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Deer Vigilance and Movement Behavior Are Affected by Edge Density and Connectivity

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ABSTRACT

Animal behavior is an important component of individual, population, and community responses to anthropogenic habitat alteration. For example, antipredator behavior (e.g., vigilance) and animal movement behavior may both be important behavioral responses to the increased density of habitat edges and changes in patch connectivity that characterize highly modified habitats. Importantly, edge density and connectivity might interact, and this interaction is likely to mediate animal behavior: linear, edge-rich landscape features often provide structural connectivity between patches, but the functional connectedness of patches for animal use could depend upon how edge density modifies animal vigilance and movement. Using remote cameras in large-scale experimental landscapes that manipulate edge density (high- vs. low-density edges) and patch connectivity (isolated or connected patches), we examined the effects of edge density and connectivity on the antipredator behavior and movement behavior of white-tailed deer (*Odocoileus virginianus*). Deer vigilance was 1.38 times greater near high-density edges compared to low-density edges, regardless of whether patches were connected or isolated. Deer were also more likely to move parallel to connected high-density edges than all other edge types, suggesting that connectivity promotes movement along high-density edges. These results suggest that increases in edge density that accompany human fragmentation of existing habitats may give rise to large-scale changes in the antipredator behavior of deer. These results also suggest that conservation strategies that simultaneously manipulate edge density and connectivity (i.e., habitat corridors) may have multiple effects on different aspects of deer behavior: linear habitat corridors were areas of high vigilance, but also areas where deer movement behavior implied increased movement along the habitat edge.

1 | Introduction

Behavior is a critical determinant of individual growth, survival, and reproductive success (Preisser et al. 2005). Behavior is also an essential component of how species will respond to increasing global change (Guiden et al. 2019), such as the widespread and continued modification and destruction of habitats (Haddad et al. 2015). For example, increasing edge density caused by the creation of smaller patches of habitat can lead to changes in vigilance behavior to detect predators (Caro 2005; Murphy et al. 2021), changes in animal movement behavior (Ries et al. 2004), or both (Fagan et al. 1999;

Ries et al. 2004). Similarly, changes in the degree to which habitat patches are connected can also modify perceived and actual predation risk (Orrock and Danielson 2005; Radvan et al. 2023) and may modify animal movement among habitat patches (Gilbert-Norton et al. 2010; Resasco 2019). Although vigilance and movement behavior are fundamental aspects of the ecology of animals, and although habitat fragmentation is widespread and ongoing, studies that evaluate the influence of edge density and habitat connectivity remain relatively rare (Gilbert-Norton et al. 2010; Haddad et al. 2015). This lacuna is important because edges may not only represent features of isolated habitat patches (i.e., edges may not be associated with connectivity), but edges may also be features of connected patches of habitat. For example, linear landscape elements that connect habitats (e.g., power lines, roads, conservation corridors) are often long and narrow, such that changes in animal behavior due to edge density or structural connectivity could eliminate or amplify functional connectivity among animal populations (Bélisle 2005; Haddad et al. 2015), with consequences for gene flow, population persistence, and adaptive evolution. Therefore, understanding how edges and connectivity affect animal vigilance and movement behavior is essential for understanding future changes to animal populations amidst global change, for planning effective restoration strategies, as well as for undertaking successful conservation efforts, such as implementing conservation corridors (Hilty et al. 2006).

