



Original Article

Past agricultural land use affects multiple facets of ungulate antipredator behavior

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Antipredator behavior affects prey fitness, prey demography, and the strength of ecological interactions. Although predator-prey interactions increasingly occur in habitats that experience multiple forms of human-generated disturbance, it is unclear how different forms of disturbance might affect antipredator behavior. Fire is a contemporary disturbance that has dramatic effects on terrestrial habitats. Such habitats may have also experienced past disturbances, like agricultural land use, that leave lasting legacies on habitat structure (e.g., overstory and understory composition). It is unclear how these past and present disturbances affect the use of different antipredator behaviors, like temporal avoidance and vigilance. We examined whether variation in disturbance regimes generates differences in ungulate antipredator behavior by using cameras to measure white-tailed deer vigilance and activity time across 24 longleaf pine woodlands that vary in past land use and contemporary fire regime. Regardless of land-use history, woodlands with high fire frequencies had 4 times less vegetation cover than low-fire woodlands, generating riskier habitats for deer; however, deer responded to fire with different antipredator strategies depending on land-use history. In nonagricultural woodlands, fire affected deer activity time such that activity was nocturnal in low-fire woodlands and crepuscular in high-fire woodlands. In post-agricultural woodlands, fire affected vigilance and not activity time such that deer were more vigilant in high-fire woodlands than in low-fire woodlands. These results suggest that ungulate antipredator behavior may vary spatially depending on past land use and contemporary fire regime, and such disturbances may generate “landscapes of fear” that persist for decades after agricultural use.

Key words: agricultural legacy, antipredator behavior, diel activity patterns, disturbance, fire, longleaf pine, *Odocoileus virginianus*, vigilance.

INTRODUCTION

Behaviors that mitigate the risk of predation are ubiquitous (Lima and Dill 1990; Caro 2005; Preisser et al. 2005). Understanding variation in antipredator behavior is important because it can provide insight into the factors that shape prey fitness, the strength of intra- and interspecific interactions, as well as community-level processes, such as disease transmission and trophic cascades (reviewed in Pace et al. 1999; Schmitz et al. 2004; Peckarsky et al. 2008; Preisser and Bolnick 2008; Terborgh and Estes 2010; Estes et al. 2011). The characteristics of the habitat in which predator-prey interactions occur can play a fundamental role in shaping antipredator behavior (Guiden et al. 2019) by altering the likelihood of an encounter between predators and prey, the likelihood that prey detect predators before an attack is initiated, and the likelihood that prey can escape an attack once initiated (Lima and Dill 1990; Lima and Bednekoff 1999; Sheriff et al. 2020). Understanding how environmental variation shapes antipredator behavior may be particularly important

given that anthropogenic activities are leading to rapid changes in habitats throughout the globe (Haddad et al. 2015; IPBES 2018).

Disturbances, such as fire, forest harvest, and drought, are common in terrestrial habitats (Sousa 1984; Pickett and White 1985) and can lead to profound changes in habitat characteristics. Disturbances vary not only in form, but also in the possible duration of their effects (Dobson et al. 1997; Buma 2015). Human disturbances, in particular, can lead to rapid and persistent changes to habitats and the species they contain. For example, human conversion of natural habitats to agriculture, leading to degraded land after agricultural abandonment, is one of the biggest factors contributing to the current biodiversity crisis (Sisk et al. 1994; Pimm et al. 1995; Dobson et al. 1997; Dirzo and Raven 2003; Dudley and Alexander 2017). Degraded lands once used for agriculture have increased by 10–44 × 10⁶ km² since 1700 CE (Hurt et al. 2006); and agricultural legacies can persist in these lands for decades and sometimes centuries (Foster 1993; Flinn and Vellend 2005), reflected in lasting effects on the diversity and structure of plant communities (Foster 1993; Flinn and Vellend 2005; Kopecký and Vojta 2009; Mattingly et al. 2015; Culbert et al. 2017). In contrast, disturbances caused by fire (e.g., prescribed burns or wildfire) are

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often dramatic and rapid, which can lead to significant differences in habitats on shorter time scales that affect predation risk and behavior of a broad range of animal prey, including arthropods (Karpestam et al. 2012), birds (Morris and Conner 2016), rodents (Fordyce et al. 2016), and ungulates (Eisenberg et al. 2015; Cherry et al. 2017; Kymmel 2019; Jorge et al. 2020). Animals in many terrestrial areas may be subject to both of these disturbance types, and the legacies of past disturbances, such as agricultural land use, can determine the outcomes of contemporary disturbances, such as fire (Buma 2015). For example, evidence is accumulating that agricultural legacies can modify animal foraging responses to contemporary disturbances (Hahn and Orrock 2015a, 2015b; Stuhler and Orrock 2016; Bartel and Orrock 2020). Contemporary fire and past agricultural land use may often co-occur, and evidence suggests that they interact to affect both plant and animal communities (Brudvig et al. 2014; Veldman et al. 2014; Hahn and Orrock 2015c; Mattingly et al. 2015) as well as important trophic interactions (e.g., herbivory and granivory; Hahn & Orrock 2015b; Stuhler & Orrock 2016). However, despite the importance of understanding the various components of antipredator behavior and the widespread modification of habitats via past and present disturbance, large-scale studies examining the interface of these processes are rare.

Ungulates provide an optimal study system to evaluate how past and present disturbances modify antipredator behavior across large spatial scales. Ungulates are known to utilize multiple strategies to mitigate predation risk (Lima 1995; Bednekoff and Lima 1998; Hunter and Skinner 1998; Ripple and Beschta 2003; Creel and Winnie 2005; Winnie and Creel 2007; Valeix et al. 2009; Kohl et al. 2018; Prugh et al. 2019; Smith et al. 2019); they may exhibit different forms of antipredator behavior (e.g., vigilance or spatiotemporal avoidance); and they range over large areas where they may encounter a variety of human-modified habitats. Ungulates respond to contemporary disturbances that modify habitat structure, such as fire (Eby et al. 2014; Cherry et al. 2016, 2017; Kymmel 2019); however, it is unknown if past land use generates persistent changes in habitat structure that may influence ungulate antipredator behavior and if this effect is modified by fire regime. For example, although it has been shown that fire alters vegetation structure and leads to changes in the antipredator behavior of deer in longleaf pine ecosystems (Cherry et al. 2017), habitats with a history of agriculture also have significantly different vegetation structure (Duguy and Ramón 2007; Veldman et al. 2014; Hahn and Orrock 2015b; Stuhler and Orrock 2016; Bartel and Orrock 2020) and may thus be areas that give rise to unappreciated shifts in deer antipredator behavior. This current lacuna is likely due to the logistical challenges of conducting large-scale, replicated experiments in landscapes containing habitat patches with known land-use histories and variable fire regimes that have no other environmental differences (e.g., steep slopes or soil series due to nonrandom land-use decisions; Flinn & Vellend 2005).

