Temporal trends in Florida panther food habits

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Abstract: Once on the brink of extinction, the Florida panther (*Puma concolor coryi*) has reoccupied parts of its extirpated range in southern Florida, USA over the past 20 years, which has largely been attributed to genetic restoration efforts initiated in 1995 to combat inbreeding depression and subsequent deleterious traits. Concurrent to the resurgence, an increase in documented livestock depredation events has heightened concern over human–panther conflicts. We examined 312 stomach content, scat, and feces (large intestine contents) samples collected 1989 to 2014 across the endemic range in southern Florida. We compared frequency of occurrence of prey items in samples by temporal (pre- and post-genetic restoration), geographic (north and south of 26° 10.017′ latitude), and demographic (age and sex) categories. We observed an apparent temporal shift in prey item occurrence in scats, where raccoon (*Procyon lotor*) occurrence increased while wild hog (*Sus scrofa*) occurrence decreased, whereas white-tailed deer (*Odocoileus virginianus*) occurrence appeared constant. Post-genetic restoration, we observed a geographic difference in panther prey, where white-tailed deer and raccoons were consumed more commonly in the southern part of the study area (characterized by lower soil quality and higher hydrological fluctuations), while wild hogs were consumed more frequently in the northern part of the study area. Neither sex nor age appeared to affect frequency of prey occurrence. Pets and livestock were not frequently found in the samples we examined. Overall, our results show shifts in panther diets both temporally and geographically; however, no notable changes in frequency of livestock found in panther diets were observed.

Key words: Florida panther, food habits, human–wildlife conflicts, livestock depredation, *Puma concolor coryi*

Assessment of the food habits of wildlife through the study of ingested materials (via feces, scat, and stomach contents) has been used extensively to elucidate the ecology of species, particularly as such information can play a key role in the management of species, and in particular the conservation and recovery efforts for endangered species. The collection of long-term food habit data allows for temporal comparisons, which could aid in the development of better informed management plans as species undergo range or abundance changes. Incorporating temporal effects could be especially important for imperiled species when management actions have successfully and rapidly increased the range or abundance of a species, which could in turn alter the use, availability, and selection of resources. However,

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a potential for human–wildlife conflict can arise when large predator populations recover, particularly where human property (e.g., livestock, pets) could be become prey.

The Florida panther (*Puma concolor coryi*; panther) has been listed as federally endangered since 1967, and the entire population of breeding individuals is restricted to a single population in southern Florida that encompasses <5% of the historic range (U.S. Fish and Wildlife Service [USFWS] 2008). In the early 1990s, the panther population was precariously small with probably <30 individuals remaining in the wild (Onorato et al. 2010), which led to a loss of genetic variation and subsequent inbreeding depression. To ameliorate inbreeding depression and concomitant traits (e.g., poor sperm quality, undescended testicles, atrial septal defects, kinked tail) that had impacted the small isolated endemic population of panthers, a genetic restoration program was initiated in 1995 with the release of 8 female pumas (*P. concolor stanleyana*) from Texas, USA (Onorato et al. 2010). The program proved successful at alleviating most correlates of inbreeding and also resulted in a simultaneous increase in population size (Johnson et al. 2010) to 100–180 adult and subadult panthers (Florida Fish and Wildlife Conservation Commission [FWC] 2014). However, the panther still faces a myriad of challenges, most notably human population expansion and associated habitat loss.

Puma prey is dominated by wild ungulates throughout the species' range (Robinette et al. 1959, Toweill and Meslow 1977, Thompson et al. 2009), though there is some limited evidence that age and stage (e.g., dispersing) class may affect diet (e.g., Elbroch et al. 2017). Biogeographic variation in puma diet has revealed differences in body size of prey, with the Florida subspecies characterized as an outlier from other North American populations (Iriarte et al. 1990). In Florida, panther diets have been typified by more frequent consumption of mid-size prey than most of their western counterparts, whereby raccoon (*Procyon lotor*), marsh rabbit (*Sylvilagus palustris*), nine-banded armadillo (*Dasypus novemcinctus*), and other mesomammals comprised a larger percentage (25.2%) of prey consumed (Maehr et al. 1990, Dalrymple and Bass 1996). Frequent consumption of relatively small prey has also been observed in puma populations in Mexico (Gómez-Ortiz and Monroy-Vilchis 2013). However, large prey, including wild hog (*Sus scrofa*) and white-tailed deer (*Odocoileus virginianus*; hereafter deer), were still main components of panther diets in Florida (Maehr et al. 1990, Dalrymple and Bass 1996).

