

**The roles of habitat area, fragmentation, and vegetation diversity in bird and snake  
habitat quality in agricultural landscapes in Iowa, USA**

by

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## **DEDICATION**

This work is dedicated to my wife, without whose love and support this substantial undertaking would not have been possible.

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## ABSTRACT

Widespread loss of native grasslands has led to major population declines of grassland wildlife worldwide, including in North America. Continent-wide, 71.2% of the historical extent of the North American tallgrass prairie has been converted to cropland, contributing to the decline of 74% of grassland bird species and the threat of extinction for 12% of Palearctic reptile species. In this dissertation my objectives were to investigate what environmental variables drive grassland nesting passerine nest success in extensively cropped landscapes, determine the best supported framework for explaining brown-headed cowbird (*Molothrus ater*) parasitism on grassland nesting birds, and to survey snake and lizard biodiversity in these landscapes.

I provide an in-depth examination of the factors that drive grassland-nesting passerine nest density and survival in landscapes dominated by agricultural production. Red-winged blackbirds (*Agelaius phoeniceus*) and Dickcissels (*Spiza americana*) were the only species for which we found enough nests to allow models to converge with a useful number of predictor variables, so we also modeled grassland nesting passerines as a guild which also included vesper sparrows (*Pooecetes gramineus*), common yellowthroats (*Geothlypis trichas*), meadowlarks (*Sturnella spp.*), and four other species. Nest density and survival for Red-winged blackbirds, Dickcissels, and grassland nesting passerines as a guild were best predicted by both habitat amount and configuration, often interacting such that configuration effects reversed direction depending on the amount of habitat on the landscape. Vegetation diversity and density consistently positively predicted nest density and survival, demonstrating that local habitat quality had similar effects as landscape composition. Landscape woody land cover amount had a negative effect on both nest density and survival.

I also compared three existing and two new hypotheses on how brown-headed cowbirds located nests to parasitize, including the edge effect hypothesis, the perch proximity hypothesis, the nest exposure hypothesis, the Habitat Amount Hypothesis (HAH), and the vegetation diversity hypothesis. I found that the covariates on nest parasitism occurrence that best fit the data included habitat amount and distance to crop edge. This lent support to the edge effect hypothesis but not the others.

Finally, I investigated how habitat amount, habitat configuration, and vegetation diversity affected terrestrial reptile occupancy, presence, and biodiversity in low habitat, highly fragmented agricultural landscapes. Snake and lizard encounter rates were very low. Although I encountered terrestrial reptiles infrequently in these fragmented agricultural landscapes, the majority of encounters were with Iowa Species of Greatest Conservation Need. The most important variables in a global model for detection-corrected occupancy were patch isolation, patch area, and patch count interacting with nearby habitat amount. I also found that snake presence was positively predicted by vegetation diversity, patch size, and grassland habitat amount and negatively predicted by edge density.

Through these studies I demonstrated that habitat configuration remains an important predictor of demographic parameters after accounting for habitat amount on the landscape. Additionally, I provided evidence that vegetation diversity had positive effects on presence and/or reproductive success of multiple taxa of wildlife in a landscape with a dearth of high diversity vegetation. Finally, I demonstrated that grass contour strips and terraces may be population sinks or ecological traps for grassland breeding passerines. In contrast, prairie contour strips offered similar reproductive success to larger patches of restored prairie in the landscapes

studied, but larger tracts of habitat are necessary to attract area sensitive bird species, reptiles, and lizards.

## CHAPTER 1. GENERAL INTRODUCTION

Widespread loss of native grasslands has led to major population declines of grassland wildlife worldwide (e.g., Teyssèdre and Couvet 2007), including in North America (Stanton et al. 2018). Continent-wide, 71.2% of the historical extent of the North American tallgrass prairie has been converted to cropland (White et al. 2000). The epicenter of that loss is in Iowa, United States, where 99.9% of the native tallgrass prairie land cover has been destroyed since 1833 (Smith 1998). By 2009, grass cover of varying quality had been replanted on an estimated 21.8% of Iowa's land cover (Iowa Department of Natural Resources and Kollasch 2019).

Much of the grassland that now exists in the Midwestern US is on agricultural working lands and is often configured in small, isolated patches dominated by monocultures of exotic cool-season grasses. These two attributes, habitat configuration and vegetation diversity, are likely the primary drivers of habitat quality in agricultural grasslands. I will use Johnson's (2007) definition of habitat quality- "resources and ecological constraints that govern fitness".

The relative importance of habitat area versus habitat configuration to wildlife is an actively debated topic in ecology (see Fletcher et al. 2018, Fahrig et al. 2019) and the relative importance of vegetation diversity on habitat quality for a variety of taxa is not well understood. A better understanding of how habitat area, configuration, and vegetative diversity interact to affect habitat quality for multiple taxa would allow conservationists and policy makers to improve grassland habitat on agricultural working lands and provide improved wildlife habitat across a large percentage of the grassland area in the US Midwest. One recent conservation practice that may improve the habitat quality of grasslands on farms is prairie strips (Schulte et al. 2017).



Prairie strips are buffer strips of diverse native perennial vegetation designed to intercept runoff from agricultural row-crop fields as well as provide other ecosystem benefits (Schulte et al. 2017). Prairie strips have received interest from conservationists and farmers due in part to their demonstrated soil and water conservation benefits. Research conducted at Neal Smith National Wildlife Refuge (Jasper County, Iowa, USA) beginning in 2007 demonstrated that converting as little as 10% of a row-crop catchment to prairie strips could reduce overland water flow by 1.6 times, sediment loss by 20 times, phosphorous runoff 4.3 times, and nitrogen runoff 3.3 times (Schulte et al. 2017). Prairie strips were also found to increase in-field biodiversity, with insect taxa richness 2.6 times higher than in control fields, insect pollinator abundance 3.5 times higher, bird species richness 2.1 times higher, and bird abundance 2.6 times higher (Schulte et al. 2017).

While prairie strips have been shown to provide many ecosystem services, questions about their habitat quality remain. The catchments studied in the first round of prairie strips research were small (0.47-3.19 ha) and embedded in a majority prairie landscape within a national wildlife refuge. Wildlife may interact with prairie strips differently when they are situated in a more typical Midwestern landscape dominated by row-crop agriculture (Schulte et al. 2016). One possibility is that small, linear strips of high-diversity prairie isolated within row-crop fields may act as a population sink or ecological trap for some species (Schulte et al. 2016). The goal of this dissertation was to determine if prairie strips or other agricultural conservation practices (contour grass strips, grass filter strips, grassed terraces, large patch grasslands) constitute population sinks or ecological traps for multiple taxa of vertebrate wildlife.

### **Habitat quality, population sinks, and ecological traps**

Habitat quality is a term that is often used imprecisely, limiting the ability to compare studies (Morrison and Hall 2002). For this study I will consider habitat of sufficient quality if it serves as a population source rather than a sink (Kellner et al. 1992).

Johnson (2007) provides 12 common approaches to measuring habitat quality in two broad categories—measuring habitat directly (1) and measuring wildlife responses to habitat (2). This study will utilize these approaches to varying degrees among different taxa. In this study, birds will receive the most detailed investigation. I will be measuring predators as an ecological constraint (1), vegetation diversity as a correlate of food availability (1), and measure nest density and survival as they relate to habitat characteristics (2). Johnson (2007) cautions that distribution, occupancy, and abundance are not necessarily indicators of habitat quality due to the possibility of maladaptive habitat selection. With this caution in mind, this study will also use occupancy, colonization, and extinction rates as an insight to habitat quality for reptiles and mammals.

Population sinks are patches of habitat where individuals have reduced fitness either through lower survival, lower reproductive success, or both, and thus more individuals die than are born to replace them (Pulliam 1988). An ecological trap is a population sink that also attracts wildlife to either no benefit or reduced benefit to their fitness, potentially resulting in population declines (Robertson and Hutto 2006). Attractiveness and fitness-affecting aspects of a patch are driven in part by its habitat quality (Johnson 2007).

Habitat quality can be a combination of many attributes (see Mortelliti et al. 2010), but habitat area and habitat configuration have received the bulk of the research attention (e.g., Winter et al. 2000, Chalfoun et al. 2002, Ries et al. 2004, Fahrig 2013, Fletcher et al. 2018, Fahrig et al. 2019). Another possible aspect of habitat quality that has received far less study in

vertebrate communities is vegetation diversity. This study will investigate the relative contributions of vegetation diversity, habitat area, and landscape configuration to habitat quality. Agricultural landscapes are an interesting study system to investigate these processes because there are landscapes available for study that differ primarily in their degrees of vegetation diversity, habitat area, and the degree of fragmentation that has occurred and contain extremes of all three factors.

### **Vegetation diversity effect on habitat quality**

Native plant communities with higher species alpha diversity have been shown to be higher-quality habitat than less-diverse, less-native plant communities for many invertebrate species (e.g., Isaacs et al. 2009, Winfree 2010). However, vegetation diversity may affect different wildlife taxa differently and study is needed for more taxa, notably vertebrate species.

### **Grassland birds**

Grasslands composed of native vegetation should be higher quality habitat for more species than lower-diversity, less-native grasslands as has been demonstrated for many invertebrate species, however this relationship does not appear to be well studied in vertebrates. I was unable to find any studies that directly tested the effect of vegetation diversity on bird reproductive success, but there are many studies on the effects of invasive plant species on birds, which in some landscapes may be equivalent. Nelson (2017) reviewed patterns and mechanisms of invasive plant species on birds (Figure 1-1**Error! Reference source not found.**) and found that 57.9% of tests in 7 studies found no difference in the number of nests in invaded patches, 26.3% found reduced numbers, and 10.5% found increased numbers. They also found that 57% of tests in 26 studies found neutral effects on nest survival in invaded habitat, 14% of tests found a negative effect on nest survival, 12.3% were positive, and 15.8% were conditional. The diversity of responses across all systems may indicate highly situational responses from specific

species in specific habitat types, highlighting the importance of research conducted on the species and within the landscape of conservation interest.

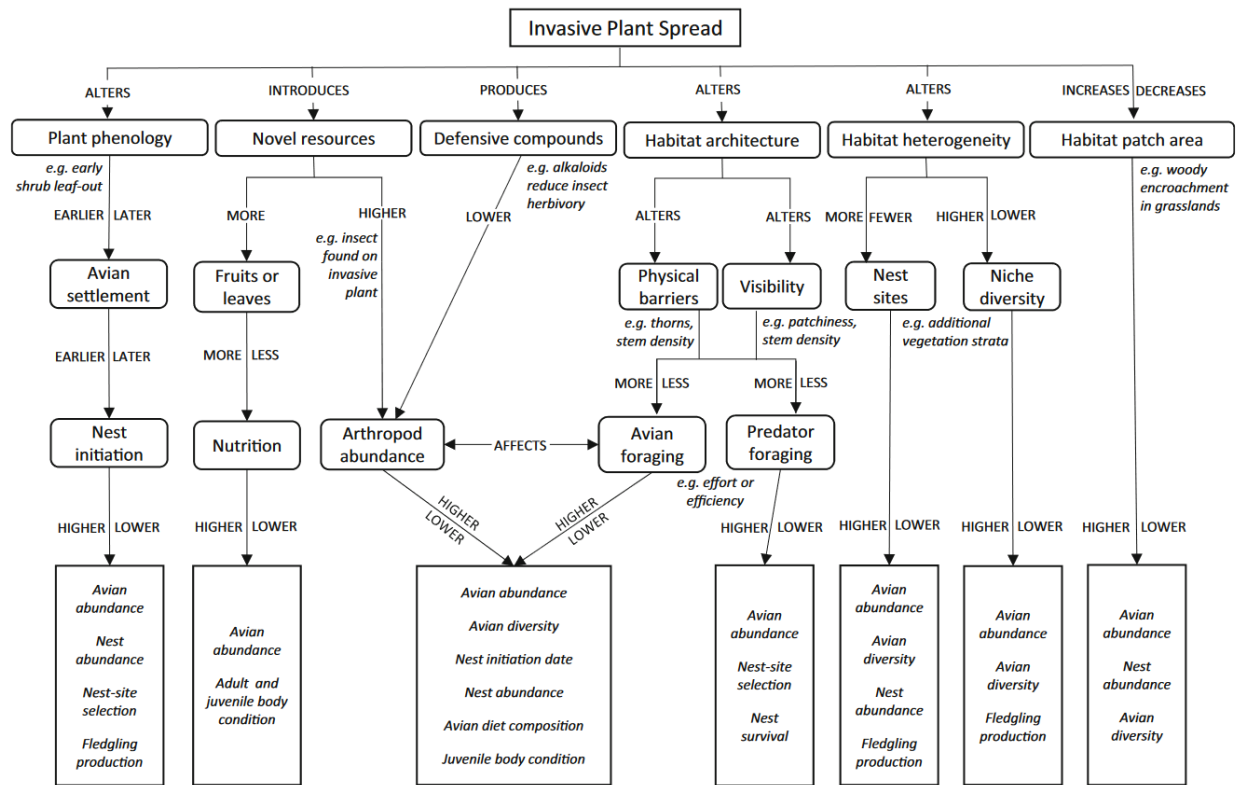


Figure 1-1. From Nelson et al. (2017). A conceptual diagram depicting many of the mechanisms by which invasive plants can influence birds. Many of these effect pathways could also describe how vegetation diversity affects avian reproductive success.

The effect of habitat vegetation diversity on nest survival does not appear to have been directly investigated at the level of individual nests. Several studies have found higher nest survival rates for grassland bird species nesting in categorically defined areas of native plant communities versus exotic (Lloyd and Martin 2005, Conover et al. 2011, Monroe et al. 2016, Davis 2018). More directly, Beyers et al. (2017) found plot-level plant species richness had a positive relationship with Grasshopper sparrow (*Ammodramus savannarum*) nest survival and Shew et al. (2019) found that a principal component containing species richness was important to

above-ground-nesting grassland-bird nest survival, but I was unable to locate any studies that modeled nest survival as a function of directly measured plant species diversity at each nest and not as a group, categorical, or principal component variable. Modeling the effect of measured, continuous vegetation diversity on nest survival would allow a comparison of the importance of vegetation diversity to other biological and environmental variables.

## **Reptiles**

The effect of habitat vegetation diversity on reptile habitat quality seems similarly understudied. At the community level, Michael et al. (2014) found that vegetation species richness positively predicted herpetofaunal richness, and at the species level Mizsei (2020) found that compositional diversity of vegetation negatively predicted the presence and abundance of a snake of conservation concern and was not important in predicting the presence or abundance of three species of lizard. I could not locate any other studies that investigated the effect of plant species diversity on grassland snake habitat quality.

### **Habitat area and configuration effects on habitat quality**

Habitat area and configuration are also important metrics of habitat quality in agricultural grasslands. Habitat configuration is defined as the spatial organization of habitat on the landscape and can be measured in many ways. In this study, I will focus on patch number, patch size, patch isolation, and amount of edge (see below). One of the processes through which configuration changes is habitat fragmentation. Habitat fragmentation is conceptualized as the process by which a continuous area of suitable habitat is converted to a configuration with more, smaller, and more-isolated patches, usually through loss of habitat area (Fahrig 2003).

However, although habitat configuration often have more, smaller, and more-isolated patches after habitat-loss-induced fragmentation, these correlations may be non-linear, with the strongest correlations at intermediate habitat areas (~30%) (Flather and Bevers 2002), and

sometimes reversing direction at extremely low habitat areas. When small patches of habitat are created within a severely depleted landscape (e.g., landscapes dominated by row crops), common measures of habitat configuration associated with fragmentation (e.g., patch number, patch size, isolation, amount of edge) can increase, even though habitat area is also increasing, not decreasing (Figure 1-2). This study will investigate landscapes as they are currently configured, acknowledging that fragmentation has likely occurred both through the destruction and then the creation of habitat area.

Landscapes with many, small, and isolated habitat patch are often thought to be less suitable for wildlife (Stephens et al. 2003, Ries et al. 2004, Fahrig et al. 2019), having reduced populations through lower reproductive success, lower survival, or lower immigration and higher emigration rates, but in review, Fahrig (2017) did not find that to be true in most cases. In that study, Fahrig reviewed 118 studies that reported 381 significant wildlife responses to fragmentation tested independently of habitat area and found that 76% of reported responses were positive.

In an earlier article, Fahrig (2003) provides a framework for describing fragmentation, consisting of four or five processes:

1. A reduction in habitat amount,
2. An increase in number of habitat patches,
3. A decrease in size of habitat patches,
4. An increase in isolation of habitat patches, or
5. An increase in perimeter to edge ratio.<sup>1</sup>

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<sup>1</sup>Fahrig (2003) makes the case that "amount of edge" is so strongly correlated with processes 2, 3, and 4 that it should not stand on its own. I will consider perimeter-area ratio in my study to allow comparison to previous studies and to provide a more complete test of the Habitat Amount Hypothesis (Fahrig 2013, see below).

In this study I will investigate the habitat configurations that result from these processes.

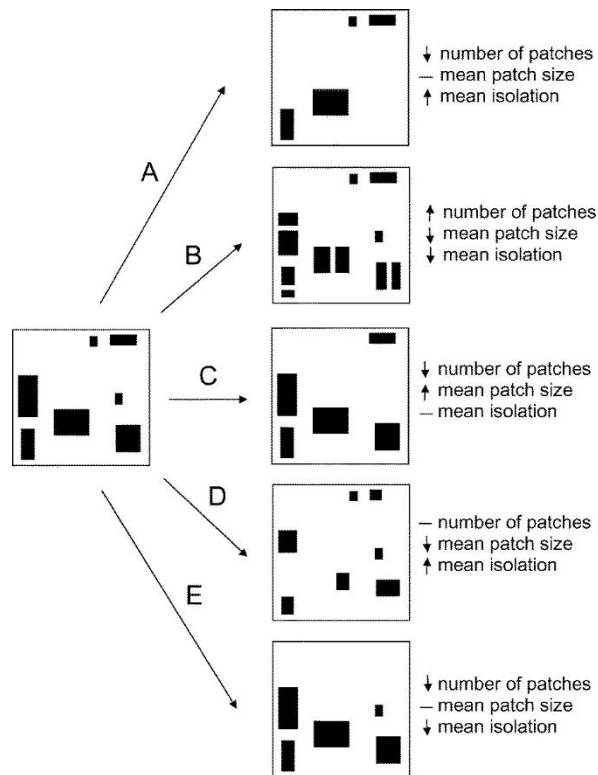


Figure 1-2. Fahrig (2003) argues that configuration metrics typically associated with fragmentation (more patches on the landscape, smaller mean patch size, and greater mean patch isolation) are strongly correlated with losing habitat area (solid arrows). However, those correlations can vary in strength relative to the amount of habitat (Andrén 1994, Betts et al. 2006), and even reverse direction when new patches are created in a severely depleted landscape (dashed arrows). For that reason, I will frame effects on wildlife as stemming from current landscape configuration and set aside the process that led to that configuration. Adapted from Fahrig (2003).

## **1. Small habitat area**

Small total habitat area can negatively affect average fitness in a population through a lack of suitable space for territories, nest sites, or access to required resources. Small areas of suitable space may trigger negative density-dependent effects such as greater conspecific competition, higher chances of predation, and reduction in per capita resource availability, as well as use of non-suitable spaces, until the population declines to the carrying capacity of the habitat area.

