:\text{CanDisF1Adv} + k:\text{Abundance} + k:\text{Sex}$) $r(k, s\&a)$	0.003	0.839 ± 0.137	-0.06 ± 0.018	0.363
S(Base + $\text{F1Adv} + k:\text{Abundance} + k:\text{Sex}$) $r(.)$	0.003	0.814 ± 0.14	-0.035 ± 0.013	0.357
S(Base + $s\&a:\text{F1Adv} + k:\text{Abundance} + k:\text{Sex}$) $r(k, s\&a)$	0.002	0.867 ± 0.105	-0.039 ± 0.013	0.363
S(Base + $\text{CanDis50TexAdv} + k:\text{Abundance} + k:\text{Sex}$) $r(k, s\&a)$	0.002	0.842 ± 0.128	-0.044 ± 0.014	0.363
S(Base + $k:50\text{TexAdv} + s\&a:\text{F1Adv} + k:\text{Abundance} + k:\text{Sex}$) $r(k, s\&a)$	0.002	0.815 ± 0.143	-0.038 ± 0.013	0.363
S(Base + $k:(50\text{TexAdv} + \text{Abundance})$) $r(.)$	0.002	0.782 ± 0.143	-0.039 ± 0.013	0.368
S(Base + $k:\text{F1Adv} + s\&a:\text{F1Adv} + k:\text{Abundance}$) $r(k, s\&a)$	0.002	0.819 ± 0.132	-0.037 ± 0.013	0.457
S(Base + $50\text{TexAdv} + k:\text{Abundance} + k:\text{Sex}$) $r(k, s\&a)$	0.002	0.837 ± 0.131	-0.039 ± 0.013	0.363
S(Base + $k:\text{F1Adv} + s\&a:\text{F1Adv} + k:\text{Abundance} + k:\text{Sex}$) $r(.)$	0.002	0.843 ± 0.124	-0.038 ± 0.013	0.357
S(Base + $k:(\text{AdmAdv} + \text{Abundance}) + k:\text{Sex}$) $r(.)$	0.002	0.78 ± 0.159	-0.039 ± 0.013	0.357
S(Base + $\text{F1Adv} + k:\text{Abundance} + k:\text{Sex}$) $r(k, s\&a)$	0.002	0.835 ± 0.137	-0.036 ± 0.013	0.363

S(Base + k :Abundance)r(.)	0.001	0.832 ± 0.114	-0.039 ± 0.012	0.368
S(Base + k :(50TexAdv + Abundance))r($k, s&a$)	0.001	0.803 ± 0.14	-0.039 ± 0.013	0.457
S(Base + k :(AdmAdv + Abundance) + k :Sex)r($k, s&a$)	0.001	0.796 ± 0.159	-0.039 ± 0.013	0.363

^a The base survival model represents survival differing between kittens, females age 1 and 2, females 3 and older, males age 1-3, and males 4 and older (Hostetler et al., 2010).

^b 2 ancestry categories: 1) canonical; 2) backcrossed to canonical, backcrossed to Everglades, backcrossed to Texas, and F₁.

^c 2 ancestry categories: 1) canonical, backcrossed to canonical, backcrossed to Everglades, and backcrossed to Texas; and 2) F₁.

^d k :Abundance refers to a linear trend in logit kitten survival by abundance index.

^e The same recovery probability for all panthers.

^f Recovery probabilities differing between kittens and older panthers.

^g 3 ancestry categories: 1) canonical; 2) backcrossed to canonical, backcrossed to Everglades, and backcrossed to Texas; and 3) F₁.

^h Kitten survival differing by sex.

ⁱ 3 ancestry categories: 1) canonical; 2) backcrossed to canonical and backcrossed to Everglades; 3) backcrossed to Texas and F₁.

^j 2 ancestry categories: 1) canonical and backcrossed to canonical; 2) backcrossed to Everglades, backcrossed to Texas, and F₁.

^k 2 ancestry categories: 1) canonical, backcrossed to canonical, and backcrossed to Everglades; 2) backcrossed to Texas, and F₁.

Table L-3. Models for density-independent canonical kitten survival, with Akaike model weights (w_i) and estimates of female canonical kitten survival ($S_k^{(c)}$). These models are > 10 QAIC_c units from the top model, but are < 10 QAIC_c units from the top density-independent model, and were therefore included in estimation of $\lambda^{(c)}$ but not in estimation of probability of extinction. For more details, see Hostetler et al. (2010).

Model	w_i	$S_k^{(c)}$
S(Base ^a + k :AdmAdv ^b + $s\&a$:F1Adv ^c)r(.) ^d	0.093	0.21 ± 0.056
S(Base + k :AdmAdv + $s\&a$:F1Adv)r($k,s\&a$) ^e	0.075	0.243 ± 0.074
S(Base + AdmAdv)r(.)	0.051	0.229 ± 0.052
S(Base + F1Adv)r(.)	0.047	0.266 ± 0.053
S(Base + AdmAdv)r($k,s\&a$)	0.039	0.265 ± 0.072
S(Base + CanDisF1Adv ^f)r(.)	0.037	0.221 ± 0.059
S(Base + F1Adv)r($k,s\&a$)	0.037	0.308 ± 0.079
S(Base + k :AdmAdv + $s\&a$:F1Adv + k :Sex ^g)r(.)	0.036	0.23 ± 0.078
S(Base + k :50TexAdv ^h + $s\&a$:F1Adv)r(.)	0.033	0.234 ± 0.057
S(Base + CanDisF1Adv)r($k,s\&a$)	0.028	0.261 ± 0.083
S(Base + k :AdmAdv + $s\&a$:F1Adv + k :Sex)r($k,s\&a$)	0.027	0.256 ± 0.093
S(Base + k :50TexAdv + $s\&a$:F1Adv)r($k,s\&a$)	0.023	0.265 ± 0.074
S(Base + F1Adv + k :Sex)r(.)	0.021	0.299 ± 0.076
S(Base + AdmAdv + k :Sex)r(.)	0.021	0.253 ± 0.073
S(Base + k :F1Adv + $s\&a$:F1Adv)r(.)	0.019	0.27 ± 0.054
S(Base + 50TexAdv)r(.)	0.019	0.242 ± 0.052
S(Base + $s\&a$:F1Adv)r(.)	0.018	0.292 ± 0.053
S(Base + CanDisF1Adv + k :Sex)r(.)	0.016	0.249 ± 0.079
S(Base + F1Adv + k :Sex)r($k,s\&a$)	0.015	0.336 ± 0.099
S(Base + AdmAdv + k :Sex)r($k,s\&a$)	0.015	0.284 ± 0.091
S(Base + k :AdmAdv)r($k,s\&a$)	0.015	0.246 ± 0.076
S(Base + k :IntAdv ⁱ + $s\&a$:F1Adv)r(.)	0.015	0.201 ± 0.079
S(Base + $s\&a$:F1Adv)r($k,s\&a$)	0.014	0.33 ± 0.073
S(Base + k :CanDis50TexAdv ^j + $s\&a$:F1Adv)r(.)	0.014	0.201 ± 0.079
S(Base + k :50TexAdv + $s\&a$:F1Adv + k :Sex)r(.)	0.014	0.262 ± 0.08
S(Base + k :AdmAdv)r(.)	0.014	0.207 ± 0.056
S(Base + 50TexAdv)r($k,s\&a$)	0.014	0.277 ± 0.072
S(Base + k :F1Adv + $s\&a$:F1Adv)r($k,s\&a$)	0.013	0.307 ± 0.076
S(Base + k :IntAdv + $s\&a$:F1Adv)r($k,s\&a$)	0.013	0.227 ± 0.093
S(Base + CanDisF1Adv + k :Sex)r($k,s\&a$)	0.011	0.285 ± 0.101
S(Base + k :CanDisF1Adv + $s\&a$:F1Adv)r(.)	0.011	0.201 ± 0.079
S(Base + k :CanDis50TexAdv + $s\&a$:F1Adv)r($k,s\&a$)	0.010	0.223 ± 0.09
S(Base + $s\&a$:F1Adv + k :Sex)r(.)	0.009	0.334 ± 0.077
S(Base + k :CanDisF1Adv + $s\&a$:F1Adv)r($k,s\&a$)	0.009	0.229 ± 0.095