Ungulates are critical components of terrestrial ecosystems whose foraging behavior and abundance can shape multiple aspects of plant (e.g., Bartel and Orrock 2023) and animal communities (e.g., Guiden et al. 2023). Evidence suggests multiple avenues by which edges and patch connectivity could generate changes in ungulate behavior. Edges can provide greater forage quality and movement efficiency (Dickie et al. 2020; Gulsby et al. 2017; Norris et al. 2008); edge-rich landscape elements (e.g., power lines, roads, habitat corridors) could provide movement conduits between connected patches (Foster and Humphrey 1995; Sparks and Gates 2012). However, an abundance of edge-rich linear habitats may also lead to greater ungulate predation risk, as predators often move or hunt along habitat edges (Clare et al. 2023; Dickie et al. 2020; Lambin et al. 2000; Whittington et al. 2011), and ungulates at a habitat edge may be less likely to detect or escape a predator approaching from the adjacent habitat patch (Bojarska et al. 2017; DeMars and Boutin 2018). Hence, ungulates may perceive greater predation risk in high-density edge habitats but may also be willing to accept those risks if foraging in high-density edges allows for greater access to resources in connected patches of habitat. Alternatively, ungulates might use movement decisions to mitigate predation risk, such as opting to avoid moving along edge habitats (Haddad et al. 2015; Ries et al. 2004). Despite the potential for both edge density and patch connectivity to affect ungulate vigilance and movement behavior, it can be difficult to disentangle the potentially unique contributions of edges and connectivity: linear elements that connect habitats (roads, corridors) are inherently edge-rich elements of the landscape. As a result, edge density and habitat connectivity often covary in field studies (Gilbert-Norton et al. 2010), and large-scale experimental studies that can disentangle the two are rare (Damschen et al. 2019; Haddad et al. 2015).

We used replicated large-scale experimental landscapes to examine how edge density and patch connectivity affect antipredator behavior and movement of white-tailed deer (*Odocoileus virginianus*). White-tailed deer are common ungulates across much of North America, including within our study area in southern South Carolina, USA (Cothran et al. 1991). In our study area, coyotes (*Canis latrans*) are the primary predators of deer, and coyote predation affects deer population dynamics and behavior (Bartel et al. 2023; Cherry et al. 2015, 2016; Gulsby et al. 2018; Kilgo et al. 2010). Coyotes have also been found to selectively utilize edge-rich habitats that often connect portions of the landscape, such as railroads, fencerows, drainage ditches, and highway underpasses (Caldwell and Klip 2020; Gehring and Swihart 2003). The experimental landscape contained two different patch types (connected and isolated patches), each containing two different edge types (low-density and high-density edges), allowing us to quantify the degree to which edge-related antipredator behavior and movement differ depending upon whether habitat patches are connected. We deployed motion-activated cameras to capture individual vigilance and movement behavior along the high- and low-density edges of both isolated and connected habitat patches (Figure 1). Based on previous work with deer, we evaluated two a priori hypotheses: (1) deer are more vigilant along high-density edges compared to low-density edges, and (2) deer are more likely to move parallel along high-density edges when those edges are between two connected patches.

2 | Methods

2.1 | Experimental Design

We conducted our experiment in seven replicated experimental landscapes (hereafter "experimental blocks") created at the Department of Energy (DOE) Savannah River Site, a National Environmental Research Park (NERP) near Aiken, South Carolina, managed by the USDA Forest Service on behalf of DOE. Each experimental block consisted of five clear-cut patches created in 1999 surrounded by mature pine forest (the matrix) and maintained by prescribed burning (for additional information, see Damschen et al. 2019). For this study, we sampled two different patches from each experimental block to explicitly focus on edge density and patch connectivity (Figure 1). The connected patch consisted of a 1-ha square patch with a 150-m-long and 25-m-wide corridor that connected it to another patch. Isolated patches consisted of a 1-ha square patch with two extending wings, each 25 m wide and 75 m long. Low-density edges did not have another edge within 25 m; high-density edges contained another edge 25 m away (Figure 1). This design independently manipulates connectivity (connected vs. isolated patches) and edge density (low- and high-density edges, identical in both connected and isolated patches). Significant differences in deer behavior between connected and isolated patches would therefore be attributable to edge connectivity. Differences between low- and high-density edges (regardless of patch type) would indicate that edge density is important for affecting deer behavior. Finally, because edge density and connectivity are independently manipulated, significant differences between low- and high-density edges,

