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ARTICLE
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Responses of a large herbivore to predation risk are modulated by intrinsic and extrinsic factors

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Abstract

Prey species can perceive and respond to spatiotemporal variation in predation risk to increase survival. In addition to adjusting spatial and temporal activity patterns to avoid predation, prey employ other antipredator behaviors, such as vigilance and fleeing, and these behaviors can be further modulated by intrinsic, environmental, and anthropogenic factors. However, few studies simultaneously examine multiple potential antipredator behavioral responses of prey or examine prey responses to multiple scales of risk. In the southeastern United States, coyotes (*Canis latrans*) have become established as the top predator of white-tailed deer (*Odocoileus virginianus*) populations mainly through fawn predation, and deer adjust behaviors in response to coyotes. Using passive camera trap data from summer 2019 to 2021, we simultaneously tested for evidence that deer adjust spatial activity patterns, diel activity patterns, and vigilance behavior in response to various abiotic and biotic factors including long-term and short-term coyote encounter risk. Overall, our results suggest that deer are unable to eliminate the risk of encountering coyotes by modifying their spatial activity and thus employ other demographic-specific behavioral adaptations to reduce coyote encounter risk. Deer nursery groups were significantly more diurnal than adult males or adult female deer traveling alone, likely in an attempt to reduce predation risk for fawns. Deer nursery groups increased spatial activity but decreased vigilance at sites the day following increased wild pig (*Sus scrofa*) activity, suggesting invasive competitors have impacts on maternal behaviors in deer. Adult female deer collectively increased vigilance at sites with greater long-term coyote encounter risk, and in support of the "many-eyes" hypothesis, were less vigilant when in larger groups. Spatial activity of adult female deer traveling alone was positively related to short-term coyote encounter risk, potentially indicating coyotes seek areas with increased doe activity to help locate fawn prey. The results of our study show that behavioral responses to predators and competitors are

modulated by individual state (demography), grouping behavior, and habitat features. Our study highlights the need to analyze multiple potential antipredator behaviors and multiple scales of risk to gain a more complete understanding of prey responses to risk.

KEYWORDS
competitors, demographics, diel activity, grouping, predation risk, risky places, risky times, ungulate behavior, vigilance

INTRODUCTION

Predation risk, defined as the probability of encounter and being killed by a predator, can drive prey to adjust behaviors to reduce the chances of being killed (Blanchard et al., 2018; Lima, 1998; Moll et al., 2017). Wild ungulate prey often alter their behaviors in response to the multiple spatial and temporal scales of predation risk (Cherry et al., 2015; Crawford et al., 2021; Gervasi et al., 2013; Kie, 1999; Thaker et al., 2011; Valeix et al., 2009) and can adjust spatial and temporal activity patterns to seek spatiotemporal refugia from predation risk (Dröge et al., 2017; Hernández & Laundré, 2005; Kautz et al., 2022; Kohl et al., 2018, 2019). Ungulates can increase antipredator responses like vigilance in the presence of immediate or short-term risk of predation (i.e., the risky times hypothesis; Creel & Christianson, 2008). Alternatively, ungulate prey can reduce predation risk by increasing antipredator responses or altogether avoiding areas of greater long-term risk (i.e., the risky places hypothesis; Creel & Christianson, 2008). Prey can also respond to spatial and temporal variation in predation risk simultaneously, where individuals can use risky habitat during temporal periods of low predation risk (Dröge et al., 2017). The predictability of risk may also interact with risk levels to impact prey behavior responses. The risk allocation hypothesis predicts that prey will exhibit stronger behavioral responses to acute risk exposure in areas perceived to have low (infrequent) long-term predation risk (Lima & Bednekoff, 1999).

How prey perceive and respond to risk is dynamic largely due to spatiotemporal variation in predator activity (e.g., seasons, diel variability; Donadio & Buskirk, 2016; Goldsmith, 1990; Thaker et al., 2011), extrinsic factors (e.g, habitat conditions, human activity, presence of other species), and state of the prey species (e.g., age, condition [locomotory/olfactory/visual/auditory capabilities], and grouping behavior) (Hayward et al., 2015; Prugh et al., 2019). In ungulates, predation risk varies among age, sex, and reproductive condition (Caughley, 1966), and responses to risk can vary across behavioral scales in accordance with vulnerability, modulated by social (e.g., group size), biotic (e.g., vegetation complexity, competitor species), and abiotic (e.g., time-of-day, weather) factors (Hebblewhite et al., 2005; Stone et al., 2017). Concurrent with predation risk, competitor species, especially invasive competitors, may present competitive risks and can impact activity patterns and behavior of native ungulates (Garabedian et al., 2023; Lewis, 2021; Saldo et al., 2023). Ungulate responses to predation risk may further be modulated by habitat complexity and human presence/activity. In some predator–prey systems, increased habitat complexity can provide prey spatial refugia from predators (Gigliotti et al., 2020; Janssen et al., 2007). Humans could provide spatial refugia for ungulate prey from predators and influence risk response behaviors because human presence and activity influences predator behavior, and most predator species generally avoid human habitation and/or human activity where possible (Hebblewhite & Merrill, 2008; Kitchen et al., 2000; Mace et al., 1996). Therefore, if ungulates perceive lower risk of predation in areas closer to human areas, it may be reasonable to expect a behavioral response whereby individuals use the "human shield" to reduce predation risk (Berger, 2007; Nowak et al., 2014), yet this concept warrants further investigation across ungulate species.

In addition to adjusting spatial and temporal activity patterns to reduce predation risk, prey employ additional antipredator behaviors, such as vigilance and fleeing (Campos & Fedigan, 2014). To detect predators, ungulates routinely use multiple senses, including visual (Barja & Rosellini, 2008; Halofsky & Ripple, 2008; Lingle & Wilson, 2001), auditory (Lynch et al., 2015), and olfactory senses (Kuijper et al., 2014). Vigilance is a specific perceptive behavior that ungulates use to detect stimuli in their surroundings with their visual, auditory, and olfactory senses. Vigilance can, in part, increase the probability of detecting predators earlier to help avoid predation (Dimond & Lazarus, 1974; Quenette, 1990). Parturition and subsequent lactation substantially increase energetic demands for mammals (Oftedal, 1985; Parker et al., 2009); thus, increasing vigilance may be costly to both mother and offspring as does spend less time foraging, possibly reducing nutritional condition (Brown & Kotler, 2004;

Christianson & Creel, 2008). Despite potential physiological costs, multiple ungulate species increase vigilance behavior in response to predation risk, such as fallow deer (*Dama dama*), vicuña (*Vicugna vicugna*), and red deer (*Cervus elaphus*; Donadio & Buskirk, 2016; Esattore et al., 2022; Kuijper et al., 2014). Predation risk can impact grouping behavior in ungulates (Creel et al., 2014), and in turn, grouping behavior may influence prey's responses to risk. For example, grouping behavior could ameliorate some of the costs associated with increased individual vigilance, even increasing individual foraging efficiency in some scenarios (i.e., the group size effect; Delm, 1990; Lima & Dill, 1990; Lipetz & Bekoff, 1982; Rieucau & Giraldeau, 2009).

Introduced ungulate species are widely known to influence the behavior of native ungulates (Galetti et al., 2015; Schuette et al., 2016; Voeten & Prins, 1999). However, comparatively little is known about how the introduction of a novel competitor influences the response of resident prey to predators and the subsequent risk of predation. Observational studies in the southeastern United States suggest that seasonally, invasive wild pig (*Sus scrofa*) site use negatively influences white-tailed deer (*Odocoileus virginianus*) and coyote (*Canis latrans*) occurrence (Garabedian et al., 2023; Saldo et al., 2023). In addition, recent experimental work further suggests that wild pigs displace deer both spatially and temporally, particularly juvenile deer, which may result in increased risk of coyote predation (Saldo et al., 2024). Thus, invasive competitors could shift predator–prey dynamics, and more research is needed on how novel competitors influence prey responses to predation risk.