To understand how past agricultural land use and contemporary fire regime affect multiple ungulate antipredator behaviors, we monitored white-tailed deer (*Odocoileus virginianus*) in a large-scale experiment in the longleaf pine ecosystem in the southeastern USA. In longleaf pine woodlands, coyotes (*Canis latrans*) are the primary predators of deer, and predation by coyotes affects deer behavior and population dynamics (Kilgo et al. 2010; Cherry et al. 2015; Cherry et al. 2016; Cherry et al. 2017; Gulsby et al. 2017). Agricultural legacies and fire regime have well-documented effects on habitat structure in longleaf pine woodlands. In our study site, nonagricultural woodlands have a mixture of hardwood and pine although post-agricultural woodlands are dominated by pine

(Brudvig et al. 2013). Post-agricultural woodlands have greater vine cover (Hahn and Orrock 2015c). Frequently burned post-agricultural woodlands have greater visible sky than frequently burned nonagricultural woodlands or infrequently burned woodlands of either land-use history (Stuhler and Orrock 2016). Across sites varying in both land-use history and fire regime, we deployed motion-activated cameras to measure deer vigilance and activity timing, evaluating two hypotheses: 1) deer are most vigilant in post-agricultural woodlands with frequent fires and least vigilant in nonagricultural woodlands with infrequent fires corresponding to the effects of land-use history and fire frequency on vegetation cover, and 2) deer show crepuscular activity in lower-risk sites (i.e., low-fire, nonagricultural woodlands) and nocturnal activity in higher-risk sites (i.e., high-fire, post-agricultural woodlands).

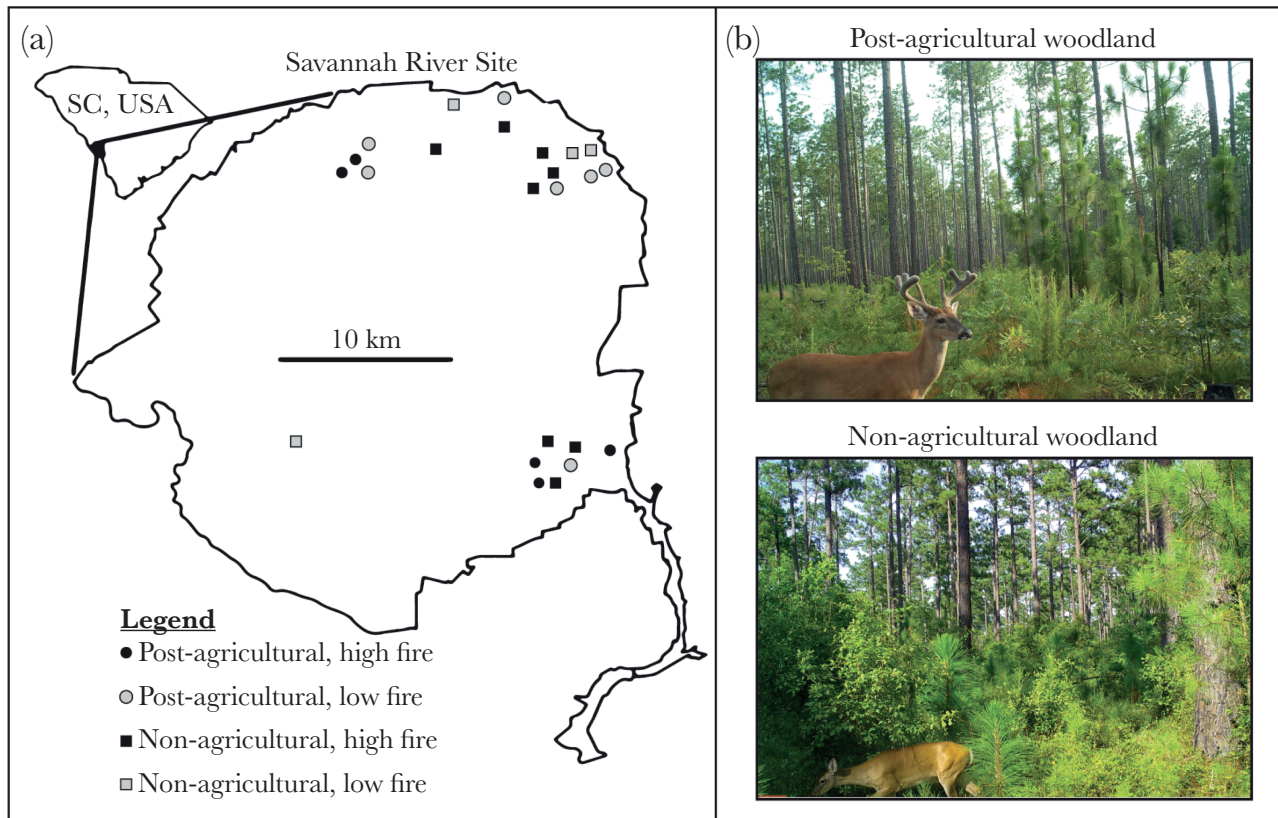
METHODS

Study area and design

This study was conducted at the Savannah River Site (SRS; Aiken, SC), an 80 125-ha National Environmental Research Park (NERP). SRS is within the historical range of the longleaf pine woodland ecosystem, much of which was converted to tillage agriculture from 1856 to 1950 (Frost 2006). Because these agricultural lands were small and dispersed, heterogeneous landscapes resulted containing patches of tilled farmland and intact forests (Kilgo and Blake 2005). Agricultural fields were abandoned in 1951 when SRS was established and have henceforth been under management as longleaf and loblolly pine plantations by the US Forest Service (Kilgo and Blake 2005). We selected 24 sites, spanning an 807-km² area, that differed in land-use history and fire frequency (Figure 1). Land-use history classification was based on aerial photography taken before land abandonment in 1951. Sites that were farmland in 1951 were classified as “post-agricultural woodlands,” and sites that were forested were classified as “nonagricultural woodlands.” Sites did not differ in other environmental variables that may be associated with nonrandom agricultural land use (e.g., topography or soil texture; see Supplementary Appendix S1 for details). The number of fires since 1991 was determined from annual fire records, and sites were characterized as low (five or less burns) or high (more than five burns) fire frequency, a metric previously used to classify these sites based on plant-community characteristics (Brudvig et al. 2014; see Supplementary Appendix S2 for site fire histories). Sites were not burned the year of the study. The resulting site classification by land-use history and fire frequency generated four distinct habitat types distributed across the study area.

Deer behavior and habitat structure

At each of our 24 sites, we deployed an unbaited, motion-activated camera trap (Bushnell 16MP Trophy Cam HD; Bushnell Corporation, Overland Park, KS) between June 8 and July 9 in 2018 for a total trapping period of 33 days. Camera traps were set to take photos at 1-second intervals whenever motion was detected, enabling us to capture individual foraging behavior at a fine scale. All photos were subsequently sorted and analyzed by a single observer, who was blind to site-level disturbance treatments, to control for possible variation in species, sex, and behavioral classifications. For every photo capturing deer activity during an independent foraging bout, the observer recorded the date and time, the sex of the individual, whether or not it was in a group, group size, and if the individual was foraging (1) or being vigilant (0) as a binomial variable. If the individual's head was up in a nonfeeding posture,

**Figure 1**

(a) We conducted our study in South Carolina, USA, at the Savannah River Site, an 80 000-ha area containing longleaf pine woodlands varying in agricultural legacies and fire frequencies. Circles and squares on the map indicate the locations of our 24 sites where camera traps were deployed to measure deer behavior. Sites were all located in flat uplands and were more than 250 m apart. (b) Agricultural legacies can affect habitat structure that is relevant for deer perceptions of risk. At Savannah River Site (SRS), post-agricultural woodlands are dominated by mature pine with depauperate understories, and nonagricultural woodlands contain mixed hardwood-pine canopies with denser understories.

then the photo was classified as vigilant, and if the individual's head was down in a feeding posture, then the photo was classified as foraging (1; Lashley et al. 2014; Cherry et al. 2017). Photos in which an individual's behavior did not clearly fall under one of these two categories (e.g., rapid movement across the camera) were not evaluated. We characterized independent foraging bouts as any sequence of deer photos of the same sex captured within 30 min at a site; a common threshold for characterizing independent detections of large mammals (Kelly 2003; Kelly and Holub 2008; Wang et al. 2015; O'Connor and Rittenhouse 2017).