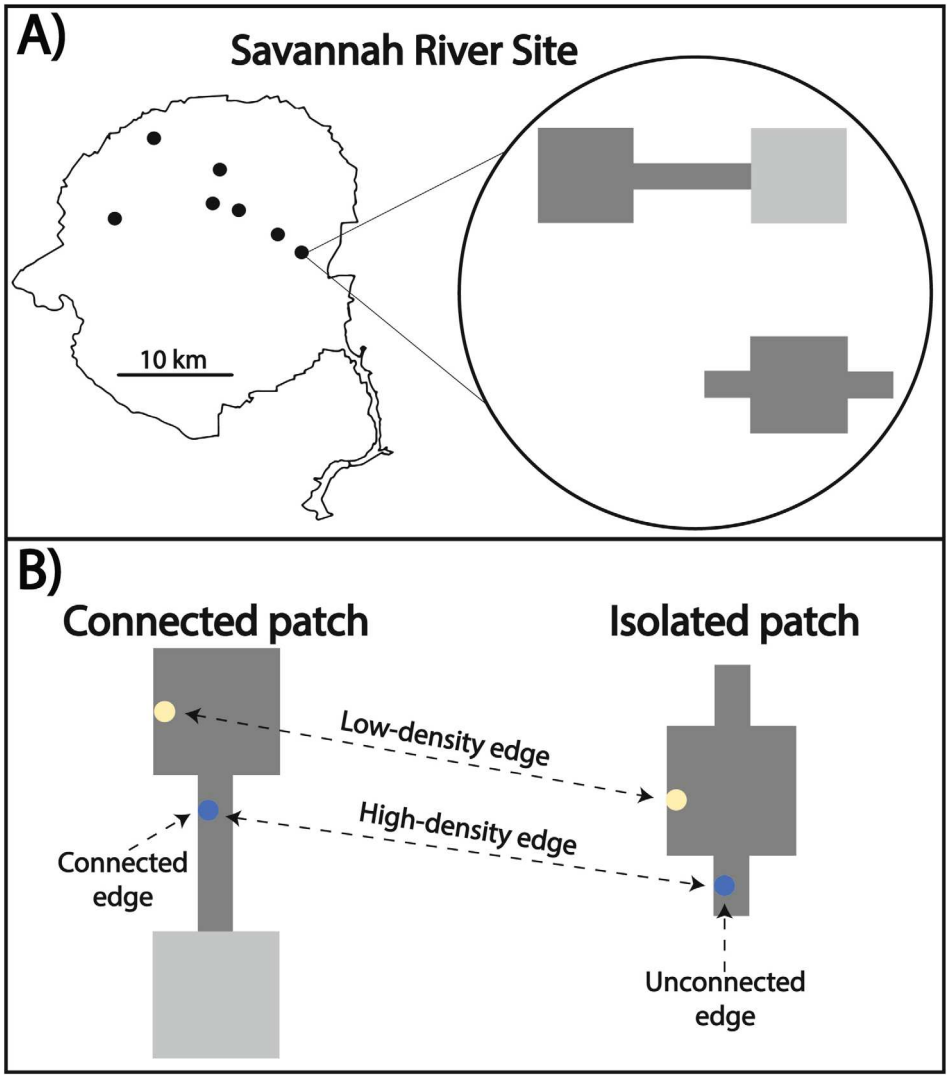

FIGURE 1 | (A) We used seven replicate experimental blocks at the Savannah River Site (left), South Carolina, USA, containing different habitat patches that allowed us to explore the role of edge density and edge connectivity in affecting deer behavior (right). (B) In order to elucidate the role of edge density and connectivity on deer behavior, we deployed motion-activated cameras along four edge locations inside each block. Cameras were located at one of two edge types: Low-density edges (yellow dots) did not have another edge nearby (i.e., within 25 m); high-density edges (blue dots) had another edge within 25 m. Edges also differed depending upon whether they were in habitat patches that were connected to other habitat patches, i.e., connected vs. unconnected edges.

the regular patch edges, and the edges of both corridors and wings would be attributable to edge density.

In July 2018, we deployed motion-activated cameras (Bushnell 16MP Trophy Cam HD; Bushnell Corporation, Overland Park, KS) for 10 days along the edges of connected and isolated patches. In both patch types, we deployed one camera along a low-density edge and another along a high-density edge (Figure 1), resulting in 28 total camera locations.