Understanding how ungulates perceive (or fail to perceive) risk is particularly important for species where top-down predation effects on populations are of management concern. Recent declines in white-tailed deer populations in the southeastern United States have been linked to reduced recruitment caused by increased fawn mortality attributed to the coyote, a recent arrival to the region (Chitwood, Lashley, Kilgo, Moorman, et al., 2015; Chitwood, Lashley, Kilgo, Pollock, et al., 2015; Gingery et al., 2018; Hody & Kays, 2018; Jackson & Ditchkoff, 2013; Kilgo et al., 2010, 2014; Shuman et al., 2017). Young fawns (<4 weeks of age) are the most susceptible deer demographic to coyote predation in the Southeast; thus, the peak fawning season is when deer populations are most impacted by predation (Chitwood, Lashley, Kilgo, Moorman, et al., 2015) and behaviors should be most responsive to variation in predation risk (Muthersbaugh et al., 2024). However, studies on deer responses to coyotes in the region have focused on other seasons (e.g., late summer or autumn) when predation risk wanes, or used supplemental feeding to study behavior, possibly clouding inference (Cherry et al., 2015; Gulsby et al., 2018). Few studies have simultaneously examined multiple potential antipredator behavioral responses of ungulate prey, and most studies on white-tailed deer responses to coyote predation risk have focused on one behavior such as foraging behavior or vigilance, or diel activity patterns alone (Crawford et al., 2021; Gulsby et al., 2018; Higdon et al., 2019; Schuttler et al., 2017). Accordingly, more research is required to simultaneously examine which behaviors deer adjust in response to coyote presence and activity at multiple spatial and temporal scales, and determine how these responses are modulated by biological, habitat, and environmental conditions.

Our objective was to simultaneously investigate multiple deer behavioral responses to predation risk among demographic groups and assess the modulating effects of invasive competitor activity, human presence, grouping behavior, abiotic factors (e.g., time of day, weather), and vegetation conditions on deer behavior during the critical fawning season. We used camera traps to quantify deer behavioral responses to coyote encounter risk (as a proxy for predation risk) in adult bucks, adult does, and nursery groups (multiple fawns and does together), and tested for evidence of spatial avoidance, temporal avoidance, and increased vigilance behavior. We broadly hypothesized that deer would adjust multiple spatial and temporal activity patterns in response to both short-term and long-term predation risk, as predicted by the predation risk allocation hypothesis (Lima & Bednekoff, 1999). Specifically, we predicted greater long-term coyote encounter risk would result in lower spatial activity, increased vigilance, and an increased likelihood for deer to seek temporal refugia as compared with short-term coyote encounter risk for all demographics. We further predicted that understory vegetation structure would affect vigilance in all demographics such that deer would be most vigilant in dense understory vegetation because of reduced predator detection (Andruskiw et al., 2008; Lagory, 1986; McCormick & Lönnstedt, 2013). We also hypothesized that deer responses to spatiotemporally variable predation risk would be modulated by individual state (i.e., demographic), grouping behavior, ambient weather and habitat conditions, and invasive competitors. Specifically, we predicted that the strength of responses for each deer demographic would scale with the vulnerability such that, across behaviors, adult bucks would display the weakest responses to both short and long-term coyote encounter risk but that nursery groups would show the strongest responses (Crawford et al., 2021; Hebblewhite et al., 2005; Stone et al., 2017). As such, we expected all demographics to be least vigilant during the day, when coyotes were least active, but for nursery groups to show the clearest patterns of temporal avoidance

(Higdon et al., 2019; Kautz et al., 2022). We predicted that does and bucks would reduce vigilance as adult group sizes increased, in support of the group size effect and "many-eyes" hypothesis (Isvaran, 2007; Lima, 1995), but that does would increase vigilance in the presence of fawns (Lashley et al., 2014). Since coyotes seem to perceive risks associated with humans at our study site (Jensen, 2023), we predicted nursery group activity would be positively related to proximity to paved roads, in partial support of the human shield hypothesis (Berger, 2007). Because wild pigs impact deer occurrence and activity likely through both interference and exploitative competition (Garabedian et al., 2023; Saldo et al., 2023) we predicted that increased pig activity at multiple scales would negatively impact deer spatial activity and increase deer vigilance.

METHODS

Study area

We studied a population of white-tailed deer on ~60.7 km^2 of privately owned lands in McCormick County, South Carolina, within the Piedmont physiographic province. The Piedmont region is characterized by a subtropical climate and rolling hills, with a diversity of land cover types including planted pine stands, riparian hardwood associations, and scattered agricultural fields (Fields, 2007). Most of the lands in our study area are maintained as various-aged managed loblolly pine (*Pinus taeda*) stands, cleared of other common competitor tree species such as sweetgum (*Liquidambar styraciflua*). Riparian areas generally are left unmanaged, with mesic hardwood associations dominant; white oak (*Quercus alba*), southern red oak (*Quercus falcata*), hickory species (*Carya* spp.), and sweetgum are common in areas where loblolly is not planted. Dominant understory plant species include blackberry (*Rubus allegheniensis*), muscadine (*Vitus rotundifolia*), fennel (*Eupatorium* spp.), poison ivy (*Toxicodendron radicans*), and broomsedge (*Andropogon virginicus*). McCormick County has a small human population, with a density of ~68.8 persons/km^2 (census.gov/quickfacts/-mccormickcountysouthcarolina), and human dwellings are rare within our study area. Numerous wildlife clearings or food plots are interspersed across the property, and most are planted with grains like sorghum (*Sorghum* spp.) and rye (*Secale* spp.); some are planted with clover (*Trifolium* spp.), and some with sunflowers (*Helianthus* spp.) and corn (*Zea mays*). Nearly all these wildlife clearings are smaller than 2.4 ha, and many are rectangular and linear, their main purpose being to provide northern bobwhite (*Colinus virginianus*) and deer forage, as well as providing open areas to hunt both species. Most inventoried forest stands are bordered by either dirt roads or paths made by log skidders for timber harvest and management activities.

Field methods

We used passive (non-baited) wildlife camera traps during summer (May 1–June 30) 2019–2021 to photograph deer, coyotes, and wild pigs. We placed 93 Bushnell Trophy Cam HD Aggressor No Glow cameras (Bushnell Corporation, Overland Park, KS, USA) 50–80 cm above ground level on trees or t-posts and angled cameras approximately 45° across roads or paths to increase viewshed and animal detection and reduce sun glare. Using a square grid cell overlay from the Fishnet tool in ArcMap 10.3 (ESRI, Redlands, CA, USA), we spatially balanced camera trap sites across the study area at a density of approximately 1 camera trap/km^2 (Appendix S1: Figure S1). We placed cameras along unpaved access roads, paths, and wildlife clearings as close as possible to the center of each grid cell and checked cameras one or more times every one to three months and set cameras to take a photograph every 0.6 s until no animal subject or subject movement was detected. Each year our goal was continuous camera operation, but due to battery failure, theft, or camera removal (and replacement) for forestry operations, some sites had truncated samples (76, 60, and 72 sites had complete sample seasons with average of 57.3, 50.6, and 58.3 sampled days in 2019, 2020, and 2021, respectively).