In the Habitat Amount Hypothesis (HAH), Fahrig (2013) strongly argues that reduced species richness attributed to habitat fragmentation is fundamentally due to reduced habitat area and all other metrics of fragmentation are unnecessary. In response, Villard (2014) makes the case that habitat amount is always important, but habitat configuration has the potential to reduce the impacts of habitat loss. In a subsequent review, Fahrig (2017) finds that 76% of ecological responses to indicators of fragmentation tested independently of habitat area were positive, including other responses beyond species diversity. To evaluate habitat quality, I am primarily interested in fitness and related rates. Although fitness is not reviewed explicitly, it is linked with abundance, which was a common response variable. This review suggests that when habitat amount is controlled for, other indicators of fragmentation may be more likely to have a positive effect than a negative effect.

## **2. Many patches**

A habitat patch can be difficult to delineate. For this study I will define a patch as "a surface area differing from its surroundings" (Kotliar and Wiens 1990). I will use vegetation community as the major distinguishing attribute and consider management regime (e.g., mowing, haying, burning) in some limited cases.



When designing reserves, conservation planners need to know if a given area of habitat should be configured as a "Single Large Or Several Small?" (SLOSS) patches. Recent reviews have found that the optimal configuration can be context-specific and dependent on the goals of the landscape manager (Tjørve 2010, McCarthy et al. 2011). When preserving biodiversity is the goal, some guiding principles can be found in Tjørve (2010), who found that more and smaller patches are favored when:

1. There is little overlap among species assemblages between patches,
2. There are few area-dependent species,
3. Area-dependent species that are present have smaller area requirements,
4. Patches are more isolated from one another, or
5. Patches have uneven numbers of species.

Prairie strips are an example of the "Several Small" landscape configuration. Following the advice of Tjørve, to maximize biodiversity, the greatest difference in species assemblages (condition 1) should be found when strips on a landscape are positioned with differing access to resources such as bodies of water or patches of woody cover. Prairie strips of a typical size will probably fail to attract most species considered area-sensitive (condition 2), however some species with moderate area requirements (condition 3) may find larger prairie strips suitable. In-field prairie strips typically meet condition 4, depending on the size of the row-crop field they are within and the dispersal ability of the taxa of interest. Prairie strips integrated into a landscape containing many other vegetated conservation features could meet the requirement of patches containing an uneven number of species (condition 5), if prairie strips are shown to have improved habitat quality relative to other conservation features.

The number of patches in a landscape primarily affects local extinction rates in the meta-population. Distribution of habitat area among several smaller patches increases local extinction rates due to demographic stochasticity, but decreases meta-population extinctions due to environmental stochasticity (Quinn and Hastings 1987). Several small prairie strips patches could buffer against meta-population extinctions due to environmental events such as severe weather, management actions such as prescribed burning, or habitat destruction such as conversion to row crops. On longer time scales, configurations with several small patches have increased probabilities of local demographic extinction events which are more likely for small populations, such as those found in a small habitat patch.

### **3. Small patches**

Studies of landscape configuration and their effect on wildlife populations frequently look at patch size as an important metric. The long-held view is that small patches are less suitable than large ones (e.g., Johnson and Temple 1990, Herkert 1994, Herkert et al. 2003). Many past studies have been hampered by the strong correlation between patch size and total habitat amount (Fahrig 2003) and more research is warranted.

In a review of the effect of patch size on grassland bird reproduction, Benson (2013) found that nest survival of grassland birds slightly increased with increasing patch size in the Great Plains, but not in the Midwest or East and that brood parasitism was higher in smaller patches and greater in the Great Plains. They defined patch size as a function of perimeter to area ratio and did not control for total habitat amount.

One reason why patch size has not been consistently shown to be important to grassland birds may be that it does not have a universal linear effect. Different species will respond differently to landscape configurations, which may make an effect difficult to detect and some effects may be non-linear (e.g., Horn et al. 2005). As an example, for grassland birds it is

possible that very small patches support very few nest predators, medium-sized patches support higher small-omnivore populations that prey on nests, due to the absence of top carnivores (i.e. meso-predator release (Soulé et al. 1988, Crooks and Soulé 1999), and large patches support enough top carnivores that omnivore populations are suppressed and nest survival is increased relative to medium-sized patches.

Patch size could also have some lower limit where it becomes unsuitable but doesn't have a strong effect at larger areas. Fahrig (2003) posits a negative effect of fragmentation at some very small threshold value where small habitat patches are unable to support a population or even a single territory. Species which are unable to easily cross the matrix will fail to form a meta-population and will become locally extinct. Due to their mobility and small resource requirements, grassland birds may have a very small lower patch size threshold (Walk et al. 2010).

Patch size may also act interactively with other factors to affect wildlife populations. For example, Zuckerberg (2018) found that nest survival was only predicted by patch size when it interacted with weather effects, but patch size on its own was not predictive.

#### **4. Isolated patches**

Bender (2003) defines patch isolation as "...a characteristic of a habitat patch that reflects how spatially inaccessible it is to dispersing organisms." They reviewed different measures of patch isolation and found they group into four categories: nearest-neighbor distances, Voronoi polygons, proximity indices, and habitat buffers. They found that the commonly used nearest-neighbor metric did not adequately match dispersal ability when patch size and shape were variable, and was outperformed by habitat amount within a radius, bolstering the position of Fahrig (2003).

The degree of isolation of a patch as it relates to dispersal ability varies considerably between taxa. For grassland birds, it may be easy to fly between grassy conservation practices separated by a row crop matrix, while that same distance of row crop to cross is a major barrier for other taxa (Richardson et al. 2006).

In landscapes where habitat is rare, restoration of even small patches may significantly increase the connectivity of existing patches. Saura et al. (2014) found that isolated patches of sufficient size to sustain reproduction were crucial to the spread of species over long distances and reduced the effective isolation of larger habitat reserves. Herrera et al. (2017) found that strategically located isolated patches of South American grasslands as small as 5 ha provided important stepping stones for species that were able to move at least 5 km. Taken together, these studies suggest that smaller prairie strip placed closer together may serve as generational stepping-stones for smaller, less mobile animals and larger prairie strips could serve as single-generation stepping stones for larger, more mobile animals.

## **5. High perimeter to area ratio**

Edge effect interactions with predators or parasites may adversely affect some wildlife species. Ries (2004) categorizes edge effects in four ways: ecological flows, access to spatially separated resources, resource mapping, and species interactions. Ecological flows are outside the scope of this dissertation, and for the majority of species present in Iowa agricultural grasslands there are only limited resources available in crop fields, diminishing the effect of spatially separated resources. Predation and parasitism are the major processes affecting my study taxa, so I will focus on resource mapping (prey/hosts) and species interactions (predation and parasitism events).

The first study to demonstrate an edge effect on grassland nesting birds and one of the first studies to demonstrate a negative edge effect in any system was by Gates and Gysel (1978).

Gates and Gysel proposed that edges serve as an ecological trap for nesting birds by increasing the density of nesting birds attracted to the edge habitat, triggering a density-dependent response from nest predators. Subsequent studies have found low nest survival in linear conservation practices (e.g., Bryan and Best 1994, Hultquist and Best 2001, Henningsen and Best 2005), which have high perimeter-area ratios.

A review Lahti (2001) found 54 studies empirically testing the edge effect hypothesis in any bird species near any edge type and, of those studies, 31 did not detect an edge effect, 13 detected an edge effect in any test conducted, and 10 detected an effect in at least one edge type but no effect in at least one other edge type. Of the 10 study sites that demonstrated an edge effect in any test conducted, five of those edge effects were negative. The author explains this by suggesting that species-specific predator behaviors are more important to understanding nest survival than a general edge effect per se.

In the absence of widespread quality information about the behavior of specific predators at habitat edges (but see Horn et al. 2005, Weatherhead et al. 2010), focusing more tightly on a particular study system may help us better understand potential edge effects in the landscape of conservation concern. In agricultural landscapes, Winter et al. (2000) found evidence to suggest edge effects on nest survival between forest and prairie edges, but none between prairie and agricultural fields. Similarly, Fletcher and Koford (2003) found edge effects on Bobolink (*Dolichonyx oryzivorus*) territory size near woodland and road edges, but not agricultural edges. Davros (2005) found that birds were more abundant in wider grass filter strips (correlated with a lower perimeter-edge ratio) and that nest survival was positively affected by grass filter strip width for Red-winged blackbirds (*Agelaius phoeniceus*) and for 10 other species pooled.

Increased nest parasitism is another edge effect often implicated in lower nest survival. In a review of 30 studies, Benson et al. (2013) found consistent evidence of increased rates of nest parasitism of grassland birds near edges. They attributed the ability to detect this edge effect but not others to brood parasitism by a single species, the Brown-headed cowbird (*Molothrus ater*), where nest survival more generally is affected by the behavior of many predator species.

### **Challenges of studying landscape configuration**

Although the effect of habitat fragmentation on habitat quality has received far more research attention than the effect of vegetation diversity, disentangling the specific mechanisms behind the purported effects caused by habitat fragmentation has been elusive. Fahrig (2003) proposes two main challenges to interpreting studies on fragmentation:

1. Habitat configuration is often measured at the patch scale and not the landscape scale, and
2. Habitat configuration metrics are often strongly correlated with habitat area.

Villard and Metzger (2014) add three additional challenges to disentangling the effects of habitat area and habitat fragmentation:

3. Configuration effects may only occur at mid-to-low habitat amounts,
4. Landscapes with similar habitat amounts but differing configurations are difficult to find for study, and
5. Ecological responses to landscape structure vary among species and/or functional groups, matrix types, geographic locations, spatial extents, or time since fragmentation.

I will briefly review each of these challenges and highlight important studies addressing them.

### **1. Habitat configuration is often measured at the wrong scale**

Fahrig (2003) argues that because fragmentation is a landscape-scale process, the appropriate sample for studying it is the landscape. She argues that many studies present only two samples: one fragmented landscape and one intact landscape with many sub-samples in each, limiting the ability to draw inference. Another consequence of this is that studies that fall into this trap are really only presenting a categorical difference: fragmented or continuous configurations, where a larger sample would allow a quantitative measure of the degree to which fragmentation has occurred in each landscape.

### **2. Configuration metrics co-vary with habitat amount**

Fahrig (2003) notes that many researchers do not report the relationships between tested configuration variables, many of which might be correlated. She gives examples both of studies that control for habitat area in manipulated landscapes (Collins and Barrett 1997, Caley et al. 2001) and those that control for habitat amount statistically (e.g., McGarigal and McComb 1995). However, Fahrig (2003) goes on to propose a simple test for differentiating habitat fragmentation and habitat loss: if the configuration of the habitat is shown to be unimportant, then any effects seen should be a result of the area lost, and not the specific pattern of the remaining habitat. Fahrig does not address the implied assumption that there are no other effects on habitat quality from other processes, such as effects of vegetation diversity.

### **3. Configuration effects may only occur at mid-to-low habitat amounts**

Another challenge of studying the effect of habitat configuration on wildlife populations is that potential effects may be non-linear. For example, Andren (1994) and Betts et al. (2006) found that effects from fragmentation were non-linear, with larger effects occurring in landscapes with less than 30% suitable habitat. However, in a review of 118 studies of

fragmentation, Fahrig (2017) looked for reported non-linear effects and did not find widespread support.

#### **4. Differing configurations are difficult to find for study**

Villard and Metzger (2014) and Fahrig (2017) discuss the difficulty of locating study landscapes with similar habitat areas arranged in different configurations. Fahrig (2017) presents three options for selecting a study landscape, starting with 1) conducting a landscape-scale experiment where habitat area is the same and habitat patches are created with the desired degree of fragmentation (With et al. 2002). Experiments of this type have been most common for studying invertebrate wildlife Debinski and Holt (2000). 2) Select study landscapes across a gradient of fragmentation while keeping the habitat amount equal Cushman and McGarigal (2003), or control for differing amounts of habitat statistically (Smith et al. 2011). 3) A single sufficiently large landscape is selected that can be repeatedly sub-sampled to produce landscapes of equal area but differing configurations at ecologically appropriate scales to the study organism (see Fahrig 2017).

#### **5. Ecological responses vary**

Although ecologists have been looking for a generalized effect of habitat configuration since MacArthur and Wilson's (1963) Theory of Island Biogeography, no consensus has been reached (Fletcher et al. 2018, Fahrig et al. 2019). Ecological responses to habitat configuration are complex and likely vary between species, habitat types, time since fragmentation, spatial scales, predator taxa, and geographic regions.

##### **Species**

The most obvious ways in which habitat configuration might affect wildlife differently is at the species level. Different life-history strategies determine how species interact with their core habitat types, nearby patches of different habitat types, and how predators of those species



will respond. Ewers and Didham (2006) describe how species traits such as trophic level, dispersal ability, and degree of specialization impact species-level responses to configuration.

### **Habitat types**

The Island Biogeography Theory (MacArthur and Wilson 1963) was quickly adapted to describe habitat "islands" in other landscapes, but the degree of habitability among "ocean" matrices varies considerably. Many of the early studies of fragmentation investigated habitat destruction in forests that resulted in sharp differences between intact forest and hard edges of grassland or agriculture. In Iowa, habitat configuration is dominated by row-crops sharing edges with scattered patches of grassland or forest- a very different system. Relevant to an agricultural grassland system, Chalfoun et al. (2002) reviewed 31 papers with testable hypotheses and found more predator effects in agricultural landscapes than forested landscapes and that local-scale effects were more common in agricultural landscapes.

### **Time since fragmentation**

Wildlife responses to fragmentation measured at one point in time may not represent the eventual cost of the fragmentation event. Tilman et al. (1994) describes the Extinction Debt theory that predicts a significant time lag between habitat destruction and the eventual extinction of some species. There is strong evidence that this is occurring in some systems (Haddad et al. 2015). Additionally, Stephens et al. (2003) found that study duration predicted the probability of detecting an effect of habitat configuration on nest success, but study sample size did not. This suggests variability in predation pressure between years that is independent of the number of nests studied in each year and underscores the importance of studying the habitat configurations resulting from fragmentation over time.

### **Spatial scales**

The spatial scale at which habitat configuration is studied has important consequences for the detectability of an effect. As discussed above, the landscape is the proper scale at which to study landscape-level processes (Fahrig 2003) and many studies improperly use the patch-level or smaller scales. Stephens et al. (2003) found that of 86 studies, those that tested at the landscape scale were more likely to find an effect of habitat configuration on avian nest success than those that focused on the edge or patch level. Further, Chalfoun et al. (2002) found studies detected predator effects more often when tested at the landscape scale than the local scale.

### **Predator taxa**

Similar to the way in which different life-history strategies of a species will affect the degree of sensitivity to habitat configuration, so too will the life-history strategies of that species' predators. Different predator species will interact differently to habitat configuration and thus will affect the system in different ways. In their review, Chalfoun et al. (2002) found more evidence for predator effects in avian than mammalian taxa, suggesting they may react to configuration differently and have different cascading effects to other species in the community.

### **Geographic regions**

There is also some evidence that effects of habitat configuration may vary by geographic region. Benson et al. (2013) found that configuration effects varied by region and attributed it to differences in predator communities. Chalfoun et al. (2002) found differences in predator effects in different bio-geographic regions and also credited it to differences in predator communities as well as prevailing land-use practices in different regions.

### **Dissertation organization**

This dissertation is organized into five chapters. This first chapter is an introduction to the concepts and themes that will be revisited throughout the document. The second chapter tests

an extension of the HAH to nest density and survival of grassland nesting birds and compares effect sizes of habitat area, habitat configuration, and vegetation diversity on habitat quality in agricultural landscapes. The third chapter compares three existing hypotheses on how brown-headed cowbirds (*Molothrus ater*) locate host nests with two new hypotheses regarding habitat amount and vegetation diversity to determine how the configuration and location of agricultural conservation practices affect grassland bird nest parasitism rates. The fourth chapter compares how habitat area, fragmentation, and vegetation diversity affect snake and lizard occupancy and presence in agricultural grasslands. The final chapter provides a synthesis of the major findings of the dissertation.

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## CHAPTER 2. HABITAT AMOUNT, CONFIGURATION, AND VEGETATION DIVERSITY PREDICT GRASSLAND BIRD NEST DENSITY AND SURVIVAL IN AGRICULTURAL LANDSCAPES

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### Abstract

Contrary to decades of biodiversity research, the Habitat Amount Hypothesis (HAH) predicted that reported effects of patch size and isolation on biodiversity were driven by habitat amount regardless of configuration. If biodiversity were affected by habitat amount and not configuration, then that relationship should also exist in population-level demographic parameters that underlie biodiversity. In addition to habitat amount or configuration, vegetation diversity also has the potential to be important to grassland habitat quality (here measured by reproductive success). Our goals were to 1) test an extension of the HAH in nest density and survival of grassland nesting birds and 2) to compare effect sizes of habitat area, habitat configuration, and vegetation diversity on habitat quality in agricultural landscapes that contained extremes of fragmentation and diversity not often studied.

From 2015-2019 we located and monitored 1475 nests of 29 species of grassland passerines on 11 sites in Iowa, USA. For one functional group and two species, we compared variable effect sizes for nest density and survival global models and predicted density and

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survival for each subset of those global models to investigate weighted-average effects over each variable's observed value range.

Grassland passerine nest density was predicted (effect direction) by amount of nearby woody land cover (–), number of patches on the landscape (+), vegetation density (+) and diversity (+), and an interaction between nearby grass land cover amount and landscape edge density (+). Nest survival was predicted by mowing (–), vegetation density (+) and diversity (+) with an interaction between diversity and mowing activity (–) and interactions between grass land cover amount and landscape patch count (–) and landscape edge density (+).

Red-winged blackbird nest density was predicted by amount of nearby woody land cover (–), distance from water body (–), annual drought conditions (–), landscape patch count (+), and an interaction between grass land cover amount and landscape edge density (+). Nest survival was predicted by vegetation density (+), an interaction between mowing intensity and vegetation diversity (–), patch area (+), and interactions between grass land cover amount and landscape edge density (+) and distance to crop (–).

Dickcissel nest density was predicted by mowing intensity (–), vegetation diversity (+), and grass land cover amount interacting with landscape edge density (+). Nest survival was predicted by mowing intensity (–), patch area (+), landscape patch count (–), landscape edge density (+), grass land cover amount (+), and an interaction between grass land cover amount and distance to crop (+).

In contrast to our predictions extending HAH to demographic parameters, after measuring fragmentation effects on the landscape scale and correcting for landscape habitat amount, configuration was an important predictor of habitat quality. Our study provides evidence

that grassland bird nesting habitat is affected by vegetation diversity, habitat configuration, and habitat amount in agricultural landscapes.

### **Introduction**

The Habitat Amount Hypothesis (HAH) (Fahrig 2013) proposes that species richness is most appropriately measured at the landscape scale and that putative effects on richness by patch size and isolation are actually driven by total amount of habitat at the landscape scale. This assertion has been contested (Hanski 2015, Haddad et al. 2017, Fletcher et al. 2018) and has stimulated a recent wave of tests of the HAH (Martin 2018). Collinearity between habitat area and fragmentation metrics makes it difficult to distinguish the most probable source of an observed effect (Fahrig 2003, Ruffell et al. 2016), either on biodiversity or on the underlying demographic parameters that give rise to community-level phenomena. Contemporaneous to the HAH, Villard and Metzger (2014) argued that instead of focusing on whether configuration or amount is the more important metric, ecologists should identify the part of the habitat amount gradient where configuration effects are most likely, due to the presence of nonlinear (e.g., threshold) or synergistic/antagonistic effects.

