

# Anthropogenic meadows provide foraging subsidies for white-tailed deer in fragmented forest ecosystems

Matthew A Wuensch

[mwuensch@kent.edu](mailto:mwuensch@kent.edu)

Kent State University <https://orcid.org/0000-0002-5826-4936>

Andrew C Eagar

Michigan State University

David Ward

Kent State University

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## Research Article

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# Abstract

White-tailed deer (*Odocoileus virginianus*) populations persist at densities higher than historical estimates throughout much of their North American range. In forest ecosystems, heavy browsing by high-density deer populations can suppress the growth and regeneration of woody plants and promote the establishment and growth of non-preferred forage items, such as grasses and ferns. Additionally, as forests are altered by anthropogenic development, grasslands and meadows are becoming increasingly common in forest landscapes where deer occur. We used activity densities to measure the seasonal patch preference of white-tailed deer between forest patches and anthropogenically-introduced meadows in northeast Ohio, a region with high-density deer populations. We also quantified the plant communities that were present in each patch type to identify forage plants that were available to deer. We found that deer preferred meadow patches and avoided forests during spring and summer. Meadow patches primarily consisted of non-native forage plants that are nutritionally beneficial to deer, whereas forests possessed fewer nutritionally beneficial plants and contained an abundance of open ground. However, as plants senesced and forage availability on the landscape decreased during autumn and winter, deer did not prefer any patch type. Our results suggest that in anthropogenically fragmented forests, meadows can provide deer with a potentially overlooked foraging subsidy that should be considered when managing high-density deer populations.

## Significance statement

In anthropogenically modified environments, populations of white-tailed deer can occur at high densities that negatively affect plant communities via heavy browsing. Anthropogenic disturbance regimes and supplemental foraging opportunities can help support overabundant deer populations; however, the seasonal patch-use of deer in anthropogenically modified environments remains less understood. By measuring activity densities, we found that deer preferred anthropogenic meadow patches rather than forest patches at times when resources were abundant, and thus deer could be selective in their patch use. Plant communities in meadow patches primarily consisted of non-native forage plants that were likely nutritionally beneficial, whereas forests contained an abundance of bare ground and few high-quality forage plants. We suggest that, in fragmented systems where forest patches have been degraded, anthropogenic meadows may provide overabundant deer populations with a foraging subsidy that helps to sustain high deer densities.

## Introduction

Throughout much of the range of white-tailed deer (*Odocoileus virginianus*, henceforth referred to as “deer”), deer populations persist at high densities that greatly exceed historic estimates (McCabe and McCabe 1997; té et al. 2004; McMahon et al. 2021). At high densities, the foraging behavior of deer can have deleterious effects on forest ecosystems by altering tree recruitment and hindering forest growth and regeneration (Goetsch et al. 2011; Rushing et al. 2020). Additionally, deer are selective in their foraging habits – typically preferring to forage on trees and shrubs in forest ecosystems rather than

nutritionally poor grasses, ferns and sedges that can be found in forests and grasslands alike (Rooney 2001; Berry et al. 2019). In some regions, this selective foraging behavior has led to forest understories that are either relatively barren or dominated by nutrient-poor sedges and ferns that deer do not prefer to forage upon (Rooney 2001; Goetsch et al. 2011). Yet, despite a relative absence of high-nutrient forage in forest understories, deer populations continue to persist at high densities in many regions, and in some areas populations continue to grow (Shafer-Nolan 1997; Stewart et al. 2007; Russell et al. 2017).

Due to the generalist foraging behavior and broad range of habitats that deer can occupy, it is typically suggested that anthropogenic modifications to the landscape may contribute to high abundances of deer (Alverson et al. 1988; Laurent et al. 2021). Anthropogenically disturbed landscapes may support overabundant deer populations by providing deer with foraging subsidies via access to agriculture in rural environments and via ornamental plants and wildlife feeders in suburban environments (Grund et al. 2002; Grovenburg et al. 2010; Potapov et al. 2014; Haus et al. 2020). Additionally, anthropogenic activities can result in heterogeneity (i.e., patchiness) within forest landscapes, which promotes plant growth at browse height that deer can use as forage (Alverson et al. 1988; Potapov et al. 2014; Darlington et al. 2022). However, there is currently limited empirical evidence that has examined the small-scale patch use, and factors within a patch, that deer prefer in anthropogenically fragmented landscapes.