2.2 | Deer Movement and Antipredator Behavior

Camera traps were set to take photos at 1-s intervals whenever motion was detected, providing fine-scale monitoring of individual behavior. Since we did not exclude subjects, we assume there is no systematic sampling bias (Webster and Rutz 2020). All photos were sorted and analyzed by two blind observers who measured different behaviors; photos were scored without knowledge of camera position (i.e., observers were blind to the treatments associated with the photos they were scoring). The first observer measured deer vigilance, then the second observer measured deer movement direction. For every photo capturing deer activity, the first observer recorded the date and time, the sex of the individual, whether it was alone or in a group, group size, and if the individual was being vigilant or foraging as a binomial variable. If the individual's head was down in a feeding posture, then the photo was classified as foraging, and if its head was up in a non-feeding, alert posture, then the photo was classified as vigilant. This method of scoring behavior has been successfully used in previous studies assessing deer vigilance (Bartel and Orrock 2021; Cherry et al. 2017; Lashley et al. 2014). Photos in which an individual's behavior did not fall under one of these two categories (e.g., rapid movement across the camera) were not evaluated. We classified independent detections

as any sequence of photos of the same-sex deer captured within 30 min at a location (Kelly and Holub 2008; Wang et al. 2015). For each detection, we calculated the total number of vigilant and foraging photos taken. We estimated the movement direction of each individual relative to the edge at four general angles: 0° or 180° for movement parallel to the edge, 90° for movement exiting the patch, and 270° for movement entering the patch from the matrix. Movement direction was estimated by monitoring the movement path of each individual deer across the camera scope during an independent detection (based on the series of photos of the individual within the detection zone).

2.3 | Data Analysis

To test how connectivity and edge density affected deer activity, we used a linear mixed effects model with patch type (connected or isolated patch), edge type (low-density or high-density edge), and the interaction of patch type and edge type as fixed effects; a random intercept varying among blocks and patches within blocks; and the log-transformed total number of detections at each location as a response variable. The total number of detections had a non-Gaussian distribution and was log-transformed to meet the linear model's assumption that response data have a Gaussian distribution and normalize variance based on residual spread (Ives 2015). To test how patch type and edge type affected deer antipredator behavior during detections, we used a binomial generalized linear mixed effects model (GLMM) with patch type, edge type, the presence of conspecifics, the individual's sex, and the interaction of patch type and edge type as fixed effects; a random intercept varying among blocks, patches within blocks, and edges within patches; and the proportion of vigilant photos for each individual detection as a response variable. To test how connectivity and edge density affected the direction of deer movement, we used a multinomial logit model with the movement direction of each individual as the response variable (parallel, enter, or exit); patch type, edge type, and the interaction of patch type and edge type as fixed effects; and block as a random intercept. All models were constructed in R version 3.6.1 (R Core Development Team 2019). The multinomial model was constructed using the *mclogit* package (Elff et al. 2022), and all other models were constructed using the *lme4* package (Bates et al. 2015).

2.4 | Ethics Statement

We used unbaited cameras to quantify the behavior of free-ranging deer in the wild. Humans had no contact with the animals as part of conducting this research, and no aspect of data collection included the physical capture or restraint of deer. The use of cameras to take photographs of free-ranging animals is approved by Research Animal Resources and Compliance at UW-Madison (permit L0005041).

3 | Results

We captured 828 photos of white-tailed deer activity across our 7 experimental blocks. The majority of detections (134 total) were single individuals not detected in a group. Groups of two individuals were detected 27 times, and only one group of three individuals was observed. Seven of the 28 cameras deployed became nonfunctional during deployment. Data from these cameras were not included in any analyses, and camera failure was distributed across all patch and edge types (one connected patch edge, one corridor edge, two isolated patch edges, three wing edges). There was no effect of patch type (connected vs. unconnected; $F_{1,17}=0.92$, $p=0.360$), edge type ($F_{1,17}=3.64$, $p=0.101$), or the interaction of patch and edge type ($F_{1,17}=2.16$, $p=0.173$; Figure 2A) on the frequency of deer activity. Deer vigilance was not affected by patch type ($X^2=0.42$, $p=0.52$), but was significantly affected by edge type ($X^2=5.27$, $p=0.022$, Odds ratio = 0.32): deer were less vigilant along low-density edges than along high-density edges (Figure 2B). There was no interaction between patch type and edge type ($X^2=0.07$, $p=0.79$), and no effect of sex ($X^2=0.31$, $p=0.58$) or the presence of conspecifics ($X^2=0.27$, $p=0.60$) on deer vigilance. Deer movement direction was significantly affected by the interaction of patch and edge type (Table 1). Deer were more likely to move parallel (i.e., travel along) a high-density connected edge than along all other edge types and were less likely to exit a patch at a high-density connected edge than at all other edge types (Figure 3). The main effects of patch type and edge type were also significant. Averaged across edge type, deer were more likely to move parallel along edges, rather than enter a patch at the edge, if those edges were in connected patches vs. isolated patches (Table 1; Figure 3). Averaged across patch type, deer were more likely to exit a patch (vs. moving along the edge) if the edge was a high-density edge rather than a low-density edge (Table 1; Figure 3).