The Habitat Amount Hypothesis includes specific, testable hypotheses: 1) the parameter of interest should change with the total amount of habitat on the landscape at an appropriate scale and 2) should not change with the size of the patch where the parameter was measured. In their rebuttal to the HAH, Fletcher et al. (2018) also called for tests of the specific mechanisms through which configuration affects wildlife and how configuration interacts with other human-induced changes. We propose an extension of the HAH that hypothesizes that population-level demographic parameters underlie community-level descriptors such as biodiversity and so could also be affected by the choice of measurement at the patch or landscape scale and whether any

putative effects of configuration may be better described by total habitat amount on the landscape (Fahrig 2013).

Another prominent category of habitat configuration metrics not addressed in the HAH are edge effects. Edge effects are posited to be due to differences in ecological flows, access to spatially separated resources, resource mapping, and/or species interactions (Ries et al. 2004), but no consensus has been reached on their importance. For example, in two Midwest agricultural landscapes, Winter et al. (2000) found evidence of edge effects on nest success near woody edges but not agricultural edges in a study in Missouri, but Walk et al. (2010) failed to find an effect in an agricultural area of Illinois. Meta-analyses have also failed to find consistent effects (Lahti 2001, Benson et al. 2013), with differing behaviors of individual predator species often given as an explanation (Lahti 2001, Benson et al. 2010, 2013).

The Island Biogeography Theory (IBT) of biodiversity (MacArthur and Wilson 1967) is often invoked when making the conservation decision of choosing a “Single Large Or Several Small?” patches (SLOSS), but applying the IBT to terrestrial “islands” is less well established than its original scope (McCarthy et al. 2011). The IBT predicts that fewer, larger patches should host greater biodiversity, but tests have found varying outcomes for patches of habitat in matrices other than ocean (Tjørve 2010, Fahrig 2017). Recently, the importance of preserving small patches has been highlighted (Wintle et al. 2018), particularly in regions where few large patches remain, such as agricultural areas (Lindenmayer 2018).

Aside from habitat amount and configuration, one of the most important human-induced changes in grassland agroecosystems is the altered diversity of plant communities. The effect of vegetation diversity on demographic parameters has been documented directly for invertebrates (Isaacs et al. 2009, Winfree 2010), but studies on vertebrates are less common. For grassland



birds, Byers et al. (2017) found measured, plot-level plant species richness had a positive relationship with Grasshopper sparrow (*Ammodramus savannarum*) nest survival and Shew et al. (2019) found that a principal component containing species richness was important to above-ground-nesting grassland bird nest survival. There is a larger body of evidence on the effect of invasive plant species, such as those demonstrating lower survival or breeding success in invaded areas (Lloyd and Martin 2005, Nelson et al. 2017, Maresh Nelson et al. 2018), but we were unable to locate any studies that modeled nest survival as a function of directly measured plant species diversity at each nest. Although plant invasion may be of management concern, we expect that effects of invasive plants on grassland bird populations to be driven by a more generalized effect of vegetation diversity. Vegetation diversity may then serve as a more insightful mechanism to explain ecological relationships, particularly in landscapes with variation in both plant diversity and nativity and in systems with multiple competing invaders.

Grassland-nesting passerines in agricultural landscapes in the US Midwest region is an ideal study system to investigate these relationships. If habitat area or configuration effects operate at threshold levels rather than as continuous effects (e.g., Andr  n 1994, Betts et al. 2006), then studies are needed at the extremes of both patch size and total habitat area.

Widespread loss of grasslands have led to major population declines of wildlife worldwide (e.g., Teyss  dre and Couvet 2007), including in North America (Stanton et al. 2018). Continent-wide, 71.2% of the historical extent of the North American tallgrass prairie has been converted to cropland (White, Murray, and Rohweder 2000), contributing to a more than 40% decline in the abundance of grassland birds since 1970 (Rosenberg et al. 2019).

Iowa, USA, has perhaps the most highly fragmented grasslands in North America (Smith 1998, Gallant et al. 2011, Wright and Wimberly 2013), with habitat patches ranging in size from

thousandths to thousands of hectares and landscapes with very low percentages of perennial vegetation are common. Previous work on habitat configuration has frequently focused on the larger end of the patch-size scale (Winter et al. 2006, Benson et al. 2013, Zuckerberg et al. 2018), but Iowa landscapes in the prairie pothole ecoregion provide access to the less-well studied patch sizes from the thousandths to tenths of hectares and includes patches in to the hundreds of hectares. Additionally, much of Iowa's grassland habitats are dominated by agricultural grass mixes, typically of low diversity and high proportion of exotic species. Higher-diversity grasslands are also available for study, including prairie reconstructions and pollinator habitat planted on private and public lands. This gradient of diversity in agricultural grasslands, sometimes across very limited spatial extents, provides an opportunity to study how plant diversity affects habitat quality for wildlife at both patch and landscape scales.

In addition to filling a gap in the range of landscapes represented in the HAH-related research, the paucity of habitat in some Iowa agricultural landscapes is in itself a conservation issue. Prairie strips have been demonstrated to provide multiple ecological services (Schulte et al. 2017), including bird habitat. In a watershed scale experiment, Schulte et al. (2016) found a 1.5 – 2.9 fold increase in birds and a 1.5 – 2.1 fold increase in bird species in fields assigned prairie contour strips compared to those with no conservation practices. However, the scale of that study and its situation within a single landscape also containing a national wildlife refuge leaves open the question of whether prairie strips implemented on commercial scale farms in landscapes more representative of Iowa and the Midwest constitute quality habitat or may function as population sinks or ecological traps.

The goal of this study is to 1) test an extension of the Habitat Amount Hypothesis (Fahrig 2013) to population-level demographic parameters that underlie observed community-level

effects, 2) to test the relative importance of vegetation diversity on those same demographic parameters, and 3) to compare habitat quality of conservation practices that vary in size, configuration, and vegetation diversity. To accomplish this, we estimated grassland-nesting passerine nest density and survival across a range of landscape grassland amounts, configurations, and vegetative diversity in small conservation practices (0.05 – 8 ha) on commercial-scale corn and soy farms and larger grassland restorations (8 – 60 ha) designed explicitly as nature reserves. We developed multiple competing hypotheses (Chamberlin 1890) with specific predictions on how habitat amount and configuration and vegetation diversity might affect nest density and survival (Appendix S1), meeting the call for specific mechanistic hypotheses presented in Fletcher et al. (2018).

## Methods

### Study sites

Our study sites (Appendix S2) were located on monocultural row-crop farms growing corn (*Zea mays* Gaertn.) and soybeans (*Glycine max* L.) within 100 km of Ames, Iowa, USA. Initial site selection was a census of all known farms containing prairie strips within 100 km of Ames, Iowa for which we were able to secure access. Most sites contained multiple conservation practices (Table 2-1, Table S2-1). We defined conservation practices as prairie if they contained an average of at least 15 native plant species in a 0.1 ha nest search plot. Prairies contained both warm- and cool-season plants including species such as big bluestem (*Andropogon gerardi*), little bluestem (*Schizachyrium scoparium*), wild bergamot (*Monarda fistulosa*), gray-headed coneflower (*Ratibida pinnata*), and golden alexanders (*Zizia aurea*). Non-prairie grassy conservation practices were typically dominated by exotic cool-season grasses such as smooth brome (*Bromus inermis*), reed canary grass (*Phalaris arundinacea*), and Kentucky bluestem (*Poa pratensis*). Older (>8 years) perennial conservation practices had shrub components such as

mulberry (*Morus* sp.), eastern redcedar (*Juniperus virginiana*), and Siberian elm (*Ulmus pumila*) to varying extents.

Most sites included prairie strips, which were located only on the study sites and not in the surrounding landscape. Landscapes surrounding study sites were characterized by many small, low-diversity, isolated patches such as ditches, waterways, grass contour strips, grass filter strips, and grassed terraces. The land cover within 1 km of our sites averaged 63.1% row crop (28.6 – 84.8%), 25.2% grassland (11.1 – 51.1%), 7.7% woody (0.9-15.6%), 3.1% developed (1.2 – 6.1%), and 0.9% water (0.16 – 2.7%) and landscapes had average patch sizes of 1 – 7 ha. Large patch grassland sites were more intact internally than farm sites, with mid-high diversity plantings of 40 – 60 ha, a typical size for private prairie restorations in Iowa, and were also situated in more intact landscapes with higher percentages of grassland or forest cover. Differing amounts of habitat area at our study sites were controlled for with interaction effects to isolate effects of configuration from the effect of habitat area. Data collection took place between 2015 – 2019. Not all sites were used in every year.

### **Sampling design**

To estimate nest density, systematic plot searches were conducted weekly during the nesting season (May – July) from 2016 – 2019. Plots were sampled based on categorical land cover classes that varied in area, configuration, and vegetation diversity, and included prairie strips (narrow [ $<10\text{m}$ ] and wide [ $\geq 10\text{ m}$ ]), grass contour strip, grass filter strip, grassed terrace, and large patch grassland. Plots in linear features (all except large-patch grasslands) were the same width as the linear feature with a variable length that resulted in the target area. Plots in linear features were 0.1 ha except for terrace plots, which were 0.05 ha due to a paucity of terraces 0.1 ha or larger.

Plots boundaries were determined using a Geographic Information System program (ArcMap 10.5, ESRI, Redlands, CA) by randomly selecting a starting point within the conservation practice or large grassland patch and delineating a grid of adjacent plots until no more complete plots would fit within the patch. At each site, the entire available area of the land cover categories of interest was delineated with grids of plots and 25-30 plots of each category across all sites were randomly selected for searching; all available plots were searched in cases where there were not enough plots available in a category to randomly sample. Plot selection was retained from year-to-year except in cases where patches were destroyed or an entire site was discontinued or added, in which case plots were discontinued or new plots were randomly selected from the existing grids to balance the number of plots in each category. Individual plots were searched from 1 – 4 years.

In 2017 we lost access to one private farm (MCC) and establishment-phase mowing of prairie strips continued longer than anticipated on other farms (GUT, RHO, WHI, WOR), which caused us to rebalance our sites. We added one site (INH) that contained a large prairie strip that would not be mowed and a large site (NIR) that contained many grassed terraces, which were limited at our existing sites. Initial selection of conservation practices focused on in-field conservation practices and so did not include filter strips, but in 2018 filter strip search plots were added at existing sites (KAL, NIR, SMI) and a second prairie large patch site with ponds (TER) was added to improve our distribution of the plot distance-to-water configuration metric that we believed to be a missing major predictor of Red-winged blackbird nest density.

## **Field methods**

### **Nest density**

Plots were systematically searched for bird nests by a pair of observers for 3 minutes per 0.1 ha by walking back-and-forth abreast, sweeping the vegetation with 1 m sticks, and watching

for flushes or other behavioral cues that a nest was nearby. When a flush or behavioral cue was observed, the timer was paused, and a secondary search timer was started. The observers then conducted a thorough search of the small ( $< 10 \text{ m}^2$ ) area the cue indicated. Length of the secondary search was dependent on the strength of the cue but was typically 1 – 5 min.

Plots were searched weekly using a lagged double-observer study design where observers alternated plots each week to allow calculation of nest detection probability. When a nest was located within a plot, its precise location was measured with a sub-meter-accurate GPS (Trimble™ GeoXT™ or Geo7x™, Sunnyvale, CA) but was otherwise not flagged. Searchers were careful to minimize trampling of the vegetation nearby and conducted several measurements around the nest (see *Search plot habitat*).

Each plot was searched once per week by a pair of observers who did not search that plot the previous week. Pairs of searchers alternated which plots they searched each week and did not share information about number or locations of nests found with the other search teams. This set up trials where plots with known nests were searched by naive observers and the re-discovery or non-discovery of nests formed the basis of a detection probability estimation. Nests discovered independently by different pairs of observers were later matched by GPS coordinates, species, count and age of eggs/young, and notes about nest position.

Weather data was summarized from raw data downloaded from the Automated Surface Observing System (National Weather Service 2022). Sites were matched to the nearest weather station that gathered data for that timeframe, with mean site-to-station distance of 65.5 km (SD = 21.9).

### **Search plot habitat**

In August of each year, we conducted vegetation surveys for each plot. Plots had vegetation sampling locations laid down in a 3x3 grid of points equidistant from each other and

plot boundaries laterally and longitudinally. At the six sampling points closest to a longitudinal edge, we placed a 1 m<sup>2</sup> quadrat and identified all vegetation to species when possible (otherwise to genus) and estimated percent cover for each species. At the three center sampling points we measured obstruction due to vegetation as a correlate to density with a Robel pole from 5 m in each of the cardinal directions and 1 m in height (Robel et al. 1970). Search plots were given a mowing intensity score of 0 – 9 by counting the number of the nine sampling locations that were mowed between May – Aug.

Patch and landscape-level land cover metrics were calculated in R using package `landscapemetrics` (Hesselbarth et al. 2019) and a land cover polygon layer that we hand-digitized in ArcMap 10 (ESRI, Redlands, CA, USA). Land cover classes (Table S2-2) were determined based on interpretation of National Agriculture Imagery Program aerial images (Farm Service Agency 2021), LiDAR (Iowa LiDAR Consortium 2021), and on-the-ground verification. Polygon-based land covers were converted to a 3 m pixel land cover raster with patches defined using rook's case. Landscape metrics calculated included the patch area, nearest patch neighbor, patch perimeter-area ratio, plot centroid distance to crop and water, and proportion of grassland and woody cover, count of patches, mean nearest neighbor, and edge density at 150 and 200 m radii.

The radii at which we chose to measure landscape metrics was based on the mean published territory size in similar habitat (Harmeson 1974, Finck 1984, Dechant et al. 2002, Searcy and Yasukawa 2014). We assumed circular territories, calculated a mean territory radius, and multiplied that by 5 to represent the area roughly covering the focal territory and two ranks of surrounding territories. This is a more localized interpretation of landscape than many published studies and was intended to follow a middle path between measuring at the patch

scale, which may not be appropriate for landscape-level processes (Fahrig 2003, Stephens et al. 2003) and defining landscapes at the kilometer scale or greater, which would have limited the sample size of landscapes and reduced our power to distinguish effects. Measuring landscape metrics at a finer scale increased the distribution of observed values while retaining an ecologically relevant, landscape-based perspective as called for in the HAH (Fahrig 2013).

We also developed an index of the mean cover of preferred nesting plant species present in each plot. For every nest in the study, at the predicted fledging date we identified and estimated coverages of plants within 1 m<sup>2</sup> quadrats placed directly over the nest and 5 m in the 0°, 120°, and 240° headings. For every plant species identified during the study, we determined if it was a preferred species for grassland nesting birds by conducting a repeated-measures ANOVA comparing percent cover in the central nest quadrats to three other locations available within 5 m. Plant species were defined as preferred nesting plant species if they appeared in nest quadrats more often than non-nest quadrats ( $\alpha = 0.05$ ) and where variance explained by quadrat location was greater than 0.05. The mean combined cover of preferred nesting substrates was then calculated for each plot and nest for use as covariates.

### **Nest survival**

Nests of grassland-, ground-, and shrub-nesting birds were located during plot searches, searches of targeted habitats, and opportunistically while conducting other tasks. When a nest was found directly or a behavioral nest cue was given by a parent bird, observers were careful to immediately minimize their footfalls to avoid trampling the vegetation (Martin and Geupel 1993) and potentially affect the nest outcome (Götmark 1992, Ibáñez-Álamo et al. 2012). The nest and all eggs were identified to species (with the exception of *Sturnella spp.*), eggs or young were counted and aged (Lokemon and Koford 1996), presence and behavior of adults were noted, the supporting or sheltering plant substrate was identified, nest condition was noted, a miniature



thermal data logger (iButton Thermochron DS1921G, Maxim Integrated, San Jose, California, USA) was installed inside the nest (Hartman and Oring 2006, Stephenson et al. 2021), a GPS position with sub-meter accuracy was recorded, and nests outside plots were flagged 2.5 m from the nest on two sides. To minimize footfalls, if the nearest crop or water edge was within 5 m, we visually estimated the distance-to-edge using a 1 or 1.5 m reference. If the distance was further than 5 m, we measured it using a GIS system.

On the first visit when the nest was no longer active, we noted the nest condition, number and condition of non-viable eggs and young, and retrieved the temperature data logger. Any evidence as to the fate of the nest was also recorded, such as damage to the nest, remaining eggs and their condition, flattening of the rim, or presence of fecal sacs or feather sheaths.

After a nest succeeded or failed and had reached the predicted fledging date, we determined vegetation composition in 4 quadrats, 1 m<sup>2</sup> in size, with one centered on the nest and three spread around the nest 5 m away in the 0°, 120°, and 240° directions. Within each quadrat, we identified vegetation to species, when possible, otherwise to genus level and estimated percent cover for each. We conducted a search of up to 5 person-minutes within 5 m of the nest to locate and identify any plant species not already recorded within one of the four quadrats. We measured vegetation obstruction as a correlate of density with a Robel pole marked with alternating red and white decimeters from each cardinal direction at a distance of 5 m and a height of approximately 1 m (Robel et al. 1970). Notes were taken on mowing, spraying, or other human disturbance within 5 m of the nest.

### **Statistical methods**

All analyses were conducted in R version 4.0+ (R Foundation for Statistical Computing 2020). All GIS data were curated in ArcGIS Desktop 10.6 (ESRI 2020) and spatial measurements were conducted in R with packages ‘*landscapemetrics*’, ‘*rgeos*’, and ‘*raster*’

(Bivand et al. 2017, Hesselbarth et al. 2019, Hijmans et al. 2022). A categorical land cover map was hand-digitized for each site based on high-resolution NAIP aerial imagery (Farm Service Agency 2021) and versioned annually to reflect changes in land cover. Land cover maps were digitized out to 1 km from all features of interest. As a condition of the HAH, we matched our definition of habitat to the species of interest (Fahrig 2013) and lumped all perennial herbaceous cover into “grassland” (Table S2-2). To make patch and habitat area measurements we rasterized the land cover map by sampling the polygon layers with a 3 m pixel size. A 3 m pixel size was chosen because it allowed very narrow grass features to serve as break points between patches, avoiding landscapes with a single lace-like patch of grass land cover broken only by roads.

### **Nest detection**

We estimated the probability of re-locating a nest to determine if detection probabilities differed across conservation practices. Detection probability was modeled as a binary response variable (detection/non-detection) in a generalized linear mixed effects model using the R package ‘glmmTMB’ (Brooks et al. 2017). Each line of data ( $n = 1$ ) represented a single opportunity for a pair of naïve observers to locate a known-active nest. In addition to single-visit detection probabilities, we also calculated the probability of detecting a nest over its lifetime, given one search per week and an estimated daily survival rate (after Smith et al. 2009).

To develop a fully parameterized global model, we created a list of covariates of interest and vetted them against model assumptions (after Zuur et al. 2010), removing or transforming variables as needed. Fixed effects of interest included nest age, time elapsed since sunrise, temperature, wind speed, precipitation, patch area, patch width, a location predictability index (see below), observer cumulative prior searches, and vegetation density and diversity (Table 2-2). Species, and nest name nested within species were included as random effects.

We examined the variables of interest for outliers by viewing their distributions as box plots and any extreme observations that could be verified as errors (e.g., data entry errors) were censored. The relationship between detection and each variable was plotted to determine what transformations to consider. Due to variation in field methods, visual obstruction reading scores recorded as higher than 150 cm (the height of the Robel measuring pole) were capped at 150 cm. Interactions between variables of interest were considered based on stated hypotheses or expert knowledge. Missing values were typically caused by missed vegetation surveys and were replaced with means by species, site, and year. Nests that were not aged were excluded from the analysis. All continuous response variables were centered and scaled to improve the likelihood of model convergence and interpretation of the coefficients.