To test the hypothesis that habitat characteristics relevant to perceived predation risk for deer varied with land-use history and fire frequency, we measured vertical vegetation cover at every site. Vertical vegetation cover was measured by a single observer using a density board that estimated the percentage of visibility across 1 x 1 foot quadrats (Griffith and Youtie 1988; Nudds 2018). The density board was placed 15 m from the observer standing at the camera-trap station. The observer took four measurements (one in each cardinal direction from the station) at each site. To account for the potential effects of forage quality on deer vigilance, we measured the presence of plant species preferred by deer in the southeast (Supplementary Appendix S3) within 8 x 8 m vegetation plots used for long-term vegetation monitoring at 18 of our sites. We estimated forage species richness at these sites by calculating the number of species present in each plot.

Data analysis

To test how land-use history and fire frequency affect vegetation cover, we employed a linear model with land-use history, fire frequency, and the interaction of land-use history and fire as fixed effects and proportion of vegetation cover as a response variable. To test how land-use history and fire frequency affect spatial patterns of deer activity, we used a linear model with land-use history, fire frequency, the interaction of land-use history and fire as fixed effects, and the log-transformed total number of foraging bouts at each site as a response variable. To test how land-use history and fire frequency affects deer antipredator behavior during foraging bouts, we used a binomial generalized linear mixed effects model (GLMM) with land-use history and fire frequency, the interaction of land-use history and fire frequency, the presence of conspecifics, and the individual's sex as fixed effects; site as a random intercept; and proportion of vigilant photos for each individual bout as a response variable. To test how forage quality affects deer antipredator behavior during foraging bouts, we used a binomial GLMM with forage species richness as a fixed effect, site as a random intercept, and proportion of vigilant photos as a response variable.

We measured the temporal patterns of deer foraging bouts using the *activity* package (Rowcliffe 2019) in R (R Core Development Team 2019) after the methods of Rowcliffe et al. (2014) and Ridout and Linkie (2009). The time of individual bouts was converted to radians to fit circular kernel densities of deer activity

for each land-use history and fire-regime treatment combination. Temporal patterns of deer activity were plotted using a von Mises kernel (Ridout and Linkie 2009; Rowcliffe et al. 2014), and 95% confidence intervals for the distributions were obtained from 999 smoothed bootstrap samples. We measured the overlap of circular distributions using the *compareCkern* function in the *activity* package (Rowcliffe 2019). This function calculates an overlap index (Δ ; Ridout and Linkie 2009) of two fitted distributions, generates a null distribution of overlap indices using randomly sampled data from the combined dataset and estimates the probability that the

observed overlap arose by chance (Rowcliffe 2019). We conducted pairwise comparisons to measure the overlap of circular distributions across the four land-use history and fire-regime treatment combinations.

RESULTS

We captured 158 independent white-tailed deer foraging bouts across 22 of the 24 sites in our study. The majority of foraging bouts (80% of 158) were from individuals detected alone and not

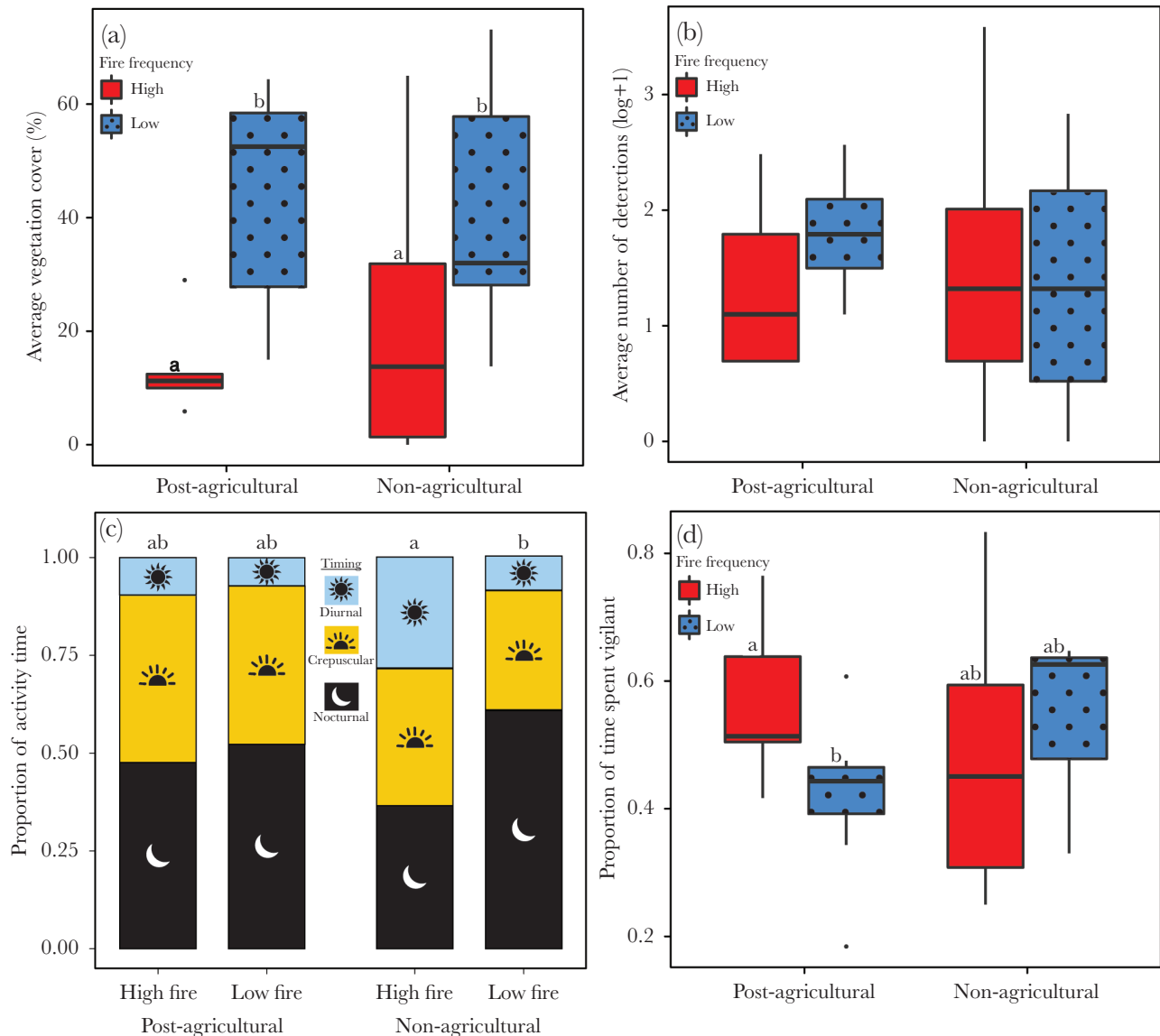


Figure 2

Past land use and contemporary fire frequency significantly affected vegetation cover, deer activity timing, and deer vigilance. (a) Sites with frequent fire regimes had significantly lower vertical vegetation cover in both post-agricultural and nonagricultural woodlands. (b) The frequency of deer foraging activity across sites did not differ with land-use history or fire frequency. (c) Independent deer detections were categorized as crepuscular, diurnal, or nocturnal using daily sunrise and sunset times. We calculated the proportion of total deer detections occurring within each timing category for each land-use history and fire frequency category. There was no difference in activity timing between post-agricultural woodlands of different fire frequencies. In nonagricultural woodlands, deer exhibited greater nocturnal activity and less crepuscular or diurnal activity in woodlands with low fire frequencies than in woodlands with high fire frequencies. (d) The effect of fire frequency on deer vigilance was contingent on land-use history. In post-agricultural woodlands, deer allocated a higher proportion of their time to vigilance in sites with frequent fire regimes, but there was no effect of fire on deer vigilance in nonagricultural woodlands. Lowercase letters indicate significant differences between group means at an alpha level of 0.05.