We collected several site-specific measurements to assess support for our 3 habitat-related hypotheses (habitat complexity, human shield, risky places) on deer space use and vigilance. We took the average of five laser rangefinder distance readings (straight, and right and left at 11° and 43°) to measure detection distance in front of each camera and used these measures as a proxy of understory vegetation density for each camera site. We used the Near tool in ArcGIS Pro 2.8.6 (Ersi, Redlands, CA, USA) and Breaklines data and Statewide Highways data from the South Carolina Department of Natural Resources to determine distance from camera sites to the nearest riparian areas and to the nearest paved road. We measured distance to the nearest riparian area because pregnant and lactating does may have a greater need for free water compared with bucks, especially during bouts of high ambient temperature and little precipitation (Brunjes et al., 2006). For assessing the effects of event-specific environmental conditions on vigilance, we obtained ambient conditions including daily total precipitation, daily average wind speed, and daily average temperature from records for a nearby airport

(Station WBAN: 53874) accessed through the National Centers for Environmental Information (National Oceanic and Atmospheric Administration).

Photograph analysis

We used digiKam (https://www.digikam.org/) and Timelapse2 (version 2.2, Greenberg et al., 2019) software to manually classify photographs with species and counts for deer, coyotes, and wild pigs. All deer photographs were further classified by age and sex (e.g., adult buck, adult doe, adult unidentified, juvenile). To make comparisons between demographics clearer, infrequent photographs with both sexes present were excluded from analyses. We quantified deer diel activity patterns and resulting temporal overlap with coyote diel activity, relative activity (hereafter spatial activity), and vigilance behavior for adult bucks, adult does, and nursery groups. We defined nursery groups as photographs where an adult doe and at least one fawn were in the frame. We analyzed demographic groups separately because our predictions varied among these groups.

We measured multiple scales of coyote encounter risk to help account for the spatiotemporal complexity of risk and the scale of effects on deer (Moll et al., 2017). We defined long-term coyote encounter risk as the average count of coyote passes per day throughout each summer season for each year (May 1–June 30) at a given camera site, including only those days a camera was operational. We characterized short-term coyote encounter risk with two separate measures: the count of daily coyote passes and the count of coyote passes the day prior. Because we thought deer responses to risk might be lagged, we did not combine these two coyote counts. To characterize long-term and short-term risk of encounter with competitors (i.e., wild pigs), we applied the same methods we used for coyotes to pig photographs. We used daily and previous-day coyote counts because our analysis of deer spatial activity was based on daily deer activity, and using these same metrics in our analysis of deer vigilance allowed for direct comparison of predator activity effects on different behaviors. We considered photographs of coyotes and pigs separated by >5 min to be independent photographic events (i.e., passes). Other studies commonly use greater time intervals (e.g., 15 min, Gulsby et al., 2018) to ensure independence, but unlike many other studies, our camera sites were non-baited and therefore not placed over a concentrated food source (Donohue et al., 2013) and were typically located on a travel corridor.

We considered deer to be vigilant when their head was above their stomach line and they appeared alert (ears erect, head up while standing or walking), and non-vigilant when their head was below their stomach line and/or they appeared relaxed (actively manipulating forage in mouth, grooming, head held low while walking; Olson et al., 2019; Schuttler et al., 2017). We did not quantify vigilance behavior in photographs where the individual's head was not visible. We determined the sex of adult deer with presence or absence of antlers or antler pedicles and determined age (adult or fawn) with the presence or absence of a spotted coat pattern. Importantly, some does photographed without fawns present likely did have fawns, but considering white-tailed deer employ a "hider strategy" for young fawns (Carl & Robbins, 1988; Jacobsen, 1979), those does were simply alone at the time of the photograph.

Statistical analyses

Spatial activity patterns

To quantify factors influencing deer spatial activity patterns, we created a set of 11 a priori candidate models representing specific hypotheses about the influence of environmental and biological factors on adult doe, adult buck, and nursery group activity. Our sampling unit was each passive camera trap site, and the response variable was the total number of deer per site for each day and we used independent photographic events (separated by >5 min) for deer in this analysis. Model covariates included additive and interactive combinations of factors including: average wild pig passes per day per site, daily count of wild pig passes, previous-day count of wild pig passes, average coyote passes per day per site, daily count of coyote passes, previous-day count of coyote passes, understory vegetation density, distance to paved road, and distance to riparian area (Appendix S1: Table S1). We fit generalized linear mixed models (GLMMs) within an Information Theoretic (IT) framework with the "glmmTMB" function from the R package glmmTMB (Brooks, 2017). We included a random intercept term to account for site-specific variation and fit models with a negative binomial distribution to account for overdispersion in the response variable. We ranked models using Akaike information criterion correction (AIC_c) for sample size using the R package MuMIn (Barton, 2009). We report only models with empirical support ($\Delta AIC_c < 2$) and considered the effects of covariates to be statistically significant when 95% CIs did not overlap 0.

Diel activity and temporal overlap

We tested for evidence of temporal activity partitioning between deer and coyotes and deer and wild pigs using

the coefficient of overlap, calculated using the program R overlap package (version 0.3.4; Meredith & Ridout, 2022). We obtained CIs using 10,000 smoothed bootstrap samples and used the $\widehat{\Delta}_4$ overlap estimator across all tested pairings. We considered photographs of focal species (deer, coyote, pigs) separated by >5 min to be independent photographic events, thinning the dataset prior to estimating temporal overlap. First, we assessed temporal overlap between deer demographic groups and coyotes and pigs across all camera sites, and considered differences in temporal overlap to be statistically significant when CIs did not overlap. To test the predation risk allocation hypothesis, for each demographic group we quantified deer–coyote temporal overlap at sites with the statistical lowest 3rd of long-term coyote encounter risk (fewest coyote passes per day—low risk), the middle 3rd of long-term coyote encounter risk (medium risk), and upper 3rd of long-term coyote encounter risk (most coyote passes per day—high risk). We did not test for the predation risk allocation hypothesis with regard to deer–wild pig temporal overlap because wild pig activity was concentrated at few sites compared with coyotes. We compared temporal overlap measures within deer demographic groups among sites with different levels of long-term coyote risk, and considered differences in temporal overlap to be statistically significant when CIs did not overlap.

Vigilance

To assess factors impacting deer vigilance, we created sets of 16, 17, and 10 a priori candidate models representing specific hypotheses about the relationship between environmental and biological factors and vigilance behavior in bucks, does, and does in nursery groups, respectively (Table 1). We used different models and numbers of models in candidate sets for each demographic because we expected vigilance behaviors would respond differently among demographics and the data used in each model set were unique. For instance, to examine buck vigilance, we did not include any models with covariates of juvenile presence because photographs with the presence of both a buck and a juvenile were rare and not included in the dataset. The response variable for the vigilance models was a count of vigilant adult individuals within an individual photograph. We used a count of individuals vigilant rather than the proportion of individuals vigilant in an individual photograph to ensure that group size did not minimize occurrences of vigilance. For example, if a group of 10 deer is present in a photograph and 2 are vigilant, and in another photograph 2 deer are present and both are vigilant, the number of vigilant deer in each photograph is the same but the proportions are widely different. We used all deer photographs in analyses of deer vigilance behavior but continued to use independent photographic events (separated by >5 min) for covariates of coyote and wild pig encounter risk. By using all deer photographs, we were better able to evaluate the potential for the group size effect because the first and last images in a series often did not capture all individuals in a group, and group size was also measured on an individual photograph basis.

For analyses of vigilance, we used the same covariates as in spatial activity analyses, with additional covariates including average daily temperature, average daily windspeed, total daily precipitation, time of day, count of adult deer (for doe and buck models only), and count of juvenile deer (for doe models only; Appendix S1: Table S2). Time of day was categorized for each photograph as day (30 min after sunrise until 30 min prior to sunset), crepuscular (30 min prior to and after sunrise and sunset), or night (30 min after sunset until 30 min prior to sunrise). Unlike the analysis of adult doe spatial activity, for the adult doe vigilance analysis, we used all photographs of adult does, including photographs where fawns were present, to determine if the presence of fawns impacted doe vigilance. For the analysis of doe vigilance in nursery groups, we used only photographs where both does and fawns were present, and covariates of group size and juvenile presence were excluded in those models (as the presence of juveniles was preestablished and does are normally solitary during fawning season).