To meet model assumptions, we tested the global model for overdispersion and zero inflation using the R package `DHARMA` (Hartig 2020). We limited multicollinearity by calculating the Variance Inflation Factor (VIF) (Zuur et al. 2010, Freckleton 2011) for each explanatory variable using R package `Performance` (Lüdtke et al. 2020) and sequentially removed the variable with the highest VIF score until no variables had a score higher than 7 (Quinn and Keough 2002), excepting interaction and polynomial terms. We also tested for spatial and temporal autocorrelation with package `DHARMA` (Hartig 2020) using Moran's I test (Moran 1948) and the Durbin-Watson test (Durbin and Watson 1950), respectively, to confirm autocorrelation in the residuals was not significant at  $\alpha = 0.05$ . To meet model assumptions we also tested for homogeneity of variance by viewing residuals plotted by observed versus expected for the global model (Hartig 2020) and also viewed plots of standardized residuals versus predicted values for each variable (Hartig 2020). We also viewed a histogram of error term residuals to confirm the global model met the assumption of normally distributed residuals.

Goodness of fit for the global model was assessed as  $R^2_{\text{GLMM}}$  derived using the delta method (Nakagawa et al. 2017).

After vetting the preferred global model, some variables were cut to reduce the overall variable count to keep the all-subsets model list within computational limits. Variables were eliminated if they were expert opinion variables that did not improve model AICc or if they were variables of interest but were correlated with other variables ( $|r| > 0.7$ ). To compare the effect sizes of variables on detection probability, we exponentiated the beta parameter estimates of the global model and their 95% confidence intervals to give odds ratios. Because all variables were centered and scaled, their effect sizes could then be directly compared (Schielzeth 2010).

To predict detection probability across conservation practices and other gradients of interest, we then fit a model list of all possible subsets of the global model and trimmed it to only those models representing 95% of the AICc model weight (Arnold 2010). We predicted detection probability (and associated standard error) for the observed mean values for each conservation practice for each model in the all-subsets list. We then calculated weighted averages of the predictions using AICc model weight (Burnham and Anderson 2002, Doherty et al. 2010). We also made predictions for variables of interest for each model and averaged the predictions by model weight. Variables of interest included each variable whose global model odds ratio did not cross one.

### **Nest density**

For our nest density analysis, the data was vetted in the same manner as the detection analysis. One observation ( $n = 1$ ) was a count of unique nests found in each plot each year by species. Plot-year nest counts were modeled as a Poisson response in a generalized linear mixed model. The global model for nest density was built by additively combining variables of research interest, variables we believed were likely to be important to nest density but that were not of

direct research interest (“expert opinion” variables), interactions which were needed to test the HAH or serve as confounding variables, a random effect for plot, and offsets for plot area and number of times the plot was searched (Table 2-3).

Fixed effects of research interest included vegetation composition, landscape configuration, habitat area, and expert opinion variables (Table 2-3). Landscape composition variables were measured within a circle covering the mean territory area plus two diameters of adjacent neighbors (30 m for Red-winged blackbird and 40 m for Dickcissel) (Temple 2020, Yasukawa and Searcy 2020). Plots with no other grassland patches within the radius of interest were assigned a mean nearest neighbor value of the radius of interest. Plot was included as a random effect and log transformations of actualized plot area and number of searches were included as offsets. We evaluated parameters as described above for detection probability modeling.

After developing the list of models that contained all subsets of the global model, predictions were made from each model and averaged by AICc model weight for nest densities across conservation practices using mean observed values for those conservation practices. We also made predictions for individual significant variables.

### **Nest survival**

We estimated nest survival using a maximum likelihood approach (Johnson 1979, Dinsmore et al. 2002) implemented through the R package RMark (White and Burnham 1999, Laake 2013). Parameters of interest included landscape configuration, vegetation composition, and expert opinion variables (Table 2-4). We evaluated parameters as described above for detection probability modeling.

No formal goodness-of-fit test is available for this analytical method in Program R (Dinsmore and Dinsmore 2007, but see Sturdivant and Hosmer 2007) so lack of fit was mitigated

by closely following the model assumptions: Nests were correctly aged at discovery, nest fates were correctly determined, nest discovery and subsequent visits did not influence survival, nest fates were independent, and daily survival rate was homogeneous. Eggs and young were aged by comparing candling views or photos to reference photos we collected from nests where incubation start date was known with high confidence based on nest temperature data. Observer effects were mitigated by using extreme care not to trample vegetation within 5 m of nests, not leaving dead-end trails to nests, and disturbing the nests as little as possible. Nest fate independence was captured to a certain degree in the slate of variables describing the environment around the nest from < 1 m to 150+ m, but otherwise assumed. The assumption of homogeneous daily survival rate was violated only to the extent that our list of variables did not approximate truth. Variable distribution was examined as outlined for the nest density analysis above.

We developed our variable list (Table 2-4) by additively combining all variables from our list of hypotheses (Appendix S1) with expert opinion variables thought to be important to nest survival but not of direct interest, with the goal of reducing un-modeled variation and improving our ability to resolve the relationships outlined in our hypotheses. We assembled the global model from this list of variables and after fitting, estimated effect sizes for each variable by exponentiating the resulting beta parameters to create odds ratios. An all-subsets model list was created as described in the nest detection methods, but we used a smaller subset of models representing 95% of the AICc model weight to make DSR and probability of fledged predictions by conservation practice and by individual variables.

### **Nest site location predictability index**

We hypothesized that predators hunting for nests might focus their effort on clearly delineated clumps of plant species favored by nesting birds. To test this, we calculated an index

of how likely a clump of plants might be to be investigated by a predator by combining a measure of how strongly nesting birds preferred each plant species with how aggregated that plant species was on the landscape. First, we determined which plant species were associated with nests by conducting a repeated-measures ANOVA for every plant species we encountered to test for differences in percent cover between the 1 m<sup>2</sup> quadrat containing the nest and each of the three surrounding quadrats 5 m from the nest. Plant species for which there was a significant difference in percent covers were considered preferred or avoided, depending on the direction of the effect. Then, for every plant species we calculated the average standard deviation of percent covers around across all nests in our database to determine the mean distribution of the plants in space. To create a measure of how likely a predator might be to be attracted to a nest-containing quadrat, we then multiplied the square of the partial Eta ( $\eta$ ) by the average standard deviation for every plant species and added one so that all scores were greater than one. That search likelihood score was then multiplied by the percent cover for each plant species in each nest-containing quadrat and summed to give an index that increased for quadrats containing plants that were preferred, often clumped, and clumped in that quadrat.

## Results

From May – Aug of 2015 – 2019 we located and monitored 1475 nests of 29 species (Table 2-5) in plots and other grassy areas of nine farms and two large patch prairie restorations in central Iowa, USA. Of those nests, 1285 belonged to nine focal species that nest in grasslands in the absence of woody vegetation, and 328 of those were found in plots (Table 2-5). Missing data for plot search covariates was rare, with 0.37% ( $n = 2$ ) of records missing.

Richness of all nesting bird species in conservation practices varied between 0.31 – 1.19 species per year per 0.1 ha plot (Table 2-6). Apparent nest densities ranged from 5.1 – 15.5

nests/ha for grassland passerines as a group, 0.41 – 10.19 nests/ha for Red-winged blackbirds, and 0.5 – 4.9 nests/ha for Dickcissels (Table 2-6).

Uncorrected nest success rates ranged from 0 – 100% among all species and from 8 – 31% for species for which we found at least 20 nests (Table 2-5). Mean uncorrected success rate was 15.5% for grassland nesting passerines, 15% for Red-winged blackbirds, and 15% for Dickcissels (Table 2-5). The most common causes of failure were predation (65.1%), nest desertion (6.5%), and egg damage caused by cowbirds (4.3%). Successful fledging of young of any species was considered a successful nest, but 0 – 50% of successful nests fledged only Brown-headed cowbird young (Table 2-5).

### **Nest detection**

We conducted 277 plot searches with naïve observers when a known nest was present. Missing data in the detection dataset were sparse, aside from location predictability index (8.8% of values missing), with the next highest missing data rate 0.7% ( $n = 2$ ). Nests where the nest was mowed over before the vegetation survey was conducted did not have a location predictability index calculated ( $n = 56$ ). After transformations and re-formulations to meet model assumptions we determined a final global model from which to develop the all-subsets model set (Equation 2-1), which contained 8800 models. The mean single-visit detection rates were 0.17 ( $PI_{95\%} = 0.11 - 0.23$ ) for Red-winged blackbirds and 0.11 ( $PI_{95\%} = 0.07 - 0.15$ ) for Dickcissels and the cumulative probability of finding a nest over its lifetime with weekly searches was 0.36 ( $PI_{95\%} = 0.26 - 0.44$ ) for Red-winged blackbirds and 0.20 ( $PI_{95\%} = 0.14 - 0.26$ ) for Dickcissels. Intercepts for the random effect of species ( $n = 16$ , Figure S2-2) ranged from -1.00 (COYE) to 0.87 (RWBL). The global model fixed effects explained 22.8% (marginal) and 30.8% (conditional) of the variance in the data.



Several terms in the global model had significant effects, although the absolute values of the untransformed 95% CIs of all significant parameters overlapped (Figure 2-1). The most important variables in the global model for predicting nest detection were search plot plant species richness (Figure 2-2a), vegetation density (Figure 2-2b), and the age of the nest relative to the start of incubation (Figure 2-2c). Location predictability index (Figure 2-2d), and recent precipitation (Figure 2-2e) also had statistically significant effects on detection. Minutes elapsed since sunrise (Figure 2-2f) was not significant at  $\alpha = 0.05$  but was at  $\alpha = 0.1$ .

Nests in large grass patches and grass filter strips were more likely to be rediscovered than nests in prairie filter strips and nests in large grass patches were more likely to be rediscovered than nests in large prairie patches. Due to violations in closure assumptions in the study design we were unable to jointly estimate detection probability with density; therefore, we assumed equal detection probabilities and estimated an index of nest abundance rather than a detection-corrected estimate. We discuss implications of differential detection rates among vegetation characteristics in the final section of the paper.

## **Grassland passerines**

### **Nest density**

Between 2016 – 2019 we found 322 nests of nine species of grassland passerines during plot searches. After transformations and re-formulations to meet model assumptions, we assembled a global model (Equation 2-2) from which to develop the all-subsets model set. The all-subsets model set contained 12,610 models initially, and 505 after trimming to 95% of the model weight (Supplementary materials). The global model explained 20.3% (marginal) and 22.1% (conditional) of the variance present in the data.

Several variables in the global model had significant effects, although the absolute values of the untransformed 95% CIs of all significant parameters overlapped (Figure 2-3). Important

predictors of nest density included vegetation density (Figure 2-4a) and diversity (Figure 2-4b), number of patches near the search plot (Figure 2-4c), proportion of woody land cover within 200 m of search plot (Figure 2-4d), and edge density interacting with grassland area near the search plot (Figure 2-4e). The interaction term between edge density and grassland area was significant (Figure 2-4e) but neither main effect was significant. Predictions by conservation practice indicated that grassland passerine apparent nest density was significantly higher in prairie filter strips than in large patch prairie, large patch grasslands, grassed terraces, or grass contour strips. We also predicted nest density to be higher in prairie contour strips than in grass contour strips, large grass patches, or large prairie patches (Figure 2-4f).

### **Nest survival**

Between 2015 – 2019 we found 1236 nests of grassland-nesting passerines that met inclusion criteria for the survival analysis. Missing nest survival data for grassland passerines was low ( $\leq 1.5\%$  per variable). We developed a global model (Equation 2-3) from which we derived a list of 4400 models representing all possible model subsets (Supplementary materials). To make predictions we used a subset of 53 models representing 95% of the AICc model weight. Several variables in the global model had significant effects (Figure 2-5). The quadratic term for daily nest age was the weakest significant effect; the absolute values of the untransformed 95% CIs of all other significant parameters overlapped (Figure 2-5). Grassland passerine nest survival (Figure 2-6, left column) and extrapolated success rates (Figure 2-6, right column) were best predicted by grass land cover within 200 m (Figure 2-6a, b), edge density (Figure 2-6c, d), patch count (Figure 2-6e, f), patch area (Figure 2-6g, h), nest age (Figure 2-6i, j), and vegetation richness (Figure 2-6k, l) and density (Figure 2-6o, p). The main effect for grassland proportion within 200 m was not significant on its own, but after partitioning variation from significant interactions with edge density, patch count, and patch area, there was a small effect of habitat

area. An interaction between vegetation diversity and mowing intensity was significant at  $\alpha = 0.05$ . Woody land cover within 200 m, an interaction between vegetation density and mowing, and an interaction between patch area and habitat area were not significant at  $\alpha = 0.05$  but were at  $\alpha = 0.1$ .

Nest success rate for grassland passerines as a functional group was significantly higher in prairie contour strips compared to grassed terraces, grass contour strips, grassed waterways, and grass filter strips (Figure 2-6o). Additionally, prairie filter strips, prairie large patch restorations, grass large patches, and grassed waterways had higher predicted daily survival rates than grassed terraces (Figure 2-6o).

## **Red-winged blackbird**

### **Nest density**

Between 2016 – 2019 we found 145 Red-winged blackbird nests during plot searches. After transformations and re-formulations to meet model assumptions, we assembled a global model from which to develop the all-subsets model set (Equation 2-2). The full all-subsets model set contained 12,610 models and after trimming to 95% of the model weight, contained 1059 models (Supplementary materials). The global model explained 26.0% (marginal) and 32.7% (conditional) of the variance present in the data.

Several variables in the global model had significant effects, although the absolute values of the untransformed 95% CIs of all significant parameters overlapped (Figure 2-7). Important predictors of nest density in plots included vegetation density (Figure 2-8a) and diversity (Figure 2-8b), distance to water body (Figure 2-8c), patch count within 150 m (Figure 2-8d), edge density within 150 m (Figure 2-8e), nearby woody land cover (Figure 8f), and year-to-date drought severity and extent (Figure 8g). Plant species richness was not significant at  $\alpha = 0.05$  but was at  $\alpha = 0.1$ . An interaction term between edge density and grassland area was significant but

neither main effect was significant, hinting that the relationship between edge density and nest density changed direction at low and high values of nearby proportion of grass land cover, but without a clear effect on average (Figure 2-8e). Predictions by conservation practice indicated that apparent nest density for Red-winged blackbirds was significantly higher in grass and prairie filter strips than in large patch restorations of grass and prairie and that apparent nest density was higher in grass filter strips than in grassed terraces, grass contour strips, and prairie contour strips (Figure 2-8h).

### **Nest survival**

Between 2015 – 2019 we found 771 nests of Red-winged blackbirds that met inclusion for the survival analysis. Missing data rates for Red-winged blackbirds were low ( $\leq 1.5\%$  per variable). We developed a global model (Equation 2-3) from which we derived a list of 4400 models representing all possible model subsets (Supplementary Materials). To make predictions we used a subset of 465 models representing 95% of the AICc model weight. Several variables in the global model had significant effects (Figure 2-9). The quadratic term for daily nest age was the weakest significant effect; the absolute values of the untransformed 95% CIs of all other significant parameters overlapped (Figure 2-9). Important predictors of Red-winged blackbird nest survival included nest age (Figure 2-10a, b), distance to crop edge (Figure 2-10c, d), edge density within 150 m (Figure 2-10e, f), area of patch containing the nest (Figure 2-10g, h), and vegetation diversity (Figure 2-10i, j) and density (Figure 2-10k, l). Distance to crop edge and edge density had significant interactions with proportion of nearby landscape in grass land cover (Figure 2-10c-f), but main effects for distance to crop edge and proportion of grass land cover were not significant at  $\alpha = 0.05$ . The main effect for edge density was significant at  $\alpha = 0.1$ , however. The main effect for vegetation diversity was not significant, but after partitioning

variance from mowing activity, there was separation between prediction intervals at minimum and maximum values for richness (Figure 2-10i, j).

Predicted nest survival for Red-winged blackbirds was significantly higher in prairie contour strips compared to grass contour strips and grassed terraces; higher in prairie filter strips and large prairie patches compared to grass contour strips; and nests in prairie contour strips, prairie filter strips, large prairie patches, grass waterways, and grass filter strips had higher predicted survival than nests in grassed terraces (Figure 2-10m, n).

## **Dickcissel**

### **Nest density**

Between 2016 – 2019 we found 126 Dickcissel nests during plot searches. After transformations and re-formulations to meet model assumptions, we assembled a global model from which to develop the all-subsets model set (Equation 2-3). The full all-subsets model set contained 12,610 models and after trimming it to 95% of the model weight it contained 4720 models (Supplementary Materials). The global model explained 9.4% (marginal) and 17.0% (conditional) of the variance present in the data. Because the Dickcissel global model fit the data less well than did the blackbird or grassland passerine models, we report density results for Dickcissels at  $\alpha = 0.1$  and include results for  $\alpha = 0.05$  in the supplementary materials.

The global model had two significant main effects and one significant interaction (Figure 2-11). The only strong effect on apparent nest density was vegetation diversity (Figure 2-12a). Mowing activity had a small but statistically significant effect (Figure 2-12b) and an interaction between edge density and nearby grass land cover was significant, but neither main effect was significant (Figure 2-12c). Predicted Dickcissel apparent nest density was higher in prairie contour strips than prairie large patches or grass filter strips, but there were no other differences between conservation practices (Figure 2-12d).

### Nest survival

Between 2015 – 2019 we found 296 Dickcissel nests suitable for inclusion in the nest survival analysis. Missing survival data rates for Dickcissels were low ( $\leq 1.5\%$ ). We developed a global model (Equation 2-3) from which we derived a list of 4400 models representing all possible model subsets (Supplementary Materials). To make predictions we used a subset of 716 models representing 95% of the AICc model weight. Several variables in the global model had significant effects (Figure 2-13). The quadratic term for daily nest age was the weakest significant effect; the absolute values of the untransformed 95% CIs of all other significant parameters overlapped (Figure 2-13). Dickcissel nest survival was predicted by proportion of the landscape in grass land cover within 200 m (Figure 2-14a, b), landscape edge density (Figure 2-14c, d), patch count within 200 m (Figure 2-14e, f), patch area (Figure 2-14g, h), nest age (Figure 2-14i, j), distance to crop (Figure 2-14k, l), and mowing intensity within 5 m (Figure 2-14m, n). Large patch prairies had higher predicted nest survival than grass terraces but there were no other significant differences between conservation practices.

### Nest site preference

Grassland bird nests had the strongest positive associations with Reed canary grass (*Phalaris arundinacea*,  $\eta^2_{\text{part}} = 0.22$ ), Canada thistle (*Cirsium arvense*,  $\eta^2_{\text{part}} = 0.18$ ), Gray-headed coneflower (*Ratibida pinnata*,  $\eta^2_{\text{part}} = 0.15$ ), Wild bergamot (*Monarda fistulosa*,  $\eta^2_{\text{part}} = 0.12$ ), Little bluestem (*Schizachyrium scoparium*,  $\eta^2_{\text{part}} = 0.11$ ), Golden alexander (*Zizia aurea*,  $\eta^2_{\text{part}} = 0.09$ ), Big bluestem (*Andropogon gerardi*,  $\eta^2_{\text{part}} = 0.08$ ), Wild parsnip (*Pastinaca sativa*,  $\eta^2_{\text{part}} = 0.07$ ), Common milkweed (*Asclepias syriaca*,  $\eta^2_{\text{part}} = 0.07$ ), and White mulberry (*Morus alba*,  $\eta^2_{\text{part}} = 0.07$ ) (Figure S2-6). Grassland nesting birds had the strongest negative associations with Smooth brome grass (*Bromus inermis*,  $\eta^2_{\text{part}} = 0.52$ ), Canada wild rye (*Elymus canadensis*,  $\eta^2_{\text{part}} = 0.14$ ), Rattlesnake master (*Eryngium yuccifolium*,  $\eta^2_{\text{part}} = 0.11$ ), Canada goldenrod

(*Solidago canadensis*,  $\eta^2_{\text{part}} = 0.10$ ), Soybean (*Glycine max*,  $\eta^2_{\text{part}} = 0.09$ ), and Switchgrass (*Panicum virgatum*,  $\eta^2_{\text{part}} = 0.07$ ). Red-winged blackbird and Dickcissel nests made up 85% of the sample, so preferences were skewed toward the preferences of these two species.