Resurgence of panther numbers post-genetic restoration has led to heightened concerns over panther depredation of livestock and pets (Jacobs and Main 2015). Low human tolerance concerning the ecology of panthers is a major challenge to their recovery (USFWS 2008), as is the case for many large predators (Naughton-Treves et al. 2003, Treves and Karanth 2003, Røskaft et al. 2007). Instances of human–panther conflict appear to be more common since the panther population has increased, particularly regarding depredation of livestock and pets. For example, from 2004 to 2007, the FWC confirmed an average of 5.25 depredation events per year (21 total), whereas 2008 to 2016 averaged 21 events per year (190 total), with a general trend of increasing depredations through time (Panther Response Plan Database, FWC, unpublished data; FWC 2015). Depredations most frequently involved domestic goats (*Capra aegagrus hircus*) or sheep (*Ovis aries*), with fewer instances of other species, including young beef calves (*Bos taurus*; FWC 2014, 2015). In other parts of their range, pumas do not appear to play a large role in depredation of domestic livestock (Spalding and Lesowski 1971, Toweill and Maser 1985, Maehr et al. 1990, Gómez-Ortiz and Monroy-Vilchis 2013; but see Cunningham et al. 1999), even in areas where their range was expanding (Thompson et al. 2009). However, animal husbandry practices are likely key in mitigating depredation events (Shaw 1977, Cunningham et al. 1999, Thompson et al. 2009).

We examined Florida panther food habits based on scat, feces (contents of the large intestine), and stomach content samples collected over a 25-year period. We evaluated whether temporal (pre- versus post-genetic restoration), geographic (differing soil and hydrological regimes), and demographic (sex and age) categories affected frequency of prey items consumed by Florida panthers, with the objective of providing stakeholders and managers with descriptive information using the only available data. Description of panther
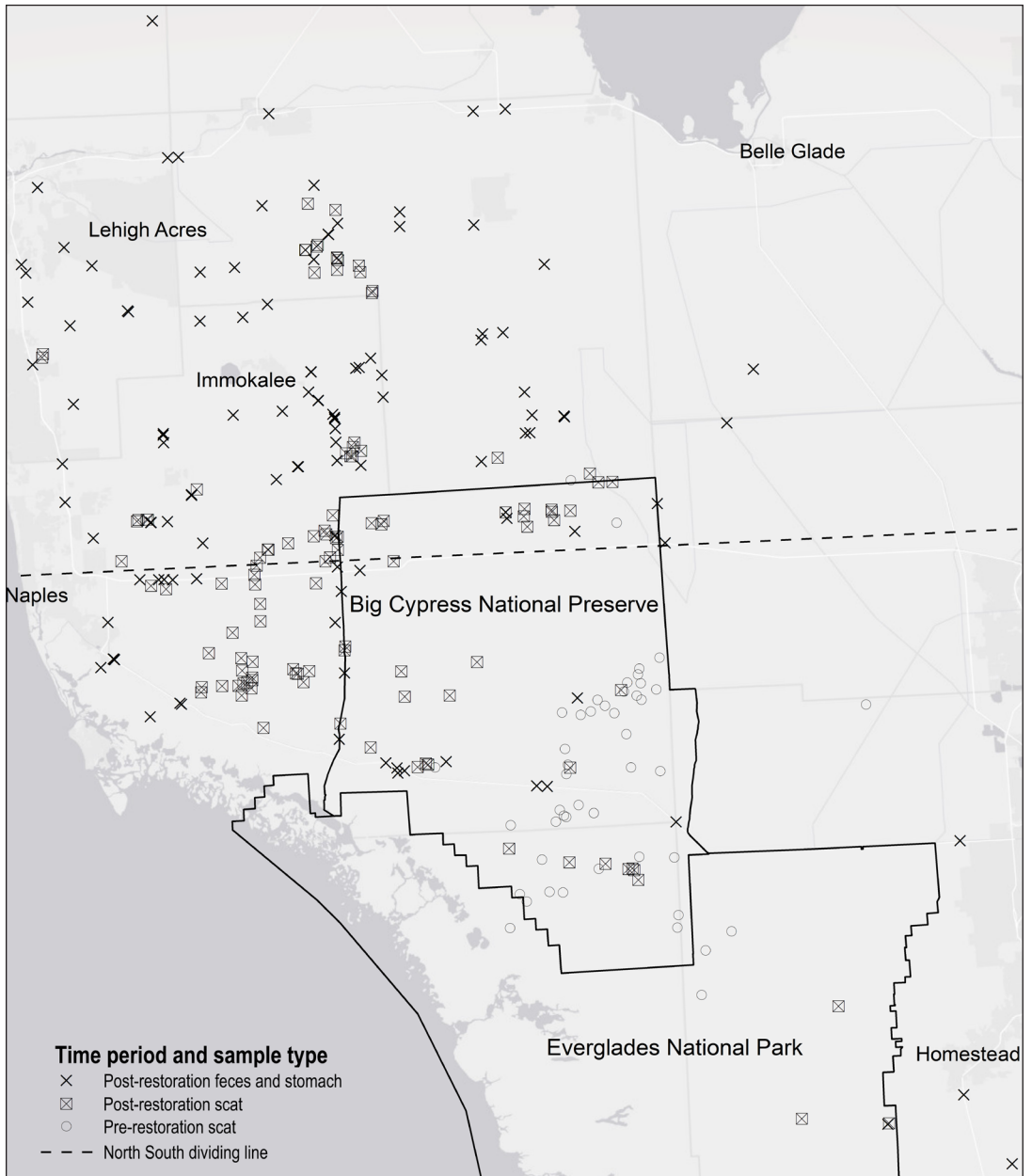
Figure 1. Locations of Florida panther (*Puma concolor coryi*) scat, stomach contents, and feces collected from 1989 to 2014 in south Florida, USA.

