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Spatiotemporal pattern of interactions between an apex predator and sympatric species

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Increases in apex predator abundance can influence the behavior of sympatric species, particularly when the available habitat and/or resources are limited. We assessed the temporal and spatiotemporal interactions between Florida panthers (*Puma concolor coryi*) and six focal sympatric species in South Florida, where Florida panther abundance has increased by more than 6-fold since the 1990's. Using camera trap data, we quantified species' diel activity patterns, temporal overlap, and time-to-encounter (i.e., time between consecutive visits of a Florida panther and a focal species and vice versa). The Florida panther and bobcat (*Lynx rufus*) displayed a nocturnal activity pattern; the black bear (*Ursus americanus*), white-tailed deer (*Odocoileus virginianus*), wild boar (*Sus scrofa*), and wild turkey (*Meleagris gallopavo*) were mostly diurnal; and the raccoon (*Procyon lotor*) was cathemeral. Prey species and black bears minimized encounters with Florida panthers by being active during the day and displaying longer time-to-encounter, whereas Florida panthers visited a site after a prey species at higher probabilities than after competitor species, and were more likely to visit an elevated site or upland habitat. Our results suggest that interactions between Florida panthers and sympatric species in our study system are driven by species-specific behavioral responses. Gaining a better understanding of the crucial interactions driving species coexistence is important for a better understanding of the structure and function of ecological communities and help manage the potential expansion of the Florida panther into Central Florida.

Keywords: adaptation, antipredator behavior, cougar, Cox proportional hazard models, large carnivore, species interactions, survival analysis, wildlife conservation

Interactions among sympatric species can strongly influence species distribution and abundance, as well as the structure and functioning of ecological communities (Paine 1966; Soulé et al. 2003; Harvey et al. 2017). In particular, predation and intraguild competition can have profound impacts on biodiversity, species distribution, and abundance (Ripple et al. 2014). For example, apex predators can control herbivore population numbers (White et al. 2013) and prevent the increase in abundance or influence the behavioral response of mid-sized carnivores, a phenomenon also known as mesopredator release (Ritchie and Johnson 2009). Due to their direct (lethal) and indirect (sublethal) effects, predators can influence the abundance and behavior of sympatric species (Linnell and Strand 2000; Soulé et al. 2003; Creel and Christianson 2008; Ritchie and Johnson 2009), which often adopt antipredator strategies to minimize the perceived predation risk either from direct encounters with a predator or from the detection of chemical cues (Lima and Dill 1990; Lima 1998; Persons and Rypstra 2001; Creel et al. 2014). Likewise, competitive interactions can lead to resource partitioning (Schoener 1974) and character displacement (Schluter and McPhail 1992; Grant 1999), potentially influencing population dynamics of the species involved, as well as the structure and function of ecological communities (e.g., Hairston et al. 1960; Tilman 1982; Leibold and McPeek 2006). In fact, competition and predation often interact, affecting the structure, function, and stability of ecological communities (e.g., Kotler and Holt 1989; Chesson and Kuang 2008). Typically, predators concentrate their foraging efforts in areas of high prey density, whereas prey avoid areas frequented by predators, particularly when predators are more active. These conflicting responses between predators and prey, termed "behavioral response race" by Sih (1984), are hypothesized to determine the spatiotemporal pattern of interactions in predator–prey systems (e.g., Sih 1984; Brown et al. 1999; Persons and Rypstra 2001).

Segregation in space or time among sympatric species has been reported for several taxa (e.g., Durant 1998; Schuette et al. 2013; Karanth et al. 2017) and is believed to reduce the intensity of species interactions while promoting coexistence and species richness (e.g., Sosa-Lopez and Mouillot 2007; Vanak et al. 2013; Sladecek et al. 2017). However, opportunities for spatial segregation are becoming limited as wildlife habitat continues to contract and species have to exist in fewer, smaller, and increasingly isolated habitat patches (Mcdonald et al. 2008). In addition, after centuries of persecution and range contractions (Woodroffe 2001), populations of predators have been able to recover in areas where favorable conservation strategies have been implemented (Linnell et al. 2001). Such an increase in predator abundance in a smaller footprint of habitat is likely to increase the frequency and intensity of species interactions such as predation and competition, where temporal and spatiotemporal segregation may drive coexistence among predator, competitor, and prey species.

The Florida panther, federally listed as endangered in 1967 and subsequently given protection under the Endangered Species Act of 1973 (Onorato et al. 2010), has increased from 20–30 individuals in the 1990s (McBride et al. 2008) to a current estimated population of 120–230 individuals (FWC 2018). A combination of conservation strategies, including a genetic introgression program implemented in 1995 (Hostetler et al. 2010; Johnson et al. 2010; van de Kerk et al. 2019), catalyzed this recovery (Onorato et al. 2010). However, the Florida panther's distribution now is restricted to less than 5% of its historic range, and the population remains threatened by factors such as inbreeding, demographic stochasticity, habitat loss, and human–panther conflicts resulting from the rapid expansion of anthropogenic development (Onorato et al. 2010; Frakes et al. 2015). The recent increase in Florida panther abundance, along with an overall net loss of quality habitat (Frakes et al. 2015) could impact the frequency and intensity of competitive and predatory interactions between the Florida panther and sympatric species. Such changes can endanger the conservation of single species within the ecological community, and the resulting interactions may compromise ecosystem integrity (Harvey et al. 2017). Understanding the mechanisms underlying coexistence among the Florida panther and its interacting species therefore is important not only for interpreting community structure and function, but also for the conservation of the Florida panther in a rapidly urbanizing landscape (Soulé et al. 2003).

Direct observation of species interactions in the wild can be challenging. However, the development of camera trapping technology offers an effective, noninvasive alternative to collect data on species occurrence and behavior (O'Connell et al. 2010). Such data have been used to discern the temporal patterns of species behavior and interactions using methods such as the temporal overlap coefficient (Ridout and Linkie 2009), or the spatiotemporal overlap among species at shared camera traps (Karanth et al. 2017). Whereas the overlap coefficient (Ridout and Linkie 2009) and related methods have yielded many important insights into how sympatric species might coexist (e.g., Lewis et al. 2015; Karanth et al. 2017), they do not consider the directionality of the interaction or account for the perceived risk in each particular situation (typically reflected in the waiting time until a visit), which can strongly influence the behavioral response of a predator, competitor, or prey species, at a certain time and location (Vanak et al. 2013; Cusack et al. 2017). For instance, prey species may delay a visit to a site recently visited by a predator to minimize the predation risk, but a predator may reduce this time to find the prey as soon as possible. An alternative analytical approach that can explicitly consider the time until an event occurs, represented as the time until the visit of a species following the visit of another species at the same camera trap (i.e., an interaction), is the "time-to-event" analysis (Hosmer, Jr. et al. 2008; Bischof et al. 2014). Using time-to-event analysis, it also is possible to assess the directionality of each interaction, and test for the effect of covariates potentially influencing species interactions (Schuette et al. 2013).