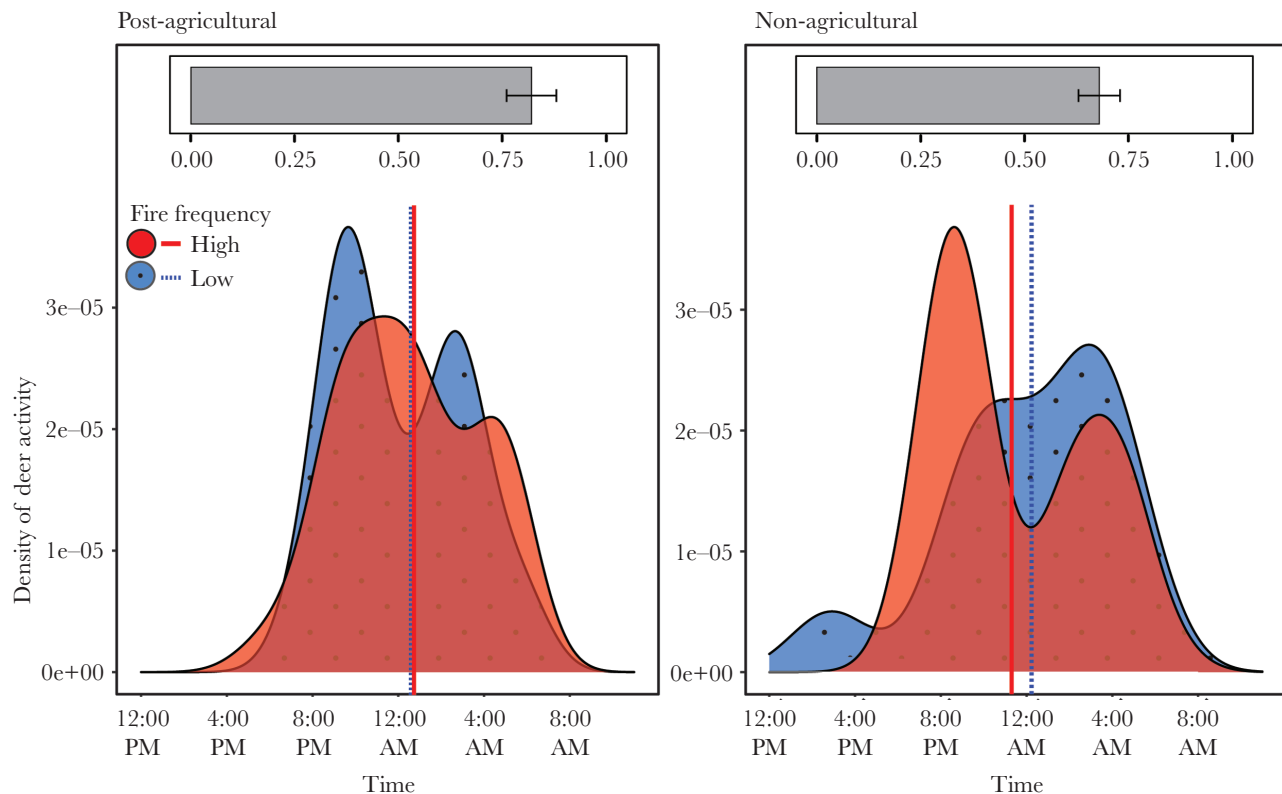


Figure 3

Deer activity patterns were significantly affected by fire frequency in nonagricultural woodlands but not in post-agricultural woodlands. In post-agricultural woodlands, the distribution of foraging bouts showed a range of activity from the evening (~9:00 PM) through the early morning (~5:00 PM). In nonagricultural woodlands, deer were primarily crepuscular in sites with high fire frequencies showing activity peaks primarily in the evening (~8:00–9:00 PM) and secondarily in the early morning (~5:00 AM). Deer were primarily nocturnal in sites with low fire frequencies, showing activity peaks only at nighttime (~2:00–3:00 AM). Vertical lines represent group means. Bars within each panel represent coefficient of overlap in distributions between fire treatments, and error bars represent bootstrapped 95% confidence intervals.

in a group. A total of 32 individuals were detected in groups of two, and groups with more than two individuals were never observed. We detected 122 bouts by female individuals, 28 bouts by male individuals, and 8 individuals could not be confidently classified by sex. There was a significant effect of fire frequency on vegetation cover ($F_{1,20} = 8.17$, $P = 0.009$), and land-use history and fire frequency did not interact to affect vegetation cover ($F_{1,20} = 0.44$, $P = 0.516$; Figure 2a). For both post-agricultural and nonagricultural woodlands, vegetation cover was significantly higher in frequently burned sites. There was not a significant interaction of land-use history and fire frequency on the frequency of deer activity ($F_{1,20} = 0.47$, $P = 0.502$; Figure 2b). Additional analyses confirmed that there were no sex-specific effects of land-use history and fire on deer activity (Supplementary Appendix S4). Because we did not observe deer foraging activity at two of the sites in our study, we did not include these sites in analyses of vigilance or activity timing patterns. Deer activity timing patterns depended on the interaction of past land use and contemporary fire regime. Whereas activity was generally crepuscular and nocturnal (Figure 2c), the frequency of nocturnal activity depended on fire frequency, but only in nonagricultural woodlands (Figure 2c). This shift in activity was not observed in post-agricultural woodlands (Figure 2c). These shifts inactivity are also reflected in patterns of overlap in activity timing (Figure 3). There was a significant lack of overlap in the temporal distribution of deer activity between nonagricultural woodlands with low fire frequencies and nonagricultural woodlands

with high fire frequencies ($\Delta = 0.68 \pm 0.05$, $P = 0.012$; Figure 3b), but not between high- and low-fire sites in post-agricultural woodlands ($\Delta = 0.82 \pm 0.06$, $P = 0.401$; Figure 3a).

There was a significant effect of fire frequency ($X^2 = 4.58$, $P = 0.032$) and the interaction of land-use history and fire frequency ($X^2 = 4.70$, $P = 0.030$) on deer vigilance such that fire only affected deer in post-agricultural woodlands. In post-agricultural woodlands, deer were significantly more vigilant in frequently burned sites (Figure 2d). Additional analyses confirmed that vigilance did not change as a function of activity timing (Supplementary Appendix S5). There was no effect of forage species richness on deer vigilance ($X^2 = 0.37$, $P = 0.546$).

DISCUSSION

Spatial and temporal variation in predation risk across heterogeneous landscapes can generate predictable patterns in prey behavior (Lima and Bednekoff 1999; Sih and Ziemba 2000; Laundré et al. 2001; Fortin et al. 2005; Hernández and Laundré 2005; Kohl et al. 2018). This study demonstrates that past disturbances can lead to long-lasting changes in the present-day antipredator behaviors employed by animals and also highlights how the effect of past disturbance on contemporary antipredator behavior depends substantially on recent disturbance by fire (Figure 2). We found that deer responded to fire-mediated changes in perceived predation risk by shifting activity timing in nonagricultural

woodlands (Figure 2c); conversely, deer responded to fire-mediated changes in risk through vigilance behavior in post-agricultural woodlands (Figure 2d). These findings have multiple implications that we discuss below. First, past land use may affect the utilization of different antipredator strategies by ungulates. Second, agricultural legacies and contemporary fire regimes may elicit landscapes of fear by generating spatiotemporal variation in antipredator behaviors.

