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Original Article

White-tailed deer responses to acoustic predator cues are contingent upon past land use and contemporary fire regime

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Prey can assess the immediate risk of predation by detecting cues of predator presence, and it is expected that prey should invest in costly antipredator behaviors when a cue of predator presence is detected. Features of the habitat in which the cue is detected, such as vegetative concealment, serve as indirect cues of risk and can mediate how prey respond to direct cues of predator presence. Past agricultural land use and contemporary fire regimes are common disturbances that may modify prey perceptions of risk and could, therefore, alter prey responses to direct cues of predator presence. We examined whether the overlap of these two disturbances affected white-tailed deer (*Odocoileus virginianus*) responses to cues of predator presence by measuring deer vigilance and foraging bout duration in response to coyote (*Canis latrans*) vocalizations across 20 woodlands that varied in past land use and contemporary fire regime. Frequent fire regimes consistently increased deer visibility to predators across both land-use history contexts. Deer exhibited no behavioral response to the predator cue in habitats containing infrequent fire regimes or agricultural legacies. Deer responded to the cue in frequently burned woodlands without agricultural legacies through increased vigilance and time spent at a foraging location. These findings reveal that land-use legacies and contemporary fire regimes can mediate how prey respond to direct cues of risk. They also suggest that prey may balance the uncertainty associated with cues of predation risk with the urgency of responding to a potential attack by being vigilant and remaining in place.

Key words: **agriculture, antipredator behavior, disturbance, fire, predator cues, vigilance.**

INTRODUCTION

Predation is among the strongest selection pressures that determine animal behavior (Lima 1998); consequently, many prey species exhibit a suite of adaptive antipredator behaviors to mitigate predation risk (Lima and Dill 1990; Caro 2005). Since antipredator behaviors entail costs (e.g., time, energy, or missed opportunities; Lind and Cresswell 2005; Preisser et al. 2005; Verdolin 2006; Zanette et al. 2011; LaManna and Martin 2016), prey may use cues from the environment to determine when to engage in potentially costly antipredator behaviors. Prey may respond to indirect cues of predation risk (i.e., characteristics of the environment, such as habitat structure, that affect prey vulnerability) that inform the probability of predator encounter, detection, or escape from attack (Orrock et al. 2004; Parsons and Blumstein 2010; Gaynor et al. 2019). Prey should use direct cues of predator presence (i.e., visual, olfactory, or acoustic cues) to evaluate the likelihood of a predator attack and modulate investment in antipredator behavior accordingly (Kats and Dill 1998; Brown 1999; Brown et al. 1999; Hettena et al. 2014; Weissburg et al. 2014). The ability of prey to detect and aptly respond to direct predator cues is particularly important in the context of global change (Guiden et al. 2019). For example, failing to respond to a direct cue of predator presence can lead to reduced survival and extinction, as has been repeatedly observed in naive, insular prey populations when predators are introduced (Savidge 1987; Blackburn et al. 2004; Roehmer et al. 2009; Hanna and Cardillo 2014) as well as in the case of predator reintroductions (Olivier et al. 2001).

In dynamic landscapes where predation risk varies across space and time, the utilization of antipredator behavior can be variable across different habitat contexts (Brown et al. 1999; Orrock et al. 2004; Hernández and Laundré 2005; Kohl et al. 2018; Gaynor et al. 2019). Since prey use many different types of

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information to assess risk, including both direct and indirect cues, our understanding of the context specificity of antipredator behavior requires embracing how context affects different types of cues. Importantly, the use of different cues is itself context specific, as prey should respond to cues that provide the most reliable information about imminent risk, which may differ depending upon characteristics of the habitat (Stankowich and Blumstein 2005; Griesser and Nystrand 2009; Parsons and Blumstein 2010; Morrison 2011; Nersesian et al. 2012; McCormick and Löonnstedt 2013) or characteristics of the cue (Kats and Dill 1998; Orrock et al. 2004; Hettena et al. 2014; Weissburg et al. 2014; Scherer and Smee 2016; Parsons et al. 2017). The primacy of habitat context in modifying prey responses to direct cues of risk is important because global changes, such as habitat fragmentation, exotic plant species, and altered disturbance regimes, may lead to significant changes in the habitats where predator–prey interactions occur, potentially modifying how prey respond to direct cues (Guiden et al. 2019). Although recent studies demonstrate how disturbance may affect indirect cues (McCormick and Löonnstedt 2013; Cherry et al. 2017; Spitz et al. 2018; Abernathy et al. 2021; Bartel and Orrock 2021), it is not clear whether the same disturbances affect how prey use direct cues. This is an important gap in our knowledge of animal behavior because the overall response to risk is a function of both cue types. For example, antipredator responses may be exacerbated when indirect and direct cues work in synergy, or they may be abated when indirect and direct cues work in opposition (Grostal and Dicke 1999; Parsons and Blumstein 2010; Morrison 2011; Nersesian et al. 2012; Farnworth et al. 2020). It is, therefore, critical to understand how disturbance affects antipredator responses to both indirect and direct cues of risk.