### **Comparison of conservation practices**

Study plots in large prairie patches had 3.1 nests/ha ( $\text{PI}_{95\%} = 2.2 - 4.4$  nests/ha) for grassland nesting passerines as a group, 0.7 Red-winged blackbird nests/ha ( $\text{PI}_{95\%} = 0.4 - 1.4$  nests/ha), and 1.4 Dickcissel nests/ha ( $\text{PI}_{95\%} = 0.8 - 2.3$  nests/ha). Nest success in large prairie patches was 13.5% ( $\text{PI}_{95\%} = 9.3 - 18.6\%$ ) for grassland nesting passerines as a group, 14.8% ( $\text{PI}_{95\%} = 9.1 - 21.9\%$ ) for Red-winged blackbirds, and 23.6% ( $\text{PI}_{95\%} = 12.5 - 36.8$ ) for Dickcissels. In addition, nest parasitism by Brown-headed cowbirds caused 13.7% of successful grassland nesting passerine nests, 8% of successful Red-winged blackbird nests, and 24% of successful Dickcissel nests to fledge only cowbird young.

Large grass patches had 2.3 times fewer nests/ha than grass filter strips, 2.1 times fewer nests/ha than prairie contour strips, and 2.7 times fewer nests/ha than prairie filter strips for grassland nesting passerines as a group (3.6 nests/ha,  $\text{PI}_{95\%} = 2.7 - 4.9$  nests/ha), 6.2 times fewer nests/ha than grass filter strips and 3.5 times fewer nests/ha than prairie filter strips for Red-winged blackbirds (0.9 nests/ha,  $\text{PI}_{95\%} = 0.5 - 1.5$  nests/ha), and similar densities to other conservation practices for Dickcissels (1.5 nests/ha,  $\text{PI}_{95\%} = 0.9 - 2.5$  nests/ha). Nest survival in grass large patches was 2.8 times higher than in grassed terraces for grassland nesting passerines as a group ( $P_{\text{fledge}} = 11.3\%$ ,  $\text{PI}_{95\%} = 8.0 - 15.2\%$ ), 2.1 times lower than in prairie contour strips for Red-winged blackbirds ( $P_{\text{fledge}} = 9.5\%$ ,  $\text{PI}_{95\%} = 5.8 - 14.3\%$ ), and similar to other conservation practices for Dickcissels ( $P_{\text{fledge}} = 15.3\%$ ,  $\text{PI}_{95\%} = 7.8 - 25.3\%$ ).

Grassland nesting passerine nest densities in grassed terraces (4.9 nests/ha,  $\text{PI}_{95\%} = 3.6 - 6.7$  nests/ha) were 1.9 times lower than in prairie filter strips, Red-winged blackbird nest

densities in grassed terraces (1.5 nests/ha,  $PI_{95\%} = 0.8 - 2.5$  nests/ha) were 3.7 times lower than grass filter strips, and Dickcissel nest densities (1.8 nests/ha,  $PI_{95\%} = 1.1 - 3.1$  nests/ha) were similar to other conservation practices. Nest success in grassed terraces was 4.1% ( $PI_{95\%} = 2.1 - 7.2\%$ ) for grassland nesting passerines, 4.0% ( $PI_{95\%} = 1.9 - 7.5\%$ ) for Red-winged blackbirds, and 5.4% ( $PI_{95\%} = 1.8 - 12.4\%$ ) for Dickcissels.

Grass contour strips had 1.5 times lower nest density than prairie contour strips and 1.9 times lower nest density than prairie filter strips for grassland nesting birds as a group (4.9 nests/ha,  $PI_{95\%} = 4.0 - 6.1$  nests/ha), 4.2 times lower nest density than grass filter strips for Red-winged blackbirds (1.3 nests/ha,  $PI_{95\%} = 0.8 - 1.9$  nests/ha), and no significant difference in Dickcissel nest density between grass contour strips (2.2 nests/ha,  $PI_{95\%} = 1.5 - 3.1$  nests/ha) and other conservation practices. Nest survival in grass contour strips was 3.1 times lower than in prairie contour strips for grassland nesting birds as a group ( $P_{fledge} = 6.0\%$ ,  $PI_{95\%} = 4.0 - 8.6\%$ ) and 3.8 times lower for Red-winged blackbirds ( $P_{fledge} = 5.2\%$ ,  $PI_{95\%} = 2.8 - 8.7\%$ ). Nest success estimates for Dickcissels in grass contour strips had overlapping prediction intervals with all other conservation practices ( $P_{fledge} = 9.9\%$ ,  $PI_{95\%} = 5.3 - 16.4\%$ ).

Grass filter strips had nest densities 2.3 times higher than large grass patches and 2.6 times higher than large prairie patches for grassland nesting passerines as a group (8.1 nests/ha,  $PI_{95\%} = 6.0 - 10.9$  nests/ha), 3.7 times higher than grassed terraces, 4.2 times higher than grass contour strips, 6.2 times higher than grass large patches, 3.2 times higher than prairie contour strips, and 7.3 times higher than prairie large patches for Red-winged blackbirds (5.3 nests/ha,  $PI_{95\%} = 3.3 - 8.5$  nests/ha), 2.5 times lower than prairie contour strips, and 1.1 times lower than large prairie patches for Dickcissels (1.2 nests/ha,  $PI_{95\%} = 0.6 - 2.3$  nests/ha). Nest success in grass filter strips was 2.4 times higher than in grass terraces and 1.9 times lower than in prairie



contour strips for grassland nesting passerines as a group ( $P_{fledge} = 9.7\%$ ,  $PI_{95\%} = 6.9 - 13.0\%$ ), 2.8 times higher than in grass terraces for Red-winged blackbirds ( $P_{fledge} = 11.3\%$ ,  $PI_{95\%} = 7.7 - 15.6\%$ ), and similar to other conservation practices for Dickcissels ( $P_{fledge} = 9.1\%$ ,  $PI_{95\%} = 4.1 - 16.6\%$ ).

Grass waterways had nest success rates 2.5 times those estimated for grassed terraces and 0.5 times those estimated in prairie contour strips for grassland nesting birds as a group ( $P_{fledge} = 10.2\%$ ,  $PI_{95\%} = 7.7 - 13.1\%$ ), 2.8 times those estimated for grassed terraces for Red-winged blackbirds ( $P_{fledge} = 11.4\%$ ,  $PI_{95\%} = 8.0 - 15.6\%$ ), and similar nest success rates compared to other conservation practices for Dickcissels ( $P_{fledge} = 9.9\%$ ,  $PI_{95\%} = 5.4 - 16.1\%$ ).

Prairie contour strips had 2.1 times the nest density of large grass patches and 2.4 times the density as large prairie patches for grassland nesting passerines as a group (7.4 nests/ha,  $PI_{95\%} = 6.1 - 9.0$  nests/ha), 3.2 times lower nest densities than grass filter strips for Red-winged blackbirds (1.7 nests/ha,  $PI_{95\%} = 1.1 - 2.5$  nests/ha), and 2.5 times the nest density as grass filter strips and 2.2 times the density as large prairie patches for Dickcissels (3.0 nests/ha,  $PI_{95\%} = 2.1 - 4.1$  nests/ha). Nest success in prairie contour strips was 2.4 times higher than in grassed terraces, 3.1 times higher than grass contour strips, 1.8 times higher than grass waterways, and 1.9 times higher than in grass filter strips for grassland nesting passerines ( $P_{fledge} = 18.8\%$ ,  $PI_{95\%} = 14.6 - 23.4\%$ ); 4.9 times higher than in grassed terraces, 3.8 times higher than in grass contour strips, and 1.8 times higher than in large grass patches for Red-winged blackbirds ( $P_{fledge} = 19.7\%$ ,  $PI_{95\%} = 14.4 - 25.7\%$ ); and similar to other conservation practices for Dickcissels ( $P_{fledge} = 13.8\%$ ,  $PI_{95\%} = 7.7 - 21.7\%$ ).

Prairie filter strips had nest densities 1.9 times higher than grassed terraces, 1.9 times higher than grass contour strips, 2.1 times higher than grass large patches, and 3.1 times higher

than prairie large patches for grassland nesting passerines as a group (9.6 nests/ha,  $PI_{95\%} = 7.2 - 12.6$  nests/ha); 3.5 times higher than large grass patches and 4.1 times higher than large prairie patches for Red-winged blackbirds (3.0 nests/ha,  $PI_{95\%} = 1.8 - 5.1$  nests/ha); and densities similar to other conservation practices for Dickcissels ( $P_{fledge} = 7.6\%$ ,  $PI_{95\%} = 3.3 - 14.4\%$ ). Nest success in prairie filter strips was 3.6 times higher than grassed terraces for grassland nesting passerines as a group ( $P_{fledge} = 14.9\%$ ,  $PI_{95\%} = 11.1 - 19.2\%$ ), 4.2 times higher than grassed terraces and 3.3 times higher than grass contour strips for Red-winged blackbirds ( $P_{fledge} = 16.9\%$ ,  $PI_{95\%} = 11.8 - 22.8\%$ ), and similar to other conservation practices for Dickcissels ( $P_{fledge} = 7.6\%$ ,  $PI_{95\%} = 3.3 - 14.4\%$ ).

## Discussion

### Habitat Amount Hypothesis

#### Habitat amount

Our findings do not support an extension of the Habitat Amount Hypothesis (Fahrig 2013) to population-level demographic parameters that underlie community-level biodiversity measures such as nest density and survival. We found that patch area was a better predictor of nest survival than landscape habitat amount for grassland nesting birds overall, as well as for Red-winged blackbirds, although both landscape habitat amount and patch size were important predictors for Dickcissels. We found few previous studies that compared patch size, landscape habitat area, and their interaction, but our findings were similar to Davis et al. (2006) who found variable effects from pasture area and its interaction with landscape habitat amount on nest density and survival on five species of grassland nesting passerines. A second study on grassland nesting passerines failed to find an effect from either patch area or landscape habitat amount (Winter et al. 2006). Neither landscape habitat amount nor patch area were important predictors of nest density for any of the three species investigated.

Our findings did not support our mechanistic hypothesis that a fixed number of birds on the landscape would crowd into the available habitat in low habitat amount landscapes, resulting in higher nest densities (Appendix S1, HA-2). Our findings of higher nest survival rates in larger patches and/or in higher habitat-amount landscapes provides evidence against our mechanistic hypothesis that birds can nest in higher densities in landscapes that are too habitat-poor to support year-round predator populations (Appendix S1, HA-3).

### **Edge effects**

Edge effects were the most consistently important predictors of nest density and survival, with edge density appearing as an important variable for both nest density and survival in all three groups tested. Additionally, distance between nest and edge as a main effect or interaction with habitat amount was important in nest survival for blackbirds and Dickcissels.

Our nest survival models showed positive relationships between edge density and nest survival in high habitat amount landscapes and negative or more weakly positive edge density-survival relationships in low-habitat amount landscapes. In addition, we found negative effects of nest distance-from-crop for Red-winged blackbirds in high habitat amount landscapes but a positive effect for high-habitat amount for Dickcissels and no effect for grassland birds overall.

Across all three groups tested, edge density only had positive effects on nest density at very high landscape habitat amounts, with negative relationships in the more common low-habitat amount landscapes. We predicted that nest density would increase with edge density because birds include both crop and grassy areas in their territories, but only the grassy areas contain suitable nesting microhabitats (excepting Vesper sparrows), resulting in a concentration of nests within grassy patches that share long borders with crop areas (Appendix S1, EE-1). Our data supports this hypothesis, with the addition of an interaction effect where in low habitat amount, high edge landscapes, all available grassland may have been more vigorously defended,

removing the ability of less dominant males to include small areas of grassland edge inside territories largely composed of crop ground.

Our nest survival data provide compelling support for our mechanistic hypothesis that nest survival is lower in linear patches because they can be searched more efficiently by predators (Appendix S1, EE-3) and provides little support for the competing mechanistic hypothesis that nest survival is not affected by edge density or proximity because the crop matrix does not contain additional predators (Appendix S1, EE-2). Red-winged blackbirds may have demonstrated a stronger positive relationship between nest survival and distance from crop edge because they flush directly from nests in a more obvious way than more circumspect species, such as Dickcissels and the rest of the species represented in our grassland nesting passerine functional group.

Renfrew et al. (2006) found a positive relationship between distance to edge and nest density of grassland nesting birds in Wisconsin, however distance to edge is a patch-scale measurement where a landscape scale measurement is more appropriate for landscape processes (Fahrig 2003) and they did not correct for landscape habitat amount. Previous studies have failed to come to a consensus on the direction or even presence of edge effects on nest survival (Lahti 2001, Benson et al. 2013). Several previous studies have found no evidence for edge effects on grassland bird nest survival near agricultural edges (Winter et al. 2000, Renfrew et al. 2006, Walk et al. 2010), however these studies also did not include interaction terms with habitat area. Given the importance of the edge density-grassland proportion interaction term in both our nest density and survival models, failure to correct for habitat amount may have resulted in a failure to detect configuration effects, or to find a weak effect in one direction when it may actually have been two strong effects in different directions.

### **Patch count**

We found that patch count was a positive predictor of nest density for grassland nesting passerines as a functional group as well as for Red-winged blackbirds but had no significant effect on Dickcissel nest density. Patch count had a negative effect on grassland nesting passerine and Dickcissel nest survival when there was more habitat on the local landscape, but had a weaker, more variable effect at very low habitat amounts and no distinguishable effect on Red-winged blackbird nest survival.

Higher nest densities in landscapes with higher patch counts provides evidence against our mechanistic hypothesis that territory borders should conform to patch borders as a landscape is divided into more patches, trending toward a single territory per patch (and thus lower nest density) (Appendix S1, PN-2). Patch count positively predicting nest survival was unexpected because predator behavior was hypothesized to be affected by patch size (Appendix S1, PS-1), isolation (Appendix S1, PI-2), and edge effects (Appendix S1, EE-2, EE-3), but we did not hypothesize an effect from patch count (Appendix S1, PN-3). We could not locate any previous studies that specifically tested grassland bird nest density or survival relative to number of patches on the landscape while controlling for landscape habitat amount.

### **Patch isolation**

Patch isolation had no effect on nest density or survival for any group tested. This provides support for our mechanistic hypothesis that patch isolation is not an important consideration for flying, migratory birds that can easily cross non-habitat matrix (Appendix S1, PI-1), but does not provide support for our mechanistic hypothesis that isolation limits the frequency with which predators visit patches, increasing nest survival rates (Appendix S1, PI-2). However, it seems likely that our non-detection of effects from patch isolation were a result of the scale at which we defined a landscape. At the scales of interest (150 m or 200 m), circular

local landscapes often contained a single patch, resulting in an inability to calculate a mean nearest-neighbor distance within the local landscape. In landscapes with only a single patch, the missing mean nearest neighbor distance was replaced with maximum distance checked for neighbors (150 or 200 m), resulting in poorly distributed data due to the frequency of occurrence and thus substantially limited statistical power to detect potential isolation effects.

### **Woody land cover amount**

Although not directly related to our study goals, we included nearby woody land cover amount in our models due to its importance in other study systems (Winter et al. 2000, Batáry and Báldi 2004, Tack et al. 2017). We found that woody land cover amount had a negative relationship to grassland passerine and blackbird nest density, with Dickcissel nest density showing the same relationship with less confidence. This suggests that birds avoided nesting near patches of woody cover proportional to their area, similarly to previous studies (Thompson et al. 2014), but see Renfrew et al. (2006). We also found a trend toward negative relationships between nearby woody land cover amount and nest survival for grassland nesting passerines and Dickcissels, but the effects were less clear than other variables.

### **Vegetation diversity**

We found that both vegetation diversity and density were important predictors of both nest density and survival for grassland nesting passerines as a functional group as well as for Red-winged blackbirds. For Dickcissels, vegetation diversity was the only significant main effect of research interest for nest density, although neither vegetation diversity nor density was an important predictor of Dickcissel nest survival. In addition, vegetation density and diversity were both negatively related to the probability of a searcher relocating a nest, indicating that the observed positive relationships between apparent nest density and vegetation density and diversity are likely conservative and the effects were stronger than estimated.

These results provided support for our mechanistic hypotheses that areas of higher vegetation diversity would have higher nest densities because of an increase in suitable microhabitats (Appendix S1, VD-1) or more abundant food resources (Appendix S1, VD-2). We also found support for our hypotheses that nest survival would increase with vegetation diversity because predators would have to search more microhabitats and a lower percentage of them would contain nests (Appendix S1, VD-3); that nest survival would be higher because, given a greater number of available microhabitats, birds could select nest sites that were more stable or better concealed (Appendix S1, VD-4); and that nest survival would be higher because parents could spend less time foraging and spend more time on nest obfuscation and defense (Appendix S1, VD-5).

### **Ecological traps**

To accurately estimate population growth rate (and thus source-sink dynamics), nest success, re-nesting rate, juvenile and adult survival, immigration, and emigration estimates are needed. Due to the expense and difficulty in estimating survival of non-game migratory birds that are not site faithful, researchers often focus on estimating nest success and then compare their estimated rates to previously published benchmarks (McCoy et al. 1999, Fletcher et al. 2006). Our study used this approach while also comparing nest survival estimates from in-field conservation practices to those of the most common “high quality” habitats in agricultural landscapes to establish relative habitat qualities among several conservation practices.

Our reference “high quality” conservation practice was field-scale (8 – 60 ha) prairie restorations. Outside of rare, widely dispersed public nature reserves, these are the largest, highest quality habitat patches that individual grassland birds are likely to encounter in Iowa. Ninety-six percent of grassland patches in Iowa are smaller than 8 ha (Figure 2-15). However, our estimated nest success rates in large patch prairies ( $s_{grassland} = 13.5\%$ ,  $PI_{95} = 9.3\% - 18.6\%$ ,

$s_{rwbl} = 14.8\%$ ,  $PI_{95} = 9.1\% - 21.9\%$ ,  $s_{dick} = 23.6\%$ ,  $PI_{95} = 12.5\% - 36.8\%$ ) were somewhat lower than published nest success estimates for large (<100 ha) patches of prairie vegetation for Dickcissels in Illinois (22.5 – 23.5%), Kansas (29.8 – 59.3%), and Missouri (37.3 – 46.9%), Grasshopper Sparrows in Illinois (22.9 – 23.6%), Kansas (8.7 – 44.6%), Missouri (13.8 – 44.6%), and Wisconsin (50.7%), and Eastern Meadowlarks (*Sturnella magna*) in Illinois (4.1 – 59.7%), Kansas (24.8 – 45.0%), Missouri (30.9 – 47.7%), and Wisconsin (47.8%) (Herkert et al. 2003, Byers et al. 2017).

