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Behavioral response of white-tailed deer to coyote predation risk

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Abstract. Behavioral responses of prey to predation risk can affect lower trophic levels. White-tailed deer (*Odocoileus virginianus*; hereafter deer) increase vigilance in response to coyote (*Canis latrans*) presence, but vigilance responses to spatiotemporal variation in coyote abundance are unknown. Therefore, we examined the relationship between deer foraging behavior and coyote abundance on two 2000-ha study areas in Georgia, USA, during 2010–2013. We used baited camera traps during fall and winter to quantify deer behavior (i.e., feeding or vigilant) and estimated coyote abundance using fecal genotyping to noninvasively mark and recapture individuals. During 2011 and 2012, coyote removals were implemented on each study area. Coyote abundance (i.e., predation risk) varied spatiotemporally and was a predictor of foraging behavior during at least one season for all sex-age classes of deer except juveniles. Adult males were more sensitive to predation risk in winter, after the breeding season, whereas adult females were sensitive to predation risk during both seasons, but more so during fall when offspring are at greater risk. Yearling males were more sensitive to predation risk than adult males, and juveniles were least sensitive to predation risk, likely because of inexperience and high energetic demands. Reproductive chronology explained sex-specific and seasonal antipredator responses to predation risk, but there was a non-linear relationship between indirect predator effects and direct predation risk for some sex-age classes. Our results suggest deer detect and respond behaviorally to variation in coyote abundance. Due to the widespread distribution of deer and their interactions at multiple trophic levels, the ecological implications of this finding may be wide-reaching.

Key words: coyote; foraging behavior; herbivore; landscape of fear; predation risk; trophic cascade; vigilance; white-tailed deer.

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Introduction

A "landscape of fear" is one in which fear of predation varies spatially in response to changing levels of predation risk (Laundré et al. 2001). Prey animals often respond to increases in predation risk by reducing foraging and/or increasing vigilance while foraging (Brown 1999). These responses have been linked to population processes (Sheriff et al. 2009, Zanette et al. 2011) and cascading effects to lower trophic levels (Ripple and Beschta 2004, Estes et al. 2011). However, the ecological role of apex predators has most often been documented in isolated landscapes and involves large predators that are no longer widely distributed (Estes et al. 2011, Ripple et al. 2014). In contrast, the landscape of fear associated with a widely distributed predator–prey system involving an herbivore that strongly interacts at multiple trophic levels, such as white-tailed deer (*Odocoileus virginianus*; hereafter deer), could have far-reaching ecological and conservation implications.

The distribution of deer encompasses the majority of North America, and deer herbivory can

indirectly affect other wildlife via trophic cascades or alteration of plant community structure and composition (Waller and Alverson 1997, Rooney and Waller 2003, Côté et al. 2004). Large predators like wolves (*Canis* spp.) and cougars (*Puma concolor*) historically limited deer populations, but nonhuman deer predators have been absent from much of their range for decades (Côté et al. 2004). Thus, deer managers have largely relied on hunting to regulate populations throughout recent history (Brown et al. 2000), and deer are North America's most economically important game species (USFWS 2011). Deer now occupy a unique role as a primary driver of conservation funding for state wildlife agencies, an agent of economic damage for forestry and agriculture, and a keystone species in forested ecosystems (Côté et al. 2004).

The relatively recent range expansion of coyotes (*Canis latrans*) into eastern North America and their impacts on deer have garnered significant attention. Coyotes are now ubiquitous throughout the region, with the Appalachian Mountains and mid-Atlantic regions being colonized as recently as the early 1990s (Parker 1995). Although typically classified as a mesopredator (Ripple et al. 2013), coyotes may act as an apex predator in the absence of larger predators like gray wolves (*Canis lupus*; Gompper 2002). For example, coyotes can be a significant mortality source for deer fawns (Kilgo et al. 2012), influencing fawn recruitment (Gulsby et al. 2015, Conner et al. 2016) and population growth (Kilgo et al. 2010, Robinson et al. 2014, Chitwood et al. 2015).

Therefore, it is plausible that coyotes have at least partially filled the ecological role of locally extirpated large carnivores by directly (i.e., numerically) affecting deer populations in eastern North America. But their indirect effects on deer remain largely unexplored and may be ecologically consequential. For example, prey vigilance generally increases with increasing predation risk (Hunter and Skinner 1998, Périquet et al. 2012), directly impacting resource acquisition rates and, by extension, prey fitness and their impacts on lower trophic levels (Lima and Dill 1990, Brown et al. 1999, Laundré et al. 2001, Childress and Lung 2003, Brown and Kotler 2004).

There is some evidence to suggest coyotes are indirectly affecting deer populations in eastern North America. For example, a study in Georgia, USA, used a series of predator exclosures and control plots in an area where coyotes were the primary nonhuman predator of deer and documented that predation risk influenced foraging behavior (Cherry et al. 2015) and space use of deer (Conner et al. 2016). However, deer in that study were presented only with areas with and without coyotes, and safe areas were consistent through time. Compared to experimental predator exclosures, predator–prey interactions in natural systems occur on dynamic landscapes where predation risk may be less predictable. For example, Schuttler et al. (2016) did not detect a relationship between deer vigilance and coyote activity under such conditions across six states in the eastern United States.

Thus, it remains unclear whether deer can detect and respond to spatiotemporal variation in predation risk in the region's natural systems. Given this uncertainty, we examined the effects of variation in coyote abundance on the age-, sex-, and season-specific foraging behavior of deer on two study areas in Georgia, USA. However, because deer vigilance also varies as a function of reproductive chronology, conspecific interactions, and group size (Cherry et al. 2015, Stone et al. 2017), we included a series of variables related to these factors in our models.