Recent work demonstrates that the overlap of multiple disturbance types in a landscape, including the legacies of historic disturbances, can shape prey foraging decisions and antipredator behavior (Abernathy et al. 2021; Bartel and Orrock 2021); however, it is unclear if prey responses to direct cues depend upon the disturbance regimes of the habitat in which the cue is detected. Past agricultural land use and contemporary fire are two common forms of disturbance that modify terrestrial habitat structure relevant to indirect cues of risk for large-mammal prey species. Fire can cause significant and rapid changes in large-mammal habitat structure by removing woody, midstory cover (Eisenberg et al. 2015; Cherry et al. 2017; Jorge et al. 2020; Abernathy et al. 2021; Bartel and Orrock 2021; Doherty et al. 2022). Vegetation cover impacts both the ability for predators to detect prey and for prey to detect predators. Ambush predators rely on dense vegetation cover to impede detection by prey (Hopcraft et al. 2005; Schmitz 2008; Abernathy et al. 2021), but cursorial predators may be better able to detect and chase prey in habitats with low vegetation cover (Creel et al. 2005; Schmitz 2008; Cherry et al. 2017). Vegetation cover can, therefore, be an important indirect cue of risk for a variety of prey species (Myserud and Østbye 1999; Orrock et al. 2004; Creel et al. 2005, 2014; Morrison 2011; Nersesian et al. 2012; Cherry et al. 2017; Smith et al. 2019). As a result, the effects of fire on prey antipredator behavior likely depend on predator hunting mode and prey escape strategies (Schmitz 2008; Thaker et al. 2011; Guiden et al. 2019; Doherty et al. 2022). For example, frequent fires that reduce vegetation cover are predicted to increase perceived predation risk for large mammals that are prey to visual, cursorial predators (Cherry et al. 2017; Bartel and Orrock 2021; Doherty et al. 2022). In contrast, frequent fires may decrease the risk of predation by ambush predators (Abernathy et al. 2021; Doherty et al. 2022).

Fire can occur in terrestrial habitats containing legacies of past disturbances, such as agricultural land use, which could alter the effects of fire on vegetation cover and hence, on animal behavior. Legacies of past agricultural land use are pervasive: since 1700, agriculture has impacted 42–68% of terrestrial land, and degraded lands previously used for agriculture increased by $10–44 \times 10^6$ km^2 (Hurtt et al. 2006). Agricultural legacies can have lasting effects on plant communities that persist for decades and sometimes centuries (Foster 1993; Flinn and Vellend 2005; Kopecký and Vojta 2009; Mattingly et al. 2015; Culbert et al. 2017), and agricultural legacies can influence animal responses to contemporary disturbances, presumably by altering habitat structure (Hahn and Orrock 2015a, 2015b; Stuhler and Orrock 2016; Bartel and Orrock 2020).

Given the potential for agricultural legacies and contemporary fire regime to drastically alter the context in which large-mammal predator–prey interactions occur, it is likely that prey will exhibit predictably different responses to direct cues of predation risk across habitats with different land-use histories and fire regimes. For example, recent work in longleaf pine woodlands has found that white-tailed deer utilize different forms of antipredator behavior in post-agricultural woodlands than in woodlands without agricultural histories when responding to changes in perceived predation risk caused by fire (Bartel and Orrock 2021). Midstory vegetation cover can provide white-tailed deer concealment from cursorial predators like coyotes (Cherry et al. 2017) and is, therefore, an indirect cue of risk. Despite the consistent suppressive effects of frequent fires on vegetation cover, deer mitigated the increased risk from frequent fires through heightened vigilance in post-agricultural woodlands and shifts in activity timing (i.e., temporal predator avoidance) in nonagricultural woodlands (Bartel and Orrock 2021). Temporal avoidance is a proactive antipredator behavior (i.e., one that may be used to avoid an encounter altogether), and vigilance is a reactive behavior to detect a predator once an encounter is likely underway (Broekhuis et al. 2013; Creel et al. 2014). Since deer only exhibited a proactive strategy to avoid an encounter with a predator in post-agricultural woodlands, these findings indicate that deer perceive post-agricultural woodlands as generally less risky spaces for encountering a predator. Despite evidence that agricultural legacies and contemporary fire regime have significant effects on deer perceptions of risk, we are aware of no studies that have investigated if the interface of these past and present disturbances affects how deer respond to direct cues of predator activity (but see Abernathy et al. 2021 for a study on how the interface of contemporary fire and contemporary flooding affect deer foraging strategies). While this knowledge gap likely exists, at least in part, because of the difficulty in replicating large-scale experiments in habitats with known land-use histories and fire regimes and no other environmental differences (Flinn and Vellend 2005), it nonetheless impedes our ability to predict how global shifts in disturbance frequency might alter predator–prey dynamics that determine species coexistence or extinction (Guiden et al. 2019).

We experimentally tested whether agricultural legacies and contemporary fire regime affect deer perceptions of risk by evaluating deer antipredator behavior in response to direct cues of predators (vocalizations of coyotes, *Canis latrans*) across longleaf pine woodlands varying in both land-use history and fire regime (Figure 1). In the longleaf pine ecosystem, coyote activity and predation