McCoy et al. (1999) estimated that a nest success rate of 29.7% for Dickcissels and 27.6% for Red-winged blackbirds was not sufficient to keep the population growth rate above  $\lambda = 1$ , but found nest success rates of 19.5% for Common yellowthroats and 29.9% for Eastern meadowlarks were sufficient to maintain population growth rates above 1 in at least 2 of 3 years. Fletcher et al. (2006) modeled the sensitivities of Dickcissel and Bobolink (*Dolichonyx oryzivorus*) population growth rates in Iowa to changes in nest survival, fecundity, number of nesting attempts, and annual juvenile and adult survival and found that Dickcissel populations with a nest success rate of 22.9% were only stable if adult survival rates increased or nest predation rates decreased and for Bobolinks with a nest success rate of 29.4%, local populations were stable when annual adult survival was  $> 0.7$  and juvenile survival was at least 0.2 – 0.5. For both species, population growth rates were most sensitive to adult annual survival.

Given the variation in our estimates, it is not clear if the nest success rates we predicted for a typical large (8 – 60 ha) patch prairie would be high enough to keep population growth rates above  $\lambda = 1$  without emigration from other populations. Even with more precise nest success estimates, it is difficult to demonstrate source-sink dynamics definitively without measuring re-nesting attempts and juvenile and adult survival. Therefore, for the purposes of this



paper we will assert that because these larger patches of prairie are the best habitat available to the large majority of individual grassland birds nesting in Iowa, but with the knowledge that grassland birds have been undergoing a long-term decline in the state, large prairie patch conservation practices may represent the minimum necessary habitat quality to remain a source and not a sink population. Due to ubiquitous presence of low-diversity conservation practices and grassland birds' continued use of them for reproduction, there may be, at minimum, a harm reduction value in replacing low-diversity plantings with high-diversity conservation practices, even when it is not clear that those patches represent source habitat on their own (Mendenhall et al. 2014, Herrera et al. 2017, Wintle et al. 2018, Estrada-Carmona et al. 2022).

Comparing other conservation practices to large prairie patches, we found that grassed terraces and grass contour strips had low nest densities and low nest survival for grassland nesting birds as a group and Red-winged blackbirds, and intermediate nest density and low nest survival for Dickcissels. Given that we estimated nest detection rates to be lower in large prairie patches, we believe our estimated differences in density between grassed terraces and grass contour strips and large patch prairies are conservative. Our estimated nest success rates almost certainly make grassed terraces and grass contour strips population sinks for Red-winged blackbirds, Dickcissels, and grassland nesting passerines as a group. In addition, because nest densities were not lower in lower-quality habitat, grass contour strips may have been ecological traps for grassland nesting passerines and Red-winged blackbirds, as were grassed terraces for Red-winged blackbirds, Dickcissels, and grassland nesting passerines as a group. The other conservation practices studied had nest survival estimate prediction intervals that overlapped those of large prairie patches, and appear to function at least as well as the best available habitat in the study landscapes.

## **Future directions**

We were unable to jointly estimate nest detection and density because we violated the assumption of demographic closure, with the second team of observers lagging a week behind the first in our double-observer searches (Royle 2004, Dail and Madsen 2011). However, we found that nest detection probability was negatively related to vegetation diversity and density and lower in prairie filter strips compared to grass filter strips or large patches and lower in large prairie patches than large grass patches. When compared to our estimated nest densities, these differences in detection would accentuate differences in our apparent density estimates. Therefore, although we have some evidence that nest detection varied by vegetation and between conservation practices, we believe our estimates of differences in apparent nest density to be conservative. Future studies should consider methods that allow joint estimation of detection and abundance to estimate detection-corrected density.

We used nest density as a metric of habitat preference, which was only one of the five approaches to measuring selection recommended by Robertson and Hutto (2006). Future studies should consider using additional approaches since our study landscapes did not offer birds a choice between all conservation practices of interest and therefore may have obscured some habitat selection dynamics.

At the inception of the study, prairie strips on commercial farms were very limited and we were not able to randomly sample sites, which would have allowed inferences more broadly beyond our study sites. In addition, we were not able to include temporal variables (e.g., year, patch age) due to the confounding effect of switching sites between years for logistical reasons. Because sites varied considerably in habitat amount, configuration, and vegetation, temporal variables had unacceptable correlations with the variables of research interest and had to be

omitted. Future studies would be improved with random selection of sites that could be monitored long-term.

Nest survival for this study was driven in large part by predation pressure. Future studies would gain more insight into the ecological mechanics of differing survival rates by studying local predator behavior concurrently (Chalfoun et al. 2002, Ibáñez-Álamo et al. 2015). Nest parasitism by Brown-headed cowbirds was also significant for some species (Table 2-5), but nests that fledged only cowbird young were still considered successful for this study, due to the uncertainty in assigning a failure date. A discussion of how landscape configuration, habitat amount, and vegetation diversity predicted cowbird parasitism can be found in Chapter 2.

We present analyses for eight grassland nesting passerines as a group and individual analyses for two common and relatively easy to find species because those were the species for which we were able to attain sample sizes sufficient to reduce uncertainty to acceptable levels. However, we also found nests of eight other grassland nesting birds and 12 shrub nesting birds that may not all demonstrate the same effects from habitat area, configuration, and vegetation diversity. Additionally, we did not locate any nests of area sensitive species (e.g., Bobolink, Henslow's sparrows) in small, linear conservation practices. We highlight here the commonalities between a functional group of grassland nesting passerines, Red-winged blackbirds, and Dickcissels (an Iowa Species of Greatest Conservation Need), but more work is needed for other species, both common and those in greatest need of conservation.

## **Conclusions**

We provided evidence against an extension of the Habitat Amount Hypothesis to demographic parameters and demonstrated several different and equivalent ways that nest density and survival varied with landscape habitat amount and configuration and vegetation diversity. Because a one standard deviation change in any predictor variable was equally as

likely in our landscapes, and because our important predictor variables were similar in magnitude with overlapping confidence intervals, a change in any one of them had the potential to improve habitat in heavily agricultural areas for a guild in long-term decline. We also provided evidence that prairie strips have similar nest survival rates as larger patches of prairie for common species of grassland nesting passerines but highlight the possibility that grassed terraces and grass contour strips could be population sinks or ecological traps based on low nest success rates without concomitantly lower nest densities.

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### **Author Contributions**

This study was conceived and executed by MS under the guidance of LAS and RK. MS designed the study and collected the data with assistance of seasonal technicians and graduate student Julia Dale. MS and JN developed the analysis approach with assistance from RK, and MS wrote and executed the statistical code. MS wrote the manuscript and prepared the figures and tables with guidance from LAS and RK and comments provided by JN. LAS secured funding for the research program.

### **Conflict of Interest Statement**

The authors have no known conflicts of interest with the publication of this manuscript. No funders had input into the content of the manuscript and no funder approval was required before submission or publication. Any mention of trade, product, or firm names is for descriptive purposes only, and does not imply endorsement by the U.S. Government.

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### Equations

Equation 2-1. Nest detection global model.

$$\begin{aligned} \text{detection} \sim & \text{nest\_age} + \text{minutes\_since\_sunrise\_log} + \text{temp\_c\_log} + \text{wind\_ms\_log} \\ & + \text{precipitation\_6\_hour\_mm\_log} + \text{observer\_prior\_searches\_log} \\ & * (\text{patch\_area\_veg\_ha\_log} + \text{feature\_width\_at\_plot\_meters\_log} \\ & + \text{location\_predictability\_sum\_log} + \text{vor\_final\_mean\_log} \\ & + \text{species\_richness\_all\_5m\_total\_log}) + (1|\text{species}) \end{aligned}$$

Equation 2-2. Nest density global model. “###” variable was 150 for Red-winged blackbirds and 200 for Dickcissels and grassland passerines.

$$\begin{aligned} \text{total\_nests} \sim & \text{species\_richness\_all\_5m\_total\_log} + \text{vor\_final\_mean\_log} \\ & + \text{quadrats\_mowed\_percent\_log} \\ & + (\text{patch\_area\_veg\_ha\_log} + \text{patch\_count\_###\_m\_radius\_log} \\ & + \text{edge\_density\_m\_per\_ha\_###\_m\_radius} \\ & + \text{mean\_nearest\_neighbor\_m\_###\_m\_radius\_log}) \\ & * \text{grassland\_area\_ppn\_###\_m\_log} + \text{woody\_cover\_ppn\_###\_m\_log} \\ & + \text{distance\_to\_water\_meters\_log} * \text{drought\_index\_mean\_jan\_aug\_log} \\ & + (1 | \text{plot\_name}) + \text{offset}(\log(\text{plot\_area\_ha})) \\ & + \text{offset}(\log(\text{search\_count})) \end{aligned}$$

Equation 2-3. Nest survival global. “sq” suffixes indicate a squared variable and “lg” suffixes indicate log-transformed variables. “###” variable was 150 for Red-winged blackbirds and 200 for Dickcissels and grassland passerines.

$$\begin{aligned} \text{daily\_survival\_rate} \sim & \text{AgeD} + \text{AgeDSq} + \text{mow\_quadlg} * (\text{vorlg} + \text{rich\_at\_lg}) \\ & + (\text{pch\_arealg} + \text{pchct###lg} + \text{edge###lg} + \text{mnn###lg} + \text{dist\_crplg}) \\ & * \text{grass###lg} + \text{woody###lg} \end{aligned}$$

## Tables

Table 2-1. Conservation practice descriptions based on patch shape, slope position, and vegetation diversity. Cost share program designations were archetypical; actual enrollment in a cost share program was not required or verified.

| Conservation practice | Example cost share program                              | Description   |
|-----------------------|---|---|
| Grass contour strip   | CP-15A  | Linear strip (3 – 100 m wide, typically ~10 m) of low diversity grass planted along a contour within a field. Often planted to exotic cool-season grass species such as smooth brome ( <i>Bromus inermis</i> ).   |
| Grassed terrace       | IA-600 grassed backslope terraces, narrow base terraces | Linear earthen berm (2 – 5 m wide) along a contour within a field, typically planted to cool-season exotic grasses (e.g., smooth brome) when established, but were frequently affected by herbicide drift and filled with annual weeds and woody species.   |
| Grass filter strip    | CP-21   | Linear strips (3 – 30 m wide, typically ~10 m) of low diversity grass planted at toe slope position adjacent to a permeant water body. Typically planted to cool-season exotic grasses such as reed canary grass ( <i>Phalaris arundinacea</i> ).   |
| Grass waterway        | CP-8A   | Linear strips (3 – 60 m wide, typically ~ 10 m) of low diversity grass planted along drainage paths to conduct surface water off fields. Typically planted with exotic cool-season grasses such as smooth brome.  |
| Grass large patch     | CP-1, CP-4D   | Low diversity grass planted in larger patches (> 8 ha) such as field corners, areas isolated by streams, or entire fields. Plantings contained exotic or native warm or cool season grasses.  |
| Prairie contour strip | CP-43   | Linear strips (3 – 100 m wide, typically ~10 m) of medium-high diversity native grasses and forbs planted along a contour within a field. Common species included big bluestem ( <i>Andropogon gerardi</i> ), little bluestem ( <i>Schizachyrium scoparium</i> ), Canada wild rye ( <i>Elymus canadensis</i> ), gray coneflower ( <i>Ratibida pinnata</i> ), wild bergamot ( <i>Monarda fistulosa</i> ), rattlesnake master ( <i>Eryngium yuccifolium</i> ), oxeye ( <i>Heliopsis helianthoides</i> ), etc. |
| Prairie filter strip  | CP-43   | Linear strips (3 – 30 m wide, typically ~10 m) of medium-high diversity native grasses and forbs planted along permeant water bodies with plant communities similar to prairie contour strips.  |
| Prairie large patch   | CP-33, CP-38, CP-42                                     | Medium-high diversity native grasses and forbs planted in larger patches (> 8 ha) such as field corners, strips wider than 100 m, or whole fields.  |

Table 2-2. Nest *detection* variables considered. Variables are divided into categories based on why they were included: “behavior” variables could affect parental behavioral cues that a nest is near, “search efficiency” variables could affect observer search patterns, “observer effect” variable captures differences between searcher ability, “nest concealment” variables could affect how effectively a nest could be concealed, and “RE” (random effect) variables were grouping variables. Interactions were included for observer prior searches with species richness, patch area, feature width, location predictability index, vegetation visual obstruction (“vor”), and vegetation richness. Bold text transformations were used in the final global model.

| Variable                              | Description  | Native units      | Transformations considered                         | Category          | Selected for final model list |
|---------------------------------------|--|-------------------|--|-------------------|-------------------------------|
| nest_age                              | age of nest  | d                 | <b>linear</b> , quadratic                          | behavior          | yes                           |
| minutes_since_sunrise                 | time elapsed since dawn  | min               | linear, quadratic, <b>log</b>                      | behavior          | yes                           |
| temp_c                                | temperature at time of search                                  | °C                | linear, quadratic, <b>log</b>                      | behavior          | yes                           |
| wind_ms                               | wind speed at time of search                                   | m/s               | linear, quadratic, <b>log</b>                      | behavior          | yes                           |
| precipitation_6_hour_mm               | total precipitation accumulation over past 6 hours             | mm                | linear, quadratic, <b>log</b>                      | behavior          | yes                           |
| patch_area_veg_ha_log                 | patch area   | ha                | linear, quadratic, <b>log</b> , <b>interaction</b> | search efficiency | yes                           |
| feature_width_at_plot_meters_log      | minimum patch width at nest                                    | log(m)            | linear, quadratic, <b>log</b> , <b>interaction</b> | search efficiency | yes                           |
| location_predictability_sum           | plant species preference divided by plant sp. mean aggregation | index             | linear, quadratic, <b>log</b> , <b>interaction</b> | search efficiency | yes                           |
| observer_prior_searches               | count of searches-conducted-to-date by both observers          | count             | linear, quadratic, <b>log</b> , <b>interaction</b> | observer effect   | yes                           |
| vor_final_mean                        | plot vegetation density measured with the Robel method         | cm obscured       | linear, quadratic, <b>log</b> , <b>interaction</b> | nest concealment  | yes                           |
| species_richness_native_quadrats_mean | count of native plant species in plot                          | log species count | linear, quadratic, <b>log</b> , <b>interaction</b> | nest concealment  | yes                           |
| species                               | species that built nest  | categorical       | -  | RE                | yes                           |
| nest_name:species                     | individual nests nested within species                         | categorical       | -  | RE                | no                            |

Table 2-3. Nest *density* variables considered. Landscape variables used 150 m (Red-winged blackbird) or 200 m (Dickcissel and grassland passerines) radii from plot centroids, denoted below as “###”. Bold text transformations were used in the final global model. Interactions were included for grassland area with patch area, patch count, edge density, and mean nearest neighbor distance within ### m, and for distance to water with drought index.

| Variable                             | Description  | Native units | Transformations considered                         | Category                | Selected for final model list |
|--------------------------------------|--|--------------|--|-------------------------|-------------------------------|
| grassland_area_ppn_###_m             | proportion of a 150/200 m radius circle in grass land cover                        | proportion   | linear, quadratic, <b>log</b> , <b>interaction</b> | landscape: habitat area | yes                           |
| patch_area_veg_ha                    | area of patch using vegetation communities and 3 m pixels                          | ha           | linear, quadratic, <b>log</b> , <b>interaction</b> | landscape: patch size   | yes                           |
| patch_nearest_neighbor_veg_m         | distance to nearest similar-community patch  | m            | linear, quadratic, log                             | landscape: isolation    | no                            |
| patch_count_###_m_radius             | count of distinct patches within 150/200 m   | count        | linear, quadratic, <b>log</b> , <b>interaction</b> | landscape: patch count  | yes                           |
| perimeter_area_ratio_veg_m_per_sq_m  | perimeter:area ratio of patch using vegetation community definition and 3 m pixels | m            | linear, quadratic, <b>log</b> , <b>interaction</b> | Landscape: edge effects | no                            |
| distance_to_crop_meters              | distance to nearest row crop land cover  | m            | linear, quadratic, log, interaction                | landscape: edge effects | no                            |
| feature_width_at_plot_meters         | patch width at plot center   | m            | linear, quadratic, log, interaction                | landscape: edge effects | no                            |
| edge_density_m_per_ha_###_m_radius   | length of edge per unit area within 150/200 m                                      | m/ha         | linear, quadratic, <b>log</b> , <b>interaction</b> | landscape: edge effects | yes                           |
| mean_nearest_neighbor_m_###_m_radius | mean nearest-neighbor distance for patches within ## m radius                      |              | linear, quadratic, <b>log</b> , <b>interaction</b> | landscape: isolation    | yes                           |
| vor_final_mean                       | mean vegetation density measured with a Robel pole from 5 m (10 – 150)             | cm obscured  | linear, quadratic, <b>log</b> , <b>interaction</b> | vegetation: density     | yes                           |

Table 2-3 continued

| Variable                                   | Description  | Native units  | Transformations considered                         | Category              | Selected for final model list |
|--|--|---------------|--|-----------------------|-------------------------------|
| species_richness_all_5m_total              | plant species count within plot                          | count         | linear, quadratic, <b>log</b> , <b>interaction</b> | vegetation: diversity | yes                           |
| preferred_species_cover_grassland_mean_all | mean cover of preferred plant species within plot        | percent cover | linear, quadratic, log, interaction                | vegetation: diversity | no                            |
| <i>Expert opinion variables</i>            |  |               |  |                       |                               |
| quadrats_mowed_percent                     | percent of quadrats mowed                                | percentage    | linear, quadratic, <b>log</b> , <b>interaction</b> | confounding           | yes                           |
| woody_cover_ppn_###_m_r                    | proportion of a ## m radius circle in woody land cover   | proportion    | linear, quadratic, <b>log</b>                      | life history          | yes                           |
| distance_to_water_meters                   | distance to nearest water land cover                     | m             | linear, quadratic, <b>log</b> , <b>interaction</b> | life history          | yes                           |
| drought_index_mean_jan_aug                 | North America Drought Monitor index mean from Jan to Aug | index         | linear, quadratic, <b>log</b> , <b>interaction</b> | life history          | yes                           |
| plot_name                                  | individual plot  | categorical   | none   | random effects        | yes                           |
| site                                       | individual site  | categorical   | none   | random effects        | no                            |
| plot_area_ha                               | area of actualized search plot                           | ha            | <b>log</b>   | offset                | yes                           |
| search_count                               | number of searches for the plot that year                | count         | <b>log</b>   | offset                | yes                           |

Table 2-4. Nest *survival* variables considered. Landscapes were scaled based on mean territory size: “###” was 150 for Red-winged blackbirds and 200 for Dickcissels and grassland birds. We included interactions for *mow\_quadlg* with *vorlg* and *rich\_at\_lg*, and for *grass###lg* with *pch\_arealg*, *pchct###lg*, *edge###lg*, *mnn###lg*, and *dist\_crplg*. Bold transformations were used in the final global model.