S(Base + CanDis50TexAdv)r(.)	0.009	0.219 ± 0.057
S(Base + k:50TexAdv + s&a:F1Adv + k:Sex)r(k,s&a)	0.009	0.288 ± 0.094
S(Base + k:F1Adv + s&a:F1Adv + k:Sex)r(.)	0.008	0.305 ± 0.077
S(Base + 50TexAdv + k:Sex)r(.)	0.008	0.269 ± 0.074
S(Base + k:IntAdv + s&a:F1Adv + k:Sex)r(.)	0.007	0.234 ± 0.101
S(Base + CanDis50TexAdv)r(k,s&a)	0.006	0.252 ± 0.076
S(Base + s&a:F1Adv + k:Sex)r(k,s&a)	0.006	0.365 ± 0.093
S(Base + IntAdv)r(.)	0.006	0.216 ± 0.057
S(Base + k:F1Adv + s&a:F1Adv + k:Sex)r(k,s&a)	0.006	0.336 ± 0.095
S(Base + k:CanDis50TexAdv + s&a:F1Adv + k:Sex)r(.)	0.005	0.226 ± 0.099
S(Base + 50TexAdv + k:Sex)r(k,s&a)	0.005	0.3 ± 0.091
S(Base + k:IntAdv + s&a:F1Adv + k:Sex)r(k,s&a)	0.005	0.253 ± 0.112
S(Base + k:(AdmAdv) + k:Sex)r(k,s&a)	0.005	0.255 ± 0.095
S(Base + k:(AdmAdv) + k:Sex)r(.)	0.005	0.224 ± 0.077
S(Base + k:50TexAdv)r(.)	0.005	0.231 ± 0.056
S(Base + IntAdv)r(k,s&a)	0.005	0.252 ± 0.076
S(Base + k:CanDisF1Adv + s&a:F1Adv + k:Sex)r(.)	0.005	0.23 ± 0.1
S(Base + k:50TexAdv)r(k,s&a)	0.004	0.266 ± 0.075
S(Base + k:CanDis50TexAdv + s&a:F1Adv + k:Sex)r(k,s&a)	0.004	0.242 ± 0.109
S(Base + CanDis50TexAdv + k:Sex)r(.)	0.004	0.244 ± 0.077
S(Base + k:F1Adv)r(.)	0.004	0.267 ± 0.053
S(Base + k:CanDisF1Adv + s&a:F1Adv + k:Sex)r(k,s&a)	0.003	0.25 ± 0.113
S(Base + IntAdv + k:Sex)r(.)	0.003	0.247 ± 0.077
S(Base + CanDis50TexAdv + k:Sex)r(k,s&a)	0.003	0.274 ± 0.093
S(Base + k:(F1Adv + IntAdv))r(.)	0.002	0.199 ± 0.079
S(Base)r(.)	0.002	0.29 ± 0.053
S(Base + IntAdv + k:Sex)r(k,s&a)	0.002	0.279 ± 0.094
S(Base + k:CanDis50TexAdv)r(.)	0.002	0.198 ± 0.078
S(Base + k:(50TexAdv) + k:Sex)r(.)	0.002	0.256 ± 0.079
S(Base + k:IntAdv)r(k,s&a)	0.002	0.226 ± 0.093
S(Base + k:CanDis50TexAdv)r(k,s&a)	0.002	0.223 ± 0.091
S(Base)r(k,s&a)	0.002	0.33 ± 0.074
S(Base + k:IntAdv)r(.)	0.002	0.199 ± 0.078
S(Base + k:(F1Adv) + k:Sex)r(.)	0.002	0.299 ± 0.077
S(Base + k:(50TexAdv) + k:Sex)r(k,s&a)	0.002	0.285 ± 0.095
S(Base + k:Sex)r(.)	0.001	0.331 ± 0.077
S(Base + k:(F1Adv + IntAdv) + k:Sex)r(.)	0.001	0.226 ± 0.099
S(Base + k:Sex)r(k,s&a)	0.001	0.365 ± 0.094
S(Base + k:(IntAdv) + k:Sex)r(.)	0.001	0.23 ± 0.099
S(Base + k:CanDis50TexAdv + k:Sex)r(.)	0.001	0.221 ± 0.097
S(Base + k:(IntAdv) + k:Sex)r(k,s&a)	0.001	0.25 ± 0.111

S(Base + k :CanDis50TexAdv + k :Sex) $r(k,s&a)$	0.001	0.239 ± 0.109
---	-------	---------------

^a The base survival model represents survival differing between kittens, females age 1 and 2, females 3 and older, males age 1-3, and males 4 and older (Hostetler et al., 2010).

^b 2 ancestry categories: 1) canonical and backcrossed to canonical; 2) backcrossed to Everglades, backcrossed to Texas, and F_1 .

^c 2 ancestry categories: 1) canonical, backcrossed to canonical, backcrossed to Everglades, and backcrossed to Texas; and 2) F_1 .

^d The same recovery probability for all panthers.

^e Recovery probabilities differing between kittens and older panthers.

^f 3 ancestry categories: 1) canonical; 2) backcrossed to canonical, backcrossed to Everglades, and backcrossed to Texas; and 3) F_1 .

^g Kitten survival differing by sex.

^h 2 ancestry categories: 1) canonical, backcrossed to canonical, and backcrossed to Everglades; 2) backcrossed to Texas, and F_1 .

ⁱ 2 ancestry categories: 1) canonical; 2) backcrossed to canonical, backcrossed to Everglades, backcrossed to Texas, and F_1 .

^j 3 ancestry categories: 1) canonical; 2) backcrossed to canonical and backcrossed to Everglades; 3) backcrossed to Texas and F_1 .

Table L-4. Models for sub-adult and adult canonical probability of breeding. Includes Akaike model weights (w_i), estimates of sub-adult female canonical probability of breeding ($q_{sa}^{(c)}$), prime-adult female canonical probability of breeding ($q_{pa}^{(c)}$), older-adult female canonical probability of breeding ($q_{oa}^{(c)}$), the effects of abundance index and abundance index squared on monthly complementary log-log probability of breeding ($\beta_{abundance}$ and $\beta_{abundance2}$, respectively), and temporal standard deviation (σ_t). Density-independent models are in bold. Probability of breeding estimates for density-dependent models are for abundance index 0.