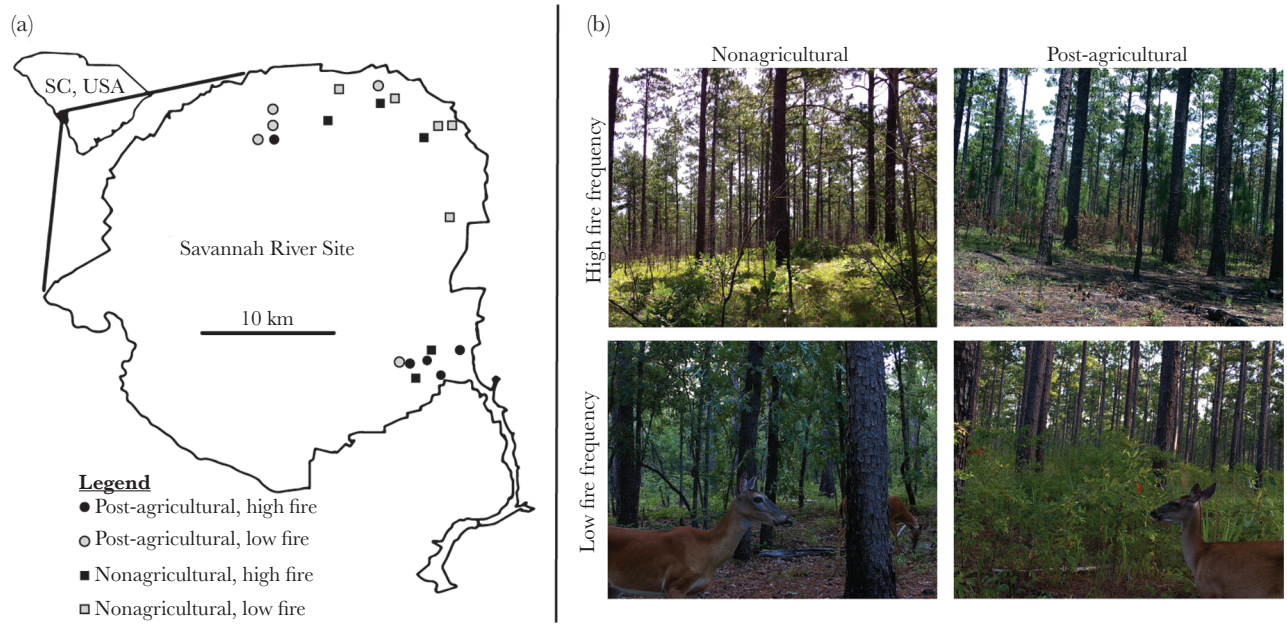

Figure 1
We conducted our experiment at 20 longleaf pine woodlands within the Savannah River Site near Aiken, SC, USA. Woodlands were classified by past land use and contemporary fire frequency, yielding five replicate woodlands for each disturbance category. The images above were captured within our sites during the experimental period and are representative of the variation in habitat structure captured in this study. The two photos on the bottom row from low-fire woodlands depict vigilant white-tailed deer in the foreground. Further in the background of the low-fire, nonagricultural woodland photo, a second white-tailed deer is foraging.

affect deer behavior and population dynamics (Kilgo et al. 2012; Cherry et al. 2015, 2016, 2017; Chitwood et al. 2015; Gulsby et al. 2017). Historically, longleaf pine woodlands were maintained by surface fires ignited by lightning and humans that occurred at an interval of every 1–6 years (Frost 2006; Oswalt et al. 2012); however, contemporary fire suppression is now widespread in these woodlands (Frost 2006). Contemporary fires in longleaf pine woodlands are typically implemented through prescribed burning (Kilgo and Blake 2005; Frost 2006; Oswalt et al. 2012). Frequent fires reduce vegetative concealment for deer from coyotes in longleaf pine woodlands (Cherry et al. 2017; Bartel and Orrock 2021). Nonagricultural woodlands often have a mixture of hardwood and pine trees, while post-agricultural woodlands are dominated by pine (Brudvig et al. 2013). Habitats characterized by hardwoods are preferred denning sites for coyotes (Hickman et al. 2015) with greater coyote densities in the southeastern United States (Jorge et al. 2020). As a result, deer may perceive a higher likelihood of a coyote encounter or attack in nonagricultural woodlands, and deer may be more vulnerable to being detected by coyotes in frequently burned woodlands. We, therefore, hypothesized that the overlap of past land use and contemporary fire frequency shapes deer perceptions of predation risk by coyotes. To evaluate this hypothesis, we deployed motion-activated cameras to measure how deer activity, vigilance, and foraging bout duration responded to acoustic cues of coyote presence under different disturbance contexts. We predicted that vegetation cover would be lower in frequently burned woodlands than in nonagricultural woodlands. We predicted that deer would only reduce activity and increase vigilance in response to coyote vocalizations in frequently burned, nonagricultural woodlands. We also predicted that the duration of foraging bouts would decrease in response to coyote vocalization in frequently burned, nonagricultural woodlands to reduce the likelihood of a coyote encounter.

METHODS

Study area

We conducted this experiment at the Savannah River Site (SRS; Aiken, SC), an ~80,000-ha National Environmental Research Park. SRS is located in the historic range of the longleaf pine ecosystem, much of which was converted to tillage agriculture between 1856 and 1950 (Frost 2006). Agricultural lands in SRS were small and dispersed, which created heterogeneous landscapes containing a mixture of patches of tilled farmland and intact forests (Kilgo and Blake 2005). When SRS was established in 1951, agricultural fields were abandoned and were planted in longleaf and loblolly pine by the US Forest Service, which has managed them since (Kilgo and Blake 2005). We selected 20 longleaf-pine woodland sites, spanning an 807-km^2 area, that differed in land-use history and fire frequency. We classified site land-use history based on aerial photography captured before land abandonment in 1951. We classified sites that were forested at the time as "nonagricultural woodlands" and sites that were farmland as "post-agricultural woodlands." We used annual fire records to determine the number of fires at each site since 1991. Sites were classified as high (five or more burns) or low (less than five burns) fire frequency. This classification scheme was used to characterize these sites based on plant-community characteristics (Brudvig et al. 2014) and has been used in past studies investigating the effects of fire frequency on deer behavior (Bartel and Orrock 2021). This site classification by land-use history and

fire frequency resulted in four distinct habitat types (five site replicates of each) equally distributed across the study area (Figure 1).