diets will aid in decision making for managers, particularly as it relates to human–wildlife conflict for residents and livestock owners. It is important to note that our study is descriptive in nature and uses observational data collected by varying methods over decades. While these data were opportunistically collected, and therefore do not represent a random sample collected systematically over geography and time, they are the most complete data available on Florida

panther diets, particularly as our study area encompasses most of the endemic range of the subspecies. Herein, we present an exploratory analysis describing the patterns observed, but acknowledge the potential bias inherent in those analyses given the nature of the data.

Study area

Our study area included lands encompassing the current Florida panther range in south

Florida (USFWS 2008). We collected samples from public lands (58% of samples) and private lands (42%; Figure 1). Southern Florida is subtropical with average temperatures in the mid-20°C range and average annual rainfall of 137 cm (USFWS 2015). Typical habitats in the study area were cypress forests, freshwater marshes, prairies, grasslands, hardwood hammocks, and pine flatwoods. The general habitat trend shifts from poor soil hydric dominated landscapes (e.g., wetlands, marshes) in the south to more fertile soil mesic landscapes (e.g., uplands, forests) in the north. Land uses included citrus agriculture, cropland, pastureland, rock mining, and both low- and high-density residential development.

Methods

Florida panthers have been routinely captured and fitted with radio-transmitters since 1981 (see McCown et al. 1990, McBride and McBride 2007), and all known mortalities, including those of uncollared individuals (e.g., roadkills), have undergone necropsy (see Cunningham et al. 2008). Radio-marked individuals were routinely monitored throughout any given year from 1989 to 2014 by FWC staff and the National Park Service. We categorized panthers into age classes by sex, whereby adults were at least 2 or 3 years old for females and males, respectively, subadults were 1 to <2 or 1 to <3 years old for females and males, respectively, and kittens were <1 year old regardless of sex. A latitude of approximately 26° 10.017′ generally represents a transition from poor soil and hydric-dominated habitats to more fertile soil and mesic-dominated habitats (Leighty 1954), and accordingly we used this latitude as a dividing line (i.e., north or south of) to describe broad scale habitat categories. Scats were collected opportunistically and during routine radio-tracking of marked individuals, and subsequently frozen for storage. Locations for most scats collected after 2002 were recorded using handheld global positioning system units. We approximated all other scat locations from detailed descriptions recorded in the field. Scats were placed in nylon bags and washed in a household washing machine to break apart dried and hardened samples and clean the remains (McDonald et al. 2005). Stomach contents and feces (contents of the

large intestines) were collected at necropsy from 2003 to 2014 by FWC staff. We rinsed stomach contents through a #10-mesh sieve to remove bile, mucus, and debris. Samples were sorted to allow macroscopic identification of prey via body parts, teeth, skeletal remains, and hair. Hair identification was confirmed microscopically by comparison to reference hairs and material. Puma stomachs typically contain only 1 unique prey item (Robinette et al. 1959, Spalding and Lesowski 1971); hence, we generally assumed all contents were from the same prey species unless strong evidence suggested otherwise ($n = 15$). When samples contained >1 apparent prey item ($n = 15$), we included both items in the analyses. We omitted samples that were empty ($n = 40$) from analyses. Contents that were unidentifiable, as well as contents that were observed infrequently, were categorized as "Other."