Within an Information Theoretic (IT) framework we fit vigilance models with the "glmmTMB" function from the R package glmmTMB (Brooks, 2017). We included a random intercept term of site nested within date and fit models with a Poisson distribution as those response variables were counts but were not over-dispersed. We used counts as the response variable instead of proportions, because beta regression (for proportion response) does not allow for "0" or "1," and implementation of random effects in beta regression remains limited. We included an offset term taking the log of either count of adult does or count of adult bucks to maintain direct proportionality with the count response variable (Bolker, 2015). We ranked models using AIC_c using the R package MuMIn (Barton, 2020), and report only models with empirical support ($\Delta AIC_c < 2$).

Prior to all analyses we centered and scaled continuous covariates and tested for multicollinearity between continuous covariates using the R package corr (Ruiz et al., 2019), and we did not include highly correlated variables in any models ($R^2 > 0.6$; e.g., maximum daily temperature and minimum daily temperature were correlated with average daily temperature; therefore, only

TABLE 1 Overview of the relationships we found between deer spatial activity ("Space"), vigilance ("Vig"), diel activity patterns ("Diel") and environmental, biological, and habitat conditions.

Hypothesized factors influencing deer responses to risk	Associated hypothesis	Model predictor(s)	Bucks			Does			Nursery group		
			Space	Vig	Diel	Space	Vig	Diel	Space	Vig	Diel
Biological	Many-eyes hypothesis	Group size	x		x	x	−	x	x		x
Environmental	Risky allocation hypothesis	Average coyote passes per day Nighttime hours Daily coyote passes Previous-day coyote passes			±			±*			±*
	Risky times hypothesis	Nighttime hours	x	−		x	−		x	−	
		Previous-day coyote passes		+	x			x			x
		Daily coyote passes		−	x	+		x			x
		Previous-day wild pig passes			x			x	+	−	x
	Risky places hypothesis	Average coyote passes per day				±	+				
		Average wild pig passes per day	+		x	±		x			x
Habitat	Human shield hypothesis	Distance to paved road			x	±		x			x
	Risky places hypothesis	Distance to riparian area			x			x		−	x
	Habitat complexity hypothesis	Understory vegetation density		−	x		−	x			x

Note: A positive relationship is denoted with a "+" and a negative relationship with a "−." An interactive relationship is denoted with a "±." If no significant relationship was found between a predictor and any behavior for any demographic, the predictor is not included in the table; otherwise, cells are left blank where no significant relationship was observed. Predictors that were not present in an analysis are denoted with an "x." An "*" indicates partial support (does and nursery groups had less diel overlap with coyotes at sites of high coyote activity compared with sites of medium coyote activity, but diel overlap was comparable between sites of high and low coyote activity).

average daily temperature was retained). We conducted all analyses in program R, version 4.2.0 (R Core Team, 2021).

RESULTS

For analyses of spatial activity patterns and temporal overlap, in total we collected and analyzed 260, 3655, and 1238 photographs of nursery groups, does, and bucks, respectively. For the analysis of vigilance, in total we collected and analyzed 2612, 52,266, and 19,195 photographs of nursery groups, does, and bucks, respectively. Across all three study years, photographs of nursery groups, does, and bucks were taken at 62, 89, and 88 sites, respectively. The average daily coyote passes at a site (short-term risk) were 0.127 (range 0–3), 0.230 (range 0–24), and 0.284 (range 0–26) at sites and dates where nursery groups, does, and bucks were also detected, respectively. The average coyote passes per day throughout each summer season for each year (May 1–June 30) at a given camera site (long-term risk) were 0.215 (range 0–3.21), 0.225 (range 0–3.21), and 0.292 (range 0–3.21), across sites and years where nursery groups, does, and bucks were detected, respectively.

Spatial activity patterns

Adult buck spatial activity was best described by a univariate model with average wild pig passes per day, and two other models were competitive (Appendix S1: Table S3).

Buck spatial activity was positively related to average wild pig passes per day, but CIs were broad (Figure 1), and no other variables were significantly related to buck spatial activity. Adult doe spatial activity was best described by a global model (Appendix S1: Table S4). Doe spatial activity was positively related to short-term coyote encounter risk, although the effect size was small (Figure 1). Doe spatial activity was related to an interaction between average coyote passes per day and average wild pig passes per day (Appendix S1: Table S5) such that doe activity was only

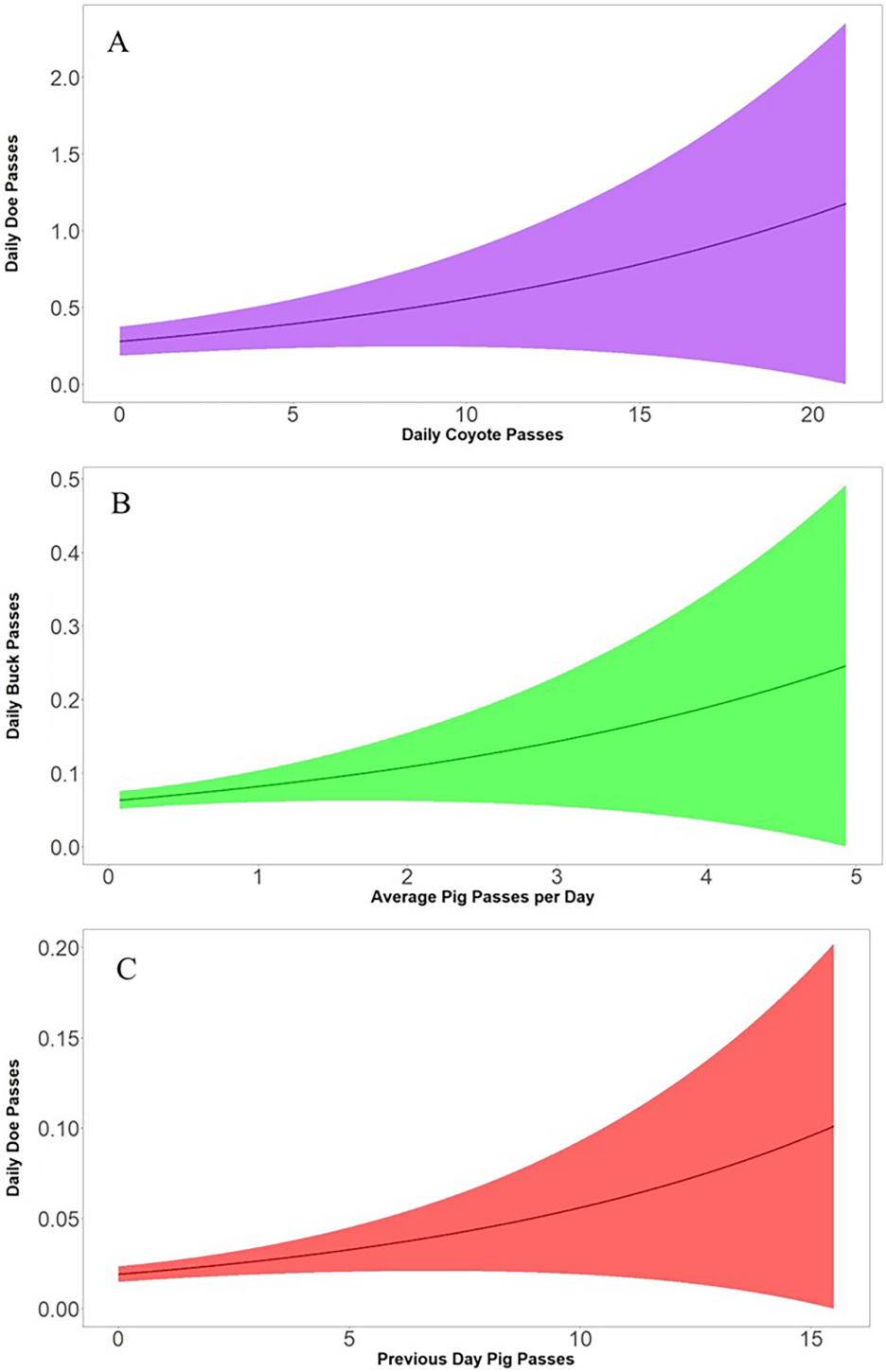

FIGURE 1 Fitted relationships between (A) adult doe spatial activity and daily coyote passes, (B) adult buck spatial activity and average wild pig passes per day, and (C) the spatial activity of adult does in nursery groups and wild pig passes on the day prior (95% CIs shown). Spatial activity was determined based on frequency of passes made in front of remote camera traps.