Our goal was to discern the temporal and spatiotemporal interactions between the Florida panther and six sympatric species (hereafter "focal species"): four prey species (white-tailed deer, *Odocoileus virginianus*; wild boar, *Sus scrofa*; raccoon, *Procyon lotor*; and wild turkey, *Meleagris gallopavo*); and two potential competitors (bobcat, *Lynx rufus*; and black bear, *Ursus americanus*). To better understand the mechanisms driving the temporal and spatiotemporal patterns of interspecific interactions, we specifically: (1) quantified the species' diel activity pattern and the temporal overlap pattern between the Florida panther and each of the focal species; and (2) analyzed the spatiotemporal interactions between the Florida panther and each of the focal species in both directions of the interaction (the detection of a focal species following a Florida panther' visit [Fig. 1a] and the detection of a Florida panther following a focal species' visit [Fig. 1b]). We hypothesized that: (1) species perceiving high predation risk would minimize the risk of predation from the Florida panther either by exhibiting low temporal overlap or an increased time-to-encounter; and (2) the Florida panther would reduce the time-to-encounter after a visit by a preferred prey species but not after a visit by a potential competitor.

Materials and Methods

Study area and data collection.—The study was conducted in the Addition Lands Unit of Big Cypress National Preserve (BCNP), Florida, United States (Fig. 2). The study area, centered approximately on 26°13′N, 81°03′W covered 225 km^2 north of Interstate Highway 75 (I-75) in Collier County and was predominantly composed of cypress swamp. Other

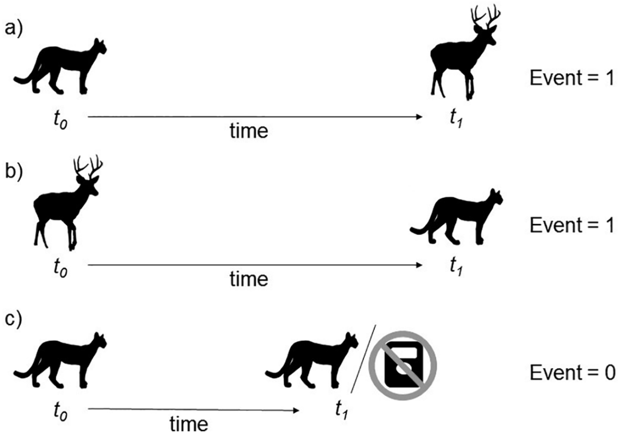

Fig. 1.—Diagram depicting the direction of interaction between Florida panther and focal species. The time-to-encounter is represented by time difference between the photographic capture of the first species (t_0) and photographic capture of the second species (t_1). (a) P–Sp interaction: a Florida panther is recorded first and a focal species second; (b) Sp–P interaction: a focal species is recorded first and a Florida panther second; (c) the interaction starts with the detection of the first species, but is not finalized either due to: (1) consecutive independent detection of the same species, (2) camera malfunctioning, or (3) end of the survey before the second species was detected.

habitat types included mixed wetland forest, freshwater marsh, pinelands, and hardwood swamp (Kautz et al. 2006). In South Florida, temperatures remain stable throughout the year (18–29°C), but humidity and rainfall define two seasons: wet (May–October) and dry (November–April—United States Climate Data 2017). The present study started in the late dry season (1 April 2014) and lasted until the wet season (19 September 2014), coinciding with the rise of the surface water level (Frakes et al. 2015). Recreational activities, such as hiking and camping were allowed in the Addition Lands Unit, but hunting was prohibited during the study period.

We divided the study area into 50 4.5-km^2 grid cells, with a single camera trap (Reconyx HC500; Reconyx, Holmen, Wisconsin) deployed at a location as close to the grid cell center as possible (Fig. 2). Sampling did not take place in inaccessible grid cells. All 50 cameras were secured to trees ca. 45 cm aboveground and were frequently placed along designated or historic off-road vehicle (ORV) trails, game trails, or other favorable sites, so as to maximize the probability of photographic captures of Florida panthers and other species. We visited the camera trap sites once per month to check batteries and functionality, download pictures, and trim the surrounding vegetation.

Diel activity patterns.—We pooled together all pictures where a species was identified. Analyses were conducted for each species separately. We assessed the temporal autocorrelation of subsequent photographic captures of a given species using the "acf" function in the "Stats" package (R Core Team 2019), and defined the independence threshold as the time lag in which autocorrelation became nonsignificant. We considered two photographic records to be independent if the time between them was longer than the independence threshold. Using the independent detections, we quantified the diel activity pattern of each species by assessing the recorded frequency (number of independent photographic captures per hour) throughout the diel period (Table 1). We classified activity patterns into four categories: diurnal (1 h after sunrise to 1 h before sunset), nocturnal (1 h after sunset to 1 h before sunrise), crepuscular (1 h before and after sunrise and sunset), and cathemeral (irregular throughout the day). We obtained sunrise and sunset times for every day of camera deployment using the NOAA Solar Calculator (NOAA 2017). For each species, we conducted a chi-square test to assess differences in the observed and expected number of detections during each diel period, considering all diel period categories independent as null hypothesis.

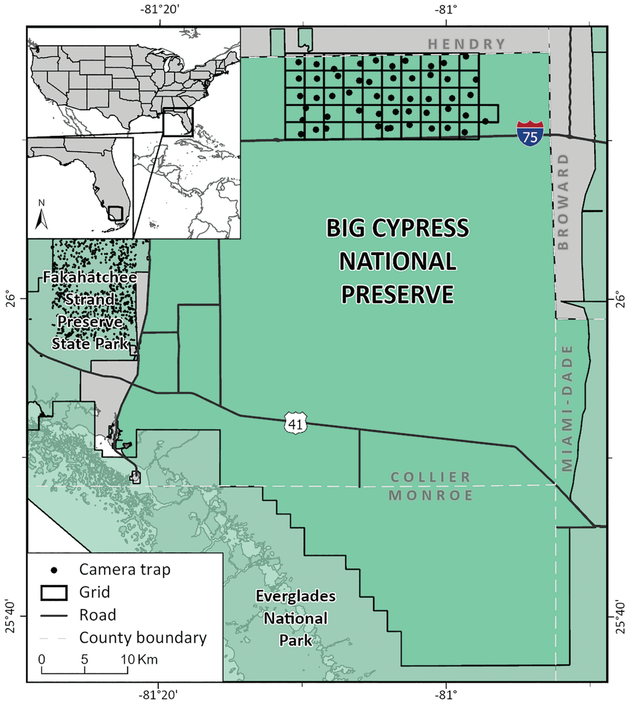

Fig. 2.—Location of the study area, grid, and camera trap sites within the Addition Lands Unit of Big Cypress National Preserve, Florida, United States.