| Variable          | Description  | Native units     | Transformations considered | Category                              | Selected for final model list |
|-------------------|--|------------------|----------------------------|---------------------------------------|-------------------------------|
| <i>grass###lg</i> | proportion of a ### m radius circle in grass land cover  | proportion       | quadratic, <b>log</b>      | landscape configuration: habitat area | yes                           |
| <i>pchct###lg</i> | count of distinct patches within ### m                   | count            | quadratic, <b>log</b>      | landscape configuration: patch count  | yes                           |
| <i>mnn###lg</i>   | mean nearest neighbor distance within ### m              | m                | quadratic, <b>log</b>      | landscape configuration: isolation    | yes                           |
| <i>edge###lg</i>  | density of edges within ### m                            | m/ha             | quadratic, <b>log</b>      | landscape configuration: edge effects | yes                           |
| <i>pch_parlg</i>  | patch length of edge per unit area                       | m/m <sup>2</sup> | quadratic, <b>log</b>      | landscape configuration: edge effects | yes                           |
| <i>dist_crplg</i> | log-distance to nearest row crop land cover              | log(m)           | quadratic, <b>log</b>      | landscape configuration: edge effects | no                            |
| <i>pch_arealg</i> | patch area   | ha               | quadratic, <b>log</b>      | landscape configuration: patch size   | yes                           |
| <i>vorlg</i>      | vegetation density measured with a Robel pole from 5 m   | cm               | quadratic, <b>log</b>      | vegetation: density                   | yes                           |
| <i>rich_at_lg</i> | log-count of plant species within 5 m                    | count            | linear, <b>log</b>         | vegetation: diversity                 | yes                           |
| <i>pref_subst</i> | indicator if nest was built in a preferred plant species | indicator        | binary                     | vegetation: diversity                 | yes                           |
| <i>pref_spcvr</i> | mean cover of preferred plant species within 5 m         | percent cover    | linear                     | vegetation: diversity                 | no                            |
| <i>mow_quadlg</i> | index of mowing activity within 5 m (0 – 4)              | index            | linear, <b>log</b>         | vegetation: confounding               | no                            |
| <i>wndlmax</i>    | maximum wind speed                                       | m/s              | linear, <b>log</b>         | vegetation: confounding               | no                            |

Table 2-4 continued

| Variable   | Description   | Native units      | Transformations considered | Category       | Selected for final model list |
|------------|---|-------------------|----------------------------|----------------|-------------------------------|
| woody###lg | proportion of a ### m radius circle in woody land cover | proportion        | linear, <b>log</b>         | expert opinion | yes                           |
| AgeD       | Days since incubation start                             | days              | <b>linear</b>              | expert opinion | yes                           |
| AgeDSq     | Days since incubation start squared                     | days <sup>2</sup> | <b>quadratic</b>           | expert opinion | yes                           |

Table 2-5. Raw counts and demographic rates of nests found from 2015 – 2019 at 11 sites in central Iowa, US. Focal species were passerines that nest in grasslands with or without woody vegetation. Species indicated with \* are Iowa Species of Greatest Conservation Need. ‘Nests (plots)’ contains the raw sum of nests found in a search plot during a structured search. ‘Nests (total)’ contains the raw count of all nests found while active and revisited at least once. ‘Success rate’ is the raw success rate and ‘Ppn of failures predations’ gives the fraction of failed nests that were attributed to a predation event. ‘Host...’ and ‘Cowbird young fledged’ columns contain the counts of young at the time of fledging and ‘Cowbird-only fledge rate’ gives the proportion of nests that fledged cowbird but not host young. Nest totals presented in ‘Nests (plots)’ and ‘Nests (total)’ columns may not match the numbers included in the final density and survival analyses due to some nests violating inclusion criteria.

| Species   | Nests (plots) | Nests (total) | Success rate | Ppn of failures predations | Host young fledged (mean) | Host young fledged (se) | Cowbird young fledged (mean) | Cowbird young fledged (se) | Cowbird-only fledge rate |
|---|---------------|---------------|--------------|----------------------------|---------------------------|-------------------------|------------------------------|----------------------------|--------------------------|
| <i>Focal species</i>                                  |               |               |              |                            |                           |                         |                              |                            |                          |
| American Goldfinch ( <i>Spinus tristis</i> )          | 6             | 16            | 0.33         | 0.8                        | 2.8                       | 0.2                     | 0                            | 0                          | 0                        |
| *Common Yellowthroat ( <i>Geothlypis trichas</i> )    | 11            | 48            | 0.08         | 0.82                       | 0.25                      | 0.25                    | 0.75                         | 0.25                       | 0.5                      |
| *Dickcissel ( <i>Spiza americana</i> )                | 126           | 304           | 0.17         | 0.8                        | 1.67                      | 0.21                    | 0.69                         | 0.12                       | 0.24                     |
| *Grasshopper Sparrow ( <i>Ammodramus savannarum</i> ) | 4             | 6             | 0.17         | 0.8                        | 1                         | -                       | 0                            | -                          | 0                        |
| *Meadowlark Species ( <i>Sturnella sp.</i> )          | 10            | 44            | 0.14         | 0.92                       | 2                         | 0.58                    | 0.33                         | 0.33                       | 0.17                     |
| Red-winged Blackbird ( <i>Agelaius phoeniceus</i> )   | 145           | 781           | 0.16         | 0.81                       | 2.24                      | 0.12                    | 0.22                         | 0.05                       | 0.08                     |
| *Sedge Wren ( <i>Cistothorus platensis</i> )          | 1             | 3             | 0.33         | 1                          | -                         | -                       | -                            | -                          | 0                        |



Table 2-5 continued

| Species  | Nests (plots) | Nests (total) | Success rate | Ppn of failures predations | Host young fledged (mean) | Host young fledged (se) | Cowbird young fledged (mean) | Cowbird young fledged (se) | Cowbird-only fledge rate |
|--|---------------|---------------|--------------|----------------------------|---------------------------|-------------------------|------------------------------|----------------------------|--------------------------|
| Song Sparrow ( <i>Melospiza melodia</i> )          | 4             | 14            | 0.14         | 0.75                       | 2.5                       | 0.5                     | 0                            | 0                          | 0                        |
| Sparrow Sp. ( <i>Emberizidae</i> )                 | 0             | 2             | 0            | 1                          | -                         | -                       | -                            | -                          | -                        |
| Vesper Sparrow ( <i>Pooecetes gramineus</i> )      | 21            | 67            | 0.24         | 0.69                       | 1.62                      | 0.34                    | 0.31                         | 0.15                       | 0.19                     |
| <i>Non-focal species</i>                           |               |               |              |                            |                           |                         |                              |                            |                          |
| American Robin ( <i>Turdus migratorius</i> )       | 6             | 66            | 0.23         | 0.96                       | 2.59                      | 0.26                    | 0                            | 0                          | 0                        |
| *Brown Thrasher ( <i>Toxostoma rufum</i> )         | 12            | 33            | 0.09         | 0.97                       | 2.67                      | 0.67                    | 0                            | 0                          | 0                        |
| Cedar Waxwing ( <i>Bombycilla cedrorum</i> )       | 0             | 1             | 0            | 1                          | -                         | -                       | -                            | -                          | -                        |
| Chipping Sparrow ( <i>Spizella passerina</i> )     | 0             | 2             | 0.5          | 1                          | 4                         | -                       | 0                            | -                          | 0                        |
| Eastern Bluebird ( <i>Sialia sialis</i> )          | 0             | 1             | 1            | -                          | 2                         | -                       | 0                            | -                          | 0                        |
| *Eastern Kingbird ( <i>Tyrannus tyrannus</i> )     | 0             | 1             | 0            | 1                          | -                         | -                       | -                            | -                          | -                        |
| Gray Partridge ( <i>Perdix perdix</i> )            | 0             | 1             | 0            | 1                          | -                         | -                       | -                            | -                          | -                        |
| Gray Catbird ( <i>Dumetella carolinensis</i> )     | 3             | 10            | 0.3          | 0.86                       | 2.33                      | 0.67                    | 0                            | 0                          | 0                        |
| Killdeer ( <i>Charadrius vociferus</i> )           | 1             | 11            | 0.91         | 0                          | 3.1                       | 0.46                    | 0                            | 0                          | 0                        |
| Lark Sparrow ( <i>Chondestes grammacus</i> )       | 0             | 1             | 0            | 1                          | -                         | -                       | -                            | -                          | -                        |
| *Loggerhead Shrike ( <i>Lanius ludovicianus</i> )  | 0             | 1             | 0            | 0                          | -                         | -                       | -                            | -                          | -                        |
| Mallard ( <i>Anas platyrhynchos</i> )              | 1             | 3             | 0.33         | 1                          | 10                        | -                       | 0                            | -                          | 0                        |
| Mourning Dove ( <i>Zenaida macroura</i> )          | 3             | 28            | 0.32         | 0.89                       | 1.89                      | 0.11                    | 0                            | 0                          | 0                        |
| Northern Cardinal ( <i>Cardinalis cardinalis</i> ) | 2             | 3             | 0            | 1                          | -                         | -                       | -                            | -                          | -                        |

Table 2-5 continued

| Species  | Nests (plots) | Nests (total) | Success rate | Ppn of failures predations | Host young fledged (mean) | Host young fledged (se) | Cowbird young fledged (mean) | Cowbird young fledged (se) | Cowbird-only fledge rate |
|--|---------------|---------------|--------------|----------------------------|---------------------------|-------------------------|------------------------------|----------------------------|--------------------------|
| Rose-breasted Grosbeak<br>( <i>Pheucticus ludovicianus</i> ) | 1             | 1             | 0            | 1                          | -                         | -                       | -                            | -                          | -                        |
| Ring-necked Pheasant<br>( <i>Phasianus colchicus</i> )       | 3             | 15            | 0.33         | 0.6                        | 11                        | 1.79                    | 0                            | 0                          | 0                        |
| Spotted Sandpiper ( <i>Actitis macularius</i> )              | 0             | 3             | 0.67         | 1                          | 2.5                       | 1.5                     | 0                            | 0                          | 0                        |
| *Upland Sandpiper<br>( <i>Bartramia longicauda</i> )         | 1             | 7             | 0.29         | 0.6                        | 2.5                       | 1.5                     | 0                            | 0                          | 0                        |
| Wild Turkey ( <i>Meleagris gallopavo</i> )                   | 0             | 1             | 0            | 0                          | -                         | -                       | -                            | -                          | -                        |
| *Yellow-billed Cuckoo<br>( <i>Coccyzus americanus</i> )      | 0             | 1             | 0            | 1                          | -                         | -                       | -                            | -                          | -                        |

Table 2-6. Conservation practice plot search summary for nest searches conducted on 11 properties in central Iowa May – Aug between 2016 – 2019. Richness (species count of nests found) includes all species, normalized to a 0.1 ha sampling area. Mean annual apparent nest densities were normalized to 10 searches per season.

| Conservation practice | Plot search-years | Mean richness | Nest density (grassland passerines) |      | Nest density (Red-winged blackbird) |      | Nest density (Dickcissel) |      |
|-----------------------|-------------------|---------------|-------------------------------------|------|-------------------------------------|------|---------------------------|------|
|                       |                   |               | Nests/ha                            | SE   | Nests/ha                            | SE   | Nests/ha                  | SE   |
| Grassed terrace       | 85                | 0.96          | 6.53                                | 1.23 | 2.33                                | 0.74 | 3.03                      | 0.84 |
| Grass contour strip   | 133               | 0.51          | 5.1                                 | 0.61 | 1.82                                | 0.36 | 2.33                      | 0.41 |
| Grass filter strip    | 60                | 0.56          | 8.18                                | 1.18 | 7.33                                | 1.12 | 0.51                      | 0.3  |
| Grass large patch     | 12                | 0.83          | 7.38                                | 2.46 | 1.64                                | 1.16 | 4.92                      | 2.01 |
| Prairie contour strip | 118               | 0.68          | 7.89                                | 0.78 | 2.63                                | 0.45 | 3.79                      | 0.54 |
| Prairie filter strip  | 26                | 1.19          | 15.48                               | 2.42 | 10.19                               | 1.96 | 4.15                      | 1.25 |
| Prairie large patch   | 96                | 0.31          | 2.48                                | 0.51 | 0.41                                | 0.21 | 1.24                      | 0.36 |

## Figures

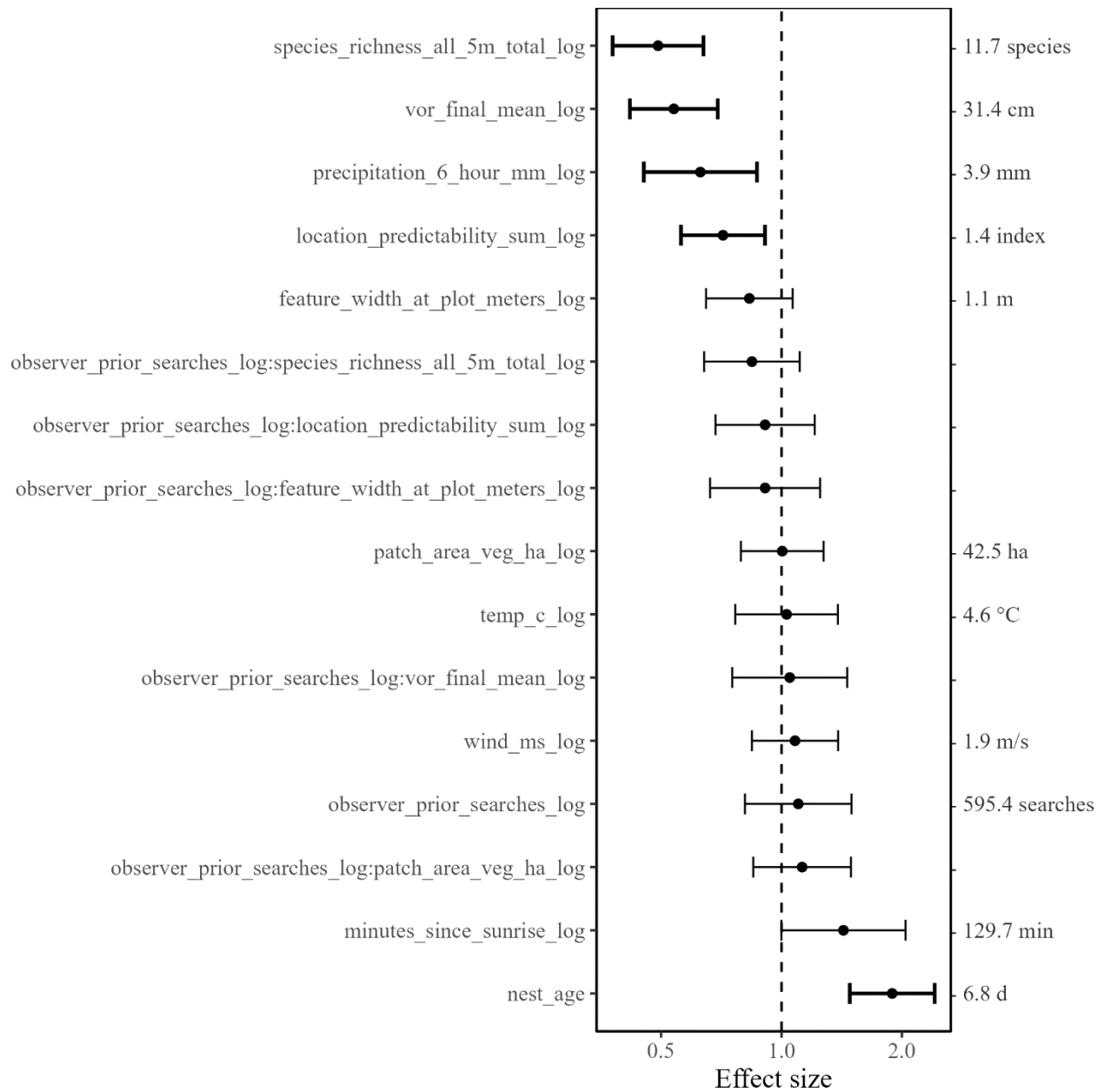


Figure 2-1. Odds of detection by predictor variable for all grassland species. A one standard deviation change (right axis) in the predictor variable multiplied the odds of detection by the indicated amount. Descriptions of variables are provided in Table 2-2.

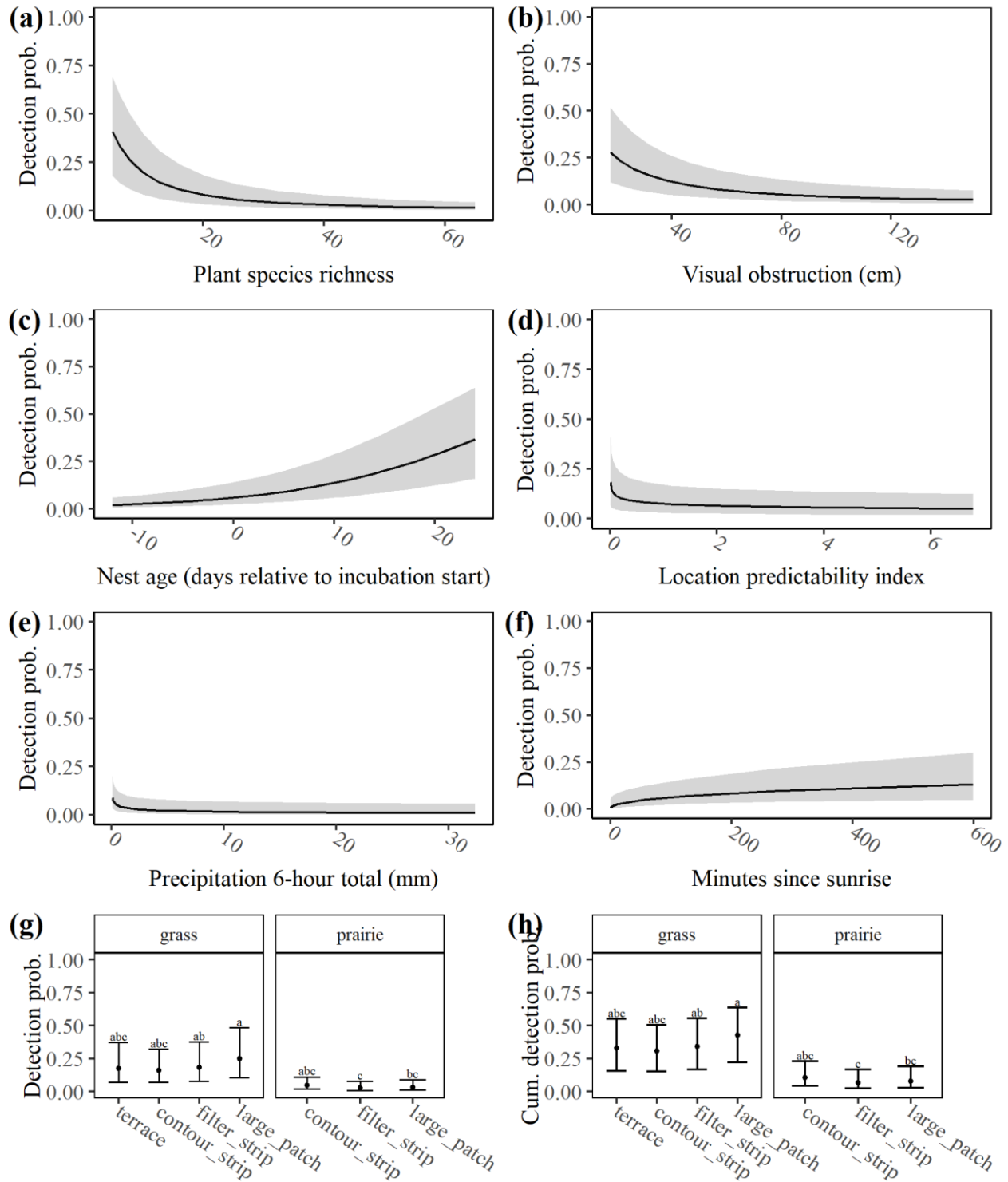


Figure 2-2. Grassland bird nest detection probability predicted for each of 398 models that represented 95% of the AICc model weight of all possible models. Mean predictions of nest

detection by nest age (a), time of day (b), location predictability index (c), precipitation (d), vegetation diversity (e), visual obstruction as a correlate of vegetation density (f), and by conservation practice (g-h). Cumulative detection probability (h) compounds detection over multiple visits after accounting for the probability a nest fails ( $DSR = 0.91$ ) and is not available for detection. 95% prediction intervals are indicated by the shaded area (a-f) and whiskers (g-h). Groups that do not share letters (g-h) are significantly different.

