Genetic introgression and the survival of Florida panther kittens

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ABSTRACT

Estimates of survival for the young of a species are critical for population models. These models can often be improved by determining the effects of management actions and population abundance on this demographic parameter. 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 (*Puma concolor coryi*) kittens (age 0–1 year). Overall, annual survival of Florida panther kittens was 0.323 ± 0.071 (SE), which was lower than estimates used in previous population models. In 1995, female pumas from Texas (*P. c. stanleyana*) were released into occupied panther range as part of an intentional introgression program to restore genetic variability. 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 results provide strong evidence for the positive population-level impact of genetic introgression on Florida panthers. Our approach to integrate data from multiple sources was effective at improving robustness as well as precision of estimates of Florida panther kitten survival, and can be useful in estimating vital rates for other elusive species with sparse data.

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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 and NPS, unpublished data). The Florida panther is now restricted to < 5% of its historic range in south Florida (Maehr et al. 2002), 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., 1993). Based on this recommendation, eight 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., 2006). There have been two other documented releases of captive pumas into south Florida, one resulting in panthers with partial Central American ancestry in the Everglades (Johnson et al., in press; O'Brien et al., 1990).

In 2003, the US 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., 2002) were not based on reliable inference methods and raised doubt on predictions regarding the persistence of the panther population (Beier et al., 2003, 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 analysed 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 Sweanor, 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).

2. Materials and methods

2.1. Field methods

Florida panthers and Texas pumas were captured and monitored by radio-telemetry from 1982 to 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 and 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 $\leqslant 12$ 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 $\leqslant 9$ 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.

2.2. 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 23 microsatellite loci following previously described PCR amplification conditions (Johnson et al., in press; Menotti-Raymond et al., 1999, 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 (see also Johnson et al., in press): 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 descendents of the introduced female Texas pumas released in 1995, except for six 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 (four 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 A.

2.3. 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 analysed annual kitten survival for periods extending from June to 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 Section 3), 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.

2.4. 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 B.

We analysed 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., 2009) 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., 2009). Transitions at these ages were impossible with a 1-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 ($\Delta QAIC_{ci}$, difference between $QAIC_c$ value of the ith 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 1000 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 1). The models for ancestry (Table 1A, models 3–6, Table 1B) and heterozygosity (Table 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

Table 1
(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 2). *s&a* indicates an effect on sub-adult and adult survival and *k* indicates an effect on kitten survival.

Model	Description
(A) All models	
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 on kitten survival
4. S(Base + ancestry)[*]	Additive ancestry effect on survival of panthers of all ages
5. S(Base + $s\&a$:F1Adv)[*]	Additive F_1 ancestry effect on survival of sub-adult and adult panthers only
6. S(Base + k:ancestry + $s\&a$:F1Adv)[*]	Separate additive ancestry effects 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

Term	Definition	Hypothesis
(B) Ancestry models		
IntAdv	Two ancestry categories: (1) canonical and (2) backcrossed to canonical, backcrossed to Everglades, backcrossed to Texas, and F_1	General introgression advantage (or disadvantage)
AdmAdv	Two ancestry categories: (1) canonical and backcrossed to canonical and (2) backcrossed to Everglades, backcrossed to Texas, and F_1	General admixture advantage (or disadvantage), but with backcrossed to canonical reverting to canonical
50TexAdv	Two ancestry categories: (1) canonical, backcrossed to canonical, and backcrossed to Everglades and (2) backcrossed to Texas, and F_1	Survival advantage (or disadvantage) for those $\geqslant$50% Texas
CanDisF1Adv	Three 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	Three 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, $\geqslant$50% Texas, and intermediate types
F1Adv	Two 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

[*] Ancestry stands for six different hypothesis driven models of the effect of ancestry on survival; specifically, F1Adv divides F_1 admixed from other panthers. See part B of this table for descriptions of ancestry models.

(4) panthers of all ages. Based on previous results (Benson et al., 2009), however, we only considered two ancestry categories for sub-adult and adult panthers (F1Adv; Table 1B).

We tested for the effect of abundance on kitten survival (Table 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 $\hat{\sigma}$; for without abundance index model) and the kitten survival computed for the mean abundance (to σ_{res}; for 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 4000 tuning samples and 1000 burn-in samples.