Activity pattern overlap.—We quantified the temporal overlap of each pair of Florida panther–focal species activity pattern using the overlap coefficient (Δ) described by Ridout and Linkie (2009) in the "overlap" package (Meredith and Ridout 2016). Using the independent detections and for each pair of interacting species, we obtained the diel activity patterns using the kernel density estimation method with the von Mises distribution for circular data. We calculated the overlap coefficient, which quantifies the overlapping area under density curves, using the two recommended nonparametric estimators for small ($\hat{\Delta}_1$) and large ($\hat{\Delta}_4$) sample sizes (≤ 50 and ≥ 75 samples, respectively). For each overlap coefficient, we obtained 95% confidence intervals (*CI*s) by computing 10,000 bootstrap samples (Linkie and Ridout 2011).

Spatiotemporal interactions.—We used a time-to-event approach to analyze the interactions in the spatiotemporal scale. Time-to-interaction data are akin to time-to-event data typically

Table 1.—Number of independent photographic captures of each species included in our study (n) conducted in the Addition Lands Unit of Big Cypress National Preserve, Florida, United States; time lag (min) in which the temporal autocorrelation became nonsignificant (independence threshold); naïve occupancy calculated as the number of sites present/total number of sites; frequency of independent photographic captures within each diel period: diurnal (1 h after sunrise to 1 h before sunset), nocturnal (1 h after sunset to 1 h before sunrise), and crepuscular (1 h before and 1 h after sunrise and sunset); activity pattern category; and chi-square values[a] and associated P-values to assess differences in the observed and expected number of detections during each diel period.

Species	n	Independence threshold (min)	Naïve occupancy	Diurnal	Nocturnal	Crepuscular	Activity pattern	χ^2	P-value
Florida panther	286	16	0.94	0.20	0.61	0.19	Nocturnal	56.84	< 0.001
Bobcat	415	15	0.96	0.22	0.59	0.19	Nocturnal	69.64	< 0.001
Black bear	653	14	0.98	0.67	0.08	0.25	Diurnal	305.60	< 0.001
White-tailed deer	1,368	17	1	0.74	0.09	0.17	Diurnal	707.46	< 0.001
Raccoon	371	29	0.9	0.41	0.52	0.07	Cathemeral	28.22	< 0.001
Wild boar	25	224	0.18	0.96	0	0.04	Diurnal	30.54	< 0.001
Wild turkey	982	32	0.94	0.93	0	0.07	Diurnal	1,098.94	< 0.001

[a] Expected values were calculated by weighting each category by its duration in a day (day = 10 h, night = 10 h, and crepuscule = 4 h) to account for the difference in length.

used in survival analysis (Pollock et al. 1989; Bischof et al. 2014). In our case we defined an event (henceforth referred to as "interactive event") as the detection of a species following a visit by another species (Cusack et al. 2017): the consecutive detections at a site of a focal species (t_1) following a Florida panther visit (t_0; Fig. 1a, henceforth referred to as "P–Sp interaction"), or the consecutive detections of a Florida panther (t_1) following a focal species visit (t_0; Fig. 1b, henceforth referred to as "Sp–P interaction"). We calculated the minimum time-to-encounter in hours (time difference $t_1 - t_0$) using the raw photographic capture data to obtain the last visit of the first species (t_0) and the first visit of the second species (t_1). We used Cox proportional hazard (CPH) regression models (Cox 1972) to analyze the time-to-encounter data and estimate the probability of a species visiting a site at a given time (t_1) after the visit of the first species (t_0).

The CPH regression method is a semiparametric approach that allows the evaluation of the multiplicative effect of explanatory variables on the instantaneous rate of occurrence of an event (baseline hazard) without specifying the shape of the underlying distribution (Cox 1972; Hosmer, Jr. et al. 2008). When the event times are continuously distributed, the hazard function (i.e., instantaneous rate at which an interactive event occurs—Cox 1972; Lee 1992; Hosmer, Jr. et al. 2008) is calculated as

$$h(t|x) = h_0(t)\ \exp(\beta_1 x_1 + \beta_2 x_2 + \ldots + \beta_p x_p)$$

where $h_0(t)$ is the baseline hazard (i.e., hazard when values of all covariates are zero), x is a matrix of p covariates, and β_i is the regression coefficient for covariate i. The above equation is equivalent to

$$S(t) = S_0(t)\exp(\beta_1 x_1 + \beta_2 x_2 + \ldots + \beta_p x_p)$$

(e.g., Lee 1992) where $S(t)$ is the survival (or interactive event) function, $S_0(t)$ is the baseline survival (i.e., value of survival function when all covariates are ignored).

We used an interactive event as unit of analysis, which was assumed to occur with probability $\Pr\{T > t_1\}$, where T is the maximum time in which an interaction can occur. We restricted the maximum time-to-encounter to seven consecutive days (i.e., $T = 7$ days), because detection of chemosensory cues of the presence of a species would be stronger in the short term as cues fade or become less detectable over time due to weather conditions (Lima 1998; Parsons et al. 2018). We used the time-to-encounter as the response variable, right-censoring observations if the interaction was not finalized either due to: (1) consecutive independent detection of the same species, (2) camera malfunctioning, or (3) end of the survey before the second species was detected (Fig. 1c). Site-specific information such as elevation and habitat type were used as explanatory variables. We used elevation, ranging from 2.08 to 7.04 m a.s.l. in our study area, as a surrogate for hydrology, which is a strong determinant of Florida panther presence (Frakes et al. 2015) and movement rates (Criffield et al. 2018), and can also affect survival and habitat use patterns of other species considered in this study (MacDonald-Beyers and Labisky 2005). We extracted elevation data from the 1/3 arc-second 3D Elevation Program data set (U.S. Geological Survey 2014), and obtained habitat type by reclassifying the land cover classes of the Cooperative Land Cover (FWC 2016) into two categories: upland and wetland. The ArcGIS Pro (ESRI 2019) program was used for spatial calculations. We tested for the proportionality of hazards of the explanatory variables using the "cox.zph" function in the "survival" package by assessing if the significance level for the fitted model was < 0.05 (Therneau 2015). The magnitude of covariate effect is indicated by 1 − hazard ratio (HR), and can be interpreted as the probability of an event occurring before time T. A HR > 1 represents a higher probability of an event occurring before time T (i.e., if HR = 1.x, the probability of an event occurring before time T is x times higher), whereas HR < 1 represents a lower probability of an event occurring before time T (i.e., if HR = 0.y, the probability of an event occurring before time T is 1 − y times lower). We included camera trap ID in the CPH models as random effect using the "frailty" function in the "survival" package (Therneau 2015) to account for the possible lack of independence of photographic captures at the same camera trap.

We used Akaike's Information Criterion corrected for small sample size (AICc) for multimodel comparison and statistical inference. Models with ΔAICc ≤ 2 were considered to be comparable (Burnham and Anderson 2002). We evaluated the effect of covariates by comparing AICc values for the models with and without a particular covariate (null model), and by assessing if the 95% *CI*s for the HR included 1. We excluded wild boar from these analyses because we only had five Florida panther–wild boar interactions and six wild boar–Florida panther interactions; these sample sizes were too small to warrant statistical analyses.