positively correlated with coyote activity at sites with little pig activity, and that sites with high pig activity had low coyote and deer activity (Figure 2). In support of the human shield hypothesis, doe spatial activity was also related to an interaction between average wild pig passes per day and distance to paved road (Appendix S1: Table S5) such that in the presence of high pig activity, doe activity was greater at sites closer to paved roads (Figure 2). Nursery group spatial activity was best described by a model including both measures of wild pig short-term activity (Appendix S1: Table S6) and was positively related to the previous-day count of wild pig passes (Figure 1; Appendix S1: Table S7).

Diel activity and temporal overlap

Deer temporal behavioral responses to coyote encounter risk generally varied among demographic groups. Coyotes were generally nocturnal, whereas nursery groups were largely diurnal. Adult bucks and adult does traveling alone were largely nocturnal. Thus, the coefficient of temporal overlap between nursery groups and coyotes was significantly lower ($\widehat{\Delta}_4 = 0.52$ CI 0.47–0.57; Appendix S1: Figure S2) compared with both does traveling alone ($\widehat{\Delta}_4 = 0.80$ CI 0.78–0.82; Appendix S1: Figure S2) and bucks ($\widehat{\Delta}_4 = 0.74$ CI 0.71–0.77; Appendix S1: Figure S2). In the absence of fawns (i.e., not a nursery group), does had a significantly higher coefficient of temporal overlap with coyotes compared with bucks. Temporal overlap between adult bucks and coyotes decreased as relative coyote activity increased, but this linear pattern was not present for does or nursery groups (Figure 3). For all demographics, diel overlap with coyotes was lowest at sites with lowest relative coyote activity, although the amount of overlap was not significantly lower than sites with higher relative coyote activity in most cases (Figure 3). Wild pig diel activity patterns were similar to coyote diel activity patterns. Thus, coefficients of temporal overlap between nursery groups and wild pigs was significantly lower ($\widehat{\Delta}_4 = 0.64$ CI 0.57–0.70; Appendix S1: Figure S3) compared with both does traveling alone ($\widehat{\Delta}_4 = 0.86$ CI 0.83–0.89; Appendix S1: Figure S3) and bucks ($\widehat{\Delta}_4 = 0.81$ CI 0.77–0.85; Appendix S1: Figure S3).

Vigilance

Adult buck vigilance was best described by a model including previous-day count of coyote passes, daily count of coyote passes, daily count of wild pig passes, previous-day count of wild pig passes, time of day, and an interaction between the count of adult deer and understory vegetation density (Appendix S1: Table S8). Bucks were more vigilant as the previous-day coyote passes increased, but less vigilant as the daily count of coyote passes increased (Figure 4). Bucks were also more vigilant at sites with lower understory density and less vigilant at night (Appendix S1: Table S9).

Adult does' vigilance was best described by a model including average coyote passes per day, the count of adult deer, the count of juvenile deer, understory vegetation density, average wild pig passes per day, and time of day (Appendix S1: Table S10). Does were more vigilant at sites with greater average coyote passes per day (Figure 5), during the day, and at sites with lower understory vegetation density, but less vigilant as the number of adult deer present increased (Figure 5; Appendix S1: Table S11).

Vigilance of adult does in nursery groups was best described by a model including average coyote passes per day, previous-day count of coyote passes, daily count of coyote passes, previous-day count of pig passes, distance to paved road, distance to riparian area, understory vegetation density, and time of day (Appendix S1: Table S12). Does in nursery groups were less vigilant as the previous-day count of pig passes increased (Figure 5), at sites farther from riparian areas, and at night (Appendix S1: Table S13). In summary, deer response to long-term, short-term coyote encounter risk, or other factors hypothesized to modulate deer behaviors was variable among behaviors and deer demographic groups (Table 1; Appendix S1: Table S14).

DISCUSSION

We found that each deer demographic adjusted at least one behavior in response to some scale of coyote encounter risk, and deer spatial activity patterns and vigilance behavior were related to a diversity of predictors. Generally, our results suggest that deer are unable to eliminate the risk of encountering coyotes by modifying their spatial activity and thus employ other behavioral adaptations to reduce coyote encounter risk and ultimately predation risk. Deer must concurrently balance behavioral modification in response to both competitor and predator species (Gurevitch et al., 2000), and our results suggest demographics perceive and respond to risk differently. Nursery groups adjusted spatial activity patterns and vigilance in response to wild pig activity but not coyote activity, instead shifting diel activity patterns to be diurnal. In contrast, bucks and does traveling alone were nocturnal along with coyotes but adjusted vigilance behavior in response to coyote encounter risk. To our knowledge, our study is the first attempt to