Utilization of different antipredator strategies is conditioned on agricultural legacies

The characteristics of the habitat in which predator-prey interactions occur can influence antipredator behavior of prey species by affecting the probability of encountering a predator, the probability of detecting a predator before an attack is initiated, or the probability of escaping an attack once initiated (Lima and Dill 1990; Lima and Bednekoff 1999; Guiden et al. 2019; Sheriff et al. 2020). Our results suggest that past land use influences the utilization of different antipredator behaviors that either reduce the probability of encountering a predator (activity timing) or increase the probability of detecting a predator (vigilance). By reducing vegetation cover, frequent fires increase white-tailed deer visibility to cursorial predators, and our results confirm past research finding that white-tailed deer vigilance responds to fire-mediated changes in perceived risk (Cherry et al. 2017). Although these parallel results suggest that the effects of fire regime on deer perceived risk are generalizable beyond our study system, our findings illuminate the role of land-use history in mediating behavioral responses to fire regime and perceived risk.

In nonagricultural woodlands, deer exhibited crepuscular activity in sites with high fire frequencies (i.e., riskier sites) and primarily nocturnal activity in sites with low fire frequencies (i.e., safer sites). Coyotes are primarily nocturnal in areas where populations are persecuted by humans (Kitchen et al. 2000; Gallo et al. 2019), which is incentivized in South Carolina. Because coyotes in our study area are likely nocturnal, we expect that deer are mitigating risk in nonagricultural woodlands by limiting nocturnal activity to safer, infrequently burned sites. Interestingly, these findings of deer using risky habitats at safe times and safe habitats at risky times parallel the results of spatiotemporal habitat partitioning in a classic predator-prey system, elk and wolves in Yellowstone National Park (Kohl et al. 2018). Elk activity in risky locations was greatest at night when wolf activity is at its lowest (Kohl et al. 2018). Similar patterns were also documented among white-tailed deer within the Florida panther's range: deer were more likely to use risky habitats during panther downtimes (Crawford et al. 2019). In finding that deer modified activity timing in response to perceived risk only under specific habitat contexts (nonagricultural woodlands), our study contributes to the growing body of literature documenting habitat-specific activity timing among mammals as an antipredator strategy (Connolly and Orrock 2018; Gaynor et al. 2018; Kohl et al. 2018; Crawford et al. 2019; Higdon et al. 2019; Smith et al. 2019). Moreover, our study provides further evidence of the role of fire in mediating ungulate activity time as demonstrated in Oregon elk populations by Spitz et al. (2018), while also revealing that the effects of fire on ungulate activity time may depend on past land use.

Our finding that deer modified vigilance, not activity time, in post-agricultural woodlands suggests that habitat context may play an important role in affecting the costs or benefits of behaviors that either decrease the probability of a predator encounter

(activity time) or increase the probability of detecting a predator (vigilance; Figure 2d). Changing activity timing in nonagricultural woodlands may be beneficial because the increased density of predators in those habitats makes vigilance too costly or ineffective (Illius and Fitzgibbon 1994; Fortin et al. 2004). In our study site, nonagricultural woodlands have a mixture of hardwood and pine whereas post-agricultural woodlands are dominated by pine (Brudvig et al. 2013). Nonagricultural woodlands may be areas of higher coyote activity because habitats characterized by hardwoods are preferred denning sites for coyotes (Hickman et al. 2015) and exhibit greater coyote densities (Jorge et al. 2020). In post-agricultural woodlands, deer vigilance was greater in sites with high fire frequencies (Figure 2d). This suggests that in habitats where the probability of an encounter might be generally low, vigilance may become the optimal strategy for reducing predation risk while also allowing deer to access food resources. Alternatively, the foraging trade-offs associated with vigilance (Illius and Fitzgibbon 1994; Fortin et al. 2004) may vary with land-use history, modifying the utility of this strategy. For example, although we did not find an effect of forage species richness on deer vigilance, land-use history does affect plant community composition in this system (Brudvig and Damschen 2011; Brudvig et al. 2014). It is possible that deer foraging efficiency may be greater in post-agricultural woodlands (e.g., more nutritious species available), permitting deer to sacrifice foraging time for vigilance in risky conditions. We also note the possibility that plant nutritional quality could change after fire; therefore, deer may need less foraging time (i.e., fewer bites and more time being vigilant) in frequently burned sites to acquire the same amount of nutrients as in infrequently burned sites. Because most sites in our study had at least two full years of recovery since the last fire (Supplementary Appendix S2), we expect that potential differences in forage quality would be the result of plant community composition, not changes in plant nutritional quality soon after the fire.

Vegetation cover is one of the most common metrics employed in studies predicting ungulate demography and behavior (Myserud and Østbye 1999), including in ecosystems of high conservation concern (e.g., Bro-Jørgensen et al. 2008; Creel et al. 2014). Our results show that agricultural legacies may have important implications for ungulate conservation efforts by altering the relationship between vegetation cover and important ungulate behaviors. In finding that deer responses to fire differed with land-use history despite the consistent effects of fire on vegetation cover across land-use histories (Figure 2), our results highlight that habitats with similar vegetation cover – a frequently used metric for predation risk – may still vary substantially from the prey's perspective. Recent work has shown that predictive models of antipredator behavior may benefit from including not only vegetation cover but also information regarding predator activity (see Moll et al. 2017) and habitat characteristics that modify the potential of escape during an attack (see Sheriff et al. 2020). In addition to these suggestions, our results indicate that agricultural legacies can alter habitats in a way that may compromise model predictions of ungulate behavior and predator-prey dynamics when land-use history is not taken into account.

Agricultural legacies and contemporary fire regimes may generate landscapes of fear

Contemporary landscapes are mosaics affected by multiple disturbances that operate at different spatial and temporal scales (Pickett and White 1985; Vitousek et al. 1997; Buma 2015). In

revealing that deer antipredator behavior is contingent on both past and present disturbances, our work provides two means to further refine behavioral models that characterize the nature and extent of the “landscape of fear.” First, our results show that understanding how multiple forms of disturbance interact may elucidate spatial patterns in antipredator behavior. It is appreciated that the legacies of past disturbances can alter the likelihood, severity, and outcome of contemporary disturbances (Buma 2015), and our study demonstrates how the interaction of multiple disturbances may give rise to dynamic landscapes of fear in animal populations. Second, landscapes of fear are often quantified by measuring spatial variance in a single antipredator behavior (Laundré et al. 2001; Moll et al. 2017; Gaynor et al. 2019); however, recent work has revealed spatiotemporal variability in antipredator strategies (Kohl et al. 2018). Our results show that ungulates may employ multiple antipredator strategies in different environmental contexts across a landscape. Consequently, accurately detecting landscapes of fear may hinge on the measurement of a suite of antipredator behaviors and accounting for multiple disturbance regimes. In finding that agricultural legacies change the antipredator strategies of deer, this study demonstrates the value of evaluating landscapes of fear in degraded habitats. Although protected areas provide invaluable ecological baselines for understanding large-scale patterns in predator-prey dynamics (Boyce 2018), as much as 75% of the earth’s land cover is considered degraded (IPBES 2018). The ubiquity of human disturbances necessitates research that applies basic principles of predator-prey dynamics to human-modified landscapes (Guiden et al. 2019). Because as much as 80% of forest cover in North America and Europe is on post-agricultural land (Flinn and Vellend 2005), restoration of degraded forests may benefit from the knowledge of how agricultural legacies affect ungulate behavior, particularly when efforts include the reintroduction of predators. Our results show that ungulates may not exhibit the same behavioral responses to predation risk in restored habitats as they do in remnant habitats, necessitating the measurement of multiple antipredator behaviors to accurately detect the effects of predator reintroduction.