We used a bootstrapping approach (Efron and Tibshirani 1993) to test if the observed pattern of spatiotemporal interactions for a focal species differed from that expected at random (i.e., null hypothesis assuming no spatiotemporal interaction). We randomized the frequency of detections generating 1,000 randomized data sets for each species and comparing the observed data and one randomized data set at a time using CPH models. In each iteration, we created a data set of equal length to the observed data set by: (1) maintaining the capture date and time of the first species (t_0); (2) generating random capture date and time for the second species (t_1) by sampling with replacement from each species' observed activity pattern probability density function to obtain the time, and randomly selecting a day from 0–7 if $t_1 > t_0$, or randomly selecting a day from 1–7 if $t_1 < t_0$; (3) maintaining the proportion of finalized events from the observed data (z) by randomly sampling a number $0 \le j \le 1$, and assigning event = 1 if $j \le z$ or event = 0 if $j > z$; and (4) censoring the interactions with date after the observed end date of the study, assigning event = 0. We combined the observed data with each randomized data set and fitted a CPH model with the type of data ("original" or "random) as a covariate; we then performed the log-rank test and computed HR values. We considered results to be significant if 95% of log-rank test *P*-values < 0.05. We assessed the magnitude of difference between observed and randomized patterns by calculating the mean HR and 95% *CI*s for the 1,000 bootstrap samples. We carried out all analyses using the R software (R Core Team 2019).

Results

Diel activity patterns.—The sampling period comprised 7,984 camera trap nights, with each of the focal species (except for wild boar) detected at least once at > 90% of the sites (Table 1). The independence threshold was different for each species, ranging from 14 to 224 min and yielding a total of 4,100 independent pictures. Diel activity patterns differed substantially among species (Table 1). The Florida panther and bobcat primarily were nocturnal, showing one activity peak before sunrise and one after sunset. Black bear, white-tailed deer, wild boar, and wild turkey, exhibited a predominantly diurnal activity pattern, whereas raccoon exhibited a cathemeral pattern. For all species, chi-square tests revealed that observed frequencies of detections differed significantly from expected frequencies based on chance alone (Table 1).

Activity pattern overlap.—The diel activity pattern of the Florida panther extensively overlapped with that of bobcat ($\hat{\Delta}_4$ = 0.89 (0.83–0.95)) and raccoon ($\hat{\Delta}_4$ = 0.77 (0.71–0.83)), suggesting that these species were active at similar times throughout the day (Fig. 3). There was less temporal overlap for those species that were predominantly diurnal, and therefore less active or inactive during highest Florida panther activity (black bear: $\hat{\Delta}_4$ = 0.47 (0.41–0.52); white-tailed deer: $\hat{\Delta}_4$ = 0.42 (0.37–0.47); wild turkey: $\hat{\Delta}_4$ = 0.27 (0.22–0.31); and wild boar: $\hat{\Delta}_1$ = 0.27 (0.16–0.33); Fig. 3).

Spatiotemporal interactions.—For the P–Sp interaction, wild turkey and black bear showed the shortest time-to-encounter, whereas white-tailed deer waited the longest after a Florida panther visited a site (median (interquartile range; sample size)): wild turkey = 36.7 h (13–75.6; 109); black bear = 47.2 h (22.7–94.3; 110); raccoon = 58.2 h (27–116; 41); bobcat = 58.6 h (27.8–101; 75); white-tailed deer = 66.5 h (23.8–113; 86). The CPH models did not unveil significant patterns of spatiotemporal interactions, but did provide further details of the species response to a recent Florida panther visit (Supplementary Data SD1). Black bear and raccoon showed lower probabilities of visiting a site after a Florida panther in wetland habitat than upland habitat (HR and 95% *CI*s): HR = 0.67 (0.42–1.07), and HR = 0.48 (0.15–1.57), respectively. Wild turkey also showed higher probabilities of visiting a site after a Florida panther at higher elevations (HR = 1.20 (0.93–1.55)). We found no pattern of spatiotemporal interactions for bobcat or white-tailed deer (Supplementary Data SD1).

The median time-to-encounter for the Sp–P interaction was similar for all species, but it was lowest for wild turkey (median (interquartile range; sample size)): wild turkey = 38.4 h (19.2–84.2; 111); raccoon = 54.3 h (20.4–88.1; 54); black bear = 55.5 h (26.2–97.9; 101); white-tailed deer = 58.3 h (19.2–113; 97); bobcat = 61.5 h (24.3–113; 78). The CPH models for the Sp–P interaction revealed significant lower probabilities of a Florida panther visiting a site in wetland habitat than upland habitat following a visit by black bear (HR and 95% *CI*s): HR = 0.54 (0.31–0.96), and raccoon: 0.38 (0.17–0.87). The Florida panther also showed a higher probability of visiting a site at higher elevations after visits by white-tailed deer, HR = 1.40 (1.06–1.85) and wild turkey, HR = 1.29 (1.12–1.49; Fig. 4) (Supplementary Data SD2).

CPH models testing whether the observed P–Sp patterns differed from random indicated that bobcat, black bear, white-tailed deer, and wild turkey would visit a site after a Florida panther with significantly higher probabilities than by chance (proportion of *P*-values > 0.05, bobcat = 0.013; black bear = 0; white-tailed deer = 0.02; and wild turkey = 0; Supplementary Data SD3), suggesting no avoidance. White-tailed deer and raccoon showed the lowest HRs from all species (HR = 1.70 (1.69–1.72) and HR = 1.74 (1.72–1.76), respectively). For the Sp–P interaction, the Florida panther also showed significantly higher probabilities of visiting a site following visits by all species (proportion of *P*-values > 0.05, bobcat = 0.008; black bear = 0; white-tailed deer = 0; raccoon = 0.001; and wild turkey = 0; Supplementary Data SD4), with higher HRs for wild turkey (HR = 2.79 (2.77–2.81)), white-tailed deer (HR = 2.44 (2.42–2.46)), and raccoon (HR = 2.35 (2.33–2.37)). Combined, these results suggest that the Florida panther did not