Model	w_i	$q_{sa}^{(c)}$	$q_{pa}^{(c)}$	$q_{oa}^{(c)}$	$\beta_{abundance}$	$\beta_{abundance2}$	σ_t
Age2 ^a + Ancest2 ^b + Abundance ^c	0.183	0.301 ± 0.100	0.301 ± 0.100	0.024 ± 0.025	0.009 ± 0.005	0	0.378
Age2 + Ancest2	0.107	0.498 ± 0.040	0.498 ± 0.040	0.038 ± 0.037	0	0	0.420
Age1 ^d + Ancest2 + Abundance	0.088	0.271 ± 0.102	0.326 ± 0.110	0.025 ± 0.026	0.008 ± 0.005	0	0.373
Age2 + Ancest1^e	0.084	0.443 ± 0.060	0.443 ± 0.060	0.038 ± 0.037	0	0	0.420
Age2 + Ancest2 + Abundance + Abundance ²	0.076	0.412 ± 0.275	0.412 ± 0.275	0.035 ± 0.044	-0.003 ± 0.025	0.0001 ± 0.0002	0.378
Age2 + Ancest1 + Abundance	0.076	0.305 ± 0.102	0.305 ± 0.102	0.026 ± 0.027	0.008 ± 0.006	0	0.378
Age1 + Ancest2	0.067	0.416 ± 0.089	0.518 ± 0.044	0.038 ± 0.037	0	0	0.407
Age1 + Ancest1	0.061	0.353 ± 0.092	0.458 ± 0.062	0.038 ± 0.037	0	0	0.407
Age1 + Ancest1 + Abundance	0.039	0.272 ± 0.103	0.337 ± 0.115	0.027 ± 0.028	0.006 ± 0.006	0	0.373
Age1 + Ancest2 + Abundance + Abundance ²	0.035	0.350 ± 0.262	0.410 ± 0.273	0.033 ± 0.042	-0.001 ± 0.025	0.0001 ± 0.0002	0.373
Age2 + Ancest1 + Abundance + Abundance ²	0.033	0.444 ± 0.292	0.444 ± 0.292	0.040 ± 0.052	-0.007 ± 0.026	0.0001 ± 0.0002	0.378
Age2 + Abundance	0.030	0.274 ± 0.094	0.274 ± 0.094	0.024 ± 0.025	0.009 ± 0.005	0	0.378
Age2	0.019	0.459 ± 0.037	0.459 ± 0.037	0.038 ± 0.037	0	0	0.420
Age1 + Ancest1 + Abundance + Abundance ²	0.016	0.376 ± 0.277	0.451 ± 0.293	0.040 ± 0.051	-0.005 ± 0.026	0.0001 ± 0.0002	0.373
Age2 + Abundance + Abundance ²	0.016	0.473 ± 0.297	0.473 ± 0.297	0.046 ± 0.057	-0.012 ± 0.025	0.0001 ± 0.0002	0.378
Age1 + Abundance	0.014	0.249 ± 0.096	0.297 ± 0.104	0.025 ± 0.026	0.008 ± 0.005	0	0.373
Age2 + Ancest3 + Abundance	0.012	0.273 ± 0.094	0.273 ± 0.094	0.023 ± 0.024	0.010 ± 0.006	0	0.378
Age1	0.012	0.382 ± 0.083	0.477 ± 0.041	0.038 ± 0.037	0	0	0.407
Age2 + Ancest3^f	0.007	0.443 ± 0.060	0.443 ± 0.060	0.038 ± 0.037	0	0	0.420
Age1 + Abundance + Abundance ²	0.007	0.418 ± 0.292	0.476 ± 0.296	0.044 ± 0.055	-0.011 ± 0.025	0.0001 ± 0.0002	0.373
Age2 + Ancest3 + Abundance + Abundance ²	0.006	0.458 ± 0.297	0.458 ± 0.297	0.043 ± 0.055	-0.010 ± 0.026	0.0001 ± 0.0002	0.378
Age1 + Ancest3 + Abundance	0.005	0.250 ± 0.096	0.295 ± 0.104	0.024 ± 0.025	0.009 ± 0.006	0	0.373

Age1 + Ancest3	0.005	0.361 ± 0.093	0.457 ± 0.062	0.038 ± 0.037	0	0	0.407
Age1 + Ancest3 + Abundance + Abundance ²	0.003	0.410 ± 0.292	0.465 ± 0.298	0.042 ± 0.054	-0.009 ± 0.026	0.0001 ± 0.0002	0.373

^a Age2 divides panthers into young-adults (1-10 years old) and older-adults (≥10 years old).

^b Ancest2 divides panthers into two ancestry categories: F₁ admixed, and other admixed and pre-introgression type combined.

^c Abundance refers to a linear trend in monthly complementary log-log probability of breeding by abundance index.

^d Age1 divides the female panthers into sub-adults (1-2.5 years old), prime-adults (2.5-10 years old) and older-adults (≥10 years old).

^e Ancest1 divides panthers into three ancestry categories: F₁ admixed, other admixed, and pre-introgression type.

^f Ancest3 divides panthers into two ancestry categories: pre-introgression type, and other admixed and F₁ admixed combined.

Table L-5. Models for sub-adult and adult average number of kittens produced (for canonical females that bred in a year). Includes Akaike model weights (w_i), estimates of sub-adult canonical dam kittens ($v_{sa}^{(c)}$), adult canonical dam kittens ($v_a^{(c)}$), and the effects of abundance index on cumulative logit number of kittens ($\beta_{abundance}$). Density-independent models are in bold. Number of kittens estimates for density-dependent models are for abundance index 0.

Model	w_i	$v_{sa}^{(c)}$	$v_a^{(c)}$	$\beta_{abundance}$
Age3^a	0.186	3.13 ± 0.28	2.69 ± 0.12	0
Constant^b	0.160	2.76 ± 0.12	2.76 ± 0.12	0
Age3 + Abundance ^c	0.089	2.87 ± 0.44	2.41 ± 0.38	0.006 ± 0.009
Age3 + Ancest2^d	0.082	3.15 ± 0.28	2.71 ± 0.13	0
Ancest2	0.071	2.79 ± 0.12	2.79 ± 0.12	0
Age3 + Ancest3^e	0.069	3.11 ± 0.33	2.67 ± 0.19	0
Abundance	0.069	2.55 ± 0.39	2.55 ± 0.39	0.005 ± 0.009
Ancest3	0.061	2.73 ± 0.19	2.73 ± 0.19	0
Age3 + Ancest2 + Abundance	0.038	2.90 ± 0.45	2.45 ± 0.39	0.006 ± 0.009
Age3 + Ancest3 + Abundance	0.034	2.86 ± 0.44	2.40 ± 0.39	0.008 ± 0.010
Age3 + Ancest1^f	0.031	3.10 ± 0.33	2.67 ± 0.19	0
Ancest2 + Abundance	0.030	2.59 ± 0.40	2.59 ± 0.40	0.005 ± 0.009
Ancest1	0.029	2.73 ± 0.19	2.73 ± 0.19	0
Ancest3 + Abundance	0.025	2.55 ± 0.39	2.55 ± 0.39	0.005 ± 0.010
Age3 + Ancest1 + Abundance	0.014	2.90 ± 0.45	2.44 ± 0.40	0.007 ± 0.011
Ancest1 + Abundance	0.011	2.60 ± 0.40	2.60 ± 0.40	0.004 ± 0.010

^a Age3 divides female panthers into sub-adults (1-2.5 years old) and adults (≥ 2.5 years old).

^b No predictor variables.

^c Abundance refers to a linear trend in log-hazard by abundance index.

^d Ancest2 divides panthers into two ancestry categories: F₁ admixed, and other admixed and pre-introgression type combined.

^e Ancest3 divides panthers into two ancestry categories: pre-introgression type, and other admixed and F₁ admixed combined.

^f Ancest1 divides panthers into three ancestry categories: F₁ admixed, other admixed, and pre-introgression type.