4 | Discussion

Vigilance and movement are key decisions that animals make in human-modified landscapes (Doherty et al. 2021; Guiden et al. 2019; Tucker et al. 2018). As a result, understanding how these behaviors are affected by habitat modification and fragmentation is important for predicting individual foraging and space use that underpins population connectivity and the nature of predator–prey interactions. Our results, collected from seven replicated large-scale landscapes, reveal the unique and interactive effects of edge density and connectivity on deer behavior. While deer movement behavior at a habitat edge depended upon the interplay of connectivity and edge density, deer vigilance was greatest at high-density edges and unaffected by connectivity. In revealing the unique and interactive effects of edges and connectivity on deer behavior, our results have several implications that may guide future research. Because deer were less vigilant at low- compared to high-density edges, widespread increases in edge density may have large-scale effects on deer antipredator behavior. Additionally, understanding deer movement behavior requires understanding habitat connectivity, and conservation strategies that modify connectivity (i.e., habitat corridors) may be effective for promoting deer movement. Finally, edges may indirectly affect plant communities by altering deer behavior and movement.

4.1 | Edge Density and Edge Connectivity Affect Different Aspects of Deer Behavior

We found that one aspect of landscapes (edge density) affects antipredator behavior, while another aspect (connectivity) affects movement behavior. This distinction is important because these