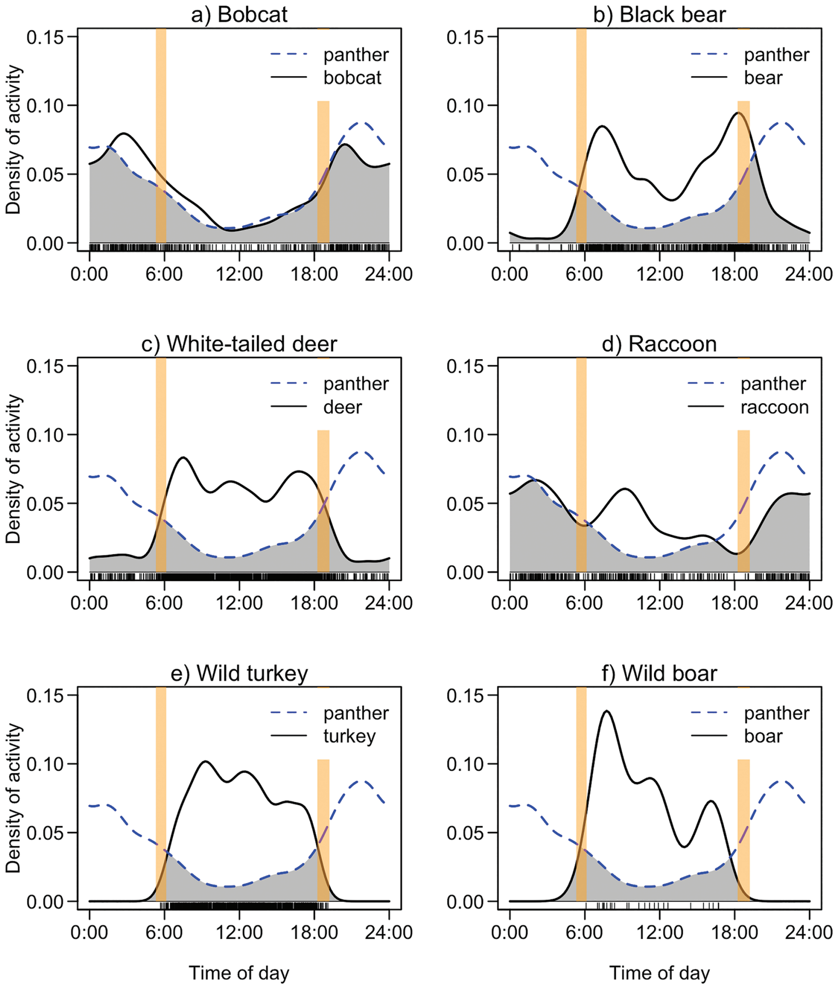

Fig. 3.—Kernel density estimates of diel activity pattern overlap for the Florida panther, potential competitors, and prey species in the Addition Lands Unit of Big Cypress National Preserve, Florida, United States. Blue dashed lines indicate Florida panther density estimates; solid lines indicate potential competitor or prey species density estimates; orange shaded areas represent sunrise and sunset times. Individual photograph times are represented by the solid vertical lines immediately above the x-axis. The overlap coefficient (Δ) is represented by the shaded area.

avoid any of the species and was more likely to move through a site after a prey than a competitor species.

Discussion

While Florida panther abundance has increased more than 6-fold since the 1990s (Onorato et al. 2010; FWC 2018), habitat loss and fragmentation have continued to reduce the habitat available to wildlife species (Kautz et al. 2006; Frakes et al. 2015). Such an increase in density of an apex predator can affect the frequency and intensity of interspecific interactions, as well as the "behavioral response race" (cf. Sih 1984) between Florida panthers and sympatric species.

Our results support the hypothesis that prey species, likely perceiving higher predation risk, would avoid the Florida panther by reducing the temporal overlap and increasing the time-to-encounter (Sih 1984; Brown et al. 1999). Two major prey species of the Florida panther, the white-tailed deer and wild boar (Maehr et al. 1990a; Maehr 1997; Onorato et al. 2010), showed a predominantly diurnal activity pattern, minimizing their activity when the Florida panther was most active (Fig. 3). White-tailed deer and wild boar have been reported to adapt their behaviors to the local environmental conditions and risk perception (Thurfjell et al. 2013; Little et al. 2014). While white-tailed deer are typically crepuscular, with activity peaks around sunrise and sunset (Beier and McCullough 1990), they have been reported to become more nocturnal in response to hunting pressure in areas without large nocturnal predators such as the Florida panther (Kilgo et al. 1998). Because predation by Florida panthers was likely the most important cause of white-tailed deer mortality in our study area, the observed predominantly diurnal activity pattern of white-tailed deer, in conjunction with longer time-to-encounter, could be a strategy to minimize risk of predation from the Florida panther.

Similarly, raccoons could minimize encounters with the Florida panther by being partially active during daytime (Fig. 3). Although raccoons primarily are nocturnal animals (Lesmeister et al. 2015), they have been reported to adapt their activity patterns to local conditions, and found to be active in Florida both during daytime and nighttime (Munscher 2006). This strategy could reduce predation risk, as previous studies have reported that raccoons are the most common mid-sized prey species in the Florida panther's

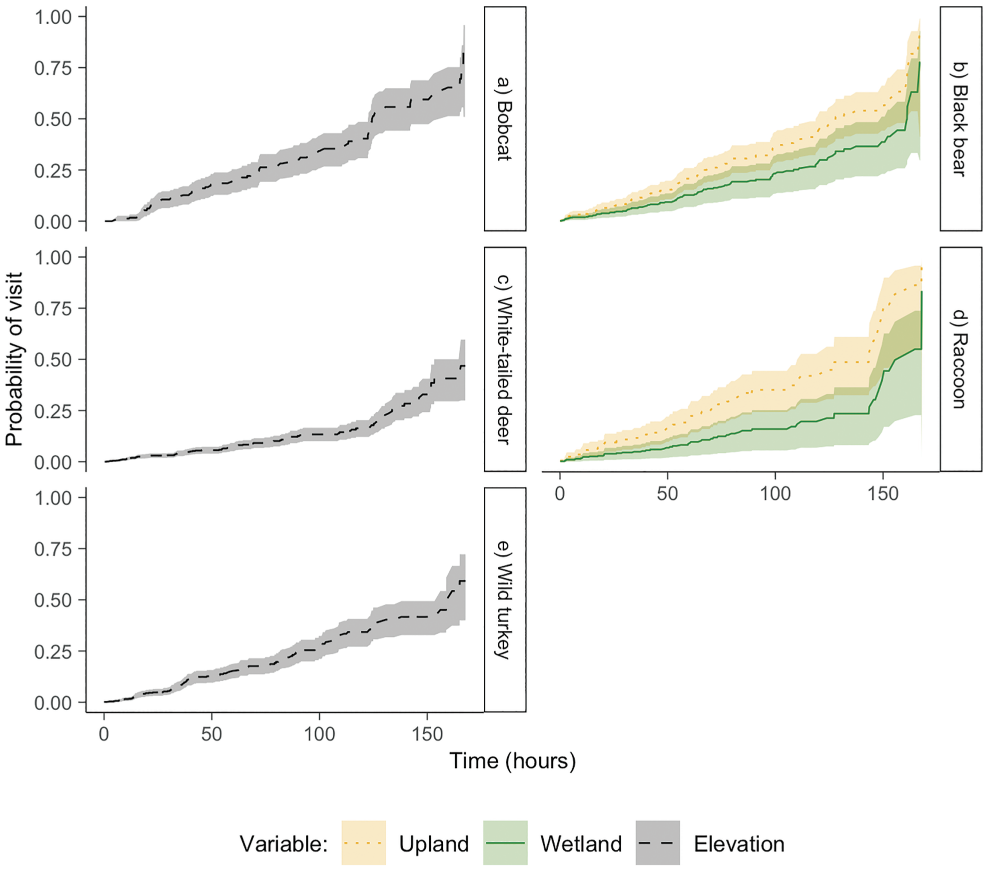

Fig. 4.—Probability of visit over time for a Florida panther after the presence of a focal species (Sp–P interaction) within a 7-day period (x-axis; time in hours). Results are presented for the top Cox proportional hazard models for each species (Supplementary Data SD2). Variables include wetland (green, solid), upland (yellow, dotted), and elevation (black, dashed). Shaded areas indicate 95% confidence intervals.