We used chi-square analysis to compare prey identified in scat samples pre- and post-genetic restoration ($n_{pre} = 59$, $n_{post} = 132$). Most post-genetic restoration samples were collected from 2002 to 2014 ($n_{1997–2001} = 4$). We performed several chi-square analyses with post-genetic restoration samples, excluding kittens given their low number ($n = 11$) and dependence on their mother, to compare prey contents between collection methods ($n_{scat} = 132$, $n_{stomach} = 77$), latitudinal zone ($n_{north} = 131$, $n_{south} = 89$), and sex ($n_{female} = 51$, $n_{male} = 72$). Because only feces and stomach contents can be collected from mortality events, we did not include scat samples in comparisons between causes of death. We used a chi-square analysis to compare age groups ($n_{kitten} = 11$, $n_{subadult} = 29$, $n_{adult} = 58$) using post-genetic restoration fecal and stomach samples. Scat samples were not included in the age comparison because we could not identify the age of individuals for every scat. Binomial proportions of post-genetic restoration data were used to estimate the prevalence and associated 95% confidence intervals for all content types.

All analyses were performed using PROC FREQ in SAS v9.3 (Cary, North Carolina, USA) with a Fisher's exact test (Freeman and Halton 1951). We present the results from all analyses as: (chi-square test statistic, P = Fisher's exact test). Due to relatively small sample sizes and generally high variability observed in our data,

we defined significance at α = 0.10. Relaxed significance thresholds helped mitigate the potential to miss significant effects in variable datasets, such as ours (Dytham 2003).

Results

We collected 312 scat, feces, or stomach content samples containing 291 unique prey items (n_{empty} = 40, $n_{two\ items}$ = 19). There appeared to be a difference in percent occurrence of prey items in panther scats collected pre- versus post-genetic restoration (χ_9 = 30.54, P <0.001). The most noticeable differences were an increase in the presence of raccoons and a decline in the presence of wild hogs (Table 1) in the post-restoration period. The most common prey items observed from all post-restoration samples (scat, feces, and stomach contents) were raccoons, followed by deer and wild hogs (Table 2). A latitudinal shift in prey items was observed in post-genetic restoration samples when the study area was divided into zones north and south of 26° 10.017′ (χ_9 = 27.31, P <0.001; Table 3). Deer and raccoons were the most common prey items found in samples collected in the southern zone, while wild hogs were the most common prey item found in the northern zone (Table 3). There were no apparent differences across age categories in post-genetic restoration samples (χ_{18} = 17.55, P = 0.245), nor were there

Table 1. Percent occurrence (and number of observations) of prey item found in scat samples of Florida panthers (*Puma concolor coryi*) pre-(1989–2005; n = 59) and post-genetic restoration (1996–2014; n = 132), south Florida, USA.

Prey item	Pre % (n)	Post % (n)
Wild hog (*Sus scrofa*)	55.93 (33)	21.97 (29)
White-tailed deer (*Odocoileus virginianus*)	27.12 (16)	28.03 (37)
Raccoon (*Procyon lotor*)	5.08 (3)	21.97 (29)
Nine-banded armadillo (*Dasypus novemcinctus*)	3.39 (2)	6.82 (9)
Rodentia	1.69 (1)	2.27 (3)
Virginia opossum (*Didelphis virginiana*)	0.00 (0)	3.79 (5)
Domestic cat (*Felis catus*)	0.00 (0)	3.79 (5)
Rabbit (*Sylvilagus* spp.)	0.00 (0)	4.55 (6)
Other	6.8 (4)	5.3 (7)
Livestock (only goats present)	0.00 (0)	1.52 (2)

Table 2. Probability of occurrence (and number of observations) of prey item found in scat, feces, and stomach contents (n = 232) of Florida panthers (*Puma concolor coryi*) post-genetic restoration (1996–2014), south Florida, USA.