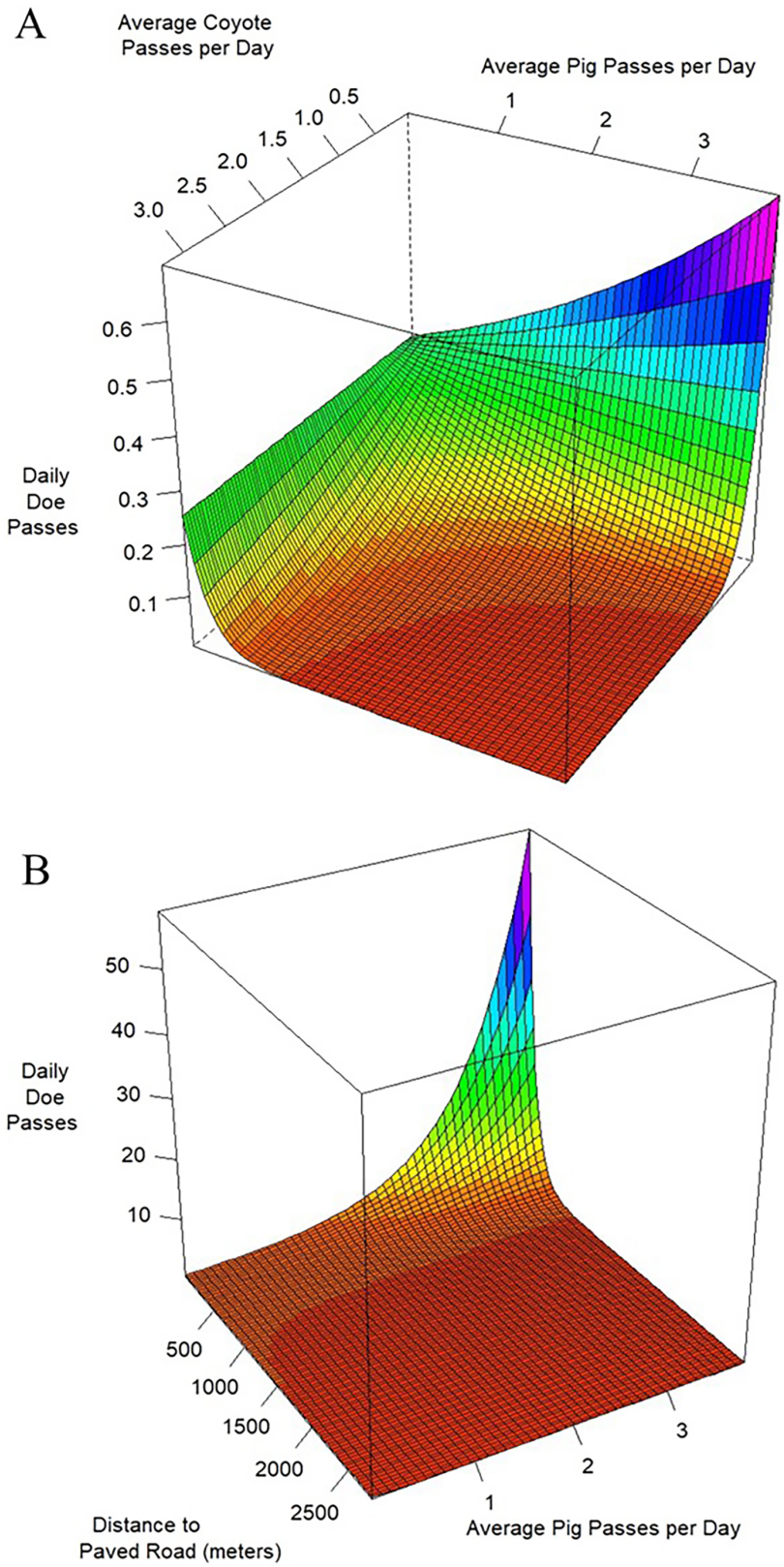

FIGURE 2 Interactive plots showing (A) the effects of average coyote passes per day and average wild pig passes per day and (B) the effects of distance to paved road and average wild pig passes per day on adult doe spatial activity. Doe spatial activity was lower at sites where the long-term risk of encountering both coyotes and pigs was greatest. Doe spatial activity was greater at sites closer to paved roads where the long-term risk of encountering pigs was greatest.

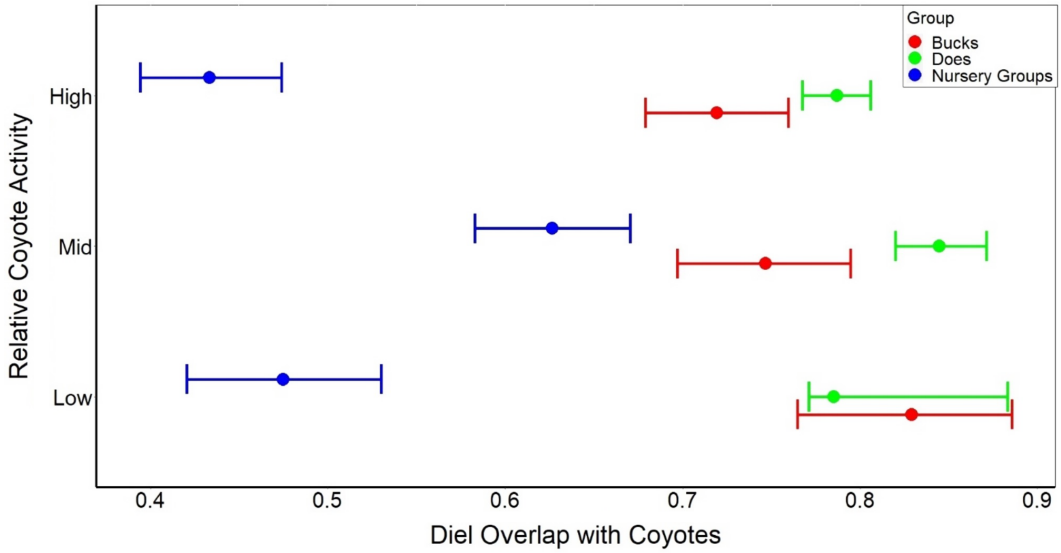

FIGURE 3 Temporal overlap between coyotes and adult bucks (red), adult does (green), and nursery groups (blue), at sites with low, medium (mid), and high levels of relative coyote activity (mean and 95% CI).

simultaneously quantify three different measures of white-tailed deer behavioral responses to long-term and short-term coyote encounter risk during the summer months when coyote predation is likely most impactful to deer populations through fawn predation (Chitwood, Lashley, Kilgo, Moorman, et al., 2015).

Coyotes were detected at most camera sites across our camera array during each study season (92.5%, 87.1%, and 90.3% of sites in 2019, 2020, and 2021, respectively), suggesting that deer were unlikely to find spatial refugia from coyotes (Esattore et al., 2022; Kilgo et al., 2019). Thus, the rather ubiquitous spatial presence of coyotes could be the reason no measure of long-term or short-term coyote encounter risk appeared in the best supported spatial activity model for nursery groups, and contrary to our predictions, long-term coyote encounter risk was positively related to doe spatial activity. We suggest coyotes may be able to perceive and subsequently seek areas of higher doe activity in order to increase their chances of encountering fawns (Chitwood, Lashley, Kilgo, Pollock, et al., 2015). Does with fawns may be attempting to avoid coyotes at finer spatial scales than we could detect using our camera trap data (Cusack et al., 2020). By tracking individual doe–fawn pairs, we found evidence that does did not adjust maternal behaviors in response to long-term coyote encounter risk (Muthersbaugh, 2023).

Predators generally demonstrate predictable diel activity patterns (Kronfeld-Schor & Dayan, 2003), which prey are capable of detecting and exploiting (Kohl et al., 2018). Our study indicates that in systems where predators occur across the landscape, prey may attempt to reduce predation risk by seeking temporal refugia (Higdon et al., 2019; Kautz et al., 2022). Nursery groups were largely diurnal, resulting in a lower amount of temporal overlap with coyotes compared with adult does and adult bucks, corroborating research in North Carolina and Michigan (Higdon et al., 2019; Kautz et al., 2022). Similarly, we tracked doe–fawn pairs and found that 68% of visits between doe–fawn pairs occurred after sunrise and before sunset (Muthersbaugh, 2023). Thus, it appears adult white-tailed does with fawns may exploit temporal refugia by limiting fawn visits (and resulting fawn activity) to times of day with lower risk of coyote encounter (Cusack et al., 2020; Dröge et al., 2017; Esattore et al., 2022; Higdon et al., 2019; Smith et al., 2019).

In partial support of the predation risk allocation hypothesis, we found that nursery groups were significantly more active during the day at sites with high long-term coyote encounter risk compared with medium levels of long-term coyote encounter risk. This result suggests baseline spatial risk affected how deer responded to risk on diel time scales, as coyote activity was largely nocturnal. However, we also found that nursery group diel activity patterns at sites with high long-term coyote encounter risk were not significantly different from sites of low long-term coyote encounter risk. In support of the predation risk allocation hypothesis, nursery groups were largely diurnal at high levels of long-term coyote encounter risk and possibly less predictable, low levels of long-term encounter risk (Ferrari et al., 2008; Trussell et al., 2011). Compared to nursery groups, adult bucks are likely less susceptible to coyote predation during summer, but our results suggest they may still adjust their diel activity patterns to reduce the risk of encountering