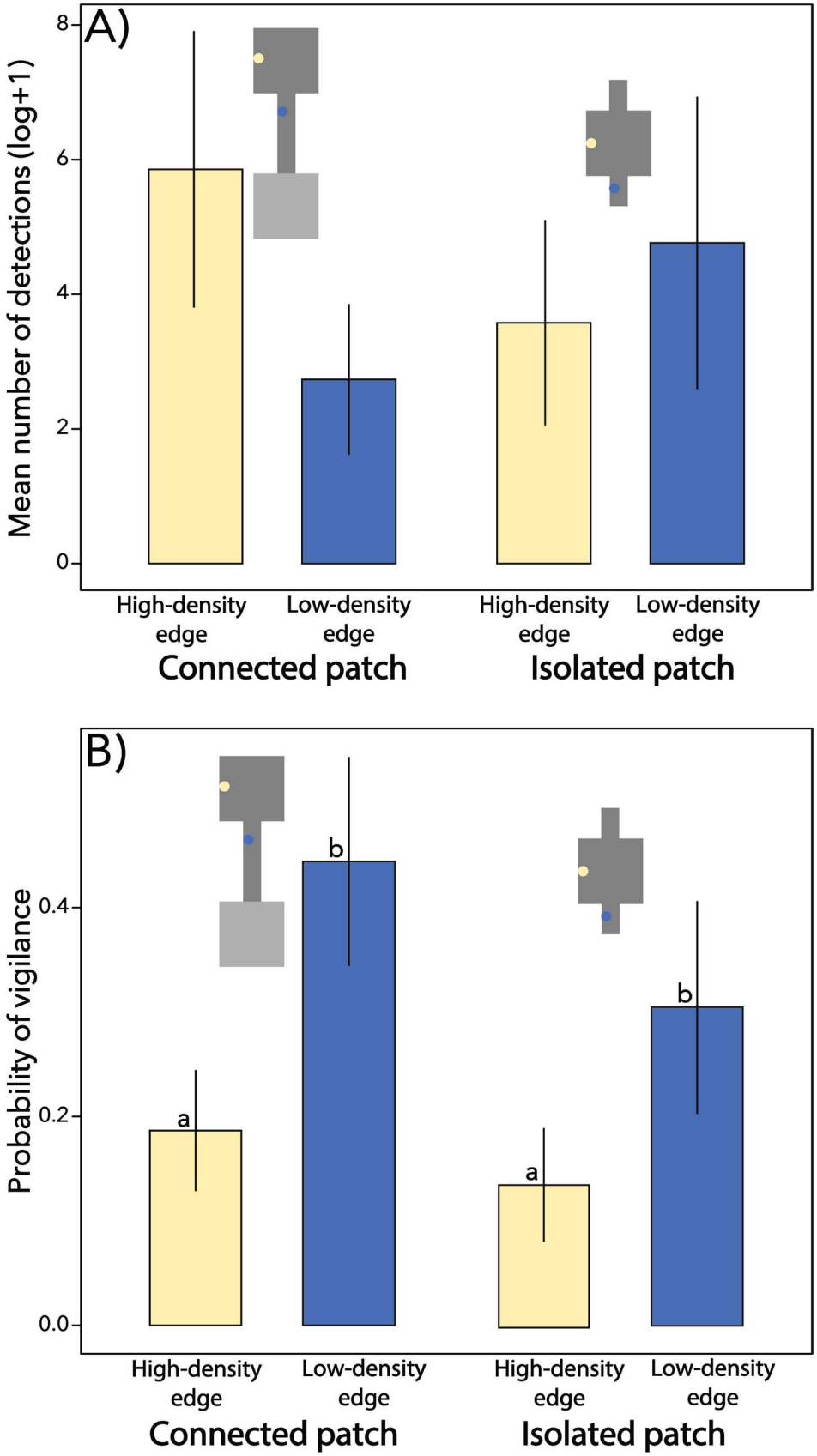

FIGURE 2 | (A) White-tailed deer activity did not differ with edge density or edge connectivity. Bars show estimated marginal means and standard error for each group. (B) Deer were significantly more vigilant during independent detections at high-density edges (blue) than at low-density edges, indicating that increased edge density, not edge connectivity, increases perceived predation risk. Bars show estimated probabilities and standard error for each group, and shared lowercase letters between groups indicate probabilities that were not significantly different from each other ($p < 0.05$ using sequential Benjamini-Hochberg correction (Benjamini and Hochberg 1995).

TABLE 1 | Summary table of the multinomial logistic model investigating the effects of patch type (unconnected vs. connected) and edge density (high vs. low) on deer movement direction.

	Coefficient (SE)	
	Enter/parallel	**Exit/parallel**
Intercept	−0.00 (0.43)	1.13 (0.35)**
Patch type: isolated/connected	1.47 (0.77)*	0.66 (0.71)
Edge type: high density/low density	−0.62 (0.63)	−3.00 (0.84)***
Patch type × edge type	1.35 (1.39)	3.61 (1.48)*

Note: *p*-values based on *Z* statistics.
*$p < 0.05$.
**$p < 0.01$.
***$p < 0.001$.

two behaviors may have different consequences for individual fitness and population dynamics. For example, changes in foraging behavior caused by predation risk can affect individual diet choices (Cherry et al. 2016), body condition, survival, and reproductive output (Abernathy et al. 2022; Ellsworth et al. 2024; Lind and Cresswell 2005; Watson et al. 2007). Changes in movement caused by connectivity could alter patterns of gene flow and effective population size, which are important components of population viability and affect the potential for adaptation in changing environments (John L Orrock 2005). As a result, our findings may be helpful for informing models seeking to understand and predict white-tailed deer behavior in human-altered landscapes (Abernathy et al. 2022; Chitwood et al. 2017; Delisle et al. 2024; Gulsby et al. 2018).