LIST OF REFERENCES

- Agresti, A., 2007. An introduction to categorical data analysis, 2nd edn. John Wiley & Sons, Hoboken, NJ, USA.
- Alberts, S.C., Altmann, J., 2003. Matrix models for primate life history analysis, in: Kappeler, P.M., Pereira, M.E. (Eds.), Primate life histories and socioecology. University of Chicago Press, Chicago, IL, USA, pp. 66-102.
- Allendorf, F.W., Leary, R.F., Spruell, P., Wenburg, J.K., 2001. The problems with hybrids: Setting conservation guidelines. *Trends in Ecology & Evolution* 16, 613-622.
- Arnold, M.L., Hodges, S.A., 1995. Are natural hybrids fit or unfit relative to their parents? *Trends in Ecology & Evolution* 10, 67-71.
- Ashman, D.L., Greer, K., 1976. Age techniques, in: Christensen, G.C., Fisher, R.J. (Eds.), Transactions of the Mountain Lion Workshop. U.S. Fish and Wildlife Service, Portland, Oregon.
- Bakker, V.J., Doak, D.F., Roemer, G.W., Garcelon, D.K., Coonan, T.J., Morrison, S.A., Lynch, C., Ralls, K., Shaw, R., 2009. Incorporating ecological drivers and uncertainty into a demographic population viability analysis for the island fox. *Ecological Monographs* 79, 77-108.
- Ball, S.J., Lindenmayer, D.B., Possingham, H.P., 2003. The predictive accuracy of population viability analysis: a test using data from two small mammal species in a fragmented landscape. *Biodiversity and Conservation* 12, 2393-2413.
- Barone, M.A., Roelke, M.E., Howard, J., Brown, J.L., Anderson, A.E., Wildt, D.E., 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.
- Beier, P., Vaughan, M.R., Conroy, M.J., Quigley, H., 2003. An analysis of scientific literature related to the Florida panther. Florida Fish and Wildlife Conservation Commission, Tallahassee.
- Beier, P., Vaughan, M.R., Conroy, M.J., Quigley, H., 2006. Evaluating scientific inferences about the Florida panther. *Journal of Wildlife Management* 70, 236-245.
- Belden, R.C., Frankenberger, W.B., 1990. Biology of a feral hog population in south central Florida. *Proceedings of Annual Conference of Southeastern Association of Fish and Wildlife Agencies* 44, 231-242.
- Belden, R.C., Frankenberger, W.B., McBride, R.T., Schwikert, S.T., 1988. Panther habitat use in southern Florida. *Journal of Wildlife Management* 52, 660-663.

- Benson, J.F., Hostetler, J.A., Onorato, D.P., Johnson, W.E., Roelke, M.E., O'Brien, S.J., Jansen, D., Oli, M.K., in revision. Intentional genetic introgression improves survival of F₁ adults and sub-adults in a small, inbred felid population. *Journal of Animal Ecology*.
- Benson, J.F., Lotz, M.A., Jansen, D., 2008. Natal den selection by Florida panthers. *Journal of Wildlife Management* 72, 405-410.
- Birchler, J.A., Auger, D.L., Riddle, N.C., 2003. In search of the molecular basis of heterosis. *Plant Cell* 15, 2236-2239.
- Bishop, C.J., White, G.C., Lukacs, P.M., 2008. Evaluating dependence among mule deer siblings in fetal and neonatal survival analyses. *Journal of Wildlife Management* 72, 1085-1093.
- Bolker, B.M., Brooks, M.E., Clark, C.J., Geange, S.W., Poulsen, J.R., Stevens, M.H.H., White, J.-S.S., 2009. Generalized linear mixed models: a practical guide for ecology and evolution. *Trends in Ecology & Evolution* 24, 127-135.
- Brito, D., 2009. Genetic consequences of population subdivision: the marsupial *Micoureus paraguayanus* (Mammalia: Didelphimorphia) as a case study. *Zoologia* 26, 684-693.
- Brook, B.W., Burgman, M.A., Akçakaya, H.R., O'Grady, J.J., Frankham, R., 2002a. Critiques of PVA ask the wrong questions: Throwing the heuristic baby out with the numerical bath water. *Conservation Biology* 16, 262-263.
- Brook, B.W., O'Grady, J.J., Chapman, A.P., Burgman, M.A., Akçakaya, H.R., Frankham, R., 2000. Predictive accuracy of population viability analysis in conservation biology. *Nature* 404, 385-387.
- Brook, B.W., Tonkyn, D.W., O'Grady, J.J., Frankham, R., 2002b. Contribution of inbreeding to extinction risk in threatened species. *Conservation Ecology* 6, 16.
- Buerkle, C.A., Morris, R.J., Asmussen, M.A., Rieseberg, L.H., 2000. The likelihood of homoploid hybrid speciation. *Heredity* 84, 441-451.
- Burke, J.M., Arnold, M.L., 2001. Genetics and the fitness of hybrids. *Annual Review of Genetics* 35, 31-52.
- Burnham, K.P., 1993. A theory for combined analysis of ring recovery and recapture data, in: Lebreton, J.-D., North, P.M. (Eds.), *Marked individuals in the study of bird population*. Birkhäuser Verlag, Boston, MA, pp. 199-213.
- Burnham, K.P., Anderson, D.R., 2002. *Model selection and multimodel inference*, 2nd edn. Springer, New York.

- Cam, E., Link, W.A., Cooch, E.G., Monnat, J.Y., Danchin, E., 2002. Individual covariation in life-history traits: Seeing the trees despite the forest. *American Naturalist* 159, 96-105.
- Campbell, D.R., Waser, N.M., 2001. Genotype-by-environment interaction and the fitness of plant hybrids in the wild. *Evolution* 55, 669-676.
- Caswell, H., 2001. *Matrix population models*, Second edn. Sinauer Associates, Sunderland, MA.
- Caswell, H., 2005. Sensitivity analysis of the stochastic growth rate: Three extensions. *Australian & New Zealand Journal of Statistics* 47, 75-85.
- Caughley, G., 1994. Directions in conservation biology. *Journal of Animal Ecology* 63, 215-244.
- Caughley, G., Gunn, A., 1996. *Conservation biology in theory and practice*. Blackwell Science, Cambridge, MA, USA.
- Charpentier, M.J.E., Tung, J., Altmann, J., Alberts, S.C., 2008. Age at maturity in wild baboons: genetic, environmental and demographic influences. *Molecular Ecology* 17, 2026-2040.
- Comiskey, E.J., Bass, O.L., Gross, L.J., McBride, R.T., Salinas, R., 2002. Panthers and forests in South Florida: an ecological perspective. *Conservation Ecology* 6.
- Cooch, E., White, G.C. eds., 2008. *Program MARK - 'a gentle introduction'* 7th Edition. <http://www.phidot.org/software/mark/docs/book/>.
- Cooley, H.S., Wielgus, R.B., Koehler, G., Maletzke, B., 2009. Source populations in carnivore management: cougar demography and emigration in a lightly hunted population. *Animal Conservation* 12, 321-328.
- Coulson, T., Mace, G.M., Hudson, E., Possingham, H.P., 2001. The use and abuse of population viability analysis. *Trends In Ecology & Evolution* 16, 219-221.
- Cox, D.R., 1972. Regression models and life-tables. *Journal of the Royal Statistical Society Series B-Statistical Methodology* 34, 187-220.
- Creel, S., 2006. Recovery of the Florida panther - genetic rescue, demographic rescue, or both? Response to Pimm et al. (2006). *Animal Conservation* 9, 125-126.
- Crnokrak, P., Roff, D.A., 1999. Inbreeding depression in the wild. *Heredity* 83, 260-270.
- Crow, J.F., 1948. Alternative hypotheses of hybrid vigor. *Genetics* 33, 477-487.
- Culver, M., Johnson, W.E., Pecon-Slattery, J., O'Brien, S.J., 2000. Genomic ancestry of the American puma (*Puma concolor*). *Journal of Heredity* 91, 186-197.