Prey item	Occurrence (n)	95% CI
Raccoon (*Procyon lotor*)	24.42 (53)	18.86–30.70
White-tailed deer (*Odocoileus virginianus*)	23.04 (50)	17.61–29.22
Wild hog (*Sus scrofa*)	22.12 (48)	16.78–28.24
Nine-banded armadillo (*Dasypus novemcinctus*)	10.60 (23)	6.84–15.48
Rodentia	5.99 (13)	3.23–10.03
Virginia opossum (*Didelphis virginiana*)	5.07 (11)	2.56–8.89
Domestic cat (*Felis catus*)	5.07 (11)	2.56–8.89
Rabbit (*Sylvilagus* spp.)	3.23 (7)	1.31–6.53
Livestock	1.84 (4)	0.50–4.65
Other	5.53 (12)	2.89–9.46

Table 3. Percent occurrence (and number of observations) of prey item found in scat, feces, and stomach contents consumed by Florida panthers (*Puma concolor coryi*) post-genetic restoration (1996–2014) north (*n* = 131) and south (*n* = 89) of 26° 10.017′, south Florida, USA.

Prey item	North % (*n*)	South % (*n*)
Wild hog (*Sus scrofa*)	29.01 (38)	11.24 (10)
Raccoon (*Procyon lotor*)	19.08 (25)	28.09 (25)
White-tailed deer (*Odocoileus virginianus*)	16.79 (22)	29.21 (26)
Nine-banded armadillo (*Dasypus novemcinctus*)	13.74 (18)	4.49 (4)
Domestic cat (*Felis catus*)	4.58 (6)	4.49 (4)
Rodentia	3.05 (4)	6.74 (6)
Virginia opossum (*Didelphis virginiana*)	3.05 (4)	6.74 (6)
Rabbit (*Sylvilagus* spp.)	1.53 (2)	5.62 (5)
Livestock	3.05 (4)	0 (0)
Other	6.11 (8)	3.37 (3)

differences between sexes (χ_9 = 3.28, *P* = 0.975). Livestock and pets were found in 5.5% of the 272 unique samples collected (i.e., not counting sample with multiple items twice). Cattle was found in 1 sample (0.4%), domestic goats (1%) in 3 samples, and domestic cats (*Felis catus*) in 11 samples (4%). Prey contents appeared different when comparing stomachs to scat (χ_9 = 14.73, *P* = 0.088), with nine-banded armadillo and Rodentia found more often in stomach contents and deer found more commonly in scat. Atypical items ("other" classification; *n* = 12) observed a single time were coyote (*Canis latrans*), American alligator (*Alligator mississippiensis*), North American river otter (*Lontra canadensis*), and striped skunk (*Mephitis mephitis*). We also classified 5 records as unknown mammal, 3 records as unknown avian, and 3 records as unknown.

Discussion

Our results largely parallel previous findings (Maehr et al. 1990, Dalrymple and Bass 1996) as panthers continue to rely heavily on deer, wild hogs, and raccoon, though the degree to which they use these prey items shifted between pre- and post-genetic restoration periods. However, collection areas pre- and post-genetic restoration did differ somewhat as research priorities for the panther have changed over time and the population expanded (Onorato 2010). The causes of the difference detected in food habits between the 2 periods are likely complex and difficult to decipher as predator diets are largely influenced by intrinsic and extrinsic forces that influence demographic characteristics of the predator population, the vulnerability of available prey, and seasonal factors (e.g., winter vs. summer or wet season vs. dry season; Knopff et al. 2010).

Abundance and localized density of white-tailed deer appear to have declined in parts of south Florida over the past several decades, most notably in the Stairsteps Unit of Big Cypress National Preserve (E. Garrison, FWC, personal communication), which was partly predicted (Labisky et al. 1999). This decline led to speculation that an expanding panther population may have played a role, but direct evidence to support such claims is difficult to garner because of the complexity of predation patterns, prey population demographics, and abiotic factors that impact both predator and prey. We found little evidence that the frequency of deer occurrence in panther diets has increased over time (Table 1), though deer occurrence was more frequent in the southern portion of the study area post-genetic restoration. White-tailed deer in Florida are known to be susceptible to population fluctuations due to intermittent and extensive flood and drought patterns (Fleming et al. 1994, Labisky et al. 1999, MacDonald-Beyers and Labisky 2005), which are common in south Florida. Apparent deer declines could be tied to a multitude of factors including fluctuating water levels, disease, illegal harvest, increasing and expanding predator populations, and poor

habitat (McCown et al. 1991, Fleming et al. 1994).

Panthers relied more heavily on small and meso-mammals, particularly raccoons, in the southern, less fertile portion of the study area (Table 3). Occurrence of raccoons was also higher in the latter of the time periods we examined (post-genetic restoration; Table 1). Human population centers in Florida have increased dramatically in recent decades, including in areas within panther range that have been among the fastest growing in the United States (U.S. Census Bureau 2016). Increases in available anthropogenic food sources may lead to increased stability of meso-mammal populations (e.g., raccoon; Prange et al. 2004) and, when coupled with potential meso-mammal releases resulting from the historic absence of apex predators, might provide a more abundant meso-mammal prey source for panthers.