Playback experiment

At each of our 20 sites, we deployed an infrared motion-activated camera trap (Bushnell 16MP Trophy Cam HD; Bushnell Corporation, Overland Park, KS) for the same 12-day period in July 2019. This is within the range of typical study durations for field-based, playback experiments at a single site (Pusenius and Ostfeld 2000; Schmidt 2006; Smith et al. 2017; Suraci et al. 2017, 2019). During this 12-day period, each site was exposed to three playback treatments, which were each deployed for 4 days: coyote calls (predator cue), pied butcherbird song (control sound), and silence. The pied butcherbird has been used as a control sound in past work examining ungulate responses to coyote cues because its low frequency is similar to that of a coyote call (Hettena et al. 2014). Since the pied butcherbird is native to Australia, it also represents a novel stimulus, allowing us to disentangle deer responses to predator cues from deer responses to novel stimuli. We created separate mp3 files for each treatment by obtaining 16-bit, 44 kHz vocalizations from commercial websites. The coyote vocalization was a lone howl lasting 6 s, and the pied butcherbird song lasted 7 s. Each mp3 file played the vocalization once every 5 min. A single mp3 file was uploaded to a battery-powered mp3 player (AGPTEK, Brooklyn, NY, USA) and set on continuous repeat while connected to an Eco Extreme waterproof portable speaker (ECOXGEAR, Poway, CA, USA).

Each vocalization treatment was deployed at a site for four 24-h periods. The order of treatment deployment was random and stratified across the 12 days such that every treatment was deployed once within a randomized 3-day period. For the coyote and control vocalization treatments, one portable speaker was attached to a tree 20 m away from the camera at the site. The speakers were calibrated to play a vocalization at 47 dB SPL using a digital sound level meter (BAFX, Muskego, WI, USA). Batteries in the mp3 players were replaced daily to preclude unexpected treatment cessation during deployment. To standardize forage quality and quantity at camera traps, we baited each trap with 18 L of whole corn that was checked daily and replenished as needed. Camera traps were not baited prior to the experimental period. Camera traps were set to take photos at 1-s intervals whenever motion was detected, enabling us to capture fine-scale individual behavior. To estimate the ability of predators to see deer (henceforth, "deer visibility") at each site, we measured vertical vegetation cover near each camera-trap station. Measurements were taken by a single observer using a density board that estimated percent visibility across 0.3 × 0.3 m quadrats (Griffith and Youtie 1988; Nudds 2018). The density board was positioned 15 m from the observer standing at the camera-trap station, and the observer took one measurement in each cardinal direction from the station.

All photos were subsequently sorted and analyzed by a single observer who was blind to the playback treatment and disturbance classification associated with each photo or site. For every photo capturing deer activity, the observer recorded the sex of the individual, whether or not it was in a group, group size, the date and time, and if the individual was foraging or vigilant as a binomial variable. In cases where multiple individuals were captured in one photo, the behavior of each individual was scored, and each individual was analyzed as an independent observation. If the individual's head was down in a feeding posture, then the photo was classified as foraging (1), and if the individual's head was up in a non-feeding posture, then the photo was classified as vigilant (0; Lashley et al. 2014; Cherry et al. 2017). Following standard procedure for characterizing independent detections of large mammals (Kelly 2003; Kelly and Holub 2008; Wang et al. 2015; O'Connor and Rittenhouse 2017), independent foraging bouts were characterized as a sequence of same-sex deer photos captured within 30 min of each other (i.e., photos taken within < 30 min of each other were all considered belonging to the same independent bout). For each foraging bout, we calculated the total number of vigilant and foraging photos of an individual deer as well as the bout duration based on the timestamp of the first and last photo. We did not record behavioral data on a deer detection in the rare case in which an individual was only captured in one photo and was clearly passing by the camera and bait. The minimum duration of an independent foraging bout in our data was 8 seconds, composed of three photos (two vigilant photos and one foraging photo).

Data analysis

To test how land-use history and fire frequency affect deer visibility, we employed a linear model with land-use history, fire frequency, and the interaction of land-use history and fire as fixed effects and the proportion of density-board visibility as a response variable. To test how land-use history, fire frequency, and predator vocalizations affect the frequency of deer activity, we used a linear mixed effects model (LMM) with land-use history, fire frequency, playback treatment, and the interaction of land-use, fire, and playback treatment as fixed effects; site as a random intercept; and the log-transformed total number of foraging bouts at each site for each playback treatment as a response variable (Supplementary Material 1A). To test how land-use history, fire frequency, and predator vocalizations affect deer vigilance during foraging bouts, we used a generalized linear mixed effects model with a binomial response distribution with land-use history, fire frequency, playback treatment, and the interaction of land-use history, fire frequency, and playback treatment as fixed effects; site as a random intercept; individual bout ID as a random intercept; and proportion of vigilant photos for each individual bout (i.e., number of vigilant photos vs. number of total photos in each bout) as a response variable (Supplementary Material 1B). The proportion of vigilant photos was modeled by providing the number of vigilant photos weighted by a total number of photos for each bout. The site was included as a random intercept to account for the nested experimental design (i.e., playback treatments were deployed within each site, and each site had a land-use history and fire frequency treatment). To test how land-use history, fire frequency, and predator vocalizations affect bout duration, we used an LMM with land-use history, fire frequency, playback treatment, the interaction of land-use history and fire, the interaction of land-use history and playback treatment, the interaction of fire and playback treatment, and the interaction of land-use history, fire frequency, and playback treatment as fixed effects; site as a random intercept; and bout duration (log-transformed minutes) as a response variable (Supplementary Material 1C). In all of our models, we used the interactions of land-use history, fire frequency, and playback treatment as a fixed effect in order to evaluate if the effect of the playback treatment on deer behavior depended on land-use history and fire frequency. We interpreted any predictor as having an effect if the $P < 0.05$.