- Cunningham, M.W., Brown, M.A., Shindle, D.B., Terrell, S.P., Hayes, K.A., Ferree, B.C., McBride, R.T., Blankenship, E.L., Jansen, D., Citino, S.B., Roelke, M.E., Kiltie, R.A., Troyer, J.L., O'Brien, S.J., 2008. Epizootiology and management of feline leukemia virus in the Florida puma. *Journal of Wildlife Diseases* 44, 537-552.
- Davis, J.B., Cox, R.R., Kaminski, R.M., Leopold, B.D., 2007. Survival of wood duck ducklings and broods in Mississippi and Alabama. *Journal of Wildlife Management* 71, 507-517.
- de Castro, F., Bolker, B.M., 2005. Mechanisms of disease-induced extinction. *Ecology Letters* 8, 117-126.
- Dees, C.S., Clark, J.D., Van Manen, F.T., 2001. Florida panther habitat use in response to prescribed fire. *Journal of Wildlife Management* 65, 141-147.
- Driscoll, C.A., Menotti-Raymond, M., Nelson, G., Goldstein, D., O'Brien, S.J., 2002. Genomic microsatellites as evolutionary chronometers: A test in wild cats. *Genome Research* 12, 414-423.
- Ebert, D., Haag, C., Kirkpatrick, M., Riek, M., Hottinger, J.W., Pajunen, V.I., 2002. A selective advantage to immigrant genes in a *Daphnia* metapopulation. *Science* 295, 485-488.
- Edmands, S., 2007. Between a rock and a hard place: evaluating the relative risk of inbreeding and outbreeding for conservation and management. *Molecular Ecology* 16, 463-475.
- Efron, B., Tibshirani, R.J., 1998. An introduction to the bootstrap. Chapman and Hall/CRC Press, Boca Raton, Florida.
- Ellner, S.P., Fieberg, J., 2003. Using PVA for management despite uncertainty: Effects of habitat, hatcheries, and harvest on salmon. *Ecology* 84, 1359-1369.
- Ellner, S.P., Fieberg, J., Ludwig, D., Wilcox, C., 2002. Precision of population viability analysis. *Conservation Biology* 16, 258-261.
- Federico, P., Canziani, G.A., 2005. Modeling the population dynamics of capybara *Hydrochaeris hydrochaeris*: a first step towards a management plan. *Ecological Modelling* 186, 111-121.
- Fergus, C., 1991. The Florida panther verges on extinction. *Science* 251, 1178-1180.
- Fergus, C., 1998. Swamp screamer: at large with the Florida panther. University Press of Florida, Gainesville, Florida USA.
- Ferreira, Á.G.A., Amos, W., 2006. Inbreeding depression and multiple regions showing heterozygote advantage in *Drosophila melanogaster* exposed to stress. *Molecular Ecology* 15, 3885-3893.

- Fieberg, J., DelGiudice, G.D., 2009. What time is it? Choice of time origin and scale in extended proportional hazards models. *Ecology* 90, 1687-1697.
- Fieberg, J., Ellner, S.P., 2001. Stochastic matrix models for conservation and management: a comparative review of methods. *Ecology Letters* 4, 244-266.
- Fisher, D.O., Hoyle, S.D., Blomberg, S.P., 2000. Population dynamics and survival of an endangered wallaby: A comparison of four methods. *Ecological Applications* 10, 901-910.
- Fitzpatrick, B.M., Shaffer, H.B., 2007. Hybrid vigor between native and introduced salamanders raises new challenges for conservation. *Proceedings of the National Academy of Sciences of the United States of America* 104, 15793-15798.
- Fleming, D.M., 1994. Distribution, abundance, and demography of white-tailed deer in the Everglades, In *Proceedings of the Florida Panther Conference*. ed. Jordan, D. U.S. Fish and Wildlife Service.
- Frankham, R., Ballou, J.D., Briscoe, D.A., 2002. *Introduction to conservation genetics*. Cambridge University Press, Cambridge, UK.
- Franklin, I.R., 1980. Evolutionary change in small populations, in: Soule, M.E., Wilcox, B.A. (Eds.), *Conservation Biology: An Evolutionary-Ecological Perspective*. Sinauer Associates, Sunderland, Massachusetts, USA, pp. 135-149.
- Fujiwara, M., Caswell, H., 2001. Demography of the endangered North Atlantic right whale. *Nature* 414, 537-541.
- FWC, 2008. Annual report on the research and management of Florida panthers: 2007-2008. Fish and Wildlife Research Institute and Division of Habitat and Species Conservation, Naples, Florida, USA.
- Garrison, E.P., McCown, J.W., Oli, M.K., 2007. Reproductive ecology and cub survival of Florida black bears. *Journal of Wildlife Management* 71, 720-727.
- Gascoigne, J., Berec, L., Gregory, S., Courchamp, F., 2009. Dangerously few liaisons: a review of mate-finding Allee effects. *Population Ecology* 51, 355-372.
- Gelman, A., 1996. Inference and monitoring convergence, in: Gilks, W.R., Richardson, S., Spiegelhalter, D.J. (Eds.), *Markov Chain Monte Carlo in Practice*. Chapman and Hall/CRC, Boca Raton, Florida, USA, pp. 131-143.
- Gerber, L.R., McCallum, H., Lafferty, K.D., Sabo, J.L., Dobson, A., 2005. Exposing extinction risk analysis to pathogens: Is disease just another form of density dependence? *Ecological Applications* 15, 1402-1414.

- Good, T.P., Ellis, J.C., Annett, C.A., Pierotti, R., 2000. Bounded hybrid superiority in an avian hybrid zone: Effects of mate, diet, and habitat choice. *Evolution* 54, 1774-1783.
- Grant, P.R., Grant, B.R., 1992. Hybridization of bird species. *Science* 256, 193-197.
- Greenwood, P.J., 1980. Mating Systems, Philopatry And Dispersal In Birds And Mammals. *Animal Behaviour* 28, 1140-1162.
- Greig, J.C., 1979. Principles of genetic conservation in relation to wildlife management in southern Africa. *South African Journal of Wildlife Research* 9, 57-78.
- Gross, L., 2005. Why not the best? How science failed the Florida panther. *PLoS Biology* 3, 1525-1531.
- Hallerman, E.M., 2003. Coadaptation and outbreeding depression, in: Hallerman, E.M. (Ed.), *Population Genetics: Principles and Applications for Fisheries Scientists*. American Fisheries Society, Bethesda, Maryland, USA, pp. 239-259.
- Heisey, D.M., Patterson, B.R., 2006. A review of methods to estimate cause-specific mortality in presence of competing risks. *Journal of Wildlife Management* 70, 1544-1555.
- Henle, K., Sarre, S., Wiegand, K., 2004. The role of density regulation in extinction processes and population viability analysis. *Biodiversity and Conservation* 13, 9-52.
- Henry, J.A., Portier, K.M., Coyne, J., 1994. *The climate and weather of Florida*. Pineapple Press, Sarasota, FL.
- Heppell, S.S., Caswell, H., Crowder, L.B., 2000. Life histories and elasticity patterns: Perturbation analysis for species with minimal demographic data. *Ecology* 81, 654-665.
- Heschel, M.S., Paige, K.N., 1995. Inbreeding depression, environmental-stress, and population-size variation in scarlet-gilia (*Ipomopsis aggregata*). *Conservation Biology* 9, 126-133.
- Hostetler, J.A., Onorato, D.P., Nichols, J.D., Johnson, W.E., Roelke, M.E., O'Brien, S.J., Jansen, D., Oli, M.K., 2010. Genetic introgression and the survival of Florida panther kittens. *Biological Conservation* 143, 2789 - 2796.
- Janis, M.W., Clark, J.D., 2002. Responses of Florida panthers to recreational deer and hog hunting. *Journal of Wildlife Management* 66, 839-848.
- Johnson, K.G., Land, E.D., Lotz, M.A., 1997. Florida panther genetic restoration and management. Annual Performance Report. Florida Fish and Wildlife Conservation Commission, Tallahassee, Florida.

