Notes

Reproductive Characteristics and Performance of the Florida Panther: A Retrospective Examination of Long-Term Data

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Abstract

Knowledge of reproductive characteristics and performance (RCP) is necessary to estimate a species’ breeding output and provide indicators to evaluate population health. Long-term data are important because they provide insight into the roles of intrinsic and extrinsic factors in determining RCP and lifetime breeding output of individuals and productivity of populations. Here, I examine the RCP of the Florida panther Puma concolor coryi by using an extensive data set collected from 1981 to 2019. My objective is to establish baseline RCP parameters and to determine the factors that affect lifetime breeding output. Briefly, the results from a variety of data analyses show the following: 1) Florida panthers exhibit a spring (March–May) birth pulse; 2) minimum age at sexual maturity does not differ between sexes; 3) mean annual proportion of females reproducing, litter size, and birth rate progressively decrease with increasing maternal age; 4) mean litter sex ratio is male biased; 5) mean birth interval differs between successful and unsuccessful litters; 6) proportion of kittens that recruited into the breeding population is small; and 7) distribution of parentage and mating partners among individuals in litters of known mothers and fathers is right skewed. The results indicate that breeding output is limited both by low birth rate and small proportion of offspring recruiting into the breeding population. The decreasing RCP with increasing maternal age suggests that costs of reproduction and progressive body condition senescence are important factors limiting lifetime breeding output. Despite these inhibiting factors, the data came from a period of substantial population growth and expansion since 1995, so the RCP shown is productive for this species. Outcomes from this study provide important RCP information for wildlife managers to implement measurable criteria to assess trends in Florida panther breeding output and population health.

Keywords: birth rate; litter; Puma concolor coryi; reproduction; sexual maturity

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Introduction

Knowledge of reproductive characteristics and performance (RCP) is necessary to estimate a species’ breeding output (Bronson 1989; Ellis et al. 2018). In iteroparous species, breeding output is the accumulation of an individual’s lifetime RCP. However, aging is a natural developmental process and characterized by progressive loss of biological functions (Ellis et al. 2018). The energetic resources allocated to sexual reproduction (i.e., costs of reproduction) in any one breeding period also can have consequences on succeeding maternal physiological condition and RCP (Clutton-Brock 1984; Gittleman and Thompson 1988). Consequently, a species’ RCP may increase, remain constant, or decrease with increasing maternal age (Clutton-Brock 1984; Ellis et al. 2018).
2018). In addition, a species’ RCP may vary because of differences in environmental covariates (e.g., climate, food quantity and quality, population abundance) that determine the maxima among discrete populations (Bronson 1989; Stearns 1992; Stoner et al. 2018). Life-history theory predicts that natural selection will result in the optimization of RCP within the limits imposed by trade-offs between selective factors intrinsic to the organism and extrinsic in the environment that affect resource allocation for both current and future reproduction (Clutton-Brock 1984; Stearns 1992).

Comparable long-term data are important because they provide insight into the roles of intrinsic and extrinsic factors in determining RCP and lifetime breeding output of individuals and productivity of populations. Understanding of a species’ RCP parameters will benefit wildlife managers by providing indicators to evaluate variations in breeding output and population health (e.g., population turnover and potential growth rates, meta-population dynamics, genetic persistence in a population; Williams et al. 2002; Mills 2007). Recognition of variations in a species’ RCP parameters and breeding output among different populations is also important for range-wide conservation planning and to inform regional protection and management policies and actions.

Although generally resilient to anthropogenic impacts, the puma Puma concolor (also regionally known as mountain lion, cougar, or panther) has been extirpated from throughout most of the historic North American range after European colonization (Gill 2009). The extirpation was caused by habitat loss and degradation, depletion of natural prey, and direct killing by humans (Gill 2009). Comprehensive knowledge of the pumas’ natural RCP parameters is needed to evaluate the impact that continuing anthropogenic impacts may have on the breeding output and health of extant populations. For example, understanding of variations in RCP parameters is necessary to determine what cause-specific mortality rate (e.g., predation removal, disease, sport hunting, intraspecific aggression, pathogens, vehicle collision) can be sustained. This information is also important to estimate how long a specific management strategy may take to produce a population recovery.

The RCP parameters of the puma (Table 1) have been examined to various extents for captive animals (Robinette et al. 1961; Eaton and Velander 1977) and wild populations (Logan and Sweanor 2001, 2009; Quigley and Hornocker 2009). Briefly, female pumas come into estrous year-round (Bonney et al. 1981) and are induced ovulators that require multiple copulations during the period of 1–16 d when the male remains with the female for courtship and breeding (Seidensticker et al. 1973; Eaton and Velander 1977; Logan and Sweanor 2001, 2009). In western populations, there is a summer–fall birth pulse from June to September following the peak in births of ungulate prey (Logan and Sweanor 2001; Laundré and Hernández 2007; Quigley and Hornocker 2009; Jansen and Jenks 2012). Variations in the RCP parameters reported from the wild suggest that minimum age at first parturition, proportion of females reproducing, litter size, litter sex ratio, birth interval, and birth rate are determined by factors intrinsic to the individual and can change with the local environment. For example, the mean annual proportion of females reproducing may vary by age-class (Van De Kerk et al. 2019). Similarly, a larger litter may occur during the first year of reproduction (Logan et al. 1986) and smaller litters later in life (Van De Kerk et al. 2019). In addition, fecundity (e.g., age at parturition, litter size, birth interval, birth rate) may vary over time in relation to the availability of large ungulate prey (Logan and Sweanor 2001; Wilson et al. 2004; Stoner et al. 2006; Laundré et al. 2007). Although some elements of the RCP are known for a wide range of pumas, comprehensive long-term studies are rare (e.g., Logan and Sweanor 2001; Lambert et al. 2006; Laundré et al. 2007; Cooley et al. 2009a, 2009b; Robinson et al. 2008, 2014), making it difficult to evaluate variations in breeding output among populations at different spatial and temporal scales.

The Florida panther Puma concolor coryi (but “puma” when referring to the species as a whole) has reoccurred small portions of its historic range in south Florida during the past 25 y (Onorato et al. 2010a). The increase and expansion of the extant population have been attributed mainly to genetic restoration efforts initiated in 1995 to counteract inbreeding depression and consequent detrimental health traits (Onorato et al. 2010a; Hostetler et al. 2010, 2012, 2013; Van De Kerk et al. 2019). The extensive extirpation and postgenetic restoration population increase have led to interest in some elements of the species’ RCP (Table 1) and the potential health benefits accrued via genetic introgression (Beier et al. 2003). Initially, Maehr et al. (1989, 1991) and Maehr and Caddick (1995) examined the birth timing, age at first parturition, litter size, and birth interval in successful litters for a small number of females during 1981–1993. More recently, Hostetler et al. (2012) and Van De Kerk et al. (2019) examined a larger sample of females during 1981–2013 and found weak evidence that genetic ancestry and population abundance influenced the probability of reproducing and litter size. However, although extensive long-term RCP data have been collected, most existing information is not yet comprehensively examined to understand other elements of the Florida panthers’ breeding output or to identify stochastic variations and temporal trends (Beier et al. 2003). Also, an important question remains: is the RCP of the Florida panther similar to that of other pumas?