RESULTS

We collected 4471 photos of white-tailed deer activity across 17 of the 20 sites in our study. We did not detect deer at 3 of our 20 sites: two nonagricultural woodlands with low fire frequencies and one post-agricultural woodland with low fire frequency. Out of the 155 total foraging bouts captured, 88 were from individuals foraging alone (46 individual females, 41 individual males, and 1 individual juvenile), and 67 were from individuals foraging with one or two individuals (38 individual females, 23 individual males, and 6 individual juveniles). We captured 84 individual females, 64 individual males, and 7 juveniles of indistinguishable sex.

There was a significant effect of fire frequency on deer visibility ($\beta = -23.83$, SE = 10.80, $F_{1,14} = 4.87$, $P = 0.045$) such that deer were more visible in frequently burned sites regardless of land-use history (Figure 2). There was not a significant effect of land-use history ($\beta = -12.37$, SE = 10.80, $F_{1,14} = 1.31$, $P = 0.271$) or the interaction between land-use history and fire frequency on deer visibility ($\beta = 11.80$, SE = 15.27, $F_{1,14} = 0.60$, $P = 0.453$). The frequency of deer activity was not significantly affected by land-use history, fire frequency, or playback treatment (Table 1). Deer vigilance was significantly affected by playback treatment (Table 1; $\beta = 0.16$, SE = 0.17, $P = 0.016$) and the interaction of land-use history and fire frequency (Table 1; $\beta = 1.21$, SE = 0.52, $P = 0.021$). The coyote vocalization treatment led to significantly greater levels of deer vigilance in frequently burned, nonagricultural woodlands (Figure 3A) but did not affect vigilance in post-agricultural woodlands or infrequently burned woodlands. The probability of deer vigilance was 1.68 times greater under the coyote vocalization treatment than under the silent treatment and 1.58 times greater than under the control treatment. Bout duration was significantly affected by land-use history (Table 1; $\beta = -2.15$, SE = 0.96, $P = 0.021$), the interaction of land-use history and playback treatment (Table 1; $\beta = 2.45$, SE = 0.97, $P = 0.013$) and the interactions of land-use history, fire frequency, and playback treatment (Table 1; $\beta = -2.09$, SE = 1.29, $P = 0.011$). The coyote vocalization treatment led to significantly longer bout durations in frequently burned, nonagricultural woodlands (Figure 3B) but did not affect bout durations in post-agricultural woodlands or infrequently burned woodlands.

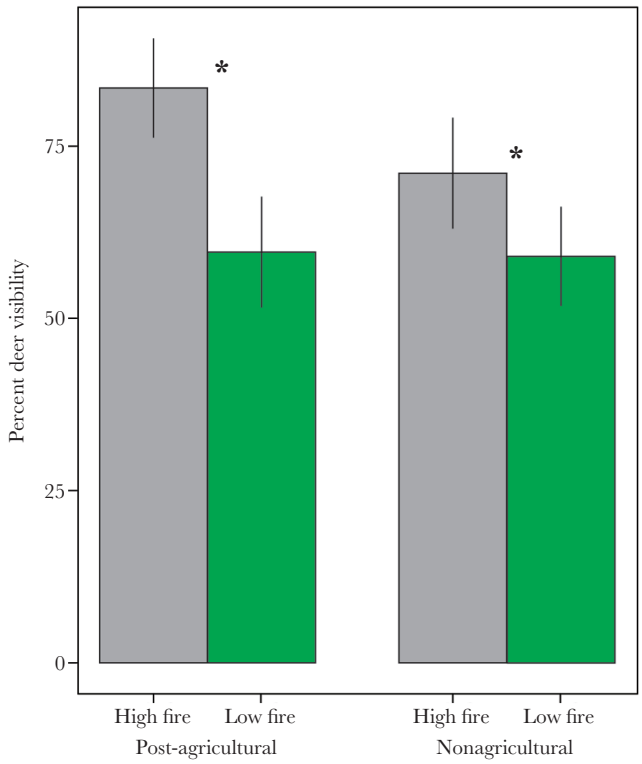

Figure 2
We estimated the visibility of deer to predators by measuring vertical vegetation cover in longleaf pine woodlands with different land-use histories that also varied in contemporary fire frequency. Post-agricultural woodlands had legacies of past agriculture, and nonagricultural woodlands had no history of agriculture. Bars represent estimated marginal means for each disturbance group, error bars represent one standard error, and asterisks denote significant differences between fire frequencies at an α level of 0.05.

DISCUSSION

Understanding how habitat context affects the antipredator behavior of ungulates is important in contemporary landscapes where animals experience multiple disturbances that modify the risk of predation. Our large-scale study reveals that habitat context is an essential component of how ungulates use cues of predation risk to modify their antipredator behavior. Moreover, we find that this context results from the interplay of contemporary disturbance (prescribed fire regime) and disturbances that occurred over 60 years ago (past agricultural land use). Deer responded to direct cues of predator presence (playbacks of coyote calls) by increasing vigilance and bout duration in frequently burned woodlands without a history of agricultural land use. In woodlands with a history of agricultural use, or infrequently burned woodlands without an agricultural history, there was no change in antipredator behavior in response to direct predator cues. These findings suggest that individual responses to direct cues of predation risk may be contingent upon indirect cues of risk produced by past and present disturbance regimes.