diet (Maehr et al. 1990a). Raccoon remains have been found in 22% of scats collected since 1995, slightly less than white-tailed deer (28%) and equal to wild boar (22%; Caudill et al. 2019). In addition, the Florida panther showed the third highest probability of visiting a site after the presence of a raccoon, suggesting some attraction to this species (Supplementary Data SD4). We found no evidence of avoidance behavior by wild turkey, with the largest HR of visiting a site after a Florida panther's visit (Supplementary Data SD3). Avian prey have been shown to comprise only a minor percentage of Florida panthers' diet (Maehr et al. 1990a, 1990b; Dalrymple and Bass, Jr. 1996; Maehr 1997); consequently, we hypothesize that wild turkeys may perceive low risk of predation from Florida panthers.

Florida panthers showed higher probabilities of interacting with prey than competitor species (Supplementary Data SD4), creating more interaction or predation opportunities with white-tailed deer, raccoon, and wild turkey. In addition, Florida panthers showed significantly higher probabilities of visiting a site at higher elevations or lower probabilities in wetland habitat after all species with the exception of bobcat. This could be a response to reduced habitat availability due to higher water levels during the wet season (Frakes et al. 2015; Criffield et al. 2018) or a hunting strategy to locate prey species, which tend to group in nonflooded areas (MacDonald-Beyers and Labisky 2005).

Our results suggest that direct or apparent competition between the Florida panther and potential competitors have remained relatively unaffected by recent increases in Florida panther abundance. Despite differences in body size, dietary preferences of Florida panthers can overlap those of bobcats, potentially resulting in competitive interactions (Land 1991; Maehr 1997; Labisky and Boulay 1998). We found a high overlap in activity patterns (Fig. 3), and no evidence of strong spatiotemporal avoidance between the Florida panther and bobcat (Supplementary Data SD1–SD4). Both Florida panther and bobcat showed two peaks of activity before sunrise and after sunset (Fig. 3), similar to previous reports for these species in South Florida when panthers occurred in low numbers (Maehr et al. 1990b; Thornton et al. 2004), suggesting no substantial change in diurnal activity patterns despite a notable increase in Florida panther population size. Black bear showed two peaks of activity after sunrise and before sunset, with a predominantly diurnal activity pattern (Table 1; Fig. 3), and significantly higher probabilities of visiting a site after a Florida panther than expected by chance (Supplementary Data SD3). The diurnal activity pattern has been attributed to the natural behavior of the species in absence of anthropogenic pressures (Amstrup and Beecham 1976; Beckmann and Berger 2003; Karelus et al. 2017), which could in fact be a mechanism to reduce apparent or direct competition and promote coexistence with the Florida panther. At low Florida panther densities (prior to 2000), coexistence among these three species was suggested to be predominantly driven by diet partitioning (Maehr 1997), because bobcat prey primarily on small mammals, whereas Florida panthers feed mainly on large- or mid-sized mammalian prey (Mahaer et al. 1990a; Hass 2009), and black bears in Florida have a predominantly plant-based diet (Dobey et al. 2005). Although Florida panthers now occur in much greater numbers (FWC 2018), dietary partitioning still could be the primary mechanism driving the coexistence between these three species.

Log-rank tests comparing time-to-encounter patterns between observed and randomly expected interactions revealed no strong spatiotemporal pattern of interaction among species, because most species showed significantly higher probabilities of visiting a site following the visit of another species. The incorporation of explanatory variables to assess time-to-encounter patterns between species revealed further details regarding the nature of interspecific interactions. The effect of site covariates on the interactive events had larger effects for the Florida panther which has been reported to adapt its movement at changing water levels (Frakes et al. 2015; Criffield et al. 2018). Site covariate patterns were less clear for competitor and prey species, but the findings are not surprising considering the limited elevation range and habitat diversity in our study site. In ecosystems with higher elevation gradient and habitat variability, this approach could yield very interesting results, as environmental conditions often influence species interactions (Schuette et al. 2013).

Competition and predation arguably are the most important species interactions, potentially influencing all levels of ecological interactions. It has become increasingly clear that these two ecological processes are equally important and often interact with each other to promote or limit species coexistence and biodiversity (Chase et al. 2002; Chesson and Kuang 2008). We found that Florida panthers' primary prey species attempt to minimize the risk of predation by means of temporal segregation. Black bears' predominantly diurnal activity pattern could relax the potential competition with Florida panthers, although other mechanisms also could be driving coexistence between these two species, as well as with bobcats. Future studies are needed to discern the behavioral response of the wild boar, and the interspecific interactions involving Florida panthers along the urban-wildland interface to provide information essential for the development of management initiatives that improve prospects for the recovery of the Florida panther. We concur with Chesson and Kuang (2008) that conservation strategies need to be much more concerned with the implications of changes in the strengths of trophic interactions. The pattern of interactions between the Florida panther and species sympatric with it will continue to change as the former recolonizes new habitats and the population size increases. Panther conservation efforts will benefit from an improved understanding of the interactions between this iconic apex predator and sympatric species.

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SUPPLEMENTARY DATA

Supplementary data are available at *Journal of Mammalogy* online.

Supplementary Data SD1.—Cox proportional hazard model selection for the P–Sp interaction.

Supplementary Data SD2.—Cox proportional hazard model selection for the Sp–P interaction.

Supplementary Data SD3.—Log-rank test *P*-value and hazard ratio distributions for the observed-randomized data sets comparison for the P–Sp interaction.

Supplementary Data SD4.—Log-rank test *P*-value and hazard ratio distributions for the observed-randomized data sets comparison for the Sp–P interaction.

LITERATURE CITED

AMSTRUP, S. C., AND J. BEECHAM. 1976. Activity patterns of radio-collared black bears in Idaho. The Journal of Wildlife Management 40:340–348.

BECKMANN, J. P., AND J. BERGER. 2003. Rapid ecological and behavioural changes in carnivores: the responses of black bears (*Ursus americanus*) to altered food. Journal of Zoology 261:207–212.

BEIER, P., AND D. R. MCCULLOUGH. 1990. Factors influencing white-tailed deer activity patterns and habitat use. Wildlife Monographs 109:3–51.

BISCHOF, R., ET AL. 2014. Using time-to-event analysis to complement hierarchical methods when assessing determinants of photographic detectability during camera trapping. Methods in Ecology and Evolution 5:44–53.