Study Areas

We conducted research on 2000-ha blocks within the interior of Cedar Creek (CC) and B.F. Grant (BFG) Wildlife Management Areas in central Georgia, USA. The areas were separated by 8 km and elevation ranged from 120 to 180 m. These sites provided an ideal study system because their proximity standardized broadscale climatic and geologic variables. Activities on the areas included hunting, fishing, and outdoor recreation. Deer were commonly pursued by hunters on both areas, and the estimated population density was 19–23 deer/km^2 on BFG and 8–12 deer/km^2 on CC. Initial occupation of these areas by coyotes likely occurred during the late 1980s, with animals becoming relatively abundant during the mid-to-late 1990s (Holzman et al. 1992, Gulsby et al. 2015).

Methods

Estimation of coyote abundance and coyote removal

We collected putative coyote scats year round on a weekly basis throughout each study area. Collection routes totaled 28 km on BFG and 20 km on CC, and were consistent among sampling occasions. We collected fecal material from the outside edges of each scat estimated to be ≤3 days old and preserved samples in 95% EtOH (Stenglein et al. 2010).

We determined species using mitochondrial sequencing, specifically the cytochrome *b* fragment amplified by primers RF14724 and RF15149 (Perrine et al. 2007), followed by BLAST search in GenBank (Gulsby et al. 2015). We used >98% homology to a single species as our criterion for accepting species-level matches during BLAST searches.

We constructed coyote genotypes using 12 microsatellites and a sex marker (based on X and Y chromosome paralogs of the amelogenin gene). We replicated all genotypes at least twice and considered high-quality samples (i.e., all loci represented in ≥1 replicate and ≥7 loci amplified in the other) complete. We replicated genotypes falling below the threshold up to five additional times and only included those with no missing loci in further analyses (Lounsberry et al. 2015). We calculated the allelic dropout rate for each heterozygous locus and used GenAlEx 6.5 (Peakall and Smouse 2006, 2012) to calculate the probability of individual identity and probability of identity for siblings for each locus and increasing combinations of the 12 loci (Waits et al. 2001). We performed pairwise genotype-matching analysis using the AlleleMatch package in R to create composite genotypes for individual coyotes (Galpern et al. 2012, R Core Team 2016).

We divided each calendar year into three seasons, with each season considered a sampling occasion (Gulsby et al. 2015). We computed abundance estimates for each site during three time periods: Year 1, January 2010–February 2011 (prior to coyote removal); Year 2, June 2011–February 2012 (year following first removal); and Year 3, April 2012 (following second removal). Abundance estimates were sufficient for detecting gross changes in coyote abundance (Gulsby et al. 2016). Professional trappers removed coyotes from the 2000-ha block on each area from March to June 2011 and March to April 2012. Capture and euthanasia procedures were approved by the University of Georgia Institutional Animal Care and Use Committee (A2009 09-157-Y3-A0).

Quantifying foraging behavior

We used digital camera traps during fall (October–November) and winter (January–February) 2009–2013 to photograph deer. We arranged camera traps across study areas systematically at a density of 1/65 ha. We pre-baited each site with corn for 1 week, then returned to position the camera over bait, and add corn as needed. We programmed cameras to take one photograph upon detection of movement, with a 15-min delay between photographs. Cameras remained in place for a 10-d period during each survey occasion.

We categorized the behavioral state of each photographed deer as actively feeding (i.e., head down actively consuming bait) or not (Cherry et al. 2015). We assigned each deer to a sex-age class of juvenile, yearling male, adult female, or adult male based on pelage (for fawns) and morphological characteristics (rostrum length, body size, and antler presence; Donohue et al. 2013). We assigned group size to each observation by tallying the number of deer in the image. We categorized each image as daylight (civil sunrise to sunset) and night (civil sunset to sunrise) based on camera-specific location and image-specific date data using algorithms provided by the National Oceanic and Atmospheric Administration. We executed the algorithms using R packages Lubridate (Grolemund and Wickham 2011) and maptools (Bivand and Lewin-Koh 2017). We elected to use this categorization to represent the effect of daylight on detectability of coyotes by deer.

We modeled the behavioral state of deer using a generalized linear mixed model with a binomial error distribution and logit link function. We modeled each sex-age class and season separately because our hypotheses regarding foraging behavior were sex-age class and season specific. Camera site-specific intercept terms were included as a random effect in each model. We assigned the estimate of site-specific annual coyote abundance (n = 6) to each observation (e.g., coyote abundance estimates for Year 1 on BFG were assigned to foraging trials conducted on BFG during fall 2010 and winter 2011). We hypothesized the probability

of feeding for all sex-age classes of deer would be influenced by study site (i.e., BFG or CC), group size, time of day (i.e., daylight vs. night), and coyote abundance (Cherry et al. 2015, 2017). For yearling males, we also included the presence of adult males because social interactions could influence foraging behavior (Stone et al. 2017). For adult females, we included the presence of adult males because dominant males could result in reduced feeding of females. We also included the presence of fawns for adult females because females may increase vigilance to protect fawns or may increase feeding to replace nutritional stores depleted by lactation. For juveniles, we included the presence of any male because both adult and yearling males are dominant over juveniles and thus may reduce feeding (Donohue et al. 2013). We scaled and centered all continuous predictors to facilitate parameter estimation. We developed a series of competing models that included all possible additive and linear subsets of these variables and a null intercept-only model for each sex-age class and season and compared models using AIC_c (Burnham and Anderson 2004). We implemented this approach because all of the variables we included were previously shown to influence foraging behavior and we were interested in evaluating variation in predation risk relative to each factor on our study areas. This resulted in 16, 33, 63, and 16 models per season for adult males, yearling males, adult females, and juveniles, respectively. We constructed model-averaged parameter estimates and associated 95% confidence intervals for each variable contained in ≥2 models with a delta $AIC_c < 2$. We considered parameters with 95% confidence intervals not overlapping zero informative (Arnold 2010). All analyses were conducted in package LME4 (Bates et al. 2015), MuMin (Bartoń 2016) using program R.