Here, I examine the RCP of the Florida panther by using an extensive data set collected by the Florida Fish and Wildlife Conservation Commission (FFWCC) and the National Park Service from 1981 to 2019. My objective is to establish baseline RCP parameters and to determine the factors that affect lifetime breeding output of the Florida panther. The results will make available the comprehensive RCP parameters against which future comparison with Florida panthers and other pumas can be made.

**Study Area**

The study area encompassed the entire breeding range of the Florida panther that included public and
private lands bordered by the Caloosahatchee River to the north, coastal mangrove swamps of the southern Everglades National Park to the south, and the urban centers of Miami-Fort Lauderdale (25.76°N, 81.19°W) and Naples-Fort Myers (26.14°N, 81.79°W) to the east and west, respectively. Habitat types included several varieties of hydric and mesic forests together with open-canopy marshes, prairies, and agricultural and rural-residential lands (Onorato et al. 2010a, 2010b). The climate (Obeysekera et al. 1999) is typical of the subtropical region, characterized by hot and wet spring (March–May) and summer (June–August) with mild and dry fall (September–November) and winter (December–February). Average winter low temperature ranges from 10 to 15°C, whereas daytime highs range from 18 to 29°C. Average summer low temperature ranges from near 21 to 27°C, whereas daytime highs range from 30 to 35°C. Rainfall averages approximately 1,600 mm annually. Most (80%) of the annual rainfall is produced by thunderstorms and tropical storms from April to July followed by a dry season from October to January. The low elevation, lack of well-defined flow channels, and semi-impervious soil severely limit the natural capacity of the landscape to drain away the abundant summer rainfall. The accumulation of rainfall results in the formation of a shallow, extensive, and slowly flowing transient surface water.

### Methods

Since 1981, FFWCC and National Park Service staff and contractors captured, radio collared, and monitored Florida panthers. The capture, handling, and monitoring procedures followed a standard data collection protocol approved by the U.S. Fish and Wildlife Service (USFWS; e.g., Endangered Species Collection Permits TE051553-4 and TE146761-2). The capture and handling procedures were consistent with guidelines of Gannon and Sikes (2007) and described in FFWCC (2019). Briefly, capture teams located individuals with trained hounds at initial ages that ranged from 0.3 to 12 y. The individuals were treed and immobilized using drugs delivered via remote injection. Capture teams 1) determined sex of individuals, 2) marked them with an ear tattoo and a

### Table 1. Reproductive characteristics and performance parameters for the puma *Puma concolor* in North America.

| Reproductive characteristics or performance parameter | Measure | Reference |
|-----------------------------------------------------|---------|-----------|
| Birth timing                                        |         |           |
| Month                                               | January–December | Laundré and Hernandez 2007 |
| Birth pulse                                         | March–July | Maehr et al. 1991a |
|                                                    | July–September | Laundré and Hernandez 2007 |
|                                                    | June–August | Jansen and Jenks 2012 |
| Minimum age (y) at first parturition                | 2.5b     | Robinette et al. 1961 |
|                                                    | 1.6b    | Maehr et al. 1989, 1991a |
|                                                    | 1.42–2.83b | Lindzey et al. 1994 |
|                                                    | 1.5b    | Lambert et al. 2006 |
|                                                    | 1.25–4.75b | Onorato et al. 2011 |
|                                                    | 1.75–6.88b | Hostetler et al. 2012a |
| Proportion of females reproducing                    | 1.92–3.08b | Robinson et al. 2014 |
|                                                    | 0.41    | Robinette et al. 1961 |
|                                                    | 0.48–0.52 | Logan and Sweanor 2001 |
|                                                    | 0.75    | Lambert et al. 2006 |
|                                                    | 0.44–0.51 | Cooley et al. 2009a, 2009b |
|                                                    | 0.41    | Hostetler et al. 2012b |
|                                                    | 0.58    | Robinson et al. 2014 |
|                                                    | 0.25–0.50d | Van De Kerk et al. 2019a |
| Litter size                                         | Wild    | Robinette et al. 1961 |
|                                                    | 2.92d   | Robinette et al. 1961 |
|                                                    | 2.7d    | Logan et al. 1986 |
|                                                    | 2.2d    | Ross and Jalkotzy 1992 |
|                                                    | 2.4d    | Lindzey et al. 1994 |
|                                                    | 2.3d    | Maehr and Caddick 1995a |
|                                                    | 3.1d    | Spreadbury et al. 2006 |
|                                                    | 1.8–1.9d | Wilson et al. 2004 |
|                                                    | 2.53d   | Lambert et al. 2006 |
|                                                    | 2.4d    | Laundré et al. 2007 |
|                                                    | 2.47d   | Cooley et al. 2009a |
|                                                    | 3.0d    | Logan and Sweanor 2010 |
|                                                    | 1.54–1.77d | Harveson et al. 2012 |
|                                                    | 2.6d    | Hostetler et al. 2012b |
| Fetal                                               | 2.92d   | Robinson et al. 2014 |
| Captivity                                           | 3.4d    | Robinette et al. 1961 |
|                                                    | 2.6d    | Eaton and Velander 1977 |
| Litter sex ratio (male:female)                      | 0.96:1  | Robinette et al. 1961 |
|                                                    | 1:2     | Seidensticker et al. 1973 |
|                                                    | 1:3:1   | Lindzey et al. 1994 |
|                                                    | 1:1:13  | Lambert et al. 2006 |
|                                                    | 0.44–2.33:1 | Harveson et al. 2012 |
| Birth interval (y)                                  |         |           |
| Successful litter                                   | 1.3–3.08 | Maehr et al. 1991a |
|                                                    | 1.64f   | Ross and Jalkotzy 1992 |
|                                                    | 2.03f   | Lindzey et al. 1994 |
|                                                    | 1.45f   | Logan and Sweanor 2001 |
|                                                    | 1.5f    | Lambert et al. 2006 |
|                                                    | 1.65f   | Cooley et al. 2009b |
|                                                    | 1.3f    | Hostetler et al. 2012b |
|                                                    | 1.65f   | Robinson et al. 2014 |
| Unsuccessful litter                                 | 0.27f   | Logan and Sweanor 2001 |

### Table 1. Continued.

| Reproductive characteristics or performance parameter | Measure | Reference |
|-----------------------------------------------------|---------|-----------|
| Birth rate (kitten/female)                           | 0.9–1.6 | Logan and Sweanor 2001 |
|                                                    | 0.32–0.62 | Lambert et al. 2006 |
|                                                    | 1.1–1.2d | Robinson et al. 2008 |
|                                                    | 1.12d   | Cooley et al. 2009a |
|                                                    | 1.29d   | Robinson et al. 2014 |

a Florida panther.  
b Female.  
c Male.  
d Mean.
subcutaneous passive integrated transponder, and 3) attached a very high frequency or global positioning system radio-collar equipped with a mortality sensor. Capture teams relocated radio-collared individuals by using aerial telemetry, generally three times per week. Successive movements of radio-collared females in the same location indicated the potential commencement of denning behavior, resulting in investigative trips by capture teams to the area to search for neonatal den sites (Benson et al. 2008). In 1992, capture teams began recording litters at initial ages ranging from 6 to 40 days postbirth. Capture teams 1) estimated birth date, 2) recorded the largest number of kittens seen in a den, and 3) implanted kittens with a passive integrated transponder. Capture teams estimated age of all individuals by using a combination of tooth wear, pelage characteristics, body size, and developmental stage of teats and reproductive organs (Ashman and Greer 1976). Capture teams collected a blood, tissue, or hair sample from individuals for genetic analysis. Technicians extracted DNA from samples and used a panel of 23 microsatellite loci to determine genotype following a method described in Johnson et al. (2010).