Predators can have nonconsumptive effects on prey fitness when predator presence elicits behavioral or physiological responses in prey (Peckarsky et al. 2008; Zanette et al. 2011; Sheriff, Peacor, et al. 2020). By reducing vegetation cover, frequent fires increase deer visibility to cursorial predators, and our results confirm emerging evidence that fire regime has substantial effects on deer perceptions of risk (Cherry et al. 2017; Bartel and Orrock 2021) and, more broadly, ungulate antipredator behavior (Spitz et al. 2018). Characteristics of the habitat that shape indirect cues of risk can affect prey responses to direct cues of risk (Grostal and Dicke 1999; Parsons and Blumstein 2010; Morrison 2011, 2011; Nersesian et al. 2012; Farnworth et al. 2020). Our results reflect past studies showing that a variety of prey species, including brushtail possums (*Trichosurus vulpecula*), Cherrie's Tanagers (*Ramphocelus costaricensis*), and Chinook salmon (*Oncorhynchus tshawytscha*), exhibit the strongest antipredator response to direct cues in contexts containing indirect cues of risk (Morrison 2011; Nersesian et al. 2012; Sabal et al. 2021). Importantly, despite the consistent effects of fire on deer visibility across woodlands with different land-use histories (Figure 2), deer only responded to direct cues of risk (coyote vocalizations) when a specific indirect cue was available (reduced vegetation cover) through increased vigilance and bout duration in woodlands without agricultural legacies (Figure 3). These findings reveal that legacies of disturbances that occurred over 60 years ago can have

Table 1

Regression coefficients and their 95% confidence intervals, test statistics, and *P*-values for the fixed effects in the LMMs and binomial GLM

LMMs

	Deer activity						
	β	SE	LCL	UCL	*F*	*P*	
Intercept	1.31	0.43	0.54	2.08	9.28	0.007	*
Land-use history	−0.76	0.61	−1.84	0.33	1.55	0.229	
Fire frequency	−0.36	0.65	−1.52	0.79	0.32	0.579	
Playback treatment	0.01	0.30	−0.53	0.55	1.16	0.328	
Land-use × fire	0.50	0.95	−1.20	2.21	0.28	0.604	
Land-use × playback	−0.07	0.43	−0.83	0.69	3.27	0.054	·
Fire × playback	−0.06	0.46	−8.70	0.75	1.12	0.342	
Land-use × fire × playback	0.39	0.68	−0.80	1.58	0.96	0.397	
	Bout duration						
	β	SE	LCL	UCL	*F*	*P*	
Intercept	5.75	0.58	4.72	6.81	95.05	<0.001	*
Land-use history	−2.15	0.96	−3.89	−0.47	4.92	0.037	*
Fire frequency	−0.62	0.92	−2.24	0.99	0.44	0.518	
Playback treatment	−0.43	0.41	−1.24	0.35	0.84	0.433	
Land-use × fire	1.64	1.51	−1.00	4.36	1.15	0.296	
Land-use × playback	2.45	0.97	0.61	4.30	4.50	0.013	*
Fire × playback	0.75	0.57	−0.33	1.87	2.39	0.095	·
Land-use × fire × playback	−2.09	1.29	−4.54	0.39	4.64	0.011	*

Binomial GLM

	Vigilance						
	β	SE	LCL	UCL	χ^2	*P*	
Intercept	0.62	0.11	0.40	0.84	32.74	<0.001	*
Land-use history	−0.61	0.43	−1.43	0.22	2.03	0.154	
Fire frequency	−0.03	0.18	−0.38	0.32	0.03	0.872	
Playback treatment	0.16	0.17	−0.18	0.49	8.29	0.016	*
Land-use × fire	1.21	0.52	0.27	2.22	5.30	0.021	*
Land-use × playback	1.54	0.65	0.31	2.78	5.63	0.060	·
Fire × playback	−0.09	0.26	−0.61	0.43	5.56	0.062	·
Land-use × fire × playback	−1.41	0.75	−2.89	0.04	4.06	0.132	

For all models, nonagricultural was the references category for land-use history, low frequency was the reference category for fire frequency, and the coyote cue was the reference category for playback treatment.

significant impacts on contemporary prey perceptions of immediate risk.

Our results demonstrate that deer may be most fearful of encountering a coyote in nonagricultural woodlands. Since past studies in the southeastern United States suggest that coyotes may prefer the mixed-canopy habitat structure found in nonagricultural woodlands (Hickman et al. 2015; Jorge et al. 2020), it is possible that differences in long-term coyote activity among woodlands of different land-use histories shaped the differences in deer antipredator behavior among these woodlands. Past work by Moll et al. (2020) evaluated mouse (*Peromyscus* spp.) antipredator responses to direct cues of risk (visual fox decoys) in forests that varied in long-term red fox (*Vulpes vulpes*) activity. This study found that mice only exhibited an antipredator response to the direct cue in forests with higher long-term levels of fox activity and did not exhibit a response to the cue in forests with lower long-term levels of fox activity (Moll et al. 2020). If long-term coyote activity is higher in nonagricultural woodlands than post-agricultural woodlands, then our results may reflect those of Moll et al. (2020): deer only responded to short-term pulses of risk in environments with high risk over long term (frequently burned nonagricultural woodlands). Our results impart a clear need for research that measures predator activity in landscapes containing agricultural legacies to elucidate how land-use history shapes long-term patterns in predation risk.