2.5. 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 C).

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 C). 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).

3. Results

The most parsimonious model (model 1, Table 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 2); the model-averaged estimate of annual kitten survival was 0.323 ± 0.065 (± 1 SE).

Table 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 bold (representing survival differing between kittens, females ages 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. $S(k, 1 \leqslant f < 3, f \geqslant 3, 1 \leqslant m < 4, m \geqslant 4)p(\cdot)r(k, s\&a)$	8	0.00	0.147	0.343 (0.070)
2. $S(k, 1 \leqslant f < 3, f \geqslant 3, 1 \leqslant m < 3, m \geqslant 3)p(\cdot)r(k, s\&a)$	8	0.19	0.134	0.342 (0.070)
3. $S(k, 1 \leqslant f < 2, f \geqslant 2, 1 \leqslant m < 4, m \geqslant 4)p(\cdot)r(k, s\&a)$	8	0.24	0.130	0.345 (0.071)
4. $S(k, 1 \leqslant f < 2, f \geqslant 2, 1 \leqslant m < 3, m \geqslant 3)p(\cdot)r(k, s\&a)$	8	0.43	0.119	0.344 (0.070)
5. $S(k, 1 \leqslant f < 3, f \geqslant 3, 1 \leqslant m < 4, m \geqslant 4)p(\cdot)r(\cdot)$	7	0.47	0.116	0.296 (0.049)
6. $S(k, 1 \leqslant f < 3, f \geqslant 3, 1 \leqslant m < 3, m \geqslant 3)p(\cdot)r(\cdot)$	7	0.62	0.108	0.296 (0.049)
7. $S(k, 1 \leqslant f < 2, f \geqslant 2, 1 \leqslant m < 4, m \geqslant 4)p(\cdot)r(\cdot)$	7	0.76	0.100	0.297 (0.049)
8. $S(k, 1 \leqslant f < 2, f \geqslant 2, 1 \leqslant m < 3, m \geqslant 3)p(\cdot)r(\cdot)$	7	0.92	0.093	0.297 (0.049)
9. $S(k + sex, 1 \leqslant f < 3, f \geqslant 3, 1 \leqslant m < 4, m \geqslant 4)p(\cdot)r(k, s\&a)$	9	2.02	0.053	0.349 (0.084)[a] 0.335 (0.089)[b]

[a] Female kitten survival.
[b] Male kitten survival.

We selected the most parsimonious model from the initial model set (model 1, Table 2) as a base model for testing the effects of covariates on kitten survival. There was no evidence of an effect of sex (Table 2) or litter size ($\Delta QAIC_c$ 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 six most parsimonious models all included ancestry effects on kitten survival (models 1–6, Table 3A).

Table 3

Model selection table for (A) ancestry effects on kitten and older survival, (B) heterozygosity effects on kitten and older survival, and (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 ($\Delta QAIC_c$), and the model $QAIC_c$ weight. See Table 1 for descriptions of the covariate models and Table 2 for the base model. All models estimate constant recapture rates and recovery rates that differ between kittens and older panthers ($p(.)r(k, s\&a)$).

Survival model	K	$\Delta QAIC_c$	Weight
A. Ancestry models			
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 + 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			
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			
1. Base + k:abundance	9	0.00	0.988
2. Base	8	8.79	0.012