I compiled radio-collar and litter data from Appendices I and II in FFWCC (2019): 1) date of birth, date of capture, date of death, and date of collar failure for 120 radio-collared females from 1992 to 2019; and 2) date of birth, litter birth date, litter size, and sex ratio for 196 litters from 84 radio-collared females from 1992 to 2019, respectively. The radio-collared female and litter information is compiled in Table S1 (Supplemental Material). Gestation ranges from 90 to 98 d (Allen 1950), and female age at conception was estimated by backdating 94 d from litter birth date. I plotted litter conception and birth dates and compared the frequency of reproductive events in a month by using chi-square analyses. I assumed an equal distribution of conceptions and births over the 12 mo to calculate expected frequencies. The association between litter size and a mother's age at conception was examined with Pearson correlation (r). I examined the effect of consecutive litter number on litter size by using analysis of covariance (F) with maternal age at conception as covariate. I estimated annual proportion of females reproducing as the number of radio-collared females ≥1.5 y (i.e., females were sexually mature from age 1.43 y) divided by the number that produced a litter in each year monitored. I estimated annual birth rate as the total number of kittens produced by all breeding females divided by the number of radio-collared females ≥1.5 y. I estimated lifetime breeding productivity by multiplying mean annual birth rate by 11 (i.e., females were reproductively active from age 2 to 13 y).

To examine relationships between RCP with maternal age, I divided the Florida panther’s lifespan into four developmental stages. The four lifespan developmental stages (LDSs) used are detailed in Text S1 (Supplemental Material): 1) juvenile (≤1.5 y), 2) young adult (>1.5–5 y), 3) prime adult (5–10 y), and 4) old adult (>10 y). The effect of LDS on annual proportion of females reproducing, annual birth rate, litter size, percentage of females and males per litter, and birth interval was examined in the same manner as litter size. I used square root transformation for percentage data (i.e., (y + 0.5)0.5). Tukey’s multiple comparisons test was used post hoc to determine differences between different levels of the main effect.

Minimum counts of dependent juveniles and adults in the population (McBride et al. 2008) estimated 1) 20–30 throughout the 1970s and early 1980s, 2) 30–50 in the late 1980s through the mid-1990s, 3) 50–70 for several years following genetic restoration in 1995, 4) 90–120 in the early 2000s, 5) 100–180 in the early 2010s, and 6) 120–230 since 2017 (FFWCC 2017). To examine the effect of population abundance on RCP, I divided the data into six temporal-classes: 1) 1992–1996, 2) 1997–2001, 3) 2002–2006, 4) 2007–2011, 5) 2012–2016, and 6) 2017–2019. The effect of population abundance on annual proportion of females reproducing, annual birth rate, litter size, percentage of females and males per litter, and birth interval was examined in the same manner as LDS.

I compiled parentage data from Johnson et al. (2010, supplemental material table 2) for 299 kittens with demographic information from 1981 to 2009. The parentage information for female and male kittens is compiled in Table S1 (Supplemental Material). I used parentage for kittens to identify known-age mothers and fathers (i.e., individuals first examined as kittens in neonatal dens). Minimum age at sexual maturity (i.e., first successful conception) in kittens monitored since birth was estimated in the same manner as birth date. Sex differences in the minimum age at sexual maturity were examined with a t-test. I determined the proportion of kittens age ≥4 y (i.e., oldest age at female sexual maturity was 3.96 y) that successfully recruited into the breeding population (i.e., produced a litter) during 1992–2005. Parentage information was only available to 2009 (Johnson et al. 2010), so I restricted the cut-off at 2005. I examined the distribution of parentage and mating pairs among individuals for 74 litters with known mothers and fathers during 1992–2008. Differences in the proportion of females and males that recruited into breeding population and the distribution of parentage and mating pairs among individuals were compared using chi-square analyses.

I conducted data analyses following the techniques in Zar (1999) by using Excel (Microsoft Corp., Redmond, WA) and Statistix 9.0 (Analytical Software, Tallahassee, FL). The RCP means are presented ± standard error, with 95% confidence interval (95% CI). I set α = 0.05 for rejection of null hypotheses in tests of statistical significance.

**Results**

Conceptions and births occurred in every month of the year (Figure 1). The conception and birth timings were not uniformly distributed throughout the year (conception: χ² = 29.42; df = 11; P = 0.002; birth: χ² = 33.21; df = 11; P < 0.001). The birth timing exhibited a seasonal birth pulse, with 42% of births in spring (Table 2; P = 0.002). Forty-one litters were born to 25 females with no evidence of previous nursing. The first litters...
Table 2. Distribution (percentage of total) of births for 196 litters of 84 female Florida panthers *Puma concolor coryi* during 1992–2019.

| Litter          | Spring | Summer | Fall | Winter |
|-----------------|--------|--------|------|--------|
| First littersa  | 20 (49)| 15 (36)| 4 (10)| 2 (5)  |
| All littersb    | 83 (42)| 53 (27)| 22 (11)| 39 (20) |

* Spring = March–May; summer = June–August; fall = September–November; winter = December–February.
* χ² = 101.2; df = 11; P < 0.001.
* χ² = 29.1; df = 11; P = 0.002.

Table 3. Mean ± standard error and 95% confidence interval (95% CI) minimum age at sexual maturity for 14 female and 7 male Florida panthers *Puma concolor coryi* monitored since birth during 1981–2009.

|          | Female | Male   |
|----------|--------|--------|
| Mean (y) | 2.47 ± 0.22 | 3.32 ± 0.65 |
| 95% CI (y) | 2.00–2.94 | 1.72–4.93 |
| Range (y)   | 1.43–3.96 | 1.64–5.83 |

* t₁₀ = −1.56; P = 0.136.

The annual proportion of females reproducing ranged from 0.00 to 1.00 (Table 4), and mean was 0.33 ± 0.03. The mean annual proportion of females reproducing in the young adults, prime adults, and old adults was dependent on LDS (F₂,80 = 21.08; P < 0.001). The mean annual proportion of old adults reproducing was significantly less (Tukey’s test: P < 0.001) than the young adults and prime adults that did not differ (Tukey’s test: P > 0.05). The mean annual proportion of females reproducing was dependent on time period (F₅,22 = 3.98; P = 0.011) and substantially increased (Tukey’s test: P < 0.05) from 1992 to 1996 (0.19 ± 0.03; 95% CI = 0.11–0.28) to 2017–2019 (0.49 ± 0.08; 95% CI = 0.14–0.85).