Results

Coyote removal and abundance estimates

We collected 238 scat samples on BFG and constructed 68 multilocus genotypes representing 38 coyotes. We collected 196 scat samples on CC and constructed 68 multilocus genotypes representing 32 coyotes. The average allelic dropout rate was 0.28 alleles/replicate, and we constructed individual genotypes from an average of 11.24 microsatellite loci (range = 7–12). For all 12 loci, probability of identity was 5.8×10^{-15}, and probability of identity for siblings was 6.4×10^{-6}. Probability of identity was 5.0×10^{-8} overall and 9.4×10^{-4} for siblings at 7 loci (minimum number of loci for individual genotype; Gulsby et al. 2015).

Trappers removed nine coyotes from CC in 2011 and one in 2012. Trappers removed 15 coyotes on BFG during 2011 and six during 2012. Coyote abundance differed spatiotemporally based on comparison of confidence intervals. The abundance estimates for BFG were 21 (95% CI = 19–33) in 2010, 4 (95% CI = 4–17) in 2011, and 16 (95% CI = 7–82) in 2012. The abundance estimates for CC were 16 (95% CI = 15–28) in 2010, 9 (95% CI = 5–40) in 2011, and 9 (95% CI = 7–22) in 2012. Time and site-specific confidence intervals were great in some cases. Because of this variation, we also conducted all analyses using a categorical coyote abundance index (high, medium, and low abundance) by discretizing the continuous abundance estimates.

Specifically, the abundance estimates from BFG during 2010 and 2012 (21 and 16 coyotes, respectively) and the abundance estimate from CC during 2010 (16 coyotes) were ≥4 times greater than that of the lowest abundance (i.e., BFG 2011, four coyotes). Thus, we categorized these estimates as high abundance, the CC estimates from 2011 and 2012 (nine coyotes) as medium abundance, and the estimate from BFG during 2011 (four coyotes) as low abundance. Despite the fact that this approach decreased the resolution of our dataset in terms of coyote abundance, categorical coyote abundance remained an important predictor of vigilance and our biological conclusions remained unchanged. Therefore, we present results from our approach that assigned the site-specific annual abundance estimate to each deer observation.

Deer foraging behavior

We interpreted the behavioral state of deer in 27,969 images including 3201 detections of mature males, 3386 detections of yearling males, 5742 detections of juveniles, and 13,572 detections of adult females. Foraging behavior was influenced by coyote abundance, time of day, and social factors, but responses varied with season and sex-age class. The time of day model received the most support for adult males during fall (Table 1), with probability of foraging

Table 1. Competitive models, number of parameters (K), Akaike's information criterion (AIC_c), difference from lowest AIC_c (ΔAIC_c), and model weight (w_i) for models used to predict foraging behavior of adult male white-tailed deer (*Odocoileus virginianus*) at camera traps during fall (September–October) and winter (January–February) 2011–2013 on two sites in Georgia, USA.

Season	Model	K	AIC_c	ΔAIC_c	w_i
Fall	Daylight†	3	769.9	0	0.31
Fall	Daylight + Group size‡	4	770.5	0.57	0.24
Fall	Coyote§ + Daylight	4	770.9	1.01	0.19
Fall	Coyote + Daylight + Group size	5	771.5	1.62	0.14
Fall	Daylight + Site¶	4	771.8	1.89	0.12
Winter	Coyote + Group size	4	1968.1	0	0.29
Winter	Coyote	3	1968.7	0.54	0.22
Winter	Coyote + Group size + Site	5	1968.8	0.66	0.21
Winter	Coyote + Site	4	1969.2	1.08	0.17
Winter	Coyote + Daylight + Group size	5	1969.8	1.7	0.12

† Civil daylight period.
‡ Number of deer in photograph.
§ Coyote (*Canis latrans*) abundance.
¶ Study site.

decreasing during daylight hours (Table 2). However, all models in the confidence set for adult males during winter included coyote abundance, which was inversely related to probability of foraging (Tables 1 and 2, Fig. 1). All other parameters in the confidence set for adult males were uninformative.

Coyote abundance was included in all models in the confidence set for yearling males during both fall and winter (Table 3). Adult male presence was also included in the majority of models in the confidence set for yearling males during fall and winter. Both parameters were informative during fall, with probability of foraging decreasing in response to increasing coyote abundance and adult male presence (Table 2). During winter, only coyote abundance was informative for yearling males and the direction of its relationship with coyote abundance was the same as for fall (Table 2, Fig. 1).

Coyote abundance, time of day, study site, and all of the social factors included in our models

Table 2. Model-averaged parameter estimates (β), 95% confidence intervals (CI), and odds ratios (OR) for informative parameters from logistic regression models predicting the probability of foraging for various sex-age classes of white-tailed deer (*Odocoileus virginianus*) at camera traps during fall (September–October) and winter (January–February) on two sites in Georgia, USA, during 2011–2013.