BROWN, J. S., J. W. LAUNDRÉ, AND M. GURUNG. 1999. The ecology of fear: optimal foraging, game theory, and trophic interactions. Journal of Mammalogy 80:385–399.

BURNHAM, K. P., AND D. R. ANDERSON. 2002. Model selection and multimodel inference: a practical information-theoretic approach. 2nd ed. Springer. New York.

CAUDILL, G., ET AL. 2019. Temporal trends in Florida panther food habits. Human-Wildlife Interactions 13:87–97.

Chase, J. M., et al. 2002. The interaction between predation and competition: a review and synthesis. Ecology Letters 5:302–315.

Chesson, P., and J. J. Kuang. 2008. The interaction between predation and competition. Nature 456:235–238.

Cox, D. R. 1972. Regression models and life-tables. Journal of the Royal Statistical Society. Series B (Methodological) 34:187–220.

Creel, S., and D. Christianson. 2008. Relationships between direct predation and risk effects. Trends in Ecology & Evolution 23:194–201.

Creel, S., P. Schuette, and D. Christianson. 2014. Effects of predation risk on group size, vigilance, and foraging behavior in an African ungulate community. Behavioral Ecology 25:773–784.

Criffield, M., et al. 2018. Assessing impacts of intrinsic and extrinsic factors on Florida panther movements. Journal of Mammalogy 99:702–712.

Cusack, J. J., et al. 2017. Revealing kleptoparasitic and predatory tendencies in an African mammal community using camera traps: a comparison of spatiotemporal approaches. Oikos 126:812–822.

Dalrymple, G. H., and O. L. Bass, Jr. 1996. The diet of the Florida panther in Everglades National Park, Florida. Bulletin of the Florida Museum of Natural History 39:173–193.

Dobey, S., D. V. Masters, B. K. Scheick, J. D. Clark, M. R. Pelton, and M. E. Sunquist. 2005. Ecology of Florida black bears in the Okefenokee-Osceola ecosystem. Wildlife Monographs 158:1–41.

Durant, S. M. 1998. Comparative refuges and coexsistance: an example from Serengeti carnivores. Journal of Animal Ecology 67:370–386.

Efron, B., and R. J. Tibshirani. 1993. An introduction to the bootstrap. Chapman & Hall/CRC. Boca Raton, Florida.

ESRI. 2019. ArcGIS Pro. Ver 2.0. Environmental System Research Institute, Inc. Redlands, California.

Florida Fish and Wildlife Conservation Commission (FWC). 2016. Cooperative Land Cover, version 3.2. Florida Fish and Wildlife Conservation Commission. https://myfwc.com/research/gis/applications/articles/cooperative-land-cover/. Accessed 1 October 2017.

Florida Fish and Wildlife Conservation Commission (FWC). 2018. Annual report on the research and management of Florida panthers: 2017-2018. Fish and Wildlife Research Institute & Division of Habitat and Species Conservation. Naples, Florida, USA.

Frakes, R. A., R. C. Belden, B. E. Wood, and F. E. James. 2015. Landscape analysis of adult Florida panther habitat. PLoS One 10:e0133044.

Grant, P. R. 1999. Ecology and evolution of Darwin's finches. Princeton University Press. Princeton, New Jersey.

Hairston, N. G., F. E. Smith, and L. B. Slobodkin. 1960. Community structure, population control, and competition. The American Naturalist 94:421–425.

Harvey, E., I. Gounand, C. L. Ward, and F. Altermatt. 2017. Bridging ecology and conservation: from ecological networks to ecosystem function. Journal of Applied Ecology 54:371–379.

Hass, C. C. 2009. Competition and coexistence in sympatric bobcats and pumas. Journal of Zoology 278:174–180.

Hosmer, D. W., Jr., S. Lameshow, and S. May. 2008. Applied survival analysis: regression modeling of time-to-event data. 2nd ed. John Wiley & Sons. Hoboken, New Jersey.

Hostetler, J. A., et al. 2010. Genetic introgression and the survival of Florida panther kittens. Biological Conservation 143:2789–2796.

Johnson, W. E., et al. 2010. Genetic restoration of the Florida panther. Science 329:1641–1645.

Karanth, K. U., A. Srivathsa, D. Vasudev, M. Puri, R. Parameshwaran, and N. S. Kumar. 2017. Spatio-temporal interactions facilitate large carnivore sympatry across a resource gradient. Proceedings of the Royal Society B: Biological Sciences 284:20161860.

Karelus, D. L., J. W. McCown, B. K. Scheick, M. van de Kerk, B. M. Bolker, and M. K. Oli. 2017. Effects of environmental factors and landscape features on movement patterns of Florida black bears. Journal of Mammalogy 98:1463–1478.

Kautz, R., et al. 2006. How much is enough? Landscape-scale conservation for the Florida panther. Biological Conservation 130:118–133.

van de Kerk, M., D. P. Onorato, J. A. Hostetler, B. M. Bolker, and M. K. Oli. 2019. Dynamics, persistence, and genetic management of the endangered Florida panther population. Wildlife Monographs 203:3–35.

Kilgo, J. C., R. F. Labisky, and D. E. Fritzen. 1998. Influences of hunting on the behavior of white-tailed deer: implications for conservation of the Florida panther. Conservation Biology 12:1359–1364.

Kotler, B. P., and R. D. Holt. 1989. Predation and competition: the interaction of two types of species interactions. Oikos 54:256–260.

Labisky, R. F., and M. C. Boulay. 1998. Behaviors of bobcats preying on white-tailed deer in the Everglades. The American Midland Naturalist 139:275–281.

Land, E. D. 1991. Big Cypress deer/panther relationships: deer mortality. Report to the Bureau of Wildlife Research, Florida Game and Fresh Water Fish Commission. Tallahassee.

Lee, E. T. 1992. Statistical methods for survival data analysis. 2nd ed. John Wiley. New York.

Leibold, M. A., and M. A. McPeek. 2006. Coexistence of the niche and neutral perspectives in community ecology. Ecology 87:1399–1410.

Lesmeister, D. B., C. K. Nielsen, E. M. Schauber, and E. C. Hellgren. 2015. Spatial and temporal structure of a mesocarnivore guild in midwestern north America. Wildlife Monographs 191:1–61.

Lewis, J. S., L. L. Bailey, S. VandeWoude, and K. R. Crooks. 2015. Interspecific interactions between wild felids vary across scales and levels of urbanization. Ecology and Evolution 5:5946–5961.

Lima, S. L. 1998. Stress and decision making under the risk of predation: recent developments from behavioral, reproductive and ecological perspectives. Pp. 215–290 in Advances in the study of behavior. Vol. 27. Stress and behavior (A. P. Møller, M. Milinski, and P. J. B. Salter, eds.). Academic Press. San Diego, California.

Lima, S. L., and L. M. Dill. 1990. Behavioral decisions made under the risk of predation: a review and prospectus. Canadian Journal of Zoology 68:619–640.