The litter size ranged from one to four, and mean for all litters was 2.50 ± 0.06 (Table 4). The mean litter size of young adults, prime adults, and old adults was independent of LDS (F₂,192 = 2.13; P = 0.122) and dependent on maternal age (F₁,192 = 9.22; P = 0.003). The litter size decreased with increasing maternal age (r² = −0.186; P = 0.009). The mean litter size did not differ between time periods (F₅,189 = 1.92; P = 0.093). For nine mothers producing five consecutive litters (Table 5), the mean litter size was independent of sequence number (P = 0.174) and maternal age (F₁,39 = 2.02; P = 0.163).

The litter sex ratio ranged from 0 to 100% female or male (Table 4). The mean sex ratio was 45.03 ± 2.34% female and 54.97 ± 2.34% male (or 1.22 male:1 female) and differed significantly from 1:1 (t₁₉₅ = −2.16; P = 0.032). The mean percentage of females and males in litters of young adults, prime adults, and prime adults was independent of LDS (F₂,192 = 0.19; P = 0.824), maternal age (F₁,192 = 0.22; P = 0.639), and time period (F₅,189 = 1.34; P = 0.251).

The birth interval for 94 litters of 48 females monitored for 2–10 consecutive years ranged from 0.61 to 4.96 y (Table 4). The mean birth interval for all litters was 1.68 ± 0.09 y (95% CI = 1.49–1.86). The birth interval for successful litters ranged from 1.32 to 4.96 y. The mothers that had lost litters before kittens reached independence recycled back into estrous and produced another litter from 0.61 to 1.28 y later. This suggests a breeding lapse of 0.35–1.02 y following unsuccessful litters. No mothers cared for more than one litter concurrently. There was a minor trend in decreasing birth interval with increasing maternal age (r² = −0.123; P = 0.237). The mean birth interval was dependent on litter success (F₁,89 = 82.69; P < 0.001) and independent of LDS (F₂,89 = 0.14; P = 0.867) and maternal age (F₁,89 = 0.82; P = 0.369) with no success type × LDS interaction (F₁,89 = 0.13; P = 0.714). The mean birth interval for successful litters was independent of...
Table 4. Mean ± standard error and 95% confidence interval proportion of individuals reproducing, birth rate, litter size, percentage of males in a litter, percentage of females in a litter, and birth interval in successful and unsuccessful litters among three lifespan development stages of 84 female Florida panthers Puma concolor coryi during 1992–2019.

| Reproductive characteristics or performance parameter | Lifespan developmental stage* | Young adults (1.5–5 y) | Prime adults (>5–10 y) | Old adults (>10 y) | Total |
|-----------------------------------------------------|--------------------------------|-----------------------|------------------------|-------------------|--------|
| Reproducing (≥1.5 y)                                | 0.41 ± 0.04^b                  | 0.29 ± 0.04^b         | 0.11 ± 0.05^a          | 0.33 ± 0.03       |        |
| 95% CI                                              | 0.33–0.49                      | 0.21–0.39             | 0.03–0.21              | 0.28–0.36         |        |
| Range                                               | 0–1.00                         | 0.0–0.75              | 0.0–1.00               | 0.0–0.60          |        |
| n                                                   | 28                              | 28                    | 27                     | 28                |        |
| Birth rate (≥1.5 y)                                 | 1.12 ± 0.08^c                  | 0.73 ± 0.12^c         | 0.09 ± 0.04^d          | 0.87 ± 0.08       |        |
| 95% CI                                              | 0.96–1.28                      | 0.49–0.97             | 0.01–0.17              | 0.71–1.03         |        |
| Range                                               | 0.55–2.00                      | 0.0–1.88              | 0.0–1.00               | 0.20–1.80         |        |
| n                                                   | 26                              | 28                    | 27                     | 28                |        |
| Litter size                                         | 2.58 ± 0.09^b                  | 2.43 ± 0.09^b         | 2.30 ± 0.37^b          | 2.50 ± 0.06       |        |
| 95% CI                                              | 2.41–2.75                      | 2.25–2.61             | 1.47–3.13              | 2.38–2.62         |        |
| Range                                               | 1–4                            | 1–4                   | 1–4                    | 1–4               |        |
| n                                                   | 98                              | 88                    | 10                     | 196               |        |
| Male (%)                                            | 57.26 ± 3.08^b                 | 52.42 ± 3.61^b        | 55.00 ± 14.07^b        | 54.97 ± 2.34      |        |
| 95% CI                                              | 51.14–63.39                    | 45.23–59.59           | 23.16–86.84            | 50.36–59.59       |        |
| Range                                               | 0–100                          | 0–100                 | 0–100                  | 0–100             |        |
| n                                                   | 98                              | 88                    | 10                     | 196               |        |
| Female (%)                                          | 42.73 ± 3.08^b                 | 47.58 ± 3.61^b        | 45.00 ± 14.07^b        | 45.03 ± 2.34      |        |
| 95% CI                                              | 36.61–48.86                    | 40.41–54.75           | 13.16–76.84            | 40.41–49.64       |        |
| Range                                               | 0–100                          | 0–100                 | 0–100                  | 0–100             |        |
| n                                                   | 98                              | 88                    | 10                     | 196               |        |
| Birth interval (y)                                  | 2.23 ± 0.15^b                  | 2.22 ± 0.18^b         | —                      | 2.23 ± 0.12       |        |
| 95% CI                                              | 1.92–2.53                      | 1.84–2.63             | —                      | 1.99–2.46         |        |
| Range                                               | 1.41–4.96                      | 1.32–3.90             | —                      | 1.32–4.96         |        |
| n                                                   | 36                              | 18                    | —                      | 54                |        |
| Unsuccessful litter                                 | 1.01 ± 0.04^b                  | 0.82 ± 0.05^b         | —                      | 0.93 ± 0.03       |        |
| 95% CI                                              | 0.92–1.09                      | 0.71–0.94             | —                      | 0.86–1.01         |        |
| Range                                               | 0.61–1.28                      | 0.61–1.19             | 0.64                   | 0.61–1.28         |        |
| n                                                   | 25                              | 14                    | 7                      | 40                |        |

* Within rows, Tukey’s multiple comparisons test: ^bP > 0.05; ^cP < 0.05; ^dP < 0.001.

The mean annual birth rate ranged from 0.20 to 1.80 (Table 4), and mean was 0.87 ± 0.08. The mean annual birth rate of young adults, prime adults, and old adults differed significantly (F_{2,80} = 37.16; P < 0.001). The mean annual birth rate of old adults was significantly less (Tukey’s test; P < 0.001) than the young adults and prime adults that also differed significantly (Tukey’s test; P < 0.05). The mean annual birth rate was independent of time period (F_{5,22} = 2.28; P = 0.082). The overall lifetime breeding productivity was 9.57 kittens/female.

Sixteen percent of the kittens (n = 18 females and 14 males) from 1992 to 2005 (n = 95 females and 102 males) recruited into the breeding population (χ^2 = 61.64; df = 1; P < 0.001). The proportion of males (0.19) and males (0.14) that recruited into the breeding population did not differ significantly (χ^2 = 0.71; df = 1; P = 0.399). These 32 kittens were parented by 20 mothers, 9 known fathers, and 13 unknown fathers.