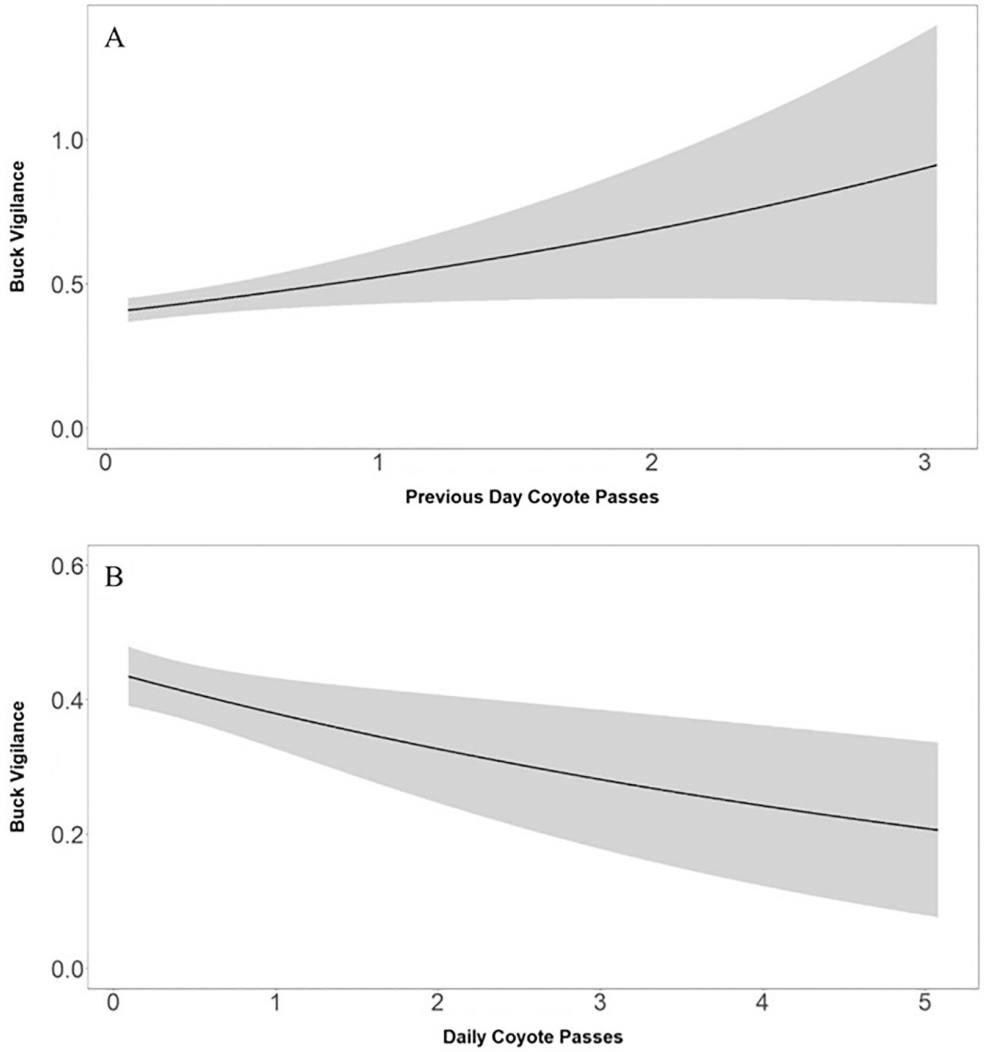

FIGURE 4 Fitted relationship between (A) vigilance in bucks and coyote passes the day prior and (B) vigilance in bucks and daily coyote passes (95% CIs shown). Bucks were increasingly vigilant at sites with greater coyote activity the day prior but were less vigilant at sites with greater coyote activity on the same day at a given site.

coyotes (Crawford et al., 2021). In further support of the predation risk allocation hypothesis, bucks had greater temporal overlap with coyotes at sites with low long-term coyote activity compared with sites with high long-term coyote activity.

Inconsistent with our prediction and the predation risk allocation hypothesis, does with fawns were not more vigilant in response to either long-term or short-term coyote encounter risk. In contrast and in support of the risky places hypothesis, does collectively were more vigilant in response to long-term coyote encounter risk, indicating that they could perceive areas of the landscape where the long-term risk of encountering coyotes was higher (Conner et al., 2016). Does collectively increased vigilance likely to increase early detection of coyotes and ultimately flee and avoid predation (Chitwood et al., 2014), or possibly inform their decision to display aggressive or defensive behavior if their fawn is nearby (Grovenburg et al., 2009; Smith, 1987). These results suggest does used vigilance behavior differently when they were with their fawns versus when they were foraging or traveling without their fawns. Indeed, many of the does photographed alone and classified as having no fawns likely had a living fawn(s), but the fawns were in hiding at the time of the photograph. Similar to Thomson's gazelle (*Eudorcas thomsoni*) that increase vigilance just prior to visiting their fawn in order to perceive immediate predation risk (Costelloe & Rubenstein, 2015), does may have been more vigilant just prior to visiting their fawn. Alternatively, it is possible does with fawns did not increase vigilance because they may have been prioritizing foraging and socialization to meet maternal demands incurred by their fawns (Caraco, 1981; Mangel & Clark, 1986). Parturition and lactation substantially increase energetic demands for white-tailed deer