- Johnson, W.E., Onorato, D.P., Roelke, M.E., Land, E.D., Cunningham, M., Belden, C., McBride, R., Jansen, D., Lotz, M.A., Shindle, D.B., Howard, J., Wildt, D.E., Penfold, L.M., Hostetler, J.A., Oli, M.K., O'Brien, S.J., 2010. Genetic restoration of the Florida panther. *Science* 329, 1641-1645.
- Kauffman, M.J., Frick, W.F., Linthicum, J., 2003. Estimation of habitat-specific demography and population growth for peregrine falcons in California. *Ecological Applications* 13, 1802-1816.
- Kautz, R., Kawula, R., Hootor, T., Comiskey, J., Jansen, D., Jennings, D., Kasbohm, J., Mazzotti, F., McBride, R., Richardson, L., Root, K., 2006. How much is enough? Landscape-scale conservation for the Florida panther. *Biological Conservation* 130, 118-133.
- Keller, L.F., Arcese, P., Smith, J.N.M., Hochachka, W.M., Stearns, S.C., 1994. Selection against inbred song sparrows during a natural population bottleneck. *Nature* 372, 303-388.
- Laake, J., Rexstad, E., 2010. RMark - an alternative approach to building linear models in MARK, in: Cooch, E., White, G.C. (Eds.), *Program MARK - 'a gentle introduction'* 9th Edition. <http://www.phidot.org/software/mark/docs/book/>, pp. C1-C108.
- Lambert, C.M.S., Wielgus, R.B., Robinson, H.S., Katnik, D.D., Cruickshank, H.S., Clarke, R., Almack, J., 2006. Cougar population dynamics and viability in the Pacific Northwest. *Journal of Wildlife Management* 70, 246-254.
- Land, E.D., Garman, D.R., Holt, G.A., 1998. Monitoring female Florida panthers via cellular telephone. *Wildlife Society Bulletin* 26, 29-31.
- Land, E.D., Shindle, D.B., Kawula, R.J., Benson, J.F., Lotz, M.A., Onorato, D.P., 2008. Florida panther habitat selection analysis of concurrent GPS and VHF telemetry data. *Journal of Wildlife Management* 72, 633-639.
- Laundré, J.W., Hernández, L., Clark, S.G., 2007. Numerical and demographic responses of pumas to changes in prey abundance: testing current predictions. *Journal of Wildlife Management* 71, 345-355.
- Levin, D.A., Francisco-Ortega, J., Jansen, R.K., 1996. Hybridization and the extinction of rare plant species. *Conservation Biology* 10, 10-16.
- Lewontin, R.C., Birch, L.C., 1966. Hybridization as a source of variation for adaptation to new environments. *Evolution* 20, 315-336.
- Lindenmayer, D.B., Possingham, H.P., Lacy, R.C., McCarthy, M.A., Pope, M.L., 2003. How accurate are population models? Lessons from landscape-scale tests in a fragmented system. *Ecology Letters* 6, 41-47.

- Logan, K.A., Sweanor, L.L., 2001. Desert puma: evolutionary ecology and conservation of an enduring carnivore. Island Press, Washington, DC.
- Loison, A., Sæther, B.-E., Jerstad, K., Røstad, O.W., 2002. Disentangling the sources of variation in the survival of the European dipper. *Journal of Applied Statistics* 29, 289-304.
- Lotz, M.A., Land, E.D., Cunningham, M.W., Ferree, B.C., 2005. Florida panther annual report 2004-2005, p. 74 pp. Florida Fish and Wildlife Conservation Commission, Tallahassee, Florida, USA.
- Lukacs, P.M., White, G.C., Watkins, B.E., Kahn, R.H., Banulis, B.A., Finley, D.J., Holland, A.A., Martens, J.A., Vayhinger, J., 2009. Separating components of variation in survival of mule deer in Colorado. *Journal of Wildlife Management* 73, 817-826.
- Madsen, T., Shine, R., Olsson, M., Wittzell, H., 1999. Restoration of an inbred adder population. *Nature* 402, 34-35.
- Maehr, D.S., 1992. Florida panther, in: Humphrey, S.R. (Ed.), *Rare and endangered biota of Florida, volume I. mammals*. University Press of Florida, Gainesville, FL, pp. 176-189.
- Maehr, D.S., Caddick, G.B., 1995. Demographics and genetic introgression in the Florida panther. *Conservation Biology* 9, 1295-1298.
- Maehr, D.S., Crowley, P., Cox, J.J., Lacki, M.J., Larkin, J.L., Hctor, T.S., Harris, L.D., Hall, P.M., 2006. Of cats and Haruspices: genetic intervention in the Florida panther. Response to Pimm et al. (2006). *Animal Conservation* 9, 127-132.
- Maehr, D.S., Lacy, R.C., Land, E.D., Bass, O.L., Hctor, T., 2002a. Evolution of population viability assessments for the Florida panther: a multiperspective approach, in: Beissinger, S.R., McCullough, D.R. (Eds.), *Population viability analysis*. University of Chicago Press, Chicago, pp. 284-311.
- Maehr, D.S., Land, E.D., Roof, J.C., McCown, J.W., 1990. Day beds, natal dens, and activity of Florida panthers, In *Annual Conference of Southeast Fish and Wildlife Agencies*. pp. 310-318.
- Maehr, D.S., Land, E.D., Shindle, D.B., Bass, O.L., Hctor, T.S., 2002b. Florida panther dispersal and conservation. *Biological Conservation* 106, 187-197.
- Maehr, D.S., Roof, J.C., Land, E.D., McCown, J.W., 1989. First reproduction of a panther (*Felis concolor coryi*) in southwestern Florida, USA. *Mammalia* 53, 129-131.