The distribution of parentage among 74 litters with known mothers (n = 42) and fathers (n = 33) was skewed to the right (Figure 2; skew u = 2.45 female and 2.47 male) with flat tail (kurtosis g = 0.51 female and 4.95 male). Twenty-four different mothers each produced 1 litter and 17 mothers produced 2 to 4 litters; 17 different fathers each produced 1 litter and 14 fathers produced 2 to 13 litters (χ^2 = 7.79; df = 6; P = 0.254). The distribution of mating partners among individuals in these litters was also skewed to the right (Figure 2; u = 2.01 female and 2.11 male) with shorter tail (g = 2.61 female and 3.01 male). Twenty-six different mothers each had one

Table 5. Mean ± standard error and 95% confidence interval litter size for 5 consecutive litters of 9 female Florida panthers Puma concolor coryi during 1992–2019.

| Litter No. | 1         | 2         | 3         | 4         | 5         |
|------------|-----------|-----------|-----------|-----------|-----------|
| Mean       | 2.44 ± 0.17| 2.11 ± 0.35| 2.89 ± 0.20| 2.33 ± 0.37| 1.89 ± 0.26|
| 95% CI     | 2.04–2.85     | 1.30–2.92     | 2.43–3.35     | 1.47–3.19     | 1.29–2.49     |
| Range      | 2–3         | 1–4         | 2–4         | 1–4         | 1–3         |

* F_{4,10} = 1.68; P = 0.174.
partner and 14 mothers had two to four partners; 20 different fathers each had one partner and 13 fathers had two to nine partners ($\chi^2 = 3.95; df = 5; P = 0.557$).

**Discussion**

Similarities and differences were detected in the RCP parameters of the Florida panther compared with other pumas. The minimum age at sexual maturity, mean litter size, and mean birth interval in successful litters of Florida panthers are within the ranges for other pumas (Table 1). The seasonal birth pulse, mean annual proportion of females reproducing, and mean annual birth rate of Florida panthers are different from those for other pumas (Table 1). The data came from a period of substantial population growth and expansion since 1995, so the RCP shown for the Florida panther is productive for this species. The results therefore provide a comprehensive set of RCP statistics representative of a stable and expanding puma population. This information provides a rational point of reference for comparison when evaluating the species’ breeding output and population health.

The Florida panther’s conceptions and births occurred in all months of the year. However, in contrast to the summer–midfall birth timing of western pumas (Logan and Sweanor 2001; Laundré and Hernandez 2007; Quigley and Hornocker 2009; Jansen and Jenks 2012), Florida panthers exhibited a spring birth pulse. The birth timing directly followed the late winter–early spring (January–March) birth pulse of the white-tailed deer _Odocoileus virginianus_ (Richter and Labisky 1985; Smith et al. 1996), the Florida panther’s primary large prey. The postparturition period is the most energetically demanding part of the reproductive cycle because mothers must maintain themselves as well as produce energy-rich milk for their rapidly growing kittens (Toweill 1986; Gittleman and Thompson 1988; Bartareau et al. 2013). Mothers also restrict their movements near den sites while nursing kittens, thereby inhibiting their ability to hunt (Seidensticker et al. 1973; Maehr et al. 1989; Laundré and Hernandez 2008; Julian 2011). During the fawning season, white-tailed deer are more abundant than at any other time of the year, and fawns are the most vulnerable component of the prey population. The birth pulse also coincided with the annual spring growing season, a time of the year when temperatures are mild and surface water levels are low following the dry season. First-time mothers were more likely to give birth in spring than succeeding litters. Differences in time for completion of the previous litter as well as physiological and social factors will create variations in the timing of subsequent births. Births timed following the birth of primary large prey will be advantaged by an abundance of food and favorable environmental conditions that enhances a mother’s ability to feed dependent offspring.

In both sexes of Florida panthers, the minimum age at sexual maturity occurred when the juveniles and young adults are still dispersing, establishing territories, and seeking mates (Maehr et al. 1989, 2002). The minimum age of females at sexual maturity is close to 1.42 y for a female puma in Utah, a female that remained and established in her deceased mother’s home territory (Lindzey et al. 1994). By contrast, the minimum age of males at sexual maturity is older than 1.25 y for a male puma in Montana (Onorato et al. 2011). Laing and Lindzey (1993) found that immigrants would not replace lost residents and breed as young as recruited progeny. The mean minimum age at sexual maturity in female Florida panthers monitored from birth is 0.1 y younger than previous estimates from field observations (Maehr et al. 1991; Hostetler et al. 2012). Using pedigree data, puma fathers in Montana were also younger at sexual maturity than estimated for putative males involved in pairings assessed from field observations (Onorato et al. 2011). However, the mean minimum age at sexual maturity showed that both sexes of Florida panthers generally first conceived at mid young-adult ages. Reproduction is energetically costly (Gittleman and Thompson 1988), and female puma sexual maturity depends on the prerequisite energetic investment in costs of reproduction that is determined by minimum body condition rather than a specific age (Robinette et al. 1961). Similarly, male puma sexual maturity also depends on the ability to grow large enough in body size to thwart competitors and successfully mate with females in estrus, which may not occur until after establishing a home range territory at varying ages.
The mean birth interval following successful litters of Florida panthers is slightly longer than 2.02 y for pumas in Utah (Lindzey et al. 1994). Like pumas in New Mexico (Logan and Sweanor 2001), females that had lost litters before kittens reached independence rapidly recycled back into estrous. Birth interval is a particularly complex reproductive performance parameter influenced by variations in intrinsic (e.g., independence and dispersal of offspring, time to come into estrous, body condition and health) and extrinsic (e.g., predators and litter mortality, food quantity and quality, social interactions) factors that will increase or decrease it. The mean birth interval following successful litters is about twice the duration of unsuccessful litters. The additional time following successful litters is consistent with the timing of juvenile independence and dispersal that occurs from age 1.0-1.5 y (Logan and Sweanor 2001; Maehr et al. 2002). The costs of reproduction are expected to be an important factor regulating duration of the birth interval (Clutton-Brock 1984; Gittleman and Thompson 1988). However, the mean birth interval following both successful and unsuccessful litters is similar in prime adults and old adults. This suggests that variations in the primary factors affecting birth interval were independent of maternal age.