	Fall				Winter			
Sex-age class	β	95% CI	OR	95% CI	β	95% CI	OR	95% CI
Juveniles, adult male†	−0.87	−1.60 to −0.14	0.42	0.20–0.87	−0.61	−1.06 to −0.16	0.54	0.35–0.86
Juveniles, group size‡	0.30	0.21 to 0.39	1.35	1.23–1.48	0.36	0.28 to 0.45	1.44	1.32–1.57
Yearling males, adult male	−0.89	−1.67 to −0.11	0.41	0.19–0.90				
Yearling males, coyote§	−0.36	−0.51 to −0.21	0.70	0.60–0.81	−0.15	−0.28 to −0.02	0.86	0.76–0.98
Adult females, adult male					−1.25	−2.16 to −0.33	0.29	0.12–0.72
Adult females, coyote	−0.30	−0.37 to −0.23	0.74	0.69–0.79	−0.14	−0.21 to −0.07	0.87	0.81–0.93
Adult females, group size	0.12	0.05 to 0.20	1.13	1.04–1.22	0.09	0.03 to 0.15	1.10	1.04–1.17
Adult males, coyote					−0.21	−0.34 to −0.08	0.81	0.71–0.92
Adult males, daylight¶	−0.70	−1.31 to −0.09	0.50	0.27–0.91				

† Presence of an adult male.
‡ Number of deer in photograph.
§ Coyote (*Canis latrans*) abundance.
¶ Civil daylight period.

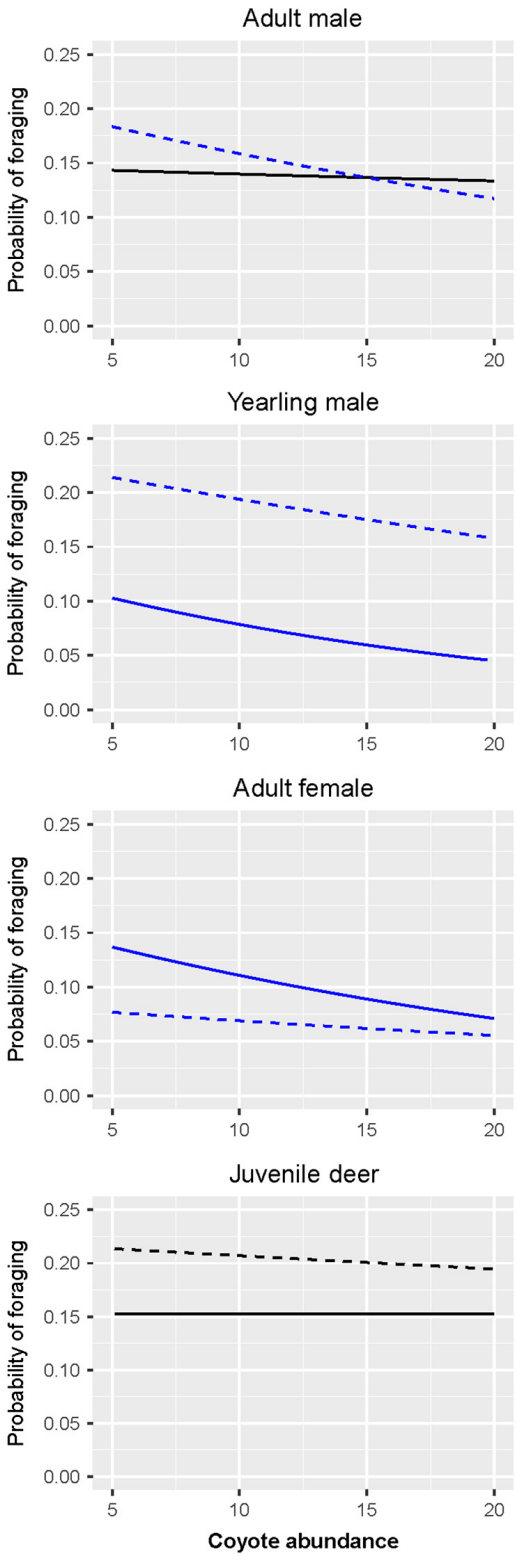

Fig. 1. Plots predicting the probability of foraging

were included in the confidence set for adult females during fall (Table 4). During winter, the confidence set for adult females included adult male presence, coyote abundance, group size, time of day, and study site (Table 4). However, the only informative predictors for adult females were coyote abundance and group size during fall, and adult male presence, coyote abundance, and group size during winter (Table 2). Specifically, foraging probability for adult females was inversely related to coyote abundance (Fig. 1), but increased with group size during both seasons. During winter, adult female foraging probability decreased in response to adult male presence (Table 2).

Adult male presence, coyote abundance, group size, and time of day were in the confidence set of models for juveniles during both seasons (Table 5), but only adult male presence and group size were informative (Table 2). Specifically, juvenile foraging probability decreased when adult males were present and increased with group size during both seasons.

Discussion

Coyote abundance influenced foraging behavior during at least one season for all sex-age classes except juveniles. This is consistent with Cherry et al. (2015), who reported deer were less vigilant inside predator exclosures, but differs from the findings of Schuttler et al. (2016). Their work occurred over a greater spatial extent, but they did not detect a relationship between deer vigilance and coyote activity. Our work offers evidence from a landscape of intermediate scale relative to these two studies and is the first to link empirical estimates of coyote abundance to deer foraging behavior.

Sex-age class specific results were also fairly consistent with previous work. Cherry et al.

(Fig. 1. *Continued*)
for white-tailed deer (*Odocoileus virginianus*) at camera traps as a function of coyote (*Canis latrans*) abundance during fall (September–October) and winter (January–February) 2011–2013 on two sites in Georgia, USA. Predictions were made by holding all other variables constant. Solid lines represent fall, dashed lines winter, and blue lines statistically significant trends.