However, Dorcas et al. (2012) postulated that small and meso-mammal densities in Everglades National Park have declined dramatically since 2000 due to increased predation from Burmese pythons (*Python bivittatus*). It is unlikely that the reported declines are representative of overall meso-mammal populations in south Florida, especially in areas occupied by panthers that are less inundated with Burmese pythons, but the reported decline seemingly coincides with the increased use of these resources by panthers. It should also be noted that pythons have been noted to prey on deer in South Florida as well, though to what degree is unknown.

The occurrence of wild hogs in panther diets has decreased markedly post-genetic restoration, although wild hog occurrence was higher in the northern, more fertile portion of the study area which parallels previous findings (Maehr et al. 1990). Wild hog populations are vulnerable to dramatic fluctuations in water levels (Fernández-Llario and Carranza 2000). Based on harvest data from the Big Cypress National Preserve, wild hog populations could have declined in the preserve since the mid-1990s (E. Garrison, FWC, personal communication). The observed shift in frequency of occurrence of wild hogs in the panther diet could reflect this potential localized decline. Moreover, apex feline predators exhibit significant selectivity for prey species (Karanth and Sunquist 1995). For example, cougars (*Puma concolor*) and

leopards (*Panthera pardus*) tended to prefer ruminants and avoid wild hogs, even in areas where ungulates were less available and hogs were more available (Karanth and Sunquist 1995, Haverson et al. 2000). Hence, our observed variability in use of wild hogs by panthers could be a result of variability in prey availability and selectivity that arises due to variability in habitat quality and moisture regimes.

When examining ingested materials, inconsistencies can arise between sampling methods (Dalrymple and Bass 1996); for example, smaller prey items could be consumed quickly and produce few scats. We did find Rodentia and nine-banded armadillos less often in scats and deer more often in scats; however, collection method did not appear to influence the frequency of raccoons and Virginia opossums (*Didelphis virginiana*). If Rodentia and nine-banded armadillos are lower-quality prey for panthers and deer are higher-quality prey, then individual quality (e.g., frailty hypothesis; Vaupel et al. 1979, Vaupel and Yashin 1985) could elucidate our results, whereby more robust individuals (i.e., living; scat collection) would consume higher-quality prey than their frail counterparts (i.e., dead individuals; stomach contents and feces samples). Further, most stomach contents and feces were collected from panthers hit by cars, which typically occurs in more marginal habitats than in the core, higher-quality habitat, range where wildlife underpasses exist.

Jacobs and Main (2015) found panther depredation rates of beef calves varied 0.5–5% on 2 separate ranches in south Florida. Our findings suggest that the Florida panther population does not use livestock to a large extent in their diet, as we only documented a single case of cow and 3 cases of goat predation. However, our data may be somewhat skewed because collection efforts were not evenly distributed across panther range and often did not include private lands where panthers have access to livestock. However, many panther mortalities sampled in our study were collected along rural roads abutted by private cattle ranches, so there were ample opportunities to document cattle remains in stomach contents and feces. Regardless of our results, agency biologists documented 56 calf depredations from 2010 to 2016 (Panther Response Team

Database, FWC, unpublished data). Current efforts to try and ameliorate some of these losses for private ranchers have focused on developing compensation programs that reimburse cattle owners who provide quality habitat for panthers for some expected level of calf loss to panthers.

Management implications

Our study has demonstrated that an expanding and growing population of panthers has resulted in changes in food habits, with less reliance on wild hogs and increased reliance on some meso-mammals. However, the changes we observed in panther food habits cannot be solely assigned to an increase in the panther population, as other often interacting factors impact prey populations (e.g., water levels, habitat loss), and untangling those variables will require more research. Deer continued to comprise a similar percentage of panther prey pre- versus post-genetic restoration, which suggested that land managers should continue to strive for initiatives that improve habitat for better recruitment rates of white-tailed deer. While domestic animals comprised a very small percentage of the prey items identified in our study, agencies should continue to work with private landowners to minimize panther depredations on livestock and pets. Given the potential for depredations to impact public sentiment and localized panther population health (e.g., feline leukemia virus; Cunningham et al. 2008), minimizing these events, no matter how infrequent they may be, should improve the long-term outlook for the continued recovery of the panther.

Acknowledgments

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