The mean annual proportion of female Florida panthers reproducing increased rapidly after attaining sexual maturity and reached a peak in young adults. The mean annual proportion of females reproducing declined thereafter in prime adults and is lowest in old adults. Although the mean annual proportion of Florida panther young adults reproducing is similar to the pooled age-class for other pumas, the overall population mean was less than that for pumas elsewhere. The potential of a female puma reproducing is regulated in part by the species’ polygynous breeding system and land-tenure social organization, whereby dominant males control large home ranges that provide access to numerous females for mating opportunities (Logan and Sweanor 2001, 2009; Quigley and Hornocker 2009; Elbroch et al. 2016). However, behavioral observations suggest that female pumas evaluate male fitness and dominance characteristics (e.g., body weight, frequency of contact) when selecting mates (Allen et al. 2014, 2015; Johansson et al. 2018). By intersecting territorial boundaries with multiple females, a male puma can display fitness to more potential mates, allowing a female to choose among dominant males. Also, many of the health weaknesses observed in the Florida panther pregenetic restoration were related to male fertility (e.g., inferior sperm quality, low testosterone levels, high incidence of cryptorchidism; Barone et al. 1994; Johnson et al. 2010). Consequently, the likelihood of a female Florida panther reproducing is exceedingly complex and includes variations in body condition, birth interval, and male fertility combined with behavioral and social dynamics. The increased mean annual proportion of female Florida panthers reproducing in recent years paralleling the larger population size suggests that reproductive output is limited by paternal function.
Corresponding with the mean annual proportion of females reproducing, the mean annual birth rate of Florida panthers reached a peak in young adults. Likewise, the mean annual birth rate declined thereafter in prime adults and rapidly dropped off in old adults. The decreasing litter size and proportion of females reproducing with increasing maternal age explains why birth rate peaked in young adults even though old adults retained the ability to reproduce, albeit at smaller litter sizes. Nevertheless, it seems unlikely that reproductive cessation and low birth rate in old adults would have much effect on the population growth and preservation. This is because it occurred late in life, the number of individuals surviving >10 y was small, and the overall contribution of old adults to the breeding output and recruitment into the breeding population was minimal.

The mean annual birth rate of the Florida panther is lower than in other pumas. However, the mean annual birth rate is similar to the 0.9 kittens/female for pumas in New Mexico in the final year of a large prey decline phase (Logan and Sweanor 2001). Logan and Sweanor (2001) suggested that the decline in large prey caused smaller litter sizes, longer birth intervals, increased the age at parturition, and consequent low annual birth rate. Pumas in New Mexico, Washington, and Montana preyed extensively on large mammals and numerous other medium-sized and small species (Logan and Sweanor 2001; Robinson et al. 2008; Cooley et al. 2009b; Robinson et al. 2014). By contrast, the Florida panther diet does not follow the typical western puma food habit pattern (Caudill et al. 2019), having the highest niche breadth and the smallest mean weight of prey (Iriarte et al. 1990). Thus, the small mean weight of prey in the diet could be an important factor limiting the annual birth rate of the Florida panther.

The extent of female and male recruitment into the breeding population influences the potential genetic variation in the inhabitants (Emlen and Oring 1977). The proportion of Florida panther kittens that successfully recruited into the breeding population is substantially small. Similarly, Hostetler et al. (2010) and Van De Kerck et al. (2019) showed that annual survival rate in both sexes of Florida panther kittens (≤1 y) was low (0.32). Although the parentage of all kittens in the population is unknown, the genotyped individuals in the sample were unlikely biased relative to the potential sex-specific survival, reproduction, and recruitment covariates (e.g., infanticide, intraspecific aggression mortality, breeding opportunities). Proportionally more female than male Florida panthers successfully recruited into the breeding population, but the differences were not significant. The results indicate a higher relative contribution to the gene pool by more females than males.

The distribution of parentage among individuals in litters of known Florida panther mothers and fathers is skewed to the right, with most parents producing one litter. However, proportionally more females produced fewer litters than males. Moreover, the distribution of mating partners among individuals in these litters is also skewed to the right. Most females and males had one mating partner, and few parents had multiple partners. As expected in this species’ polygynous breeding system and land-tenure social organization (Logan and Sweanor 2001, 2009), individual males parented a larger number of litters and had more mating partners than females. A progression toward a higher relative contribution to the gene pool by one sex in the population will increase the strength of sexual selection (Emlen and Oring 1977). The results suggest that a strong hierarchy in the individual male contribution to the gene pool will decrease the amount of genetic variability generated and increase the potential for male-biased sexual selection (e.g., male-biased litter sex ratio, male-biased sexual size dimorphism).

In conclusion, the results indicate that breeding output of the Florida panther is limited both by low birth rate and small proportion of offspring recruiting into the breeding population. The decreasing RCP with increasing maternal age suggests that costs of reproduction and progressive body condition senescence are important factors limiting lifetime breeding output. However, further studies are needed to quantify those intrinsic costs and physical differences. The results suggest that optimization of breeding output over a lifetime overrides the potential short-term benefits of increased fecundity within a year, and the additional resources allocated to larger litter size and rearing more offspring are better committed to future reproduction (e.g., maintaining a more fertile maternal body condition, shorter birth interval, costs of gestation and lactation). A low but more continuous level of offspring production seems to be the most efficient reproductive strategy because kitten survival is low and the costs of increased reproduction could reduce maternal fitness and inhibit future breeding potential. In addition, the proportion of kittens that recruited into the breeding population is small, so the low birth rate could be evolutionary stable.

Recognizing the RCP parameters has direct application to management of pumas because of the strong correlation of fecundity with physical condition and ecological covariates (Logan and Sweanor 2001; Lambert et al. 2006; Laundré et al. 2007; Cooley et al. 2009a, 2009b; Robinson et al. 2008, 2014). Further comparisons are needed to determine whether the RCP of pumas is similar among populations with different habitat quality, food habits, and social structure. A better understanding of the circumstances causing differences in RCP parameters (e.g., variation in food habits, social interactions) will help to identify ecological factors that give rise to variations in fecundity, population abundance, and human–puma conflicts. Specifically, I recommended that future studies determine the extent to which variations in maternal body condition and environmental covariates regulate RCP and lifetime breeding output. I predict that any changes in an environmental factor that alter the maternal body condition or population structure and dynamics (e.g., prey quantity and quality, habitat loss and degradation, cause-specific mortality) will affect the RCP and potential breeding output and population health.

Although research is an important part of Florida panther preservation (FFWCC 2019), the current man-
agement plan (USFWS 2008) does not specifically recognize the importance of RCP in providing quantifiable indicators to evaluate breeding output and population health. I recommend recognizing RCP in a science-based approach to Florida panther management because it will satisfy both wildlife manager and stakeholder interests, and ensure more reliability for this species’ protection and management policies and actions. Outcomes from this study provide important RCP information for wildlife managers to implement measurable criteria to assess trends in Florida panther breeding output and population health.

Supplemental Material

Please note: The Journal of Fish and Wildlife Management is not responsible for the content or functionality of any supplemental material. Queries should be directed to the corresponding author for the article.

Text S1. Text file (.doc) describing the lifespan developmental stages used to stratify the examination of lifetime reproductive characteristics and performance of the Florida panther Puma concolor coryi during 1981–2019.

Found at DOI: http://doi.org/10.3996/JFWM-20-006.S1 (63 KB DOC).

Table S1. Data file (.xls) information for litter mother, litter birth date, litter conception date, litter birth date, litter female kittens, litter male kittens, sexual maturity kitten, sexual maturity sex, sexual maturity age (y), reproduction mother, reproduction mother birth date, reproduction mother date captured, reproduction mother date of death, reproduction mother date of birth, reproductive performance year, reproductive performance females, reproductive performance females ≥1.5 y, reproductive performance females reproducing, reproductive performance kittens, recruitment kitten, recruitment sex, recruitment mother, recruitment kitten date of birth, recruitment father; known parent date litter marked, known parent mother, and known parent father of Florida panthers Puma concolor coryi during 1981–2019.