When considering how deer navigate and use heterogeneous landscapes, it is important to consider the phenology of the plants that deer are consuming because forage abundance and quality both change with plant phenology (Buxton and Marten 1989; Van der Wal et al. 2000). In temperate climates, during spring when plants begin to green up after being dormant, they are highly nutritious and easy for herbivores to digest (Fryxell 1991; Hebblewhite et al. 2008). During summer, the availability of vegetative biomass is at its peak and there is an abundance of forage available to deer across the landscape. When there are multiple foraging options available, generalist herbivores such as deer should be able to selectively forage across the landscape and select food items that are the most nutritiously beneficial (Stephens and Krebs 1986; Sauvé and Côté 2007; Dykes et al. 2020). During autumn, green biomass begins to senesce and deer are expected to opportunistically select patches that still contain high-quality forage; however, as patch quality depletes over time deer will become less selective (Dostaler et al. 2011). In winter, foraging resources in temperate areas are limited in availability and typically of poor quality compared to summer (van Beest et al. 2010; Schuyler et al. 2021). At times when foraging resources are scarce, deer broaden their dietary breadth and landscape use to meet their metabolic needs (Berteaux et al. 1998; Dumont et al. 2005).

According to optimal foraging theory, herbivores are expected to select for a patch that confers the greatest benefits and imposes the lowest costs (MacArthur and Pianka 1966; Belovsky 1984; Vincent et al. 1996; Owen-Smith et al. 2010). Typically, forest-dwelling plants such as trees and shrubs have a greater crude protein content than grasses, ferns, and sedges (Hanley 1982; Holechek 1984). This is important for large herbivores when considering forage preference and habitat selection, because crude protein is typically a limiting resource in their diets (Owen-Smith and Novellie 1982). Thus, it is typically

expected that deer, and other herbivore species that are concentrate selectors in their foraging habits will prefer patches that contain an abundance of high-quality shrubs and herbaceous plants over patches that contain nutrient-poor forage items (Demment and Van Soest 1985; McShea 2012; Pendergast et al. 2016). As foraging opportunities in forests become degraded due to heavy browsing by deer, alternative patch types may become more desirable to deer than forests if the alternative patch types provide benefits that exceed those in the forest (Hobbs and Swift 1985; Rieucan et al. 2009). Additionally, patch quality can be influenced by varying levels of predation risk on the landscape (Laundré et al. 2010). Vegetative cover that conceals predators and impedes the line of sight of prey species may result in a higher risk of predation, and therefore decrease the overall value of a patch (Lagory 1986; Brown and Kotler 2004). Patches where predator species are more active also decrease the value of a patch to mammalian herbivores due to the increased likelihood of encounters with predators (Kauffman et al. 2010; Iribarren and Kotler 2012). Thus, patches that mammalian herbivores, such as deer, should prefer are those that offer the greatest foraging benefits without increasing predation risk.

Our objective was to use activity densities to discern the patch use and preference of white-tailed deer throughout the year in an anthropogenically-fragmented forest ecosystem. Specifically, we wanted to determine if deer activity was greater in forest patches or anthropogenically modified meadows. One method that is often employed to quantify patch preference is to determine the amount of time or foraging effort that a species will allocate to different patch types (Ziv et al. 1993; Schmidt and Schaubert 2007). A simple and minimally invasive method to quantify such behaviors is through collecting activity densities – a measurement of foraging effort that accounts for the activity and number of animals foraging at a given location (China et al. 2008). Activity densities can be determined by measuring the amount of foraging effort or detection rates of animals in different patch types (Mitchell et al. 1990; Schmidt and Schaubert 2007). We also quantified the vegetative community present within both patch types to gain insight into the type and quality of forage within each patch. We predicted that deer patch preference would vary depending on the season, with high-stress periods (autumn and winter) resulting in less-selective patch use by deer and low-stress periods (spring and summer) resulting in selective behavior for higher quality patches.

## Methods

### Study area

We conducted this experiment at three field sites in suburban parks in the vicinity of Medina, Ohio, USA. The region is recorded as a cold zone with warm to hot summers, cold winters, and no dry season (Peel et al. 2007; Beck et al. 2018). We collected data from two sites in the Chandler Preserve (~ 60 ha, 41.14° N, 81.82° W), and one site in the Hinckley Reservation (~ 200 ha, 41.20° N, 81.70° W). The Chandler Preserve and Hinckley Reservation are both in suburban areas and consist of mixed hardwood forests that are fragmented by patches of meadow. The meadow habitats at both sites are comprised of a mixture of grasses and herbaceous plants, some of which are indicative of prior agricultural land use (Fig. 1). Hunting of deer is not permitted in either of the two parks, and coyotes (*Canis latrans*) are the

only natural predators of deer in our study region. However, it is uncommon for coyotes to prey on adult deer in this region (Cepek 2004). Human disturbance in both sites is limited to hiking trails that were > 100 m from any of our sites.