Table 3. Competitive models, number of parameters (K), Akaike's information criterion (AIC_c), difference from lowest AIC_c (ΔAIC_c), and model weight (w_i) for models used to predict foraging behavior of yearling male white-tailed deer (*Odocoileus virginianus*) at camera traps during fall (September–October) and winter (January –February) 2011–2013 on two sites in Georgia, USA.

Season	Model	K	AIC_c	ΔAIC_c	w_i
Fall	Adult male† + Coyote‡	4	1488.8	0	0.23
Fall	Adult male + Coyote + Site§	5	1489.3	0.55	0.18
Fall	Adult male + Coyote + Group size¶	5	1489.4	0.63	0.17
Fall	Adult male + Coyote + Daylight#	5	1490.1	1.32	0.12
Fall	Adult male + Coyote + Group size + Site	6	1490.3	1.55	0.11
Fall	Adult male + Coyote + Daylight + Group size	6	1490.6	1.81	0.09
Fall	Adult male + Coyote + Daylight + Site	6	1490.6	1.86	0.09
Winter	Coyote + Group size	4	1847.2	0	0.47
Winter	Coyote + Daylight + Group size	5	1849.1	1.94	0.18
Winter	Adult male + Coyote + Group size	5	1849.2	1.98	0.17
Winter	Coyote	3	1849.2	1.99	0.17

† Presence of an adult male.
‡ Coyote (*Canis latrans*) abundance.
§ Study site.
¶ Number of deer in photograph.
# Civil daylight period.

(2015) reported adult females fed less with increasing predation risk, and risk effects were stronger during summer than winter. Females may be more sensitive to predation risk during summer because they are invested in fawns, which are highly susceptible to predation, versus winter when maternal investment is lower. We quantified behavior during fall instead of summer, and according to Kilgo et al. (2012), fawn predation risk is minimal by this time of year. Nevertheless, some fawns are still nursing, more susceptible to predation than adults, and largely dependent on their dams for predator defense during this time. We also documented an attempted predation event of an approximately 6-month-old fawn on Cedar Creek during 2010 (Fig. 2), though we cannot be sure of the frequency at which these events occur. In contrast, predation of adult females by coyotes is very rare (Kilgo et al. 2016, but see Chitwood et al. 2014).

Table 4. Competitive models, number of parameters (K), Akaike's information criterion (AIC_c), difference from lowest AIC_c (ΔAIC_c), and model weight (w_i) for models used to predict foraging behavior of adult female white-tailed deer (*Odocoileus virginianus*) at camera traps during fall (September–October) and winter (January –February) 2011–2013 on two sites in Georgia, USA.

Season	Model	K	AIC_c	ΔAIC_c	w_i
Fall	Adult male† + Coyote‡ + Group size§ + Juvenile¶ + Site#	7	5881.2	0	0.16
Fall	Adult male + Coyote + Daylight‖ + Group size + Juvenile + Site	8	5881.36	0.16	0.15
Fall	Adult male + Coyote + Group size + Juvenile	6	5881.5	0.31	0.14
Fall	Adult male + Coyote + Daylight + Group size + Juvenile	7	5881.99	0.79	0.11
Fall	Coyote + Group size + Juvenile + Site	6	5882.49	1.30	0.08
Fall	Coyote + Daylight + Group size + Juvenile + Site	7	5882.63	1.44	0.08
Winter	Adult male + Coyote + Group size	5	7816.5	0	0.52
Winter	Adult male + Coyote + Daylight + Group size	6	7817.8	1.30	0.27
Winter	Adult male + Coyote + Group Size + Site	6	7818.3	1.78	0.21

† Presence of an adult male.
‡ Coyote (*Canis latrans*) abundance.
§ Number of deer in photograph.
¶ Presence of a juvenile.
# Study site.
‖ Civil daylight.

Table 5. Competitive models, number of parameters (K), Akaike's information criterion (AIC_c), difference from lowest AIC_c (ΔAIC_c), and model weight (w_i) for models used to predict foraging behavior of juvenile white-tailed deer (*Odocoileus virginianus*) at camera traps during fall (September–October) and winter (January–February) 2011–2013 on two sites in central Georgia, USA.

Season	Model	K	AIC_c	ΔAIC_c	w_i
Fall	Adult male† + Group size‡	4	2959.9	0	0.53
Fall	Adult male + Daylight§ + Group size	5	2961.2	1.35	0.27
Fall	Adult male + Coyote¶ + Group size	5	2961.9	1.99	0.2
Winter	Adult male + Coyote + Group size	5	4013.0	0	0.48
Winter	Adult male + Group size	4	4013.7	0.69	0.34
Winter	Adult male + Coyote + Daylight + Group size	6	4014.9	1.86	0.19

† Presence of a male.
‡ Number of deer in photograph.
§ Civil daylight.
¶ Coyote (*Canis latrans*) abundance.

Thus, we conclude the seasonal pattern we observed in adult female behavior is most logically attributed to the seasonal differences in susceptibility of fawns to predation.