- Maguire, L.A., Servheen, C., 1992. Integrating biological and sociological concerns in endangered species management: Augmentation of grizzly bear populations. *Conservation Biology* 6, 426-434.
- Mansfield, K.G., Land, E.D., 2002. Cryptorchidism in Florida panthers: Prevalence, features, and influence of genetic restoration. *Journal of Wildlife Diseases* 38, 693-698.
- McBride, R., 2002. Florida panther current verified population, distribution and highlights of field work: fall 2001 – winter 2002, p. 25. Prepared for Florida Panther SubTeam of MERIT, U.S. Fish and Wildlife Service, Vero Beach, FL, USA.
- McBride, R.T., McBride, R.T., McBride, R.M., McBride, C.E., 2008. Counting pumas by categorizing physical evidence. *Southeastern Naturalist* 7, 381-400.
- McCown, J.W., Maehr, D.S., Roboski, J., 1990. A portable cushion as a wildlife capture aid. *Wildlife Society Bulletin* 18, 34-36.
- Menotti-Raymond, M., David, V.A., Lyons, L.A., Schäffer, A.A., Tomlin, J.F., Hutton, M.K., O'Brien, S.J., 1999. A genetic linkage map of microsatellites in the domestic cat (*Felis catus*). *Genomics* 57, 9-23.
- Menotti-Raymond, M., David, V.A., Stephens, J.C., Lyons, L.A., O'Brien, S.J., 1997. Genetic individualization of domestic cats using feline STR loci for forensic applications. *Journal of Forensic Science* 42, 1039-1051.
- Miller, P.S., Lacy, R.C., 2005. VORTEX: a stochastic simulation of the extinction process. Version 9.50 user's manual. Conservation Breeding Specialist Group (SSC/IUCN), Apple Valley, MN, USA.
- Min, Y., Agresti, A., 2005. Random effect models for repeated measures of zero-inflated count data. *Statistical Modelling* 5, 1-19.
- Minch, E., Ruiz-Linares, A., Goldstein, D.B., 1995. MICROSAT. <http://hpgl.stanford.edu/projects/microsat/>.
- Moore, W.S., 1977. Evaluation of narrow hybrid zones in vertebrates. *Quarterly Review of Biology* 52, 263-277.
- Moore, W.S., Price, J.T., 1993. Nature of selection in the northern flicker hybrid zone and its implications for speciation theory, in: Harrison, R.G. (Ed.), *Hybrid Zones and the Evolutionary Process*. Oxford University Press, New York, New York, USA, pp. 196-225.
- Morris, W.F., Doak, D.F., 2002. *Quantitative conservation biology: theory and practice of population viability analysis*. Sinauer Associates, Sunderland, MA.

- Morris, W.F., Doak, D.F., 2005. How general are the determinants of the stochastic population growth rate across nearby sites? *Ecological Monographs* 75, 119-137.
- Newton, I., 2004. The recent declines of farmland bird populations in Britain: an appraisal of causal factors and conservation actions. *Ibis* 146, 579-600.
- Nichols, J.D., Kendall, W.L., Hines, J.E., Spendlow, J.A., 2004. Estimation of sex-specific survival from capture-recapture data when sex is not always known. *Ecology* 85, 3192-3201.
- Nilsson, T., 2004. Integrating effects of hunting policy, catastrophic events, and inbreeding depression, in PVA simulation: the Scandinavian wolf population as an example. *Biological Conservation* 115, 227-239.
- O'Brien, S.J., Roelke, M.E., Yuhki, N., Richards, K.W., Johnson, W.E., Franklin, W.L., Anderson, A.E., Bass, O.L., Belden, R.C., Martenson, J.S., 1990. Genetic introgression within the Florida panther *Felis concolor coryi*. *National Geographic Research* 6, 485-494.
- Oli, M.K., Dobson, F.S., 2003. The relative importance of life-history variables to population growth rate in mammals: Cole's prediction revisited. *American Naturalist* 161, 422-440.
- Onorato, D.P., Belden, R.C., Cunningham, M.W., Land, E.D., McBride, R.T., Roelke, M.E., 2010. Long-term research on the Florida panther (*Puma concolor coryi*): historical findings and future obstacles to population persistence, in: MacDonald, D.W., Loveridge, A.J. (Eds.), *Biology and conservation of wild felids*. Oxford University Press, Oxford, UK, pp. 452-469.
- Ortego, J., Calabuig, G., Cordero, P.J., Aparicio, J.M., 2007. Egg production and individual genetic diversity in lesser kestrels. *Molecular Ecology* 16, 2383-2392.
- Ozgul, A., Armitage, K.B., Blumstein, D.T., Oli, M.K., 2006. Spatiotemporal variation in survival rates: Implications for population dynamics of yellow-bellied marmots. *Ecology* 87, 1027-1037.
- Packer, C., Kosmala, M., Cooley, H.S., Brink, H., Pintea, L., Garshelis, D., Purchase, G., Strauss, M., Swanson, A., Balme, G., Hunter, L., Nowell, K., 2009. Sport hunting, predator control and conservation of large carnivores. *PLoS One* 4, e5941.
- Pankratz, V.S., de Andrade, M., Therneau, T.M., 2005. Random-effects cox proportional hazards model: General variance components methods for time-to-event data. *Genetic Epidemiology* 28, 97-109.
- Pimm, S.L., Bass, O.L., Dollar, L., 2006a. Of cats and Haruspices: genetic intervention in the Florida panther. Ockham and Garp. Reply to Maehr et al.'s (2006) response to Pimm et al. (2006). *Animal Conservation* 9, 133-134.

- Pimm, S.L., Dollar, L., Bass, O.L., 2006b. The genetic rescue of the Florida panther. *Animal Conservation* 9, 115-122.
- Pollock, K.H., 1981. Capture-recapture models allowing for age-dependent survival and capture rates. *Biometrics* 37, 521-529.
- Pollock, K.H., Winterstein, S.R., Bunck, C.M., Curtis, P.D., 1989. Survival analysis in telemetry studies: the staggered entry design. *Journal of Wildlife Management* 53, 7-15.
- Pritchard, J.K., Stephens, M., Donnelly, P., 2000. Inference of population structure using multilocus genotype data. *Genetics* 155, 945-959.
- R Development Core Team, 2010. R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria.
- Ralls, K., Ballou, J., 1983. Extinction: lessons from zoos, in: Schonewald-Cox, C.M., Chambers, S.M., MacBryde, B., Thomas, W.L. (Eds.), *Genetics and Conservation: A Reference for Managing Wild Animal and Plant Populations*. Benjamin/Cummings, Menlo Park, California, pp. 164-184.
- Rand, D.M., Harrison, R.G., 1989. Ecological genetics of a mosaic hybrid zone - mitochondrial, nuclear, and reproductive differentiation of crickets by soil type. *Evolution* 43, 432-449.
- Reed, J.M., Mills, L.S., Dunning, J.B., Menges, E.S., McKelvey, K.S., Frye, R., Beissinger, S.R., Anstett, M.-C., Miller, P., 2002. Emerging issues in population viability analysis. *Conservation Biology* 16, 7-19.
- Rhymer, J.M., Simberloff, D., 1996. Extinction by hybridization and introgression. *Annual Review of Ecology and Systematics* 27, 83-109.
- Richter, A.R., Labisky, R.F., 1985. Reproductive dynamics among disjunct white-tailed deer herds in Florida. *Journal of Wildlife Management* 49, 964-971.
- Robinson, H.S., Wielgus, R.B., Cooley, H.S., Cooley, S.W., 2008. Sink populations in carnivore management: Cougar demography and immigration in a hunted population. *Ecological Applications* 18, 1028-1037.
- Roelke, M.E., Forrester, D.J., Jacobson, E.R., Kollias, G.V., Scott, F.W., Barr, M.C., Evermann, J.F., Pirtle, E.C., 1993a. Seroprevalence of infectious-disease agents in free-ranging Florida panthers (*Felis concolor coryi*). *Journal of Wildlife Diseases* 29, 36-49.
- Roelke, M.E., Martenson, J.S., O'Brien, S.J., 1993b. The consequences of demographic reduction and genetic depletion in the endangered Florida panther. *Current Biology* 3, 340-350.