The top two 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 3A). Model-averaged kitten survival was lowest for canonical kittens and highest for F_1 kittens (Fig. 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 3B, model 1). Although this model differed from the base model by $\Delta QAIC_c < 2$, 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 (Fig. 1B).
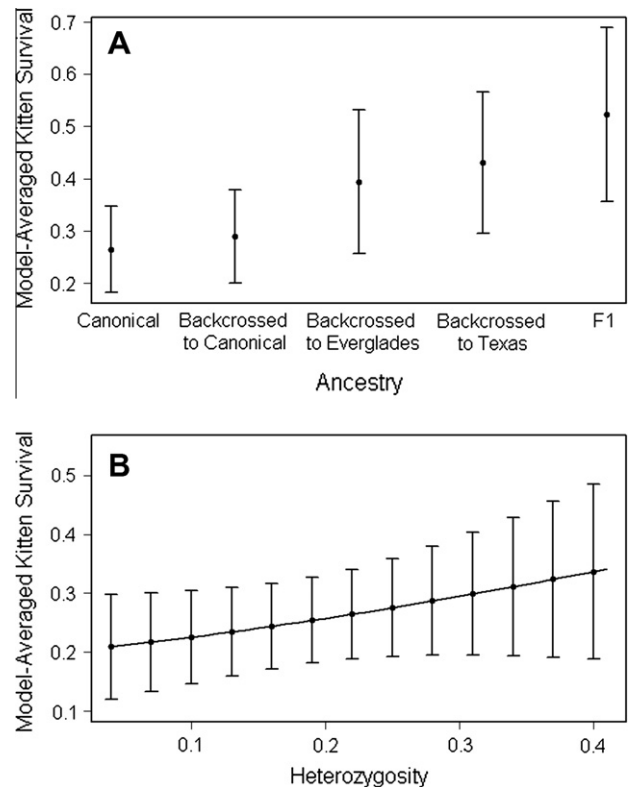

Fig. 1. The effect of genetic variables on model-averaged kitten survival estimates. A) Annual survival plotted against ancestry category. B) Annual survival plotted against heterozygosity. Error bars represent unconditional standard errors.
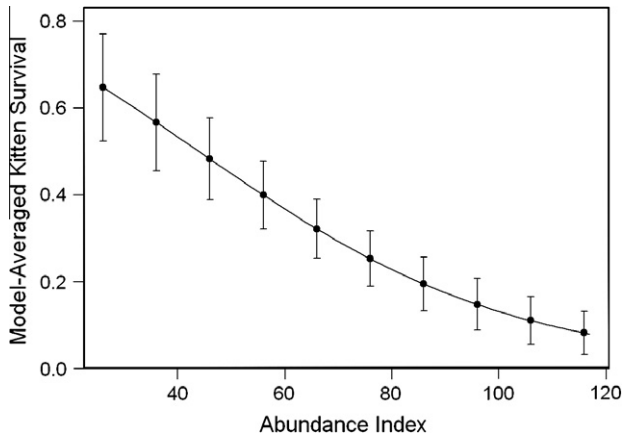
Fig. 2. The effect of a panther abundance index on model-averaged kitten survival estimates. Error bars represent unconditional standard errors.
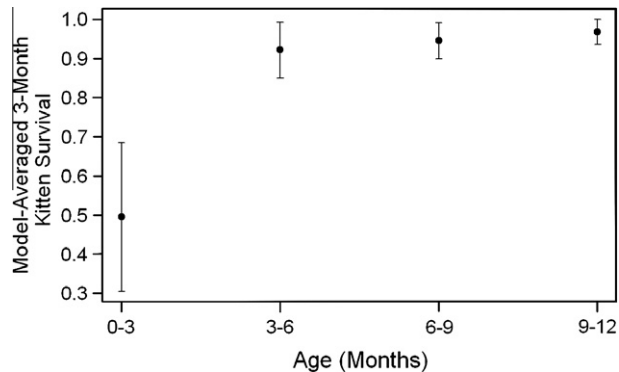

Fig. 3. Model-averaged kitten survival by 3-month age interval within the first year. Error bars represent unconditional standard errors.

There was considerable evidence that abundance negatively influenced kitten survival, with the model with no such effect having a $\Delta QAIC_c$ of 8.79 (Table 3C). Kitten survival declined with increasing population size (Fig. 2; β = −0.034, 95% CI = −0.053 to −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 eight models in Table 2 having $\Delta QAIC_c$ < 1. We reran all covariate tests using model 5 from Table 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 D).

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

4. 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., 2002; 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: 0.44–0.72; Lambert et al., 2006; Laundré et al., 2007; Logan and Sweanor, 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., 2002: 0.735–1.0; Root, 2004: 0.62). Although our estimates of kitten survival varied slightly depending on the model (0.30–0.34; Table 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 from birth 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 Sweanor, 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 eight 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., 2006). 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., in press). 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 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 C). 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., 2002) 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, F_1) 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 of the critically endangered Florida panther.

Appendix A. Supplementary material

Supplementary data associated with this article can be found, in the online version, at doi:10.1016/j.biocon.2010.07.028.

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