Found at DOI: http://doi.org/10.3996/JFWM-20-006.S2 (76 KB XLS).

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References

Allen R. 1950. Notes on the Florida panther Felis concolor coryi Bang. Journal of Mammalogy 31:279–280.

Allen ML, Wittmer HU, Houghtaling P, Smith J, Elbroch ML, Wilmers CC. 2015. The role of scent marking in mate selection by female pumas (Puma concolor). PLoS ONE 10:1–12.

Allen ML, Wittmer HU, Wilmers CC. 2014. Puma communication behaviours: understanding functional use and variation among sex and age classes. Behaviour 151:819–840.

Ashman DL, Greer K. 1976. Age techniques. Pages 199–204 in Christensen GC, Fisher RJ, editors. Mountain lion workshop. Portland, Oregon: U.S. Fish and Wildlife Service.

Barone MA, Roelke ME, Howard J, Brown JL, Anderson AE, Wildt DE. 1994. Reproductive characteristics of male panthers: comparative studies from Florida, Colorado, Latin America, and North American zoos. Journal of Mammalogy 75:150–162.

Bartareau T, Onorato D, Jansen D. 2013. Growth in body length and mass of the Florida panther: an evaluation of different models and sexual size dimorphism. Southeastern Naturalist 12:27–40.

Beier P, Vaughan MR, Conroy MJ, Quigley H. 2003. An analysis of scientific literature related to the Florida panther. Final Report. Florida Fish and Wildlife Conservation Commission, Tallahassee, Florida. Available: http://mountainlion.org/us/fl/FL-A-FFWCC-Bier-2003-Analysis-Of-Scientific-Literature-Related-To-Florida-Panther.pdf (December 2020).

Benson JF, Lotz MA, Jansen D. 2008. Natal den selection by Florida panthers. Journal of Wildlife Management 72:405–411.

Bonney RC, Moore HDM, Jones PM. 1981. Plasma concentrations of oestradiol-17B and progesterone, and laparoscopic observations of the ovary in the puma (Felis concolor) during oestrus, pseudopregnancy and pregnancy. Journal of Reproduction and Fertility 63:523–531.

Bronson FH. 1989. Mammalian reproductive biology. Chicago: University of Chicago Press.

Carranza J. 1996. Sexual selection for male body mass and the evolution of litter size in mammals. American Naturalist 148:81–100.

Caudill G, Onorato DP, Cunningham MW, Caudill D, Leone EH, Smith LM, Jansen D. 2019. Temporal trends in Florida panther food habits. Human-Wildlife Interactions 13:87–97.

Clutton-Brock TH. 1984. Reproductive effort and terminal investment in iteroparous animals. American Naturalist 123:212–229.
Cockburn A, Legge S, Double MC. 2002. Sex ratios in birds and mammals: can the hypotheses be disentangled? Pages 267–286 in Hardy ICW, editor. Sex ratios: concepts and research methods. Cambridge, UK: Cambridge University Press.

Cooley HS, Wielgus RB, Koehler G, Maletzke B. 2009a. Source populations in carnivore management: cougar demography and emigration in a lightly hunted population. Animal Conservation 12:321–328.

Cooley HS, Wielgus RB, Koehler GM, Robinson HS, Maletzke BT. 2009b. Does hunting regulate cougar populations? A test of the compensatory mortality hypothesis. Ecology 90:2913–2921.

Eaton RL, Velander KA. 1977. Reproduction in the puma: biology, behavior and ontogeny. Pages 45–70 in Eaton RL, editor. The world’s cats. Seattle: Carnivore Research Institute.

Elbroch ML, Lendrum PE, Quigley H, Caragiulo A. 2016. Spatial overlap in a solitary carnivore: support for the land tenure, kinship or resource dispersion hypotheses? Journal of Animal Ecology 2016:487–496.

Ellis S, Franks DW, Nattrass S, Cant MA, Bradley DL, Giles D, Balcomb KC, Croft DP. 2018. Postreproductive lifespans are rare in mammals. Ecology and Evolution 8:2482–2494.

Emlen ST, Oring LW. 1977. Ecology, sexual selection, and the evolution of mating systems. Science 197:215–223.

[FWCC] Florida Fish and Wildlife Conservation Commission. 2017. Determining the size of the Florida panther population. Available: https://myfwc.com/media/3107/determiningpantherpopulation2017.pdf (December 2020).

[FWCC] Florida Fish and Wildlife Conservation Commission. 2019. Annual report on the research and management of Florida panthers: 2018–2019. Fish and Wildlife Research Institute and Division of Habitat and Species Conservation; Florida Fish and Wildlife Conservation Commission. Available: https://myfwc.com/media/21759/pantherannualreport2018-19.pdf (December 2020).

Gannon WL, Sikes RS. 2007. Guidelines of the American Society of Mammalogists for the use of wild animals in research. Journal of Mammalogy 88:809–823.

Gill RB. 2009. To save a mountain lion: evolving philosophy and nature of cougars. Pages 5–16 in Hornocker MG, Negri S, editors. Cougar: ecology and conservation. Chicago: University of Chicago Press.

Gittleman JL, Thompson SD. 1988. Energy allocation in mammalian reproduction. American Zoologist 28:863–875.

Harveson PM, Harveson LA, Hernandez-Santin L, Tewes ME, Silvy NJ, Pittman MT. 2012. Characteristics of two mountain lion Puma concolor populations in Texas, USA. Wildlife Biology 18:58–66.

Hostetler JA, Onorato DP, Bolker BM, Johnson WE, O’Brien SJ, Jansen D, Oli MK. 2012. Does genetic introgression improve female reproductive perfor-

mance? A test on the endangered Florida panther. Oecologia 168:289–300.

Hostetler JA, Onorato DP, Jansen D, Oli MK. 2013. A cat’s tale: the impact of genetic restoration on Florida panther population dynamics and persistence. Journal of Animal Ecology 82:608–620.

Hostetler JA, Onorato DP, Nichols JD, Johnson WE, Roelke ME, O’Brien SJ, Jansen D, Oli MK. 2010. Genetic introgression and the survival of Florida panther kittens. Biological Conservation 143:2789–2796.

Iriarte JA, Franklin WL, Johnson WE, Redford KH. 1990. Biogeographic variation of foods habits and body size of the American puma. Oecologia 85:185–190.

Jansen BD, Jenks JA. 2012. Birth timing for mountain lions (Puma concolor); testing the prey availability hypothesis. PLoS ONE 7:1–7.

Johansson O, Koehler G, Rauzet GR, Samelius G, Andrén H, Mishra C, Lhagvasuren P, McCarthy T, Low M. 2018. Sex-specific seasonal variation in puma and snow leopard home range utilization. Ecosphere 9:1–14.