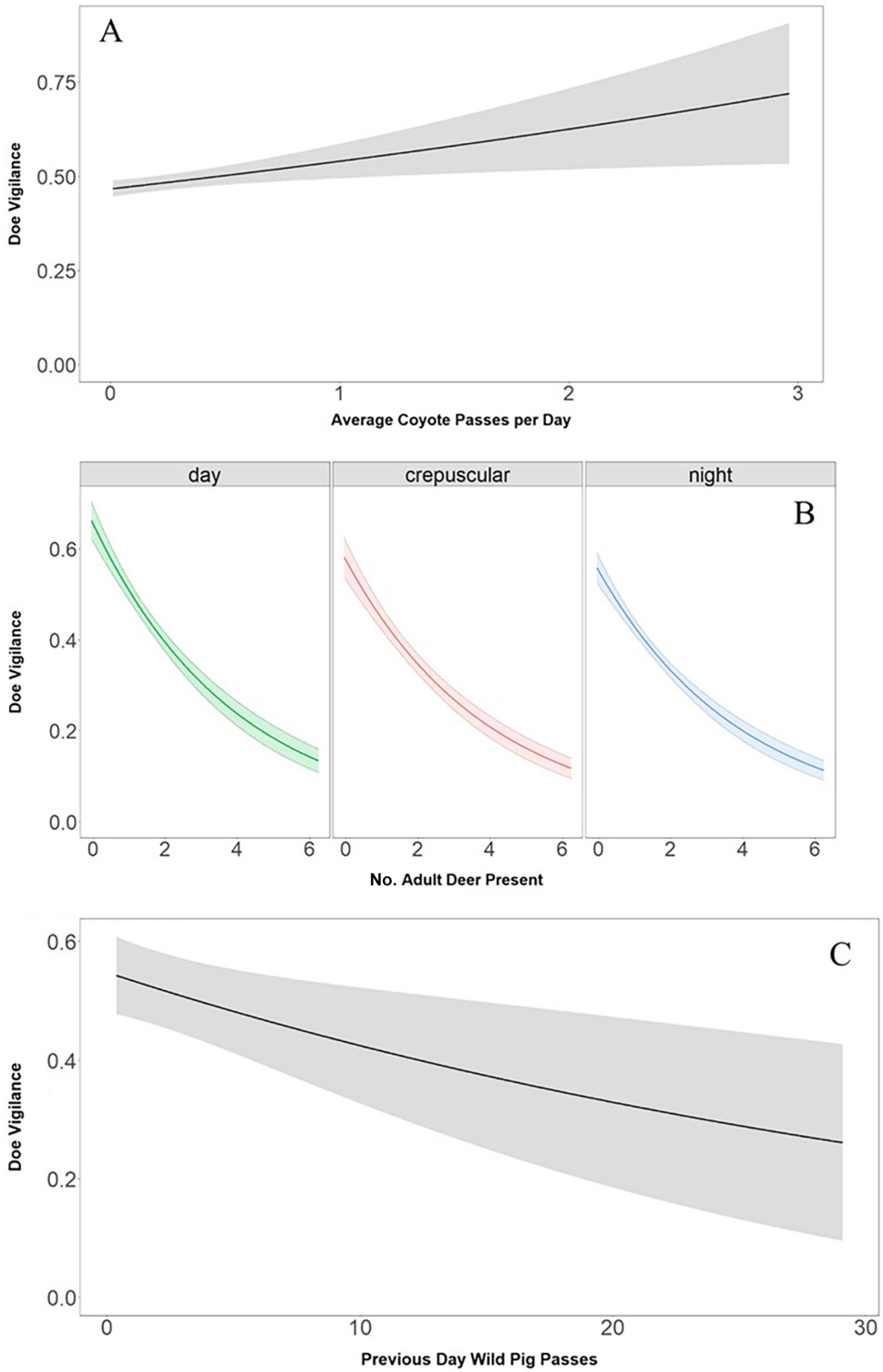

FIGURE 5 Fitted relationships between (A) vigilance in adult does and the average coyote passes per day, (B) vigilance in adult does and group size and time of day, and (C) vigilance in adult does in nursery groups and the number of wild pig passes the day prior (95% CIs shown). Does were more vigilant at sites with greater average coyote passes per day, least vigilant at night, and less vigilant as the number of adult deer present increased. Does in nursery groups were less vigilant as the wild pig activity the day prior increased.

does (Oftedal, 1985; Parker et al., 2009); thus, vigilance in does can be costly to both mother and offspring, as less time may be spent foraging, potentially impacting does' ability to meet maternal demands (Brown & Kotler, 2004). Another possible explanation for the differences in vigilance responses we observed between does and does in

nursery groups could be that vigilance is more useful for does traveling alone. In the absence of their offspring and upon detecting a coyote, does could respond with a variety of antipredator behaviors, but when does are with their offspring, early detection of a coyote might do little to increase the chance their fawn evades predation, thus rendering vigilance in these situations obsolete.

Vigilance was further modulated by environmental conditions, and contrary to our predictions, all demographic groups we analyzed were more vigilant during the day than at night. Furthermore, bucks and does were also more vigilant at sites with less understory vegetation density. There are several potential explanations for why we did not observe increased vigilance during the night in areas with more vegetative cover as we predicted. First, given deer vision is more effective during brighter hours (Newman et al., 2023), deer might be focusing vigilance during times and in places with less understory when and where they are best able to spot predators. Second, because coyotes are coursing predators and prey may be more vulnerable to predation in areas of reduced understory vegetation (Chitwood et al., 2017), predation risk may be greater in these open areas, which deer perceived and responded with increased vigilance. Third, depending on the species of vegetation present, understory cover could be associated with increased availability of suitable forage. Thus, many deer photographed with their head down could reflect more about foraging behavior than vigilance. Finally, decreased vigilance in areas of higher understory cover is consistent with the habitat complexity hypothesis, which states that encounter rates, and therefore, risk should decrease with increasing vegetation complexity (Janssen et al., 2007). We observed little evidence that other habitat features, namely paved roads, modulated deer behaviors. This suggests that paved roads could represent a weak human shield, and any potential shield effects could be nullified by roads also serving as corridors for coyote movement (Chamberlain et al., 2021; Hinton et al., 2015). Alternatively, human shield effects could exist on finer spatial scales than we measured, or perhaps deer adjust other behaviors (such as birth site selection) to utilize a human shield (Berger, 2007).

Globally, many ungulate species modulate vigilance behavior by grouping (i.e., the group size effect), and individual vigilance typically decreases with increasing group size (Berger & Cunningham, 1988; Lian et al., 2007; Matson et al., 2005; Rieucau & Martin, 2008). In partial support of our hypothesis, the group size effect was an important driver for vigilance behavior in does, but it did not influence vigilance in bucks. We did not directly test for a group size effect on does' vigilance in nursery groups because white-tailed does with fawns generally become more solitary and partition space during the fawning season (Schwede et al., 1993). However, as mentioned, many of the photographed does used in the analysis of doe vigilance likely had living fawns (the fawns were just likely out of the view of the camera). Thus, the group size effect may help does in our study system meet the high energetic demands of gestation and lactation. Like white-tailed deer research in North Carolina and Georgia by Lashley et al. (2014) and Gulsby et al. (2018), we found that does decreased vigilance as the number of adult deer present increased, possibly affording individuals increased foraging efficiency. Does in our study system may use grouping as an antipredator response, yet it remains unclear how grouping may impact resource partitioning, foraging efficiency, and ultimately individual fitness and fawn survival in southeastern white-tailed deer. Predation risk can impact fission–fusion dynamics (Kelley et al., 2011), and future studies should test how social dynamics between does differ between geographic areas with different levels of predator encounter risk and fawn predation rates.

Our results suggest that wild pigs impact deer behavior, but responses are complex and sometimes contrary to expectations (i.e., positive associations). At our study site, wild pig activity was more concentrated than that of coyotes (Saldo et al., 2023), and all demographic groups adjusted spatial activity patterns in response to wild pigs in broad support of our hypothesis that deer behaviors are impacted by multiple scales of invasive competitor species encounter risk. Crucially, our results suggest that wild pigs elicit changes in doe–fawn interactive behaviors, which could scale up to population responses if these behavioral modifications place fawns at higher or lower predator encounter risk. We found deer nursery group activity increased more at sites the day after elevated wild pig activity compared with when prior day pig activity was lower. Does with fawns typically segregate and have distinct home ranges while their fawns are young, and fawns generally have high site fidelity in the first weeks of life (Hirth, 1985). Although adult deer generally avoid wild pigs (Garabedian et al., 2023; McDonough et al., 2022; Saldo et al., 2023), doe–fawn pairs' spatial activity patterns may be less flexible, and fawns may remain hidden even if pigs have temporarily displaced their mother. Therefore, we suggest that does may have been unwilling to visit their hidden fawns if pigs were nearby, and then increased fawn visitation once pigs left the area, possibly to compensate for reduced maternal care and nursing the day prior. In contrast, perhaps does with fawns sought areas wild pigs had recently vacated because of potential refugia from coyote encounter risk. In some seasons (autumn), coyote site use was negatively related to wild pig activity at our study site (Saldo et al., 2023).

Finally, support we observed for the human shield hypothesis in that deer were positively associated with wild pig activity when near roads suggests there are external factors that are important to consider in understanding associations between wild pigs and deer. Regardless, our results add to the growing body of evidence that wild pigs impact deer behavior (Garabedian et al., 2023; McDonough et al., 2022; Saldo et al., 2023) and that there is a need for more research on the potential complex effects pigs have on deer–predator interactions.

Ungulate prey are widely known to adjust their antipredator behaviors in response to several biological and environmental factors, including predation risk (Liley & Creel, 2008; Wirsing et al., 2021). Because we found that predation risk often varies among demographics and seasons, we suggest future research on ungulate behaviors should focus on seasons when predators are most likely to impact populations. Ungulate behavioral responses to predation risk are highly context dependent, and our study shows that responses can differ widely among demographics and are modulated differentially by a suite of intrinsic, environmental, and anthropogenic factors. As we observed a diversity of behavioral responses, our study indicates that limiting research to just one potential antipredator behavior could fail to detect prey responses, leading to erroneous conclusions that prey are not responding to predation risk. In addition to investigating multiple prey behaviors and the hypothesized factors that can modulate those responses, our study shows that simultaneously investigating predation risk at different scales (i.e., risky times [short-term risk] and risky places hypothesis [long-term risk]) can maximize the inference gained from studies on prey behavioral responses.

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CONFLICT OF INTEREST STATEMENT

The authors declare no conflicts of interest.

DATA AVAILABILITY STATEMENT

Data are available from Figshare: https://figshare.com/articles/dataset/Deer_Behavioral_Responses_Data/23688831.

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SUPPORTING INFORMATION

Additional supporting information can be found online in the Supporting Information section at the end of this article.

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