## Collecting patch preference data

To quantify the patch use of deer, we measured activity densities via feeders that were constructed from polyvinyl chloride (PVC) pipe and specifically designed to restrict the access of non-target species (Wuensch et al. 2023). The PVC feeder design consisted of a feeder that was constructed from 10.2 cm pipe that created a feeding spout for deer to withdraw food. The spout of the PVC feeder was elevated 1.2 m above the ground. To prevent non-target species from climbing the steel-pipe stand, we placed a 15 cm diameter collar around the stand. We did not include any inedible substrate in the PVC feeders because it completely inhibited deer from accessing food. The lack of inedible substrate in the feeders meant that they lacked diminishing returns, which is incorporated into other foraging study designs (Brown 1988; Kotler and Brown 1990). Therefore, the activity densities that we measured from the feeders provided us with information on deer presence and foraging effort within different patch types (China et al. 2008; Wuensch et al. 2023)

At each of our three sites, we placed four PVC feeders on three 120 m transects (12 total feeders per site) that were perpendicular to the linear ecotone between the forest and meadow patches. Each transect extended 60 m from the ecotone into the forest and 60 m from the ecotone into the meadow. Each of the three transects were parallel to one another and separated by 35 m. Each transect possessed feeders that were placed at: meadow 60 m from ecotone, meadow 20 m from ecotone, forest 20 m from ecotone, and forest 60 m from ecotone. The food source that we placed in each feeder was shelled maize (*Zea mays*), due to it being a supplemental food source that white-tailed deer use when it is available (Vercauteren and Hygnstrom 1998; Grovenburg et al. 2010; Delger et al. 2011). We collected data during four sampling periods during 2019 and 2020. We selected dates that coincided with the changing of seasons in our region: spring (March 2019), summer (July 2019), autumn (October 2019), and winter (January 2020). During each season, we measured activity densities for six consecutive days. Prior to data collection, we allowed a two-week conditioning period in which the feeders were filled with maize and no data were collected. Based on preliminary trials, this provided time to allow deer to recognize the feeders as a foraging opportunity. To measure activity densities, we placed 1.6 kg of maize in each feeder and allowed deer to forage for ~ 24 h. After 24 h, we returned and collected the remaining maize and weighed it to the nearest g. The total amount of maize eaten during a 24 h period was the activity density for a given feeder. We used 1.6 kg of maize because a preliminary data collection found that deer would completely consume smaller quantities.

## Vegetation sampling

We implemented the Braun-Blanquet cover-abundance scale (Mueller-Dombois and Ellenberg 1974) to quantify the vegetative species present in the forest understory and meadow patches at all three of our sites. In the meadow and forest patches at each site we sampled twelve plots. In each patch type, we

collected data from six plots that were associated with a feeder location and six plots that were at random locations within the bounds of our transects. We placed plots that were associated with a feeder at a location of 3 m from the feeder base in a randomly determined cardinal direction. We placed random plots at locations in the forest and meadow patches by creating a grid in each patch type. To create a grid, we placed marks at 1 m intervals along an x-axis that followed the linear ecotone and a y-axis that extended 60 m from the ecotone into each patch type. We then randomly generated x and y coordinates to determine a random plot location. Any coordinates that were generated within 2 m of another plot were omitted and new coordinates were generated.

To sample our plots, we placed a 1 X 1 m frame on the ground and included any plant that possessed roots that originated from within the frame. Due to some species being indistinguishable at the time of sampling, we were only able to identify some plant species to genus. We assigned each species a Braun-Blanquet score which corresponded to the range of cover the species presented in the plot (supplementary table 1). Moreover, we estimated the proportion of bare ground within each plot. To analyze the data, we converted Braun-Blanquet coverage scores to a median coverage value (Wikum and Shanholtzer 1978), then summed the median values of all species (including open ground) present within a plot and calculated the proportional cover of each species. All Braun-Blanquet vegetation sampling was conducted after we collected summer activity densities in July.