The effects of coyote abundance on adult male feeding also varied seasonally. During fall, coyote abundance was an uninformative predictor of foraging probability. Adult male deer are in peak physical condition during fall, and testosterone concentrations are greatest during this period (Mirarchi et al. 1978). Testosterone can enhance risk tolerance in mammals (Cooper et al. 2014), and behavioral changes related to elevated testosterone can increase probability of natural mortality in deer (Ditchkoff et al. 2001), likely because adult males are less sensitive to

Fig. 2. Camera trap image of two coyotes (*Canis latrans*) attempting to kill an approximately 6-month-old white-tailed deer (*Odocoileus virginianus*) fawn on Cedar Creek Wildlife Management Area in Putnam County, Georgia, USA, in November 2010.

risk. In contrast, yearling males exhibited greater vigilance when coyote abundance increased, regardless of season. Younger males typically have lower testosterone concentrations (Bubenik and Schams 1986), likely making them more sensitive to risk. Subsequently, adult male probability of feeding decreased in response to coyote abundance during winter, a time corresponding to decreased testosterone concentrations. Cherry et al. (2015) similarly found adult males were most sensitive to predation risk during winter. Although a behavioral response of this demographic to coyote predation risk seems counterintuitive given their relatively large body size, indirect effects of predators on prey are not always proportional to the direct threat they pose (Creel and Christianson 2008).

In contrast to other sex-age classes, coyote abundance was not an important predictor of feeding probability for juveniles during any season, a finding consistent with previous work (Cherry et al. 2015) and the notion that direct and indirect predator effects are often not correlated. Juvenile deer experience the highest rate of direct predation and have the greatest energetic demands. Species or demographic groups within a species with these characteristics are not expected to exhibit antipredator behavior because they are both ineffective and too costly considering energetic demands of growth (Creel and Christianson 2008). Conversely, both juveniles and adult females were sensitive to group size during fall and winter. Feeding probability similarly increased with group size for juveniles during summer in Georgia, USA (Cherry et al. 2015), and adult males and females during summer in North Carolina, USA (Lashley et al. 2014). Because detection of risk is increased, individual vigilance and risk are reduced or diluted when deer form larger groups (Roberts 1996). In response, time spent feeding increases and time spent alert decreases (Hirth 1977).

Group size alone is insufficient to describe the effects of social factors on deer foraging behavior; group composition is important as well. Adult male presence decreased probability of feeding for yearling males during fall, juveniles during both seasons, and for adult females during winter. This is not surprising given that dominance behavior occurs in social ungulates when there is competition for resources (Taillon and Côté 2006), and male deer dominate females and juveniles (Ozoga 1972). So, although coyote abundance was an important predictor of feeding probability, group size and composition were also necessary to explain the variation in feeding probability we observed. In addition, seasonal responses of each demographic group to coyote predation risk were intrinsically tied to morphology and reproductive behavior, which also affect deer resource demands and risk sensitivity (Brown et al. 1999). Others have described how these factors lead to sex-specific resource exploitation and ultimately sexual segregation (McCullough et al. 1989, Main et al. 1996, Bowyer 2004).

It is important to account for social factors that affect probability of feeding for deer because these predictors help explain seasonal and demographic variation in risk sensitivity, but our ultimate question was whether coyote abundance influences foraging behavior of deer. Our data suggest this was the case on our study areas, but extrapolating to other areas in the eastern United States is difficult given the coyote's recent colonization of the region and the lack of study this topic has received. Behavioral responses of prey to predation risk depend on nutritional condition (Sih 1980, McNamara and Houston 1987), and deer populations in poor condition may be less sensitive to risk than the populations we studied. Differences in coyote density among the region are likely important as well. Published reports from the eastern United States are scarce, but dividing our abundance estimates by the physical area surveyed yielded a range of coyote density values comparable to estimates from elsewhere (Knowlton 1972, Knowlton et al. 1999).

Despite these uncertainties, Cherry et al. (2016) found evidence to suggest that differences in deer behavior related to coyote predation risk were sufficient to increase oak (*Quercus* spp.) recruitment and decrease abundance of more palatable forage on a study area in the eastern Unites States, facilitating a behaviorally mediated trophic cascade. Links between predation risk and population processes (Sheriff et al. 2009, Zanette et al. 2011), and cascading effects to lower trophic levels (Ripple and Beschta 2004, Estes et al. 2011) have been documented elsewhere. Although our data limit our ability to assert that this was the case on our study areas, the context of our findings within the greater

literature suggests it is plausible. Because of the widespread distribution of deer and coyotes in the eastern United States and the importance of deer as an agent of ecological change, future work should seek to link these processes, in this system, under free-range conditions.

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Literature Cited

Arnold, T. W. 2010. Uninformative parameters and model selection using Akaike's information criterion. Journal of Wildlife Management 74:1175–1178.

Bartoń, K. 2016. MuMIn: Multi-Model Inference. R package version 1.15.6. https://cran.r-project.org/web/packages/MuMIn/index.html

Bates, D., M. Maechler, B. Bolker, and S. Walker. 2015. Fitting linear mixed-effects models using lme4. Journal of Statistical Software 67:1–48.

Bivand, R., and N. Lewin-Koh. 2017. Maptools: tools for reading and handling spatial objects. R package version 0.9-2. https://CRAN.R-project.org/package=maptools

Bowyer, R. T. 2004. Sexual segregation in ruminants: definitions, hypotheses, and implications for conservation and management. Journal of Mammalogy 85:1039–1052.

Brown, J. S. 1999. Vigilance, patch use and habitat selection: foraging under predation risk. Evolutionary Ecology Research 1:49–71.

Brown, T. L., D. J. Decker, S. J. Riley, J. W. Enck, T. B. Lauber, P. D. Curtis, and G. F. Mattfeld. 2000. The future of hunting as a mechanism to control white-tailed deer populations. Wildlife Society Bulletin 28:797–807.

Brown, J. S., and B. P. Kotler. 2004. Hazardous duty pay and the foraging cost of predation. Ecology Letters 7:999–1014.

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.

Bubenik, G. A., and D. Schams. 1986. Relationship of age to seasonal levels of LH, FSH, prolactin and testosterone in male, white-tailed deer. Comparative Biochemistry and Physiology Part A: Physiology 83:179–183.