Linkie, M., and M. S. Ridout. 2011. Assessing tiger-prey interactions in Sumatran rainforests. Journal of Zoology 284:224–229.

Linnell, J. D. C., and O. Strand. 2000. Interference interactions, co-existence and conservation of mammalian carnivores. Biodiversity Research 6:169–176.

Linnell, J. D. C., J. E. Swenson, and R. Anderson. 2001. Predators and people: conservation of large carnivores is possible at high human densities if management policy is favourable. Animal Conservation 4:345–349.

Little, A. R., et al. 2014. Does human predation risk affect harvest susceptibility of white-tailed deer during hunting season? Wildlife Society Bulletin 38:797–805.

MacDonald-Beyers, K., and R. F. Labisky. 2005. Influence of flood waters on survival, reproduction, and habitat use of white-tailed deer in the Florida Everglades. Wetlands 25:659–666.

Maehr, D. S. 1997. The comparative ecology of bobcat, black bear and Florida panther in South Florida. Bulletin of the Florida Museum of Natural History 40:1–176.

Maehr, D. S., R. C. Belden, E. D. Land, and L. Wilkins. 1990a. Food habits of panthers in southwest Florida. The Journal of Wildlife Management 54:420–423.

Maehr, D. S., E. D. Land, J. C. Roof, and J. W. McCown. 1990b. Day beds, natal dens, and activity of Florida panthers. Proceedings of the Annual Conference of Southeastern Fish and Wildlife Agencies 44:310–318.

McBride, R. T., R. T. McBride, R. M. McBride, and C. E. McBride. 2008. Counting pumas by categorizing physical evidence. Southeastern Naturalist 7:381–400.

Mcdonald, R. I., P. Kareiva, and R. T. T. Forman. 2008. The implications of current and future urbanization for global protected areas and biodiversity conservation. Biological Conservation 141:1695–1703.

Meredith, M., and M. Ridout. 2016. Overlap: estimates of coefficient of overlapping for animal activity patterns. https://cran.r-project.org/package=overlap. Accessed 1 November 2016.

Munscher, E. C. 2006. Physical and health assessment of a population of raccoon (*Procyon lotor*) in Northeastern Florida. M.S. thesis, University of North Florida. Jacksonville, Florida.

National Oceanic and Atmospheric Administration (NOAA). 2017. NOAA Solar Calculator. National Oceanic & Atmospheric Administration. https://www.esrl.noaa.gov/gmd/grad/solcalc. Accessed 1 October 2017.

O'Connell, A. F., J. D. Nichols, and K. U. Karanth. 2010. Camera traps in animal ecology: methods and analyses. Springer. Berlin, Germany.

Onorato, D. P., R. C. Belden, M. W. Cunningham, E. D. Land, R. T. McBride, and M. E. Roelke. 2010. Long-term research on the Florida panther (*Puma concolor coryi*): historical findings and future obstacles to population persistence. Pp. 453–469 in Biology and conservation of wild felids (D. W. Macdonald and A. J. Loveridge, eds.). Oxford University Press. New York.

Paine, R. T. 1966. Food web complexity and species diversity. The American Naturalist 100:65–75.

Parsons, M. H., et al. 2018. Biologically meaningful scents: a framework for understanding predator–prey research across disciplines. Biological Reviews 93:98–114.

Persons, M. H., and A. L. Rypstra. 2001. Wolf spiders show graded antipredator behavior in the presence of chemical cues from different sized predators. Journal of Chemical Ecology 27:2493–2504.

Pollock, K. H., S. R. Winterstein, C. M. Bunck, and P. D. Curtis. 1989. Survival analysis in telemetry studies: the staggered entry design. The Journal of Wildlife Management 53:7–15.

R Core Team. 2019. R: a language and environment for statistical computing, version 3.6.1. R Foundation for Statistical Computing. Vienna, Austria. www.R-project.org/.

Ridout, M. S., and M. Linkie. 2009. Estimating overlap of daily activity patterns from camera trap data. Journal of Agricultural, Biological, and Environmental Statistics 14:322–337.

Ripple, W. J., et al. 2014. Status and ecological effects of the world's largest carnivores. Science 343:1241484.

Ritchie, E. G., and C. N. Johnson. 2009. Predator interactions, mesopredator release and biodiversity conservation. Ecology Letters 12:982–998.

Schluter, D., and J. D. McPhail. 1992. Ecological character displacement and speciation in sticklebacks. The American Naturalist 140:85–108.

Schoener, T. W. 1974. Resource partitioning in ecological communities. Science 185:27–39.

Schuette, P., A. P. Wagner, M. E. Wagner, and S. Creel. 2013. Occupancy patterns and niche partitioning within a diverse carnivore community exposed to anthropogenic pressures. Biological Conservation 158:301–312.

Sih, A. 1984. The behavioral response race between predator and prey. The American Naturalist 123:143–150.

Sladecek, F. X., S. T. Segar, C. Lee, R. Wall, and M. Konvicka. 2017. Temporal segregation between dung-inhabiting beetle and fly species. PLoS ONE 12:e0170426.

Sosa-Lopez, A., and D. Mouillot. 2007. Spatiotemporal segregation regulates species richness along biomass gradients in estuarine fish assemblages. Marine Ecology Progress Series 342:217–226.

Soulé, M. E., J. A. Estes, J. Berger, and C. M. Del Rio. 2003. Ecological effectiveness: conservation goals for interactive species. Conservation Biology 17:1238–1250.

Therneau, T. M. 2015. A package for survival analysis in S. https://cran.r-project.org/package=survival. Accessed 1 February 2017.

Thornton, D. H., M. E. Sunquist, and M. B. Main. 2004. Ecological separation within newly sympatric populations of coyotes and bobcats in South-Central Florida. Journal of Mammalogy 85:973–982.

Thurfjell, H., G. Spong, and G. Ericsson. 2013. Effects of hunting on wild boar *Sus scrofa* behaviour. Wildlife Biology 19:87–93.

Tilman, D. 1982. Resource competition and community structure. Princeton University Press. Princeton, New Jersey.

United States Climate Data. 2017. Climate data. https://www.usclimatedata.com/climate/naples/florida/united-states/usfl0338/2017/1. Accessed 16 September 2017.

U.S. Geological Survey. 2014. 3D Elevation Program (3DEP). https://nationalmap.gov/3DEP/index.html. Accessed 30 August 2017.

Vanak, A. T., et al. 2013. Moving to stay in place: behavioral mechanisms for coexistence of African large carnivores. Ecology 94:2619–2631.

White, P. J., R. A. Garrott, and G. E. Plumb (eds.). 2013. Yellowstone's wildlife in transition. Harvard University Press. Cambridge, Massachusetts.

Woodroffe, R. 2001. Strategies for carnivore conservation: lessons from contemporary extinctions. Pp. 61–92 in Carnivore conservation (J. L. Gittleman, S. M. Funk, D. Macdonald, and R. K. Wayne, eds.). Cambridge University Press. London, United Kingdom.

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