Variation in the employment of different antipredator strategies across a landscape may have important ecosystem consequences because different behaviors may have different ecological effects. Changes in vigilance can determine herbivory pressure on plant communities (Schmitz et al. 2004; Creel and Winnie 2005; Cherry et al. 2016) whereas increased ungulate nocturnality may increase metabolic costs, decrease visual acuity, and increase overlap with competitors (Gaynor et al. 2018). Importantly, frequent fires can reduce tick abundance (Gleim et al. 2014), and increased nocturnality among white-tailed deer in high-fire sites may affect temporal overlap with ectoparasites during times of day when environmental conditions are optimal for parasites to seek hosts (e.g., ticks; Orr et al. 2013; Dubie et al. 2018). Hence, fire-mediated shifts in activity timing in nonagricultural woodlands may modify ectoparasite load and disease transmission by altering spatiotemporal overlap with ectoparasites. Because vigilance and activity timing yield different costs to deer and modify different ecological interactions (e.g., herbivory versus parasitism), it is possible that the nature and strength of behaviorally-mediated trophic cascades may differ across habitats with different land-use histories. Past work has found evidence of behaviorally-mediated trophic cascades driven by deer antipredator behavior in longleaf pine woodlands (Cherry et al. 2016), and our findings suggest the interesting possibility

that differences in past land use found throughout the range of this ecosystem (e.g., 50% of longleaf pine acreage contains stands <50 years old; Oswalt et al. 2012) could be a significant, but unappreciated factor contributing to variation in trophic cascades.

CONCLUSIONS AND FUTURE DIRECTIONS

Land-use legacies and contemporary fire regimes can interact to modify deer vigilance and activity time, potentially generating dynamic landscapes of fear in longleaf pine woodlands. The historic diversity of understory plant communities in longleaf pine woodlands has made this ecosystem a global biodiversity hotspot (Frost 2006). Because shifts in ungulate foraging behavior in response to perceived risk can generate cascading effects on plant communities (Schmitz et al. 2000; Winnie 2012; Kauffman et al. 2013; Cherry et al. 2016), it is possible that the effects of past land use and contemporary fire regime on deer foraging behavior could have unappreciated consequences for the restoration and maintenance of understory plant diversity in longleaf pine woodlands. Variation in the employment of different antipredator strategies may also have important ecosystem consequences because different behaviors have different ecological effects. Future studies that employ herbivore exclosures to measure the effects of herbivory on understory plants across different land-use histories and fire regimes are necessary to understand the ultimate consequences of deer behavioral responses to past and present disturbances detected in our study.

SUPPLEMENTARY MATERIAL

Supplementary data are available at *Behavioral Ecology* online.

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Data availability: Analyses reported in this article can be reproduced using the data provided by Bartel & Orrock (2021).

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REFERENCES

- Bartel SL, Orrock JL. 2020. Past and present disturbances generate spatial variation in seed predation. *Ecosphere*. 11:e03116.
- Bartel SL, Orrock JL. 2021. Past agricultural land use affects multiple facets of ungulate antipredator behavior. *Behav Ecol*. doi: 10.5061/dryad.qjq2bvqg6.
- Bednekoff PA, Lima SL. 1998. Randomness, chaos and confusion in the study of antipredator vigilance. *Trends Ecol Evol*. 13:284–287.
- Boyce MS. 2018. Wolves for Yellowstone: dynamics in time and space. *J Mammal*. 99:1021–1031.