In addition to helping inform models of animal behavior and movement, our results illustrate a distinction between landscapes and animal behavior: that edge connectivity, not edge density, has unique effects on animal orientation and movement behavior. An exciting possibility is that the observed effects of edges on deer may interact with other aspects of the environment to help provide a deeper mechanistic understanding of the factors that can affect deer behavior. For example, deer in our study area also exhibit greater vigilance in habitats that have recently experienced prescribed fire (Bartel et al. 2023; Cherry et al. 2016, 2017) as well as past patch disturbances, such as past agricultural land use (Bartel et al. 2023). The strong effect of edge density on vigilance that we observed here could amplify shifts in vigilance caused by prescribed fire or past land use, giving rise to potentially large (and currently unexplored) changes in vigilance in present-day landscapes. However, it is unknown whether interactions occur between these aspects of landscape change, including whether deer movement through connected habitats is more or less likely depending on whether they were recently burned.

4.2 | Deer Behavior and Habitat Connectivity

Corridors are linear landscape elements meant to increase population viability by increasing movement of organisms between habitat patches (Gilbert-Norton et al. 2010; Haddad et al. 2015).

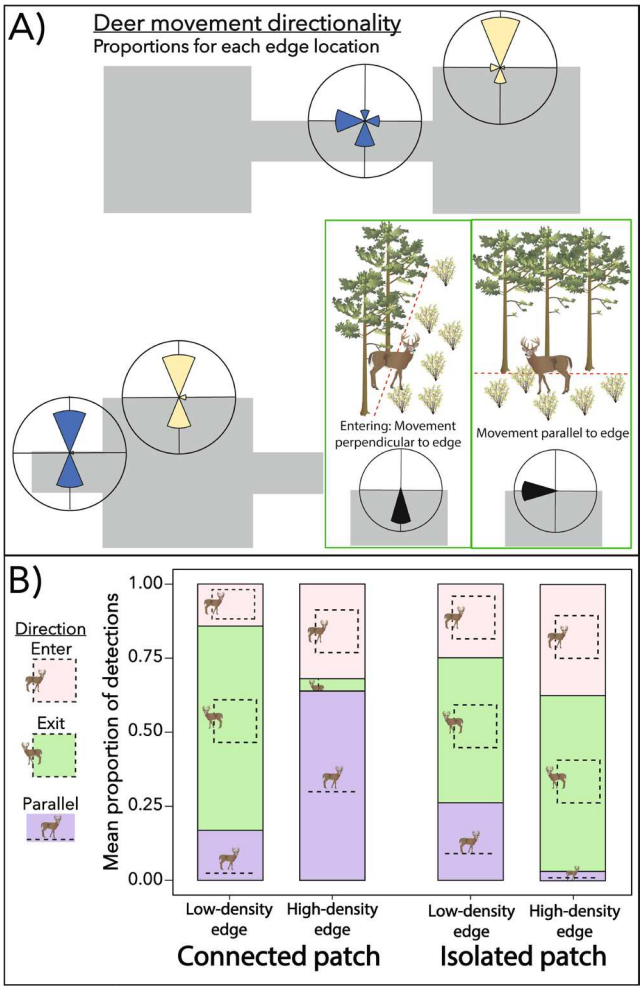

FIGURE 3 | (A) White-tailed deer movement directionality was estimated based on the angle of movement relative to the edge. In high-density connected edges, the majority of deer movement was parallel to the edge in both directions, indicating movement through the habitat corridor toward both connecting patches. Deer were more likely to enter a patch than to exit a patch along a high-density connected edge. The majority of deer movement at low-density connected edges was directed to exiting the patch. At unconnected edges, deer movement was mostly directed toward exiting or entering the patch, regardless of edge density. (B) The probability of parallel movement was greater along high-density connected edges than at all other edge types. The probability of exiting a patch was lower at high-density connected edges than at all other edge types.

Some linear landscape elements (e.g., roads, powerlines, or seismic lines) can increase perceived and actual predation risk for mammalian prey (DeMars and Boutin 2018; Dickie et al. 2020; James and Stuart-Smith 2000). Because our study explicitly manipulates both edge density and connectivity, our results indicate that the linear (edge-rich) shape of habitat corridors, not the connectivity provided by corridors, may give rise to an increase in perceived predation risk in white-tailed deer. Despite this enhanced perception of risk, our results suggest that deer movement behavior along the edges of connected patches may facilitate movement along corridors, which supports previous work showing that large mammals use corridors to reach patches of connected habitat (Bhardwaj et al. 2020; Clevenger and Waltho 2005; Hilty et al. 2006; Hilty and Merenlender 2004;

Seidler et al. 2018). Our results also illustrate that connected high-density edges may serve as 'drift fences' that intercept individuals moving through a landscape (Fried et al. 2005): deer often entered connected high-density edges, often moved parallel to them, but rarely left the patch through them (Figure 3). In contrast, unconnected high-density edges were often areas where deer entered or exited a patch, rarely moving along the edge (Figure 3).