Table 1

–  $R^2$  values for plant taxonomic groups showing their goodness of fit in relation to the first axis of a redundancy analysis that we performed to ascertain differences between vegetative communities in forest, meadow and ecotone patch types. We extracted taxonomic groups with an  $R^2$  value of greater than 0.25 because these groups provided the best depiction of which plants were strongly associated with patch type.

Plant taxonomic group	$R^2$
<i>Poa</i> spp.	0.55
Open ground	0.51
<i>S. canadensis</i>	0.40
<i>B. inermis</i>	0.37
<i>Fraxinus</i> spp.	0.35
<i>A. odoratum</i>	0.35
<i>Carex</i> spp.	0.31
<i>I. capensis</i>	0.30
<i>P. quinquefolia</i>	0.30
<i>R. acris</i>	0.28
<i>J. tenuis</i>	0.27
<i>T. repens</i>	0.27

## Statistical analyses of vegetation

To assess the variation in the understory vegetation communities, we analyzed the plant abundance data via redundancy analysis (RDA) with patch type modeled as an explanatory variable and site modeled as a conditional effect using the *vegan* package in R (Oksanen et al. 2020, R Core Team 2020). Rather than conducting RDA on values that were proportions of landcover, we transformed the proportions of each plant taxonomic group and open ground into theoretical plant communities for each plot by multiplying the proportion of cover for each taxonomic group and open ground by 1,000, thus representing a theoretical plant community. We performed a Hellinger transformation on the abundance values in our theoretical plant communities (Rao 1995; Legendre and Gallagher 2001; Borcard et al. 2018). Hellinger transformations give low weight to the importance of rare or absent species in a community (Legendre

and Gallagher 2001). This analysis allowed us to assess differences in plant community composition among habitats. We used the *goodness()* function in the package *vegan* to ascertain the goodness-of-fit ( $R^2$ ) for each plant species in relation to the first RDA axes and included any species with an  $R^2$  value of > 25% in the biplot (figure. 1).

## Statistical analyses of patch preference

We used Manly's selection ratio to determine patch preference of deer from each transect during each season (Manly et al. 2007). To calculate the selection ratio for patch  $i$  ( $w_i$ ) we divided the proportion of resources that are available within the feeders in the  $i^{th}$  patch ( $p_i$ ) by the amount of resources that were used by deer in the  $i^{th}$  patch ( $o_i$  formula:  $w_i = \frac{o_i}{p_i}$ ). We defined  $o_i$  as the sum of all daily activity densities (total maize that was consumed by deer) in a given patch during a season, and  $p_i$  as the sum of all maize that was available to deer in a given patch during a season. We used a type II design for analysis, measuring selection ratios for transects within each site, and calculated Bonferroni-corrected 95% confidence limits (CL) for each selection ratio (Manly et al. 2007). Selection ratios in which the lower Bonferroni CL was > 1 indicated that a patch was preferred by deer and selection ratios in which the upper Bonferroni CL < 1 indicated that a patch was avoided by deer. Selection ratios that had either the upper or lower Bonferroni CL intersect with a value of 1 indicate that a patch has no preference.

## Results

### Vegetation results

By performing RDA on the vegetation communities present at our field sites (Fig. 1, model adjusted  $R^2$  = 0.27), we found that the vegetation communities differed significantly among patch types ( $p < 0.001$ ,  $F = 28.83$ ,  $n = 999$  permutations). The constraining factors of the RDA were responsible for explaining 26.92% of the variance among plant communities (63.49% of the variance was unconstrained). Our conditional effect (study site) was responsible for explaining the remaining 9.60% of the variance among plant communities. We identified 12 plant species that had a goodness of fit ( $R^2$  value) greater than 0.25 with the RDA axis (Table 1).

Of the plant species included in the RDA, we found that juvenile ash trees (*Fraxinus* spp.), sedges (*Carex* spp.), Virginia creeper (*Parthenocissus quinquefolia*), and spotted jewelweed (*Impatiens capensis*) were strongly associated with plots in the forest patch type. Open ground was also associated with vegetation plots in the forest patch. Plants most associated with the meadow patch type were Canada goldenrod (*Solidago canadensis*), bluegrass (*Poa* spp.), sweet vernal grass (*Anthoxanthum odoratum*), tall buttercup (*Ranunculus acris*), smooth brome (*Bromus inermis*), white clover (*Trifolium repens*), and slender rush (*Juncus tenuis*)

### Patch preference results



During spring and summer, we found that deer activity was greater in meadow patches than in the forest (Fig. 2). During spring and summer, deer significantly preferred meadows (Fig. 2, selection ratios:  $w_{\text{meadow spring}} = 1.21$ ,  $w_{\text{meadow summer}} = 1.51$ ), and avoided forest patches (Fig. 2,  $w_{\text{forest spring}} = 0.79$ ,  $w_{\text{forest summer}} = 0.49$ ). During autumn and winter, we did not find that deer activity differed significantly between patch types. Both the forest and meadow patches were of neutral preference to deer because the Bonferroni CL overlapped with a value of 1.