Since habitat structure can be an indirect cue of risk for deer (Altendorf et al. 2001; Cherry et al. 2017; Bartel and Orrock 2021), differences in habitat structure between post-agricultural and nonagricultural woodlands may also explain why deer did not respond to predator cues in frequently burned post-agricultural woodlands. While our measures of vertical vegetation cover 15 m from an observer did not indicate a difference in deer visibility between frequently burned post-agricultural woodlands versus nonagricultural woodlands, differences in habitat structure due to past land use may manifest at longer distances from the observer. Importantly, mature trees in post-agricultural woodlands were initially planted in distinct rows typical of pine plantations at the time of restoration (Kilgo and Blake 2005), whereas nonagricultural woodlands are composed of mature trees that are more randomly dispersed. It is possible that the distinct rows of mature trees in post-agricultural woodlands improve the ability of deer to escape an attack once initiated by increasing movement efficiency. Linear habitat features, such as roads, pipelines, and seismic lines, improve movement efficiency for large mammals (DeMars and Boutin 2018; Dickie et al. 2020). However, it is unclear if the linear alignment of mature trees in post-agricultural pine stands has similar effects on large-mammal movement efficiency. Our results indicate that deer perceive lower predation risk in frequently burned post-agricultural woodlands than nonagricultural woodlands, but future research is

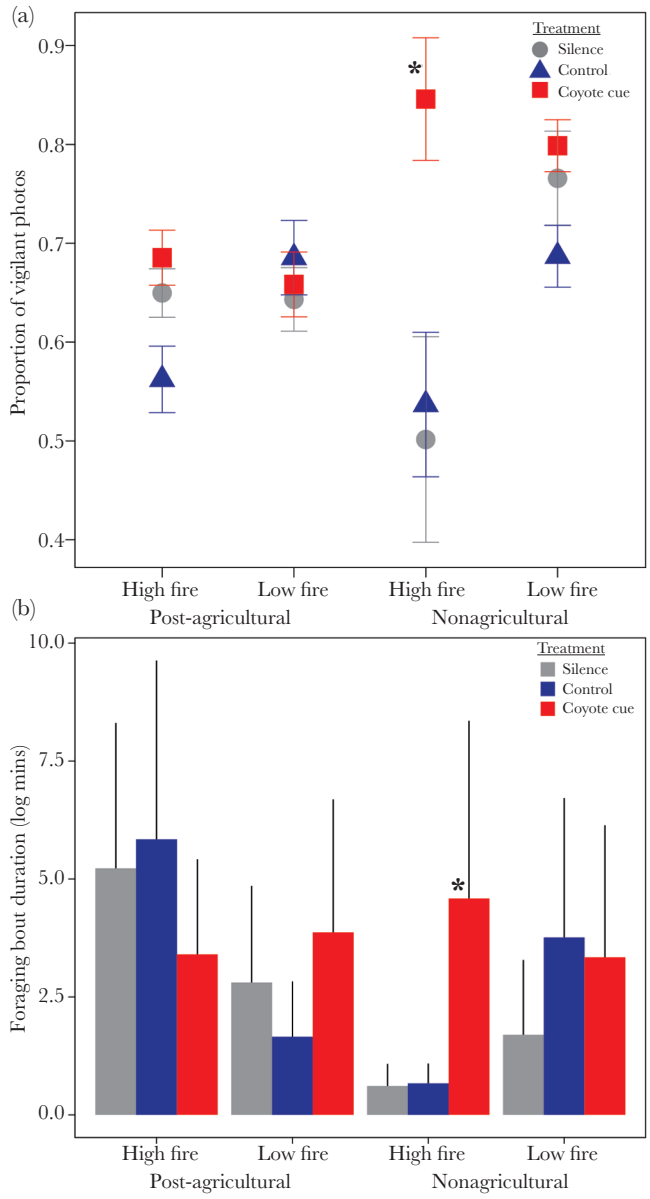

Figure 3
Using photos of deer foraging behavior captured with remote wildlife cameras, we measured deer vigilance (a; i.e., proportion of vigilant photos per bout) and duration of foraging bouts (b) in response to predator cue (coyote vocalization), control sound (pied butcherbird vocalization) and silence treatments that were deployed across longleaf pine woodlands with different land-use histories and also varied in contemporary fire frequency. Post-agricultural woodlands had legacies of past agriculture, and nonagricultural woodlands had no history of agriculture. Bars represent estimated marginal means for each disturbance and cue treatment group. Asterisks denote significant differences between the coyote cue and the other cue treatments within a disturbance group at an alpha level of 0.05.

needed to understand if the underlying mechanism is due to differences in coyote habitat use or movement efficiency among the two habitat contexts.

Importantly, our results revealed that direct cues of predation risk modify how prey budget their time on fine temporal scales, but only under certain disturbance contexts. The past work by Bartel and Orrock (2021) examining deer responses to an indirect cue of risk (reduced vegetation cover) created by fire found that this indirect cue modified how deer budgeted time over broader temporal scales in nonagricultural woodlands: deer exhibited nocturnal activity in frequently burned woodlands and crepuscular activity in infrequently burned woodlands. By evaluating how deer budget their time on a finer temporal scale (i.e., duration of foraging bout as opposed to diel timing of bout) in response to a cue of immediate predation risk, our results show that deer increase the time spent foraging in a location when there are cues of immediate risk in habitats that are generally perceived as risky (i.e., nonagricultural woodlands with frequent fires).