- Bro-Jørgensen J, Brown ME, Pettorelli N. 2008. Using the satellite-derived normalized difference vegetation index (NDVI) to explain ranging patterns in a lek-breeding antelope: the importance of scale. *Oecologia*. 158:177–182.
- Brudvig LA, Damschen EI. 2011. Land-use history, historical connectivity, and land management interact to determine longleaf pine woodland understory richness and composition. *Ecography*. 34:257–266.
- Brudvig LA, Grman E, Habeck CW, Orrock JL, Ledvina JA. 2013. Strong legacy of agricultural land use on soils and understory plant communities in longleaf pine woodlands. *For Ecol Manage*. 310:944–955.
- Brudvig LA, Orrock JL, Damschen EI, Collins CD, Hahn PG, Mattingly WB, Veldman JW, Walker JL. 2014. Land-use history and contemporary management inform an ecological reference model for longleaf pine woodland understory plant communities. *PLoS One*. 9:e86604.
- Buma B. 2015. Disturbance interactions: characterization, prediction, and the potential for cascading effects. *Ecosphere*. 6:70.
- Caro T. 2005. Antipredator defenses in mammals and birds. Chicago, IL: University of Chicago Press.
- Cherry MJ, Conner LM, Warren RJ. 2015. Effects of predation risk and group dynamics on white-tailed deer foraging behavior in a longleaf pine savanna. *Behav Ecol*. 26:1091–1099.
- Cherry MJ, Warren RJ, Conner LM. 2016. Fear, fire, and behaviorally mediated trophic cascades in a frequently burned savanna. *For Ecol Manage*. 368:133–139.
- Cherry MJ, Warren RJ, Conner LM. 2017. Fire-mediated foraging tradeoffs in white-tailed deer. *Ecosphere*. 8:e01784.
- Connolly BM, Orrock JL. 2018. Habitat-specific capture timing of deer mice (*Peromyscus maniculatus*) suggests that predators structure temporal activity of prey. *Ethology*. 124:105–112.
- Crawford DA, Cherry MJ, Kelly BD, Garrison EP, Shindle DB, Conner LM, Chandler RB, Miller KV. 2019. Chronology of reproductive investment determines predation risk aversion in a felid-ungulate system. *Ecol Evol*. 9:3264–3275.
- Creel S, Schuette P, Christianson D. 2014. Effects of predation risk on group size, vigilance, and foraging behavior in an African ungulate community. *Behav Ecol*. 25:773–784.
- Creel S, Winnie JA. 2005. Responses of elk herd size to fine-scale spatial and temporal variation in the risk of predation by wolves. *Anim Behav*. 69:1181–1189.
- Culbert PD, Dorresteijn I, Loos J, Clayton MK, Fischer J, Kuemmerle T. 2017. Legacy effects of past land use on current biodiversity in a low-intensity farming landscape in Transylvania (Romania). *Landsc Ecol*. 32:429–444.
- Dirzo R, Raven PH. 2003. Global state of biodiversity and loss. *Annu Rev Environ Resour*. 28:137–167.
- Dobson AP, Bradshaw AD, Baker AJM. 1997. Hopes for the future: restoration ecology and conservation biology. *Science*. 277:515–522.
- Dubie TR, Turner J, Noden BH. 2018. Questing behavior and analysis of tick-borne bacteria in *Ixodes scapularis* (Acari: Ixodidae) in Oklahoma. *J Med Entomol*. 55:1569–1574.
- Dudley N, Alexander S. 2017. Agriculture and biodiversity: a review. *Biodiversity*. 18:45–49.
- Duguy B, Ramón V V. 2007. Land-use and fire history effects on post-fire vegetation dynamics in eastern Spain. *J Veg Sci*. 19:97–108.
- Eby SL, Anderson TM, Mayemba EP, Ritchie ME. 2014. The effect of fire on habitat selection of mammalian herbivores: the role of body size and vegetation characteristics. *J Anim Ecol*. 83:1196–1205.
- Eisenberg C, Hibbs DE, Ripple WJ. 2015. Effects of predation risk on elk (*Cervus elaphus*) landscape use in a wolf (*Canis lupus*) dominated system. *Can J Zool*. 93:99–111.
- Estes JA, Terborgh J, Brashares JS, Power ME, Berger J, Bond WJ, Carpenter SR, Essington TE, Holt RD, Jackson JB, et al. 2011. Trophic downgrading of planet Earth. *Science*. 333:301–306.
- Flinn KM, Vellend M. 2005. Recovery of forest plant communities in post-agricultural landscapes. *Front Ecol Environ*. 3:243–250.
- Fordyce A, Hradsky BA, Ritchie EG, Di Stefano J. 2016. Fire affects microhabitat selection, movement patterns, and body condition of an Australian rodent (*Rattus fuscipes*). *J Mammal*. 97:102–111.
- Fortin D, Beyer HL, Boyce MS, Smith DW, Duchesne T, Mao JS. 2005. Wolves influence elk movements: behavior shapes a trophic cascade in Yellowstone National Park. *Ecology*. 86:1320–1330.
- Fortin D, Boyce MS, Merrill EH, Fryxell JM. 2004. Foraging costs of vigilance in large mammalian herbivores. *Oikos*. 107:172–180.
- Foster DR. 1993. Land-use history and forest transformations in Central New England. In: Humans as components of ecosystems. New York, NY: Springer New York. p. 91–110.
- Frost C. 2006. History and future of the longleaf pine ecosystem. In: Jose S, Jokela EJ, Miller DL, editors. The longleaf pine ecosystem. New York, NY: Springer-Verlag. p. 9–48.
- Gallo T, Fidino M, Lehrer EW, Magle S. 2019. Urbanization alters predator-avoidance behaviours. *J Anim Ecol*. 88:793–803.
- Gaynor KM, Brown JS, Middleton AD, Power ME, Brashares JS. 2019. Landscapes of fear: spatial patterns of risk perception and response. *Trends Ecol Evol*. 34:355–368.
- Gaynor KM, Hohnowski CE, Carter NH, Brashares JS. 2018. The influence of human disturbance on wildlife nocturnality. *Science*. 360:1232–1235.
- Gleim ER, Conner LM, Berghaus RD, Levin ML, Zemtsova GE, Yabsley MJ. 2014. The phenology of ticks and the effects of long-term prescribed burning on tick population dynamics in southwestern Georgia and northwestern Florida. *PLoS One*. 9:e112174.
- Griffith B, Youtie BA. 1988. Two devices for estimating foliage density and deer hiding cover. *Wildl Soc Bull*. 16:206–210.
- Guiden PW, Bartel SL, Byer NW, Shipley AA, Orrock JL. 2019. Predator-prey interactions in the anthropocene: reconciling multiple aspects of novelty. *Trends Ecol Evol*. 34:616–627.
- Gulsby WD, Kilgo JC, Vukovich M, Martin JA. 2017. Landscape heterogeneity reduces coyote predation on white-tailed deer fawns. *J Wildl Manage*. 81:601–609.
- Haddad NM, Brudvig LA, Clobert J, Davies KF, Gonzalez A, Holt RD, Lovejoy TE, Sexton JO, Austin MP, Collins CD, et al. 2015. Habitat fragmentation and its lasting impact on Earth's ecosystems. *Sci Adv*. 1:e1500052.
- Hahn PG, Orrock JL. 2015a. Spatial arrangement of canopy structure and land-use history alter the effect that herbivores have on plant growth. *Ecosphere*. 6:Article 193.
- Hahn PG, Orrock JL. 2015b. Land-use legacies and present fire regimes interact to mediate herbivory by altering the neighboring plant community. *Oikos*. 124:497–506.
- Hahn PG, Orrock JL. 2015c. Land-use history alters contemporary insect herbivore community composition and decouples plant-herbivore relationships. *J Anim Ecol*. 84:745–754.
- Hernández L, Laundré JW. 2005. Foraging in the 'landscape of fear' and its implications for habitat use and diet quality of elk *Cervus elaphus* and bison *Bison bison*. *Wildlife Biol*. 11:215–220.
- Hickman JE, Gulsby WD, Killmaster CH, Bowers JW, Byrne ME, Chamberlain MJ, Miller K V. 2015. Home range, habitat use, and movement patterns of female coyotes in Georgia: implications for fawn predation. *J Southeast Assoc Fish Wildl Agencies*. 2:144–150.
- Higdon SD, Diggins CA, Cherry MJ, Ford MW. 2019. Activity patterns and temporal predator avoidance of white-tailed deer (*Odocoileus virginianus*) during the fawning season. *J Ethol*. 37:283–290.
- Hunter LTB, Skinner JD. 1998. Vigilance behaviour in African ungulates: the role of predation pressure. *Behaviour*. 135(2):195–211.
- Hurt G, Frolking S, Fearon MG, Moore B, Shevliakova E, Malyshev S, Pacala SW, Houghton RA. 2006. The underpinnings of land-use history: three centuries of global gridded land-use transitions, wood-harvest activity, and resulting secondary lands. *Glob Chang Biol*. 12:1208–1229.
- Illius AW, Fitzgibbon C. 1994. Costs of vigilance in foraging ungulates. *Anim Behav*. 47:481–484.
- Intergovernmental Science-Policy Platform on Biodiversity and Ecosystem Services I. 2018. The IPBES assessment report on land degradation and restoration. Bonn, Germany: IPBES secretariat.
- Jorge MH, Garrison EP, Conner LM, Cherry MJ. 2020. Fire and land cover drive predator abundances in a pyric landscape. *For Ecol Manage*. 461:117939.
- Karpestam E, Merilaita S, Forsman A. 2012. Reduced predation risk for melanistic pygmy grasshoppers in post-fire environments. *Ecol Evol*. 2:2204–2212.
- Kauffman MJ, Brodie JE, Jules ES. 2013. Are wolves saving Yellowstone's aspen? A landscape-level test of a behaviorally mediated trophic cascade: reply. *Ecology*. 94:1425–1431.
- Kelly MJ. 2003. Jaguar monitoring in the Chiquibul Forest, Belize. *Caribb Geogr*. 13:19–32.
- Kelly MJ, Holub EL. 2008. Camera trapping of carnivores: trap success among camera types and across species, and habitat selection by species, on Salt Pond Mountain, Giles County, Virginia. *Northeast Nat*. 15:249–262.