## Discussion

We found that in forest ecosystems fragmented by anthropogenic development, deer activity varied between forest and meadow patches, and the patch type that deer preferred varied depending on season. Interestingly, deer preferred anthropogenic meadow patches during seasons when resources were abundant across the landscape (i.e., spring and summer), and deer did not prefer forest patches during any time of year. We suspect that deer patch preference varied among seasons due to shifts in plant phenology and structure throughout the year, which can consequentially change the nutritional benefits and costs that a patch confers to a herbivore (Moore et al. 2010; Middleton et al. 2018). Additionally, meadow patches may have provided deer with a patch type where they felt less at risk to predation due to shorter vertical vegetation that can conceal predators such as coyotes, thus deer could decrease vigilance behavior (Donadio and Buskirk 2016; Gulsby et al. 2018). Ultimately, we suggest that anthropogenically introduced meadow habitats will help to support overabundant deer populations by providing deer with a supplemental foraging opportunity that exceeds the value of adjacent forest landscapes that can be degraded due to heavy browsing pressure.

We initially expected that deer would have the greater activity densities in the forest patches due to forbs and woody vegetation being more nutritionally beneficial than grasses (i.e., higher crude protein and energy - Demment and Van Soest 1985, du Toit and Owen-Smith 1989, Wigley et al. 2015). However, we did not find that deer preferred forest patches during any season. Instead, we found that deer preferred meadow patches in spring and summer, likely due to an abundance of green forage that was available in meadows compared to the forest understories. We predicted that forest patches would possess an abundance of high-quality broad-leafed trees and herbaceous plants for deer to consume, but found that the forest patches possessed an abundance of bare ground, and provided relatively few shrubs and juvenile trees that are nutritionally beneficial for deer. When deer persist at high densities, forest understories become highly degraded due to heavy browsing, and no longer possess an abundance of high-quality forage (Rooney and Waller 2003; té et al. 2004; Goetsch et al. 2011; Pendergast et al. 2016). Deer densities that are greater than approximately 5 deer km<sup>2</sup> are considered harmful to understory plant species (Alverson et al. 1988; Russell et al. 2001; McShea 2012). In the vicinity of our study in northeast Ohio, previous estimates of deer densities were approximately 36 deer km<sup>2</sup> and were predicted to increase (Shafer-Nolan 1997; Fulton et al. 2004). Therefore, due to heavy browsing pressure from deer populations at high densities, the understories in the forest patches where we measured activity densities likely did not confer much foraging benefit to deer.

In addition to degraded forests, our result that deer preferred meadows in the spring and summer can be explained by the abundant and high-quality forage that we found in the meadow patches and better lines of sight to detect predators. The plant species that had the greatest associations with the meadow patches were species that are non-native and frequently associated with agricultural land use (e.g., smooth brome [*Bromus inermis*], white clover [*Trifolium repens*], bluegrass [*Poa* spp.]) (Johnson et al. 1987; Ellis-Felege et al. 2013). Cultivated forage species such as these generally have a high crude protein content and can provide wildlife high-quality foraging opportunities (Johnson et al. 1987; Dykes et al. 2020). Additionally, many cultivated forage species associated with meadows are grasses and therefore possess little to no plant secondary metabolites such as tannins or polyphenols to defend against herbivory (Orians and Ward 2010; Ward et al. 2020). Moreover, there was a greater availability of forage in the meadows, which was reflected by open ground being more abundant in forest plots. Therefore, the generalist foraging behavior of deer enabled them to use the more beneficial meadow patch during spring and summer.