Johnson WE, Onorato DP, Roelke ME, Land ED, Cunninghame M, Belden C, McBride R, Jansen D, Lotz M, Shindle D, Howard J, Wildt DE, Penfold LM, Hostetler JA, Oli MK, O’Brien SJ. 2010. Genetic restoration of the Florida Panther. Science 329:1641–1645. https://doi.org/10.1126/science.1192891

Julian P. 2011. Home range dynamics of female Florida panthers in response to kitten production. Florida Scientist 74:215–223.

Laing SP, Lindzey FG. 1993. Patterns of replacement of resident cougars in southern Utah. Journal of Mammalogy 74:1056–1058.

Lambert CMS, Wielgus RB, Robinson HS, Katnik DD, Cruickshank HS, Clarke R. 2006. Cougar population dynamics and viability in the Pacific Northwest. Journal of Wildlife Management 70:246–254.

Laundré JW, Hernández L. 2007. Do female pumas (Puma concolor) exhibit a birth pulse? Journal of Mammalogy 88:1300–1304.

Laundré JW, Hernández L. 2008. The amount of time female pumas Puma concolor spend with their kittens. Wildlife Biology 14:221–227.

Laundré JW, Hernández L, Clark SG. 2007. Numerical and demographic responses of pumas to changes in prey abundance: testing current predictions. Journal of Wildlife Management 71:345–355.

Lindzey FG, VanSickle WD, Ackerman BB, Arnhurst D, Hemker TP, Laing SP. 1994. Cougar population dynamics in southern Utah. Journal of Wildlife Management 58:619–624.

Logan KA, Irwin LL, Skinner R. 1986. Characteristics of a hunted mountain lion population in Wyoming. Journal of Wildlife Management 50:648–654.

Logan KA, Sweanor LL. 2001. Desert puma: evolutionary ecology and conservation of an enduring carnivore. Washington, D.C.: Island Press.

Logan KA, Sweanor LL. 2009. Behavior and social organization of solitary carnivore. Pages 105–117 in
Reproductive Characteristics and Performance of the Florida Panther

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Hornocker MG, Negri S, editors. Cougar: ecology and conservation. Chicago: University of Chicago Press.

Maehr DS, Caddick CT. 1995. Demographics and genetic introgression in the Florida panther. Conservation Biology 9:1295–1298.

Maehr DS, Land ED, Roof JC. 1991. Social ecology of Florida panthers. National Geographic Research and Exploration 7:414–431.

Maehr DS, Land ED, Shindle DB, Bass OL, Hocott TS. 2002. Florida panther dispersal and conservation. Biological Conservation 106:187–197.

McBride RT, McBride RM, McBride CE. 2008. Counting pumas by categorizing physical evidence. southeastern Naturalist 7:381–400.

Mills SL. 2007. Conservation of wildlife populations: demography, genetics, and management. Malden, Massachusetts: Blackwell Publishing.

Obeyesekera J, Browder J, Hornung L, Hanwell MA. 1999. The natural South Florida system I: climate, geology and hydrology. Urban Ecosystems 3:223–244.

Onorato DP, Belden C, Cunningham M, Land D, McBride R, Roelke M. 2010a. Long-term research on the Florida panther (Puma concolor coryi): historical findings and future obstacles to population persistence. Pages 452–469 in Macdonald D, Loveridge A, editors. Biology and conservation of wild felids. Oxford, UK: Oxford University Press.

Onorato DP, Griffie M, Lotz M, Cunningham M, McBride R, Leone EH, Bass OL Jr, Hellgren EC. 2010b. Habitat selection by critically endangered Florida panthers across the diel period: implications for land management and conservation. Animal Conservation 14:196–205.

Onorato D, Desimone R, White C, Waits LP. 2011. Genetic assessment of paternity and relatedness in a managed population of cougars. Journal of Wildlife Management 75:378–384.

Quigley H, Hornocker MG. 2009. Cougar population dynamics. Pages 59–75 in Hornocker MG, Negri S, editors. Cougar: ecology and conservation. Chicago: University of Chicago Press.

Richter AR, Labisky RF. 1985. Reproductive dynamics among disjunct white-tailed deer herd in Florida. Journal of Wildlife Management 49:986–971.

Robinette WL, Gashwiler JS, Morris OW. 1961. Notes on cougar productivity and life history. Journal of Mammalogy 42:204–217.

Robinson HS, Desimone R, Gude JA, Thompson MJ, Mitchell MS, Hebblewhite M. 2014. A test of the compensatory mortality hypothesis in Mountain lions: a management experiment in west-central Montana. Journal of Wildlife Management 78:791–807.

Robinson HS, Wielgus RB, Cooley HS, Cooley SW. 2008. Sink populations in carnivore management: cougar demography and immigration in a hunted population. Ecological Applications 18:1028–1037.

Ross PI, Jalkotzy MG. 1992. Characteristics of a hunted population of cougars in southwestern Alberta. Journal of Wildlife Management 56:417–426.

Seidensticker JC IV, Hornocker MG, Wiles WV, Messick JP. 1973. Mountain lion social organization in the Idaho Primitive Area. Wildlife Monographs 35:1–60.

Smith TR, Hunter CG, Eisenberg JF, Sunquist ME. 1996. Ecology of white-tailed deer in Eastern Everglades National Park, an overview. Bulletin of the Florida Museum of Natural History 39:141–172.

Spreadbury B, Musil K, Musil J, Kaisner C, Kovak J. 1996. Cougar population characteristics in southeastern British Columbia. Journal of Wildlife Management 64:962–969.

Stearns SC. 1992. The evolution of life histories. New York: Oxford University Press.

Stockley P, Hobson L. 2016. Paternal care and litter size coevolution in mammals. Proceedings of the Royal Society B 283:1–40.

Stoner DC, Sexton JO, Choate DM, Nagol J, Bernales HH, Sims SA, Ironside KE, Longshore KM, Edwards TC Jr. 2018. Climatically driven changes in primary production propagate through trophic levels. Global Change Biology 24:4453–4463.

Stoner DC, Wolfe ML, Choate DM. 2006. Cougar exploitation levels in Utah: implications for demographic structure, population recovery, and metapopulation dynamics. Journal of Wildlife Management 70:1588–1600.

[U.S.FWS] U.S. Fish and Wildlife Service. 2008. Florida panther recovery plan (Puma concolor coryi). 3rd revision. Atlanta: United States Fish and Wildlife Service. Available: https://www.fws.gov/verobeach/MSRRPDFs/FloridaPanther.pdf (December 2020).

Towell DE. 1986. Notes on the development of cougar kittens. Murrelet 67:20–23.

Van De Kerk M, Onorato DP, Hostetler JA, Bolker BM, Oli MK. 2019. Dynamics, persistence, and genetic management of the endangered Florida panther population. Wildlife Monographs 203:3–35.

Williams BK, Nichols JD, Conroy MJ. 2002. Analysis and management of animal populations. San Diego, California: Academic Press.

Wilson SF, Hahn A, Gladlles A, Goh KML, Shackleton DM. 2004. Morphology and population characteristics of Vancouver Island cougars, Puma concolor vancouverensis. Canadian Field Naturalist 118:159–163.

Zar JH. 1999. Biostatistical analysis. Fourth edition. Upper Saddle River, New Jersey: Prentice-Hall.