- Root, K.V., 2004. Florida panther (*Puma concolor coryi*): using models to guide recovery efforts, in: Akçakaya, H.R., Burgman, M.A., Kindvall, O., Wood, C.C., Sjogren-Gulve, P., Hatfield, J.S., McCarthy, M.A. (Eds.), Species Conservation and Management: Case Studies. Oxford University Press, New York, New York, USA, pp. 491-504.
- Rosenfield, J.A., Nolasco, S., Lindauer, S., Sandoval, C., Kodric-Brown, A., 2004. The role of hybrid vigor in the replacement of Pecos pupfish by its hybrids with sheepshead minnow. Conservation Biology 18, 1589-1598.
- Schortemeyer, J.L., Maehr, D.S., McCown, J.W., Land, E.D., Manor, P.D., 1991. Prey management for the Florida panther: A unique role for wildlife managers, In Transactions of the 56th North American Wildlife and Natural Resource Conference. pp. 512-526.
- Seal, U.S., 1994. A plan for genetic restoration and management of the Florida panther (*Felis concolor coryi*). Conservation Breeding Specialist Group, Apple Valley, Minnesota, USA.
- Shields, W.M., 1993. The natural and unnatural history of inbreeding and outbreeding, in: Thornhill, N.W. (Ed.), The natural history of inbreeding and outbreeding: theoretical and empirical perspectives. The University of Chicago Press, Chicago, Illinois, USA, pp. 143-169.
- Shull, G.H., 1908. The composition of a field of maize. Reports of the American Breeders Association 4, 296-301.
- Slate, J., Kruuk, L.E.B., Marshall, T.C., Pemberton, J.M., Clutton-Brock, T.H., 2000. Inbreeding depression influences lifetime breeding success in a wild population of red deer (*Cervus elaphus*). Proceedings of the Royal Society Of London Series B-Biological Sciences 267, 1657-1662.
- Slattery, M., Kamel, H.N., Ankisetty, S., Gochfeld, D.J., Hoover, C.A., Thacker, R.W., 2008. Hybrid vigor in a tropical Pacific soft-coral community. Ecological Monographs 78, 423-443.
- Stahl, J.T., Oli, M.K., 2006. Relative importance of avian life-history variables to population growth rate. Ecological Modelling 198, 23-39.
- Stoner, D.C., Wolfe, M.L., Choate, D.M., 2006. Cougar exploitation levels in Utah: Implications for demographic structure, population recovery, and metapopulation dynamics. Journal of Wildlife Management 70, 1588-1600.
- Sullivan, J.D., Jr., 2004. Florida's endangered species, threatened species, and species of special concern. Florida Fish and Wildlife Conservation Commission, Tallahassee, Florida, USA.

- Sweanor, L.L., Logan, K.A., Hornocker, M.G., 2000. Cougar dispersal patterns, metapopulation dynamics, and conservation. *Conservation Biology* 14, 798-808.
- Taylor, S.K., Buergelt, C.D., Roelke-Parker, M.E., Homer, B.L., Rotstein, D.S., 2002. Causes of mortality of free-ranging Florida panthers. *Journal of Wildlife Diseases* 38, 107-114.
- Templeton, A.R., 1999. Coadaptation, local adaptation, and outbreeding depression, in: Meffe, G.K., Carroll, C.R. (Eds.), *Principles of Conservation Biology*. Sinauer Associates, Sunderland, Massachusetts, USA, pp. 171-172.
- Thatcher, C.A., van Manen, F.T., Clark, J.D., 2009. A habitat assessment for Florida panther population expansion into central Florida. *Journal of Mammalogy* 90, 918-925.
- Therneau, T.M., Grambsch, P.M., 2000. *Modeling survival data: extending the Cox model*. Springer, New York.
- Tinker, M.T., Doak, D.F., Estes, J.A., Hatfield, B.B., Hatfield, B.B., Staedler, M.M., Bodkin, J.L., 2006. Incorporating diverse data and realistic complexity into demographic estimation procedures for sea otters. *Ecological Applications* 16, 2293-2312.
- Tuljapurkar, S.D., Horvitz, C.C., Pascarella, J.B., 2003. The many growth rates and elasticities of populations in random environments. *American Naturalist* 162, 489-502.
- USFWS, 2006. Florida panther recovery plan (*Puma concolor coryi*), 3rd revision, p. 216. United States Fish and Wildlife Service, Atlanta, GA, USA.
- Vaida, F., Blanchard, S., 2005. Conditional Akaike information for mixed-effects models. *Biometrika* 92, 351-370.
- Vrijenhoek, R.C., 1994. Genetic diversity and fitness in small populations, in: Loeschcke, V., Tomiuk, J., Jain, S.K. (Eds.), *Conservation genetics*. Birkhäuser Verlag, Boston, pp. 37-53.
- Westemeier, R.L., Brawn, J.D., Simpson, S.A., Esker, T.L., Jansen, R.W., Walk, J.W., Kershner, E.L., Bouzat, J.L., Paige, K.N., 1998. Tracking the long-term decline and recovery of an isolated population. *Science* 282, 1695-1698.
- White, G.C., 2000. Population viability analysis: data requirements and essential analyses, in: Boitani, L., Fuller, T.K. (Eds.), *Research techniques in animal ecology: controversies and consequences*. Columbia University Press, New York, NY USA, pp. 288-331.

- White, G.C., Burnham, K.P., Barker, R.J., 2009. Evaluation of a Bayesian MCMC random effects inference methodology for capture-mark-recapture data, in: Thomson, D.L., Cooch, E.G., Conroy, M.J. (Eds.), *Modeling demographic processes in marked populations*. Springer, New York, NY, pp. 1119-1127.
- White, G.C., Burnham, K.P., 1999. Program MARK: survival estimation from populations of marked animals. *Bird Study* 46, S120-S139.
- Whitlock, M.C., Ingvarsson, P.K., Hatfield, T., 2000. Local drift load and the heterosis of interconnected populations. *Heredity* 84, 452-457.
- Williams, B.K., Nichols, J.D., Conroy, M.J., 2002. *Analysis and management of animal populations*. Academic Press, San Diego, CA, USA.
- Wolf, D.E., Takebayashi, N., Rieseberg, L.H., 2001. Predicting the risk of extinction through hybridization. *Conservation Biology* 15, 1039-1053.
- Zedrosser, A., Dahle, B., Stoen, O.G., Swenson, J.E., 2009. The effects of primiparity on reproductive performance in the brown bear. *Oecologia* 160, 847-854.

BIOGRAPHICAL SKETCH

Jeffrey Hostetler was born in Cheverly, Maryland in 1974. He received a B. A. in biology from Oberlin College in 1996 (with minors in environmental studies and computer science). He worked at Patuxent Wildlife Research Center for several years, developing web applications and databases for the Breeding Bird Survey and other monitoring programs. He has done field work in Olympic National Forest, Washington, Tongass National Forest, Alaska, the Dolomite Mountains of Italy, and the outer banks of North Carolina, among other places. He earned an M.S. from North Carolina State University in 2004 in zoology (with minors in statistics and biomathematics), where his advisors were Ken Pollock and Jaime Collazo. His master's research focused on modeling the spring migration of semipalmated sandpipers. From 2004 through 2006, he worked at the University of Florida for Madan Oli and Franklin Percival, modeling the survival and population dynamics of northern bobwhite and Florida black bears. In 2006, he started as a Ph.D. student at the University of Florida under the direction of Madan Oli. He received his Ph.D. in wildlife ecology and conservation from the University of Florida in the fall of 2010.