Whereas coyotes primarily prey upon neonate deer (Vreeland et al. 2004; Kilgo et al. 2010, 2014) and hunting is not permitted in our study sites, meadow patches may have provided deer with a patch type where they felt less at risk to predation. Deer are most susceptible to predation from coyotes during the neonate and juvenile life stages; the risk of predation decreases as fawns grow and become more mobile (Vreeland et al. 2004; Rohm et al. 2007). Shorter vegetation enables prey species to visually detect predators more easily (Donadio and Buskirk 2016; Chen et al. 2021). Thus, during spring and summer when females are accompanied by fawns, deer activity may have been greater in meadow patches due a more open line-of-sight that affords a better ability to detect predators than forests that may obscure predators due to dense vertical vegetation.

During autumn, deer did not significantly prefer any patch type, and deer activity in the forest patch was relatively similar to deer activity in the meadow patch. We suspect that phenological changes in the vegetation in both the meadow and forest patches were responsible for these shifts in deer activity densities. During autumn in temperate regions, grasses, forbs and other understory species have matured and begun to senesce. As plants mature, the crude protein content deteriorates and becomes much less desirable forage to herbivores (Fryxell 1991; Van Soest 2018; Geremia et al. 2019). At this time of year, the vegetation that was present in the meadow patches was much less beneficial to deer than it was during the spring and summer months, thus explaining a decrease in deer activity in the meadow when compared to spring and summer activity densities. Additionally, as the vegetation in the meadow deteriorated in quality during autumn, mast crops such as acorns, hickory nuts and walnuts, that are a valuable foraging resource for deer and other wildlife (Harlow et al. 1975; Eagle and Pelton 1983; Elston and Hewitt 2010), became available in the forest. The forest patches at our sites consisted primarily of mixed hardwoods, of which the primary mast trees were shagbark hickory (*Carya ovata*) and various oak species (*Quercus* spp.). While forests were not significantly preferred by deer in autumn, an increase in mast crop availability likely contributed to the similar deer activity between the forest and meadow patches.

During winter, we did not discern any difference in deer activity densities in relation to patch type. In regions that experience harsh winters with cold temperatures and regular snowfall, such as northeast Ohio where this study took place, high-quality foraging opportunities for deer are scarce across all patch types because herbaceous food items have fully senesced and are of poor nutritional quality (Schmitz 1992; Van Soest 2018). Moreover, masting crops that were available during autumn have mostly been consumed by other wildlife or cached by small mammals, and are not a reliable food source (Wolff 1996; Fay et al. 2023). When there is a lack of food present on the landscape, deer employ a broad foraging strategy in which they decrease selectivity to meet their dietary needs (Berteaux et al. 1998; Dumont et al. 2005). Therefore, we expect that deer were not selective in their patch use during winter (when forage quality was likely at its lowest) and used multiple patch types across the entire landscape, rather than foraging in a single patch that may confer only minimal benefit. Moreover, because deer benefit from using agriculture as a resource subsidy during winter months (Vercauteren and Hygnstrom 1998; Grovenburg et al. 2010) it is possible that deer relocated out of the parks where we collected data and increased their activity in surrounding agricultural areas instead.

Due to the effects of global climate change, many temperate regions are predicted to experience longer, hotter summers and shorter, warmer winters with less snow (Kreyling 2010; Piao et al. 2019; Wang et al. 2021). This means that vegetation in these regions will remain green and more nutritionally beneficial to deer and other herbivores for longer periods throughout the year (Piao et al. 2019). Moreover, throughout much of North America, anthropogenic development is expanding, and deer will have increasing access to anthropogenically introduced meadow habitats in suburban and fragmented landscapes. A scenario in which non-native meadows become more abundant and growing periods increase in duration will increase forage opportunities for deer and may serve to support high-density deer populations. We suggest that in suburban landscapes where deer populations are overabundant, managing meadow patches to be less desirable to deer (e.g., seeding less nutritionally beneficial plants) may decrease the quality of landscape to deer and help reduce deer abundance.

## **Declarations**

### **Declaration of funding**

Funding was provided by the Herrick Trust, Kent State University.

### **Conflicts of interest**

The authors declare no conflicts of interest.

### **Ethics approval**

A formal, ethical review of this experiment was not required because measuring activity densities is a non-invasive technique. The use of animals adhered to the guidelines

set forth by the Animal Behavior Society/Association for the Study of Animal Behavior.

## Data availability statement

All data are made available as supplementary material for the review process. All associated data, metadata, and R code will be made publically available and assigned a DOI prior to publication of this manuscript.