Increased bout duration may be a strategy that provides several important benefits to foraging prey. Since many prey species face a behavioral trade-off of allocating time to vigilance versus foraging, heightened vigilance can lead to reduced food intake if this is not mitigated by increased bout duration (Underwood 1982; Lima and Dill 1990; Illius and Fitzgibbon 1994; Fortin et al. 2004). When deer increase vigilance in response to cues of risk, they might attempt to mitigate lost foraging opportunities through increased bout duration. Since increased bout duration may also incur costs to the prey (e.g., missed opportunity costs), prey behavioral responses to direct cues of risk can carry costs both in foraging opportunities and time. Increased bout duration may also be an adaptive antipredator strategy when prey are in risky habitats and detect cues of predator presence (Curio 1993). When prey detect the cue of a predator that uses vision to locate prey, the prey may benefit from remaining stationary to reduce visual detectability, as opposed to fleeing (Curio 1993). Remaining stationary with increased vigilance may allow prey to collect more information, such as the predator's location, movement direction, and behavioral state, which is particularly relevant for launching an effective defense against a cursorial predator (Curio 1993; Yorzinski and Platt 2012; Sheriff, Orrock, et al. 2020). Moreover, features of the habitat in which the cue is detected may affect the potential to escape an attack and should, therefore, affect the prey's decision on if and when to flee from a cursorial predator like the coyote (Lingle and Pellis 2002; Stankowich and Coss 2007). Our study indicates that both agricultural legacies and contemporary fire regimes can affect this decision. Since white-tailed deer were less likely to flee and more likely to remain stationary (i.e., increased bout duration) in response to the cue of coyote presence in frequently burned nonagricultural woodlands, our results indicate that in this disturbance context, immediate flight may not be an effective antipredator strategy or that deer require more information before launching an effective flight response.

Since we detected neither an increase nor decrease in deer bout duration in response to cues of coyote activity in woodlands with agricultural legacies or nonagricultural woodlands with infrequent fire regimes, we found no evidence that deer were modifying their behavior to mitigate predation risk, providing further evidence that deer perceive these habitats as relatively safe. However, an alternative hypothesis is that post-agricultural woodlands are also areas where deer are at high risk of coyote attack, but deer fail to optimally launch an antipredator response (i.e., deer experience an evolutionary trap; Schlaepfer et al. 2002; Sih et al. 2011; Guiden et al. 2019; Smith et al. 2021). Agricultural legacies in woodlands are a relatively new disturbance from an evolutionary perspective and may create a novel habitat context for predator–prey interactions. Since novel habitat contexts may preclude prey from

making accurate risk assessments or using effective antipredator strategies (Guiden et al. 2019), it is possible that the probability of encountering and escaping a coyote in post-agricultural woodlands is much greater than what the behavior of white-tailed deer suggests. This possible alternative hypothesis underscores the critical need for future research that evaluates how agricultural legacies affect every stage of the predator–prey encounter sequence in order to predict if this globally pervasive disturbance may generate evolutionary traps (Schlaepfer et al. 2002; Sih et al. 2011) and determine predator–prey coexistence (Guiden et al. 2019).

CONCLUSIONS AND FUTURE DIRECTIONS

In this study, we found that prey respond to information about the risk of a predator encounter differently under different disturbance contexts, illustrating how disturbances that alter indirect cues of risk mediate how prey respond to direct cues of risk. When prey detect cues of escalating risk in high-risk habitats, they may balance the urgency and the uncertainty of the situation through vigilance and by remaining in place to acquire more information about the encounter to launch an appropriate defense, if necessary. Interestingly, our findings reflect recent work showing that deer herbivory in longleaf pine woodlands depends upon fire and land-use history, as well as predation risk (Cherry et al. 2016; Bartel and Orrock 2023). Notably, Bartel and Orrock (2023) only detected a negative effect of deer herbivory on plant species diversity in frequently burned, post-agricultural woodlands. Since our results suggest that frequently burned, nonagricultural woodlands are perceived as riskier foraging habitats by deer, it is possible that the effects of fire and land-use history on deer perceptions of risk may have cascading effects on understory plant communities in longleaf pine woodlands. These findings highlight the need for future research that evaluates how the overlap of multiple disturbances shapes the nature and strength of trait-mediated trophic cascades. Despite a growing body of knowledge of how agricultural legacies affect animal behavior and species interactions in longleaf pine woodlands (Hahn and Orrock 2015a, 2016; Stuhler and Orrock 2016; Bartel and Orrock 2020), there is still limited research in other ecosystems where agricultural land-use history is pervasive. Future research evaluating past land use and contemporary disturbance regime may resolve unexplained spatial variation in large-mammal behavior, predator–prey dynamics, and trophic cascades in human-modified landscapes.

SUPPLEMENTARY MATERIAL

Supplementary material can be found at http://www.beheco.oxfordjournals.org/

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AUTHOR CONTRIBUTIONS

Savannah Bartel (Conceptualization [Equal], Data curation [Lead], Formal analysis [Lead], Investigation [Lead], Methodology [Equal], Writing—original draft [Lead], Writing—review & editing [Equal]), John Kilgo (Conceptualization [Supporting], Investigation [Supporting], Methodology [Supporting], Writing—review & editing [Equal]), and John Orrock (Conceptualization [Supporting], Formal analysis [Supporting], Funding acquisition [Lead], Investigation [Supporting], Writing—original draft [Supporting], Writing—review & editing [Equal])

DATA AVAILABILITY

Analyses reported in this article can be reproduced using the data provided by Bartel et al. (2023).

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