4.3 | Potential Implications of Edge- and Connectivity-Mediated Changes in Deer Behavior

Shifts in animal antipredator behavior can have cascading effects on communities (Schmitz et al. 1997, 2004; Werner and Peacor 2003), and a significant body of literature describes the potential implications of ungulate antipredator behavior in affecting plant communities (e.g., Callan et al. 2013; Cherry et al. 2016; Ford et al. 2014). Our results suggest that edges, by changing deer vigilance, may lead to important effects on plant communities along habitat edges. For example, deer foraging in risky environments may opt to forage on less-desirable plant species that can be consumed without compromising vigilance. Cherry et al. (2016) found that white-tailed deer foraging in riskier habitats were more likely to browse saplings (e.g., oaks) that could be consumed without lowering their heads, while deer in low-risk environments consumed greater amounts of preferred plant species, such as *Lespedeza* spp., *Rubus* spp., and *Smilax* spp. These shifts in deer behavior ultimately led to increases in the richness of deer-preferred species in riskier habitats (Cherry et al. 2016) and may contribute to similar patterns in vegetation communities in other studies (Bartel and Orrock 2023).

Our results also indicate how the effect of habitat connectivity on deer movement behavior may be an important facet of understanding interactions mediated by deer. For example, deer can be important agents of seed dispersal (Baltzinger et al. 2019; Guiden et al. 2015; Myers et al. 2004). Our results give rise to the hypothesis that edge connectivity, by affecting deer movement behavior, could ultimately affect rates of plant dispersal between patches, as well as determine the likelihood of seed dispersal at particular types of habitat (e.g., if deer spend less time at habitat edges, seed deposition may be directed away from edge habitats). Edge –and connectivity-mediated changes in deer behavior may thus contribute to the large-scale benefits of conservation corridors for plant communities, helping explain why animal-dispersed plant species are more common in habitats connected with high-edge conservation corridors (Damschen et al. 2008). The effect of landscape characteristics on animal behavior can thus be an important component of understanding patterns of plant dispersal.

4.4 | Conclusions and Future Directions

Understanding how edges and connectivity affect animal vigilance and movement behavior is essential for understanding the implications of animal behavior for individuals, populations, and communities in a world characterized by human modification of landscapes (Guiden et al. 2019). In finding a significant effect of edges and connectivity on deer behavior, our results set the stage for future studies that explore additional aspects of deer and coyote behavior in human-modified landscapes. For example, the timing of our study was selected to examine deer behavior at a time when it is likely to be sensitive to predation risk, i.e., when female deer may be wary of coyotes that attack fawns (Kilgo et al. 2012), which limits the seasonal generalizability of these findings (Webster and Rutz 2020). Given the growing appreciation for seasonal variation in deer antipredator behavior (Clare et al. 2023) and evidence that edges can drive strong changes in vigilance during the summer period we studied (Figure 2), future studies that evaluate the strength of edge-mediated changes in vigilance and movement would be useful for understanding if there are particular times and seasons when responses to edges are greatly elevated or greatly reduced. Moreover, an interesting, yet untested possibility is that increased vigilance along edges leads to shifts in coyote behavior, such as edge-mediated changes in preferred prey species.

Author Contributions

Savannah L. Bartel: conceptualization, investigation, funding acquisition, methodology, formal analysis, data curation, visualization, writing – original draft. **Leotie Hakkila:** investigation, writing – review and editing, data curation. **John L. Orrock:** supervision, resources, project administration, writing – review and editing, conceptualization, investigation, funding acquisition, methodology, visualization.

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Conflicts of Interest

The authors declare no conflicts of interest.

Data Availability Statement

Analyses reported in this article can be reproduced using the data and code provided by Bartel et al. (2025).

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