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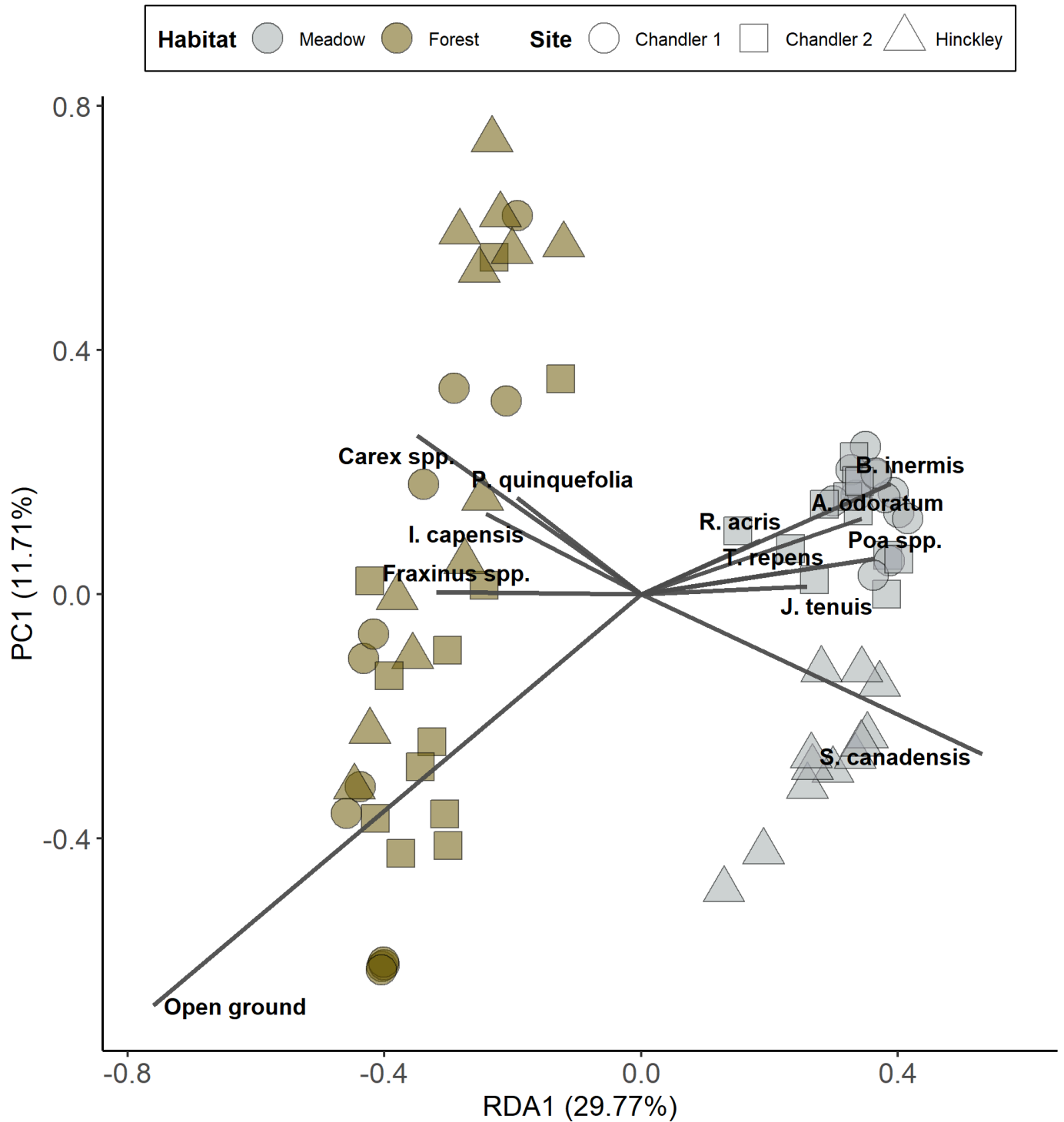
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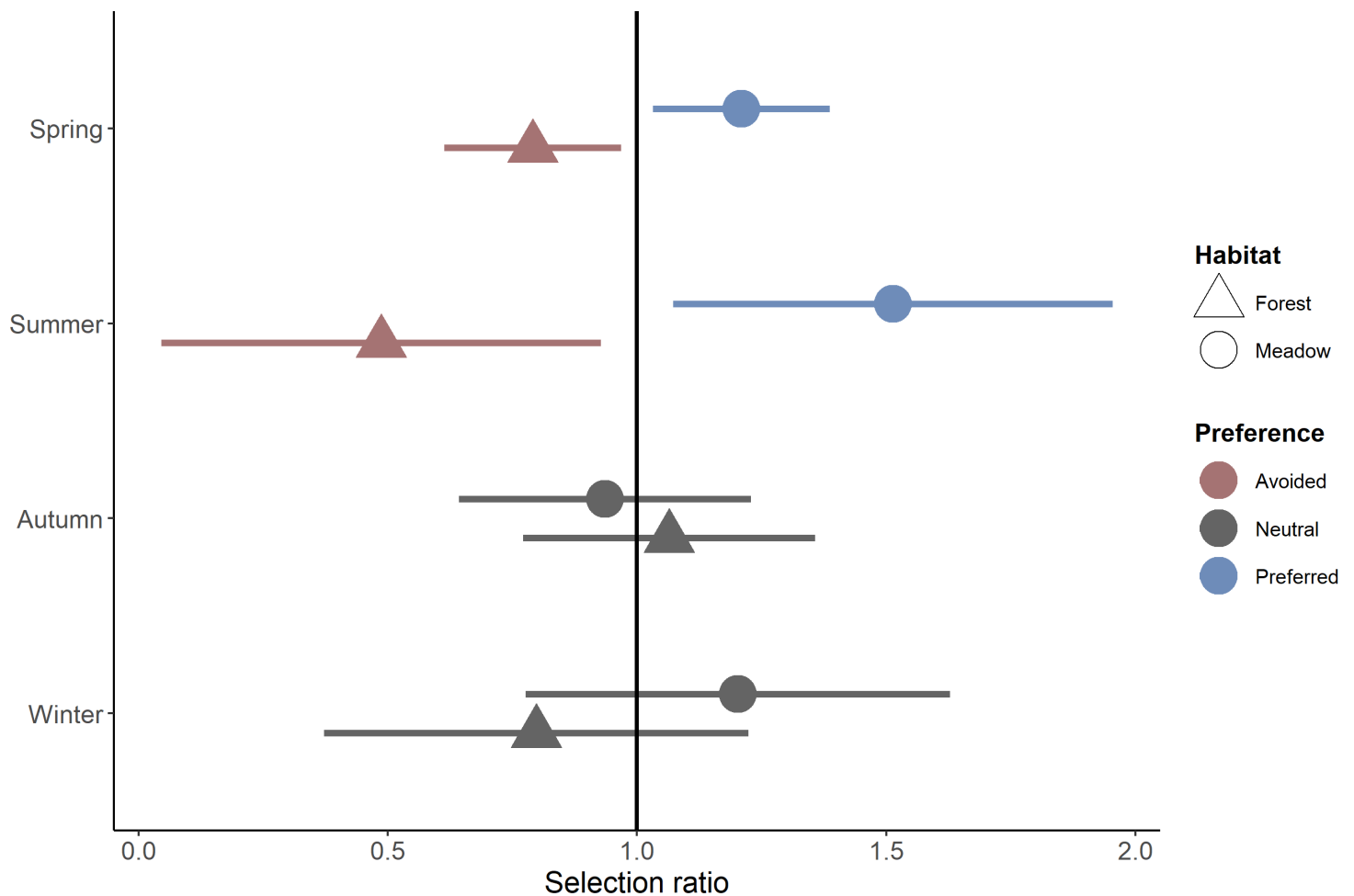
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## Figures



**Figure 1**

Plot showing redundancy analysis (RDA) scores of vegetation plots that we measured among meadow and forest patch types. RDA1 scores explained 29.77% of the variance among our plots and PC1 explained 11.71% of the variance. We included the scores of 12 species or genera of plants that had an  $R^2$  value of greater than 0.25 and are represented by grey vectors overlaid on the plot and terminate with the scientific name or genus labeling the vector. Vectors that are longer indicate a higher  $R^2$  value, and thus a stronger relationship to the plots that are located near the vector.



**Figure 2**

The patch preference scores of white-tailed deer as calculated by Manly's selection ratio during four seasons. Selection ratios were determined using the activity densities of white-tailed deer that we measured within each patch type during each season. The centroid shape of each value indicates the mean selection ratio, and the arms extending from the centroid represent upper and lower Bonferroni-corrected 95% confidence intervals. Values in which the lower Bonferroni-corrected confidence interval  $<1$  indicate that deer preferred a patch type, and values in which the upper Bonferroni-corrected confidence interval  $>1$  indicate that deer avoided that patch type. If the confidence intervals intersect 1, a plot is considered to be of neutral preference by white-tailed deer.

## Supplementary Files

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