- Kilgo J, Blake JI, editors. 2005. Ecology and management of a forested landscape: fifty years on the Savannah River Site. Washington, DC, USA: Island Press.
- Kilgo JC, Ray HS, Ruth C, Miller K V. 2010. Can coyotes affect deer populations in southeastern North America? *J Wildl Manage.* 74:929–933.
- Kitchen AM, Gese EM, Schauster ER. 2000. Changes in coyote activity patterns due to reduced exposure to human persecution human persecution. *Can J Zool.* 78:853–857.
- Kohl MT, Stahler DR, Metz MC, Forester JD, Kauffman MJ, Varley N, White PJ, Smith DW, MacNulty DR. 2018. Diel predator activity drives a dynamic landscape of fear. *Ecol Monogr.* 88:638–652.
- Kopecký M, Vojta J. 2009. Land use legacies in post-agricultural forests in the Doupovské Mountains, Czech Republic. *Appl Veg Sci.* 12:251–260.
- Kymmel D. 2019. Fire effects in a landscape of fear – food availability and perceived predation risk as potential determinants of patch utilization by herbivore prey. Umeå, Sweden: Swedish University of Agricultural Sciences.
- Lashley MA, Chitwood CC, Biggerstaff MT, Morina DL, Moorman CE. 2014. White-tailed deer vigilance: the influence of social and environmental factors. *PLoS One.* 9:90652.
- Laundré JW, Hernández L, Altendorf KB. 2001. Wolves, elk, and bison: reestablishing the “landscape of fear” in Yellowstone National Park, U.S.A. *Can J Zool.* 79:1401–1409.
- Lima SL. 1995. Back to the basics of anti-predatory vigilance: the group-size effect. *Anim Behav.* 49:11–20.
- Lima SL, Bednekoff PA. 1999. Temporal variation in danger drives antipredator behavior: the predation risk allocation hypothesis. *Am Nat.* 153:649–659.
- Lima SL, Dill LM. 1990. Behavioral decisions made under the risk of predation: a review and prospectus. *Can J Zool.* 68:619–640.
- Mattingly WB, Orrock JL, Collins CD, Brudvig LA, Damschen EI, Veldman JW, Walker JL. 2015. Historical agriculture alters the effects of fire on understory plant beta diversity. *Oecologia.* 177:507–518.
- Moll RJ, Redilla KM, Mudumba T, Muneza AB, Gray SM, Abade L, Hayward MW, Millspaugh JJ, Montgomery RA. 2017. The many faces of fear: a synthesis of the methodological variation in characterizing predation risk. *J Anim Ecol.* 86:749–765.
- Morris G, Conner LM. 2016. Effects of forest management practices, weather, and indices of nest predator abundance on nest predation: a 12-year artificial nest study. *For Ecol Manage.* 366:23–31.
- Myserud A, Østbye E. 1999. Cover as a habitat element for temperate ungulates: effects on habitat selection and demography. *Wildl Soc Bull.* 27:385–394.
- Nudds TD. 2018. Quantifying the vegetative structure of wildlife cover. *Wildl Soc Bull.* 5:113–117.
- O'Connor KM, Rittenhouse TAG. 2017. Temporal activity levels of mammals in patches of early successional and mature forest habitat in eastern Connecticut. *Am Midl Nat.* 177:15–28.
- Orr JM, Smith JD, Zawada SG, Arias JR. 2013. Diel and seasonal activity and trapping of ticks (Acari: Ixodidae) in Northern Virginia, U.S.A. *Syst Appl Acarol.* 18:111.
- Oswalt CM, Cooper JA, Brockway DG, Brooks HW, Walker JL, Connor KF, Oswalt SN, Conner RC. 2012. History and current condition of longleaf pine in the Southern United States. General Technical Report SRS-166. Asheville, NC: U.S. Department of Agriculture Forest Service, Southern Research Station.
- Pace ML, Cole JJ, Carpenter SR, Kitchell JF. 1999. Trophic cascades revealed in diverse ecosystems. *Trends Ecol Evol.* 14:483–488.
- Peckarsky BL, Abrams PA, Bolnick DI, Dill LM, Grabowski JH, Luttberg B, Orrock JL, Peacor SD, Preisser EL, Schmitz OJ, et al. 2008. Revisiting the classics: considering nonconsumptive effects in textbook examples of predator-prey interactions. *Ecology.* 89:2416–2425.
- Pickett STA, White PS, editors. 1985. The ecology of natural disturbance and patch dynamics. San Diego, CA: Academic Press.
- Pimm SL, Russell GJ, Gittleman JL, Brooks TM. 1995. The future of biodiversity. *Science.* 269:347–350.
- Preisser EL, Bolnick DI. 2008. The many faces of fear: comparing the pathways and impacts of nonconsumptive predator effects on prey populations. *PLoS One.* 3:e2465.
- Preisser EL, Bolnick DI, Benard ME. 2005. Scared to death? The effects of intimidation and consumption in predator-prey interactions. *Ecology.* 86:501–509.
- Prugh LR, Sivy KJ, Mahoney PJ, Ganz TR, Dittmer MA, van de Kerk M, Gilbert SL, Montgomery RA. 2019. Designing studies of predation risk for improved inference in carnivore-ungulate systems. *Biol Conserv.* 232:194–207.
- R Core Team. 2019. R: a language and environment for statistical computing. Vienna, Austria: R Foundation for Statistical Computing. <https://www.R-project.org/>.
- Ridout MS, Linkie M. 2009. Estimating overlap of daily activity patterns from camera trap data. *J Agric Biol Environ Stat.* 14:322–337.
- Ripple WJ, Beschta RL. 2003. Wolf reintroduction, predation risk, and cottonwood recovery in Yellowstone National Park. *For Ecol Manage.* 184:299–313.
- Rowcliffe M. 2019. Activity: animal activity statistics. CRAN, Version: 1.2.
- Rowcliffe JM, Kays R, Kranstauber B, Carbone C, Jansen PA. 2014. Quantifying levels of animal activity using camera trap data. *Methods Ecol Evol.* 5:1170–1179.
- Schmitz OJ, Hambäck PA, Beckerman AP. 2000. Trophic cascades in terrestrial systems: a review of the effects of carnivore removals on plants. *Am Nat.* 155:141–153.
- Schmitz OJ, Krivan V, Ovadia O. 2004. Trophic cascades: the primacy of trait-mediated indirect interactions. *Ecol Lett.* 7:153–163.
- Sheriff MJ, Orrock JL, Ferrari MCO, Karban R, Preisser EL, Sih A, Thaler JS. 2020. Proportional fitness loss and the timing of defensive investment: a cohesive framework across animals and plants. *Oecologia.* 193:273–283.
- Sih A, Ziemba R. 2000. New insights on how temporal variation in predation risk shapes prey behavior. *Trends Ecol Evol.* 15:3–4.
- Sisk TD, Launer A, Switky KR, Ehrlich PR. 1994. Identifying extinction threats. *Bioscience.* 44:592–604.
- Smith JA, Donadio E, Pauli JN, Sheriff MJ, Middleton AD. 2019. Integrating temporal refugia into landscapes of fear: prey exploit predator downtimes to forage in risky places. *Oecologia.* 189:883–890.
- Sousa WP. 1984. The role of disturbance in natural communities. *Annu Rev Ecol Syst.* 15:353–391.
- Spitz DB, Clark DA, Wisdom MJ, Rowland MM, Johnson BK, Long RA, Levi T. 2018. Fire history influences large-herbivore behavior at circadian, seasonal, and successional scales. *Ecol Appl.* 28:2082–2091.
- Stuhler JD, Orrock JL. 2016. Past agricultural land use and present-day fire regimes can interact to determine the nature of seed predation. *Oecologia.* 181:463–473.
- Terborgh J, Estes JA, editors. 2010. Trophic cascades: predators, prey, and the changing dynamics of nature. Washington, DC: Island Press.
- Valeix M, Loveridge AJ, Chamaillé-Jammes S, Davidson Z, Murindagomo F, Fritz H, Macdonald DW. 2009. Behavioral adjustments of African herbivores to predation risk by lions: spatiotemporal variations influence habitat use. *Ecology.* 90:23–30.
- Veldman JW, Brudvig LA, Damschen EI, Orrock JL, Mattingly WB, Walker JL. 2014. Fire frequency, agricultural history and the multivariate control of pine savanna understory plant diversity. Gilliam F, editor. *J Veg Sci.* 25:1438–1449.
- Vitousek PM, Mooney HA, Lubchenco J, Melillo JM. 1997. Human domination of Earth's ecosystems. *Science* (80-). 277:3–13.
- Wang Y, Allen ML, Wilms CC. 2015. Mesopredator spatial and temporal responses to large predators and human development in the Santa Cruz Mountains of California. *Biol Conserv.* 190:23–33.
- Winnie JA Jr. 2012. Predation risk, elk, and aspen: tests of a behaviorally mediated trophic cascade in the Greater Yellowstone Ecosystem. *Ecology.* 93:2600–2614.
- Winnie J, Creel S. 2007. Sex-specific behavioural responses of elk to spatial and temporal variation in the threat of wolf predation. *Anim Behav.* 73:215–225.