Burnham, K. P., and D. R. Anderson. 2004. Multimodel inference understanding AIC and BIC in model selection. Sociological Methods & Research 33:261–304.

Cherry, M. J., L. M. Conner, and R. J. Warren. 2015. Effects of predation risk and group dynamics on white-tailed deer foraging behavior in a longleaf pine savanna. Behavioral Ecology 26:1091–1099.

Cherry, M. J., R. J. Warren, and L. M. Conner. 2016. Fear, fire, and behaviorally mediated trophic cascades in a frequently burned savanna. Forest Ecology and Management 368:133–139.

Cherry, M. J., R. J. Warren, and L. M. Conner. 2017. Fire-mediated foraging tradeoffs in white-tailed deer. Ecosphere 8:e01784.

Childress, M. J., and M. A. Lung. 2003. Predation risk, gender and the group size effect: Does elk vigilance depend upon the behaviour of conspecifics? Animal Behaviour 66:389–398.

Chitwood, M. C., M. A. Lashley, J. C. Kilgo, C. E. Moorman, and C. S. Deperno. 2015. White-tailed deer population dynamics and adult female survival in the presence of a novel predator. Journal of Wildlife Management 79:211–219.

Chitwood, M. C., M. A. Lashley, C. E. Moorman, and C. S. DePerno. 2014. Confirmation of coyote predation on adult female white-tailed deer in the southeastern United States. Southeastern Naturalist 3: 30–32.

Conner, L. M., M. J. Cherry, B. T. Rutledge, C. H. Killmaster, G. Morris, and L. L. Smith. 2016. Predator exclusion as a management option for increasing white-tailed deer recruitment. Journal of Wildlife Management 80:162–170.

Cooper, S. E., S. P. Goings, J. Y. Kim, and R. I. Wood. 2014. Testosterone enhances risk tolerance without altering motor impulsivity in male rats. Psychoneuroendocrinology 40:201–212.

Côté, S. D., T. P. Rooney, J. P. Tremblay, C. Dussault, and D. M. Waller. 2004. Ecological impacts of deer overabundance. Annual Review of Ecology, Evolution, and Systematics 35:113–147.

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

Ditchkoff, S. S., E. R. Welch Jr., R. L. Lochmiller, R. E. Masters, and W. R. Starry. 2001. Age-specific causes

of mortality among white-tailed deer support mate-competition theory. Journal of Wildlife Management 65:552–559.

Donohue, R. N., D. G. Hewitt, T. E. Fulbright, C. A. Deyoung, A. R. Litt, and D. A. Draeger. 2013. Aggressive behavior of white-tailed deer at concentrated food sites as affected by population density. Journal of Wildlife Management 77:1401–1408.

Estes, J. A., et al. 2011. Trophic downgrading of planet Earth. Science 333:301–306.

Galpern, P., M. Manseau, P. Hettinga, K. Smith, and P. Wilson. 2012. Allelematch: an R package for identifying unique multilocus genotypes where genotyping error and missing data may be present. Molecular Ecology Resources 12:771–778.

Gompper, M. E. 2002. Top Carnivores in the Suburbs? Ecological and Conservation Issues Raised by Colonization of North eastern North America by Coyotes: The expansion of the coyote's geographical range may broadly influence community structure, and rising coyote densities in the suburbs may alter how the general public views wildlife. BioScience 52:185–190.

Grolemund, G., and H. Wickham. 2011. Dates and times made easy with lubridate. Journal of Statistical Software 40:1–25.

Gulsby, W. D., C. H. Killmaster, J. W. Bowers, J. D. Kelly, B. N. Sacks, M. J. Statham, and K. V. Miller. 2015. White-tailed deer fawn recruitment before and after experimental coyote removals in central Georgia. Wildlife Society Bulletin 39:248–255.

Gulsby, W. D., C. H. Killmaster, J. W. Bowers, J. S. Laufenberg, B. N. Sacks, M. J. Statham, and K. V. Miller. 2016. Efficacy and precision of fecal genotyping to estimate coyote abundance. Wildlife Society Bulletin 40:792–799.

Hirth, D. H. 1977. Social behavior of white-tailed deer in relation to habitat. Wildlife Monographs 53:3–55.

Holzman, S., M. J. Conroy, and J. Pickering. 1992. Home range, movements, and habitat use of coyotes in southcentral Georgia. Journal of Wildlife Management 56:139–146.

Hunter, L. T. B., and J. D. Skinner. 1998. Vigilance behaviour in African ungulates: the role of predation pressure. Behaviour 135:195–211.

Kilgo, J. C., H. S. Ray, C. Ruth, and K. V. Miller. 2010. Can coyotes affect deer populations in southeastern North America? Journal of Wildlife Management 74:929–933.

Kilgo, J. C., H. S. Ray, M. Vukovich, M. J. Goode, and C. Ruth. 2012. Predation by coyotes on white-tailed deer neonates in South Carolina. Journal of Wildlife Management 76:1420–1430.

Kilgo, J. C., M. Vukovich, M. J. Conroy, H. S. Ray, and C. Ruth. 2016. Factors affecting survival of adult female white-tailed deer after coyote establishment in South Carolina. Wildlife Society Bulletin 40:747–753.

Knowlton, F. F. 1972. Preliminary interpretations of coyote population mechanics with some management implications. Journal of Wildlife Management 36:369–382.

Knowlton, F. F., E. M. Gese, and M. M. Jaeger. 1999. Coyote depredation control: an interface between biology and management. Journal of Range Management 52:398–412.

Lashley, M. A., M. C. Chitwood, M. T. Biggerstaff, D. L. Morina, C. E. Moorman, and C. S. DePerno. 2014. White-tailed deer vigilance: the influence of social and environmental factors. PLoS ONE 9: e90652.

Laundré, J. W., L. Hernández, and K. B. Altendorf. 2001. Wolves, elk, and bison: reestablishing the "landscape of fear" in Yellowstone National Park, USA. Canadian Journal of Zoology 79:1401–1409.

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.

Lounsberry, Z. T., T. D. Forrester, M. T. Olegario, J. L. Brazeal, H. U. Wittmer, and B. N. Sacks. 2015. Estimating sex-specific abundance in fawning areas of a high-density Columbian black-tailed deer population using fecal DNA. Journal of Wildlife Management 79:39–49.

Main, M. B., F. W. Weckerly, and V. C. Bleich. 1996. Sexual segregation in ungulates: new directions for research. Journal of Mammalogy 77:449–461.

McCullough, D. R., D. H. Hirth, and S. J. Newhouse. 1989. Resource partitioning between sexes in white-tailed deer. Journal of Wildlife Management 53:277–283.

McNamara, J. M., and A. I. Houston. 1987. Starvation and predation as factors limiting population size. Ecology 68:1515–1519.

Mirarchi, R. E., B. E. Howland, P. F. Scanlon, and R. L. Kirkpatrick. 1978. Seasonal variation in plasma LH, FSH, prolactin, and testosterone concentrations in adult male white-tailed deer. Canadian Journal of Zoology 56:121–127.

Ozoga, J. J. 1972. Aggressive behavior of white-tailed deer at winter cuttings. Journal of Wildlife Management 36:861–868.

Parker, G. R. 1995. Eastern coyote: the story of its success. Nimbus Publishing, Halifax, Nova Scotia, Canada.

Peakall, R., and P. E. Smouse. 2006. GENALEX 6: genetic analysis in Excel. Population genetic software for teaching and research. Molecular Ecology Notes 6:288–295.

Peakall, R., and P. E. Smouse. 2012. GenAlEx 6.5: genetic analysis in Excel. Population genetic software for teaching and research—an update. Bioinformatics 28:2537–2539.

Périquet, S., et al. 2012. Influence of immediate predation risk by lions on the vigilance of prey of different body size. Behavioral Ecology 23:976.

Perrine, J. D., J. P. Pollinger, B. N. Sacks, R. H. Barrett, and R. K. Wayne. 2007. Genetic evidence for the persistence of the critically endangered Sierra Nevada red fox in California. Conservation Genetics 8:1083–1095.

R Core Team. 2016. R: a language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria.

Ripple, W. J., and R. L. Beschta. 2004. Wolves and the ecology of fear: Can predation risk structure ecosystems? BioScience 54:755–766.

Ripple, W. J., A. J. Wirsing, C. C. Wilmers, and M. Letnic. 2013. Widespread mesopredator effects after wolf extirpation. Biological Conservation 160:70–79.

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

Roberts, G. 1996. Why individual vigilance declines as group size increases. Animal Behaviour 51:1077–1086.

Robinson, K. F., D. R. Diefenbach, A. K. Fuller, J. E. Hurst, and C. S. Rosenberry. 2014. Can managers compensate for coyote predation of white-tailed deer? Journal of Wildlife Management 78:571–579.

Rooney, T. P., and D. M. Waller. 2003. Direct and indirect effects of white-tailed deer in forest ecosystems. Forest Ecology and Management 181: 165–176.

Schuttler, S. G., A. W. Parsons, T. D. Forrester, M. C. Baker, W. J. McShea, R. Costello, and R. Kays. 2016. Deer on the lookout: How hunting, hiking and coyotes affect white-tailed deer vigilance. Journal of Zoology 54:242–252.

Sheriff, M. J., C. J. Krebs, and R. Boonstra. 2009. The sensitive hare: sublethal effects of predator stress on reproduction in snowshoe hares. Journal of Animal Ecology 78:1249–1258.

Sih, A. 1980. Optimal behavior: Can foragers balance two conflicting demands? Science 210:1040–1043.

Stenglein, J. L., M. De Barba, D. E. Ausband, and L. P. Waits. 2010. Impacts of sampling location within a faeces on DNA quality in two carnivore species. Molecular Ecology Resources 10:109–114.

Stone, D. B., M. J. Cherry, J. M. Martin, B. S. Cohen, and K. V. Miller. 2017. Breeding chronology and social interactions affect ungulate foraging behavior at a concentrated food resource. PLoS ONE 12: e0178477.

Taillon, J., and S. D. Côté. 2006. The role of previous social encounters and body mass in determining social rank: an experiment with white-tailed deer. Animal Behaviour 72:1103–1110.

USFWS (U.S. Fish and Wildlife Service). 2011. 2011 National survey of fishing, hunting, and wildlife-associated recreation. U.S. Department of the Interior, U.S. Fish and Wildlife Service, U.S. Department of Commerce, and U.S. Census Bureau, Washington, D.C., USA.

Waits, L. P., G. Luikart, and P. Taberlet. 2001. Estimating the probability of identity among genotypes in natural populations: cautions and guidelines. Molecular Ecology 10:249–256.

Waller, D. M., and W. S. Alverson. 1997. The white-tailed deer: a keystone herbivore. Wildlife Society Bulletin 25:217–226.

Zanette, L. Y., A. F. White, M. C. Allen, and M. Clinchy. 2011. Perceived predation risk reduces the number of offspring songbirds produce per year. Science 334:1398–1401.