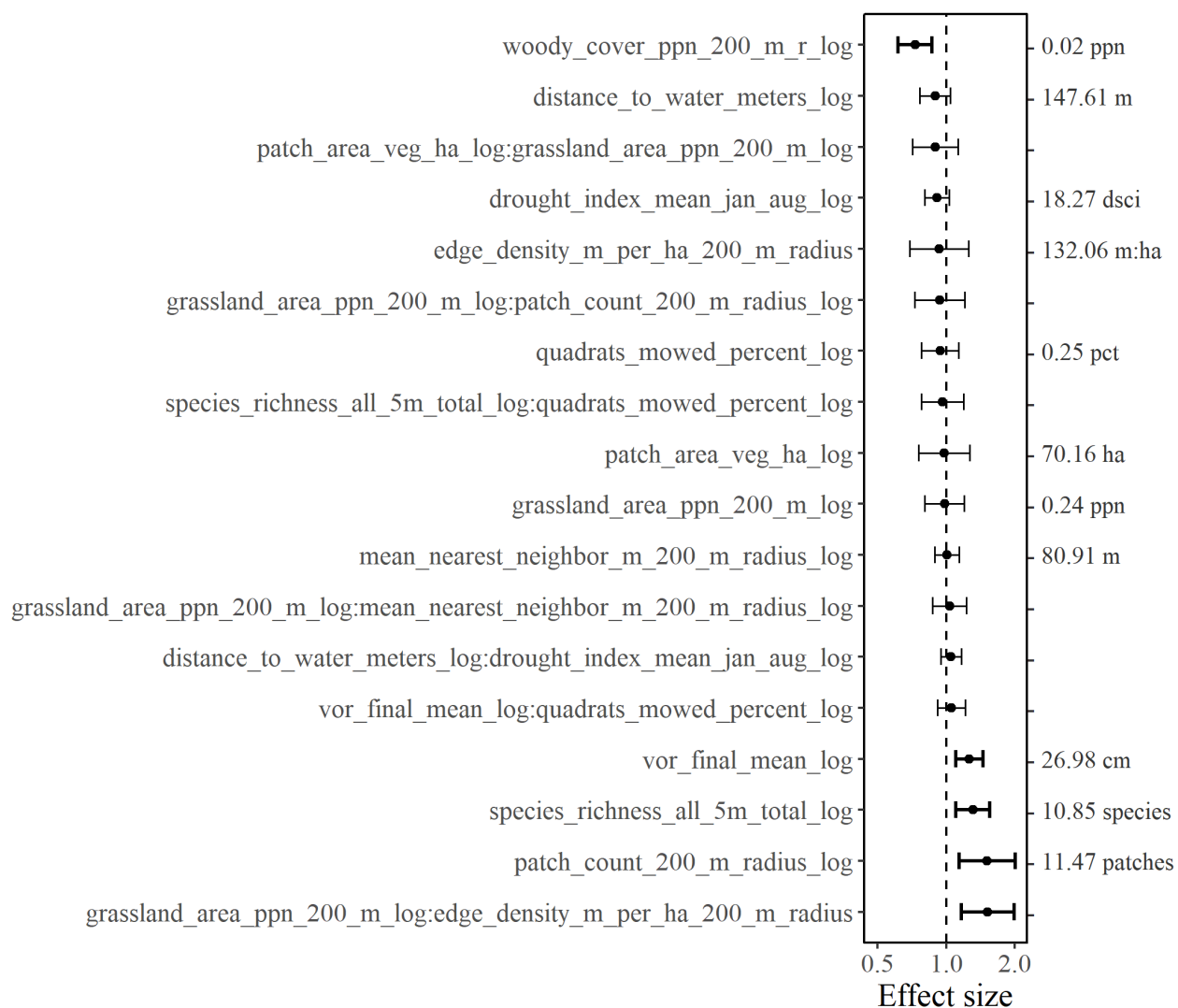


Figure 2-3. Grassland nesting passerine apparent nest density effect sizes and 95% confidence intervals derived from the global model, expressed as odds ratios. Predictor variables were centered and scaled so that a one standard deviation (right axis) change in the predictor variable multiplies apparent nest density by the indicated odds. Descriptions of variables are provided in Table 2-3.

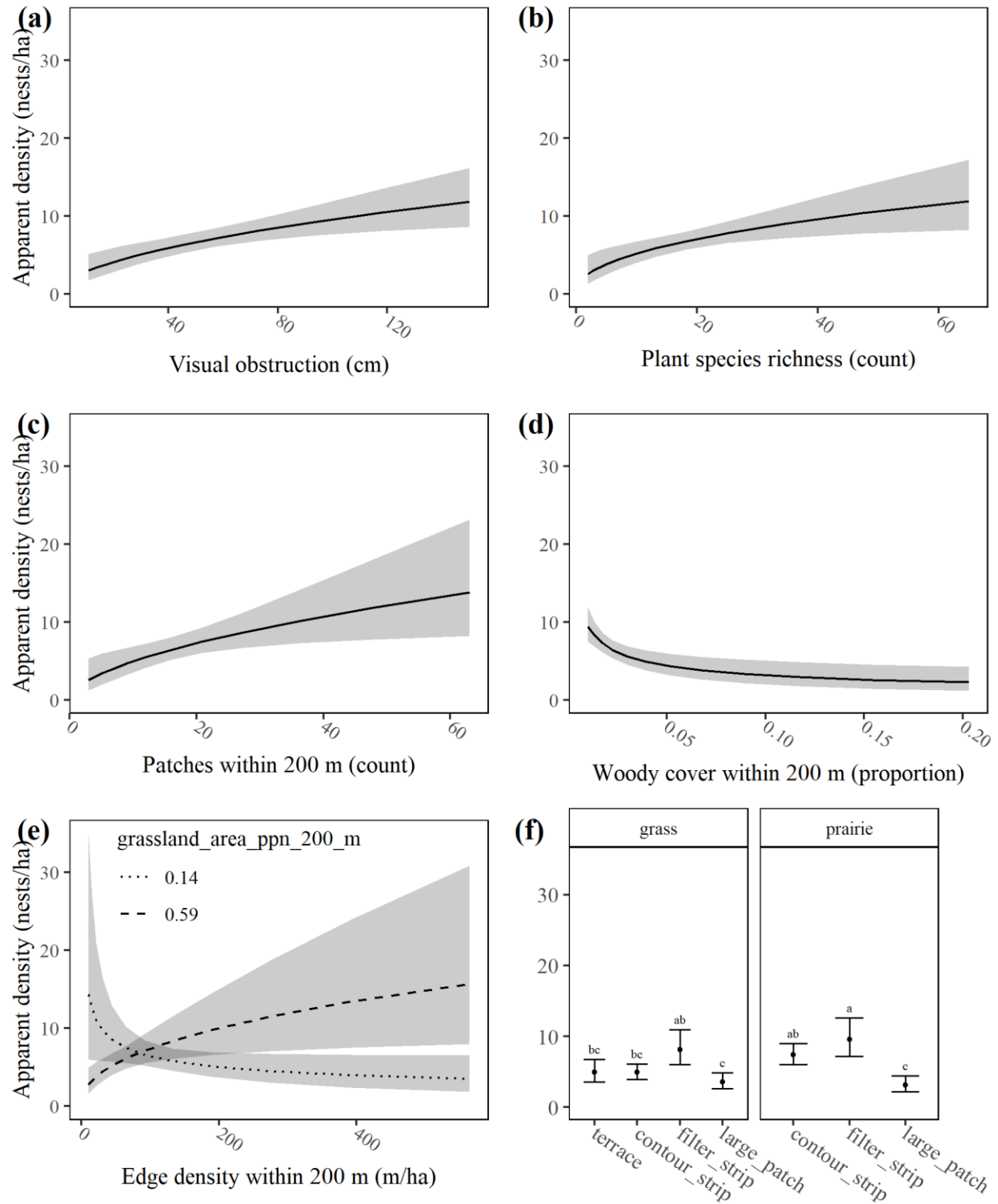


Figure 2-4. Grassland bird apparent nest density predicted for each of 505 models that represented 95% of the AICc model weight of all possible models. Mean predictions of nest

density by visual obstruction as a correlate of vegetation density (a), vegetation diversity (b), landscape patch count (c), landscape edge density with a grassland habitat amount interaction (d), landscape woody cover amount (e), and by conservation practice (f). 95% prediction intervals are indicated by the shaded area (a-e) and whiskers (f). Groups that do not share letters (f) are significantly different.



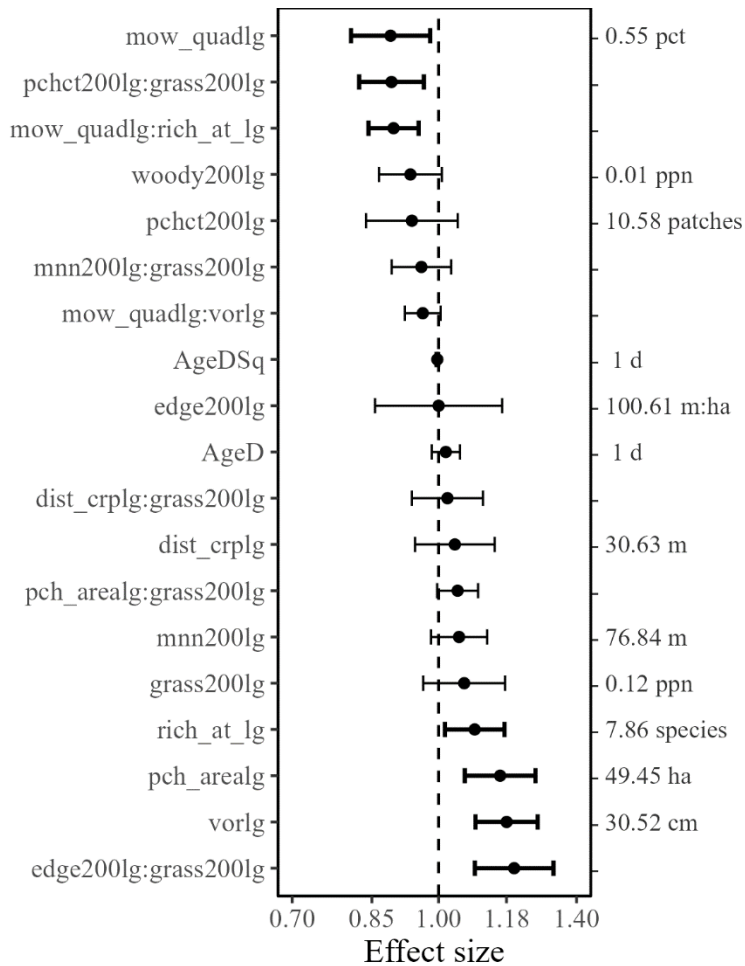


Figure 2-5. Nest survival global model effect sizes for grassland bird functional group with 95% confidence intervals, expressed as odds ratios. Predictor variables (with the exception of Age) were centered and scaled so that a one standard deviation (right axis) change in the predictor variable multiplied the estimated daily survival rate by the indicated amount. Variable descriptions are provided in Table 2-4.

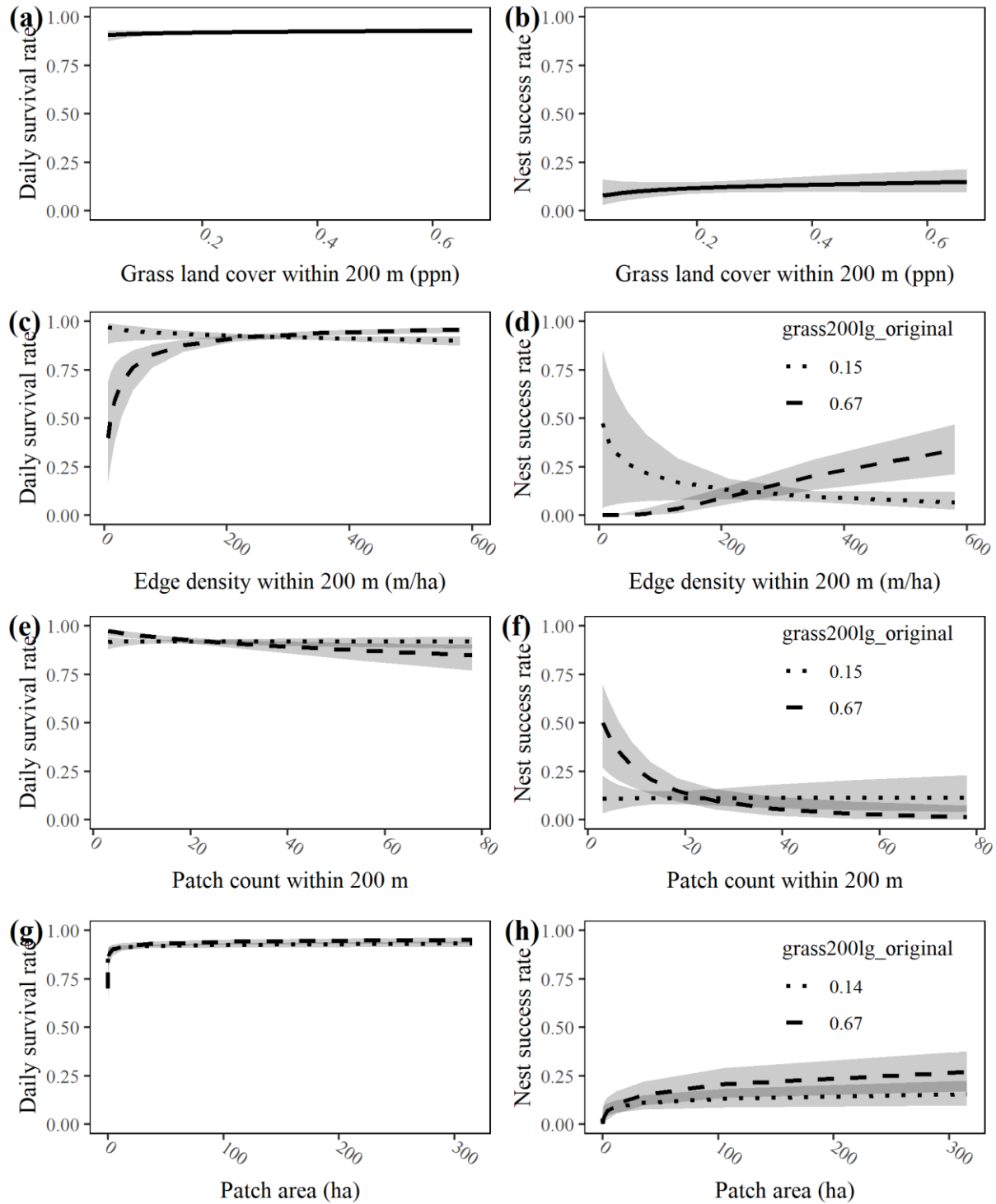


Figure 2-6. Nest daily survival rate (DSR) and overall success rate for grassland birds as a group predicted by individual variables and averaged across 53 models representing 95% of the AICc model weight : grass land cover within 200 m (a, b), edge density within 200 m (c, d), patch

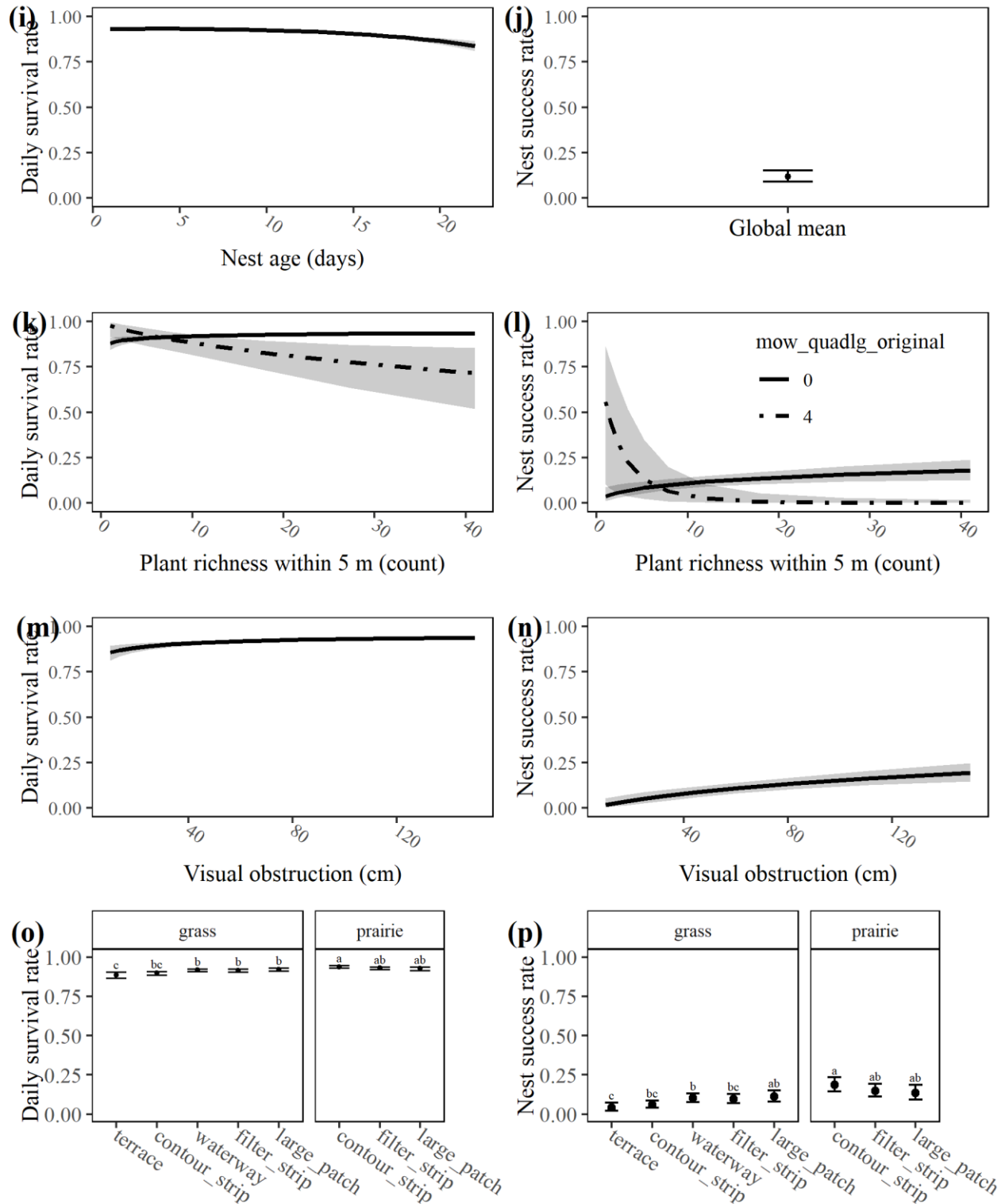


Figure 2-6 continued... count within 200 m (e, f), patch area (g, h), nest age (i), the global mean success rate (j), plant species richness (k, l), visual obstruction as a correlate of vegetation

density (m, n), and conservation practice (o, p). Daily survival rates are presented on the left and likelihood of surviving 24 days is on the right. Predictions with interaction terms include the smallest and largest observed values of the variable shown in the legend. Shaded areas indicate the 95% prediction interval and conservation practices that do not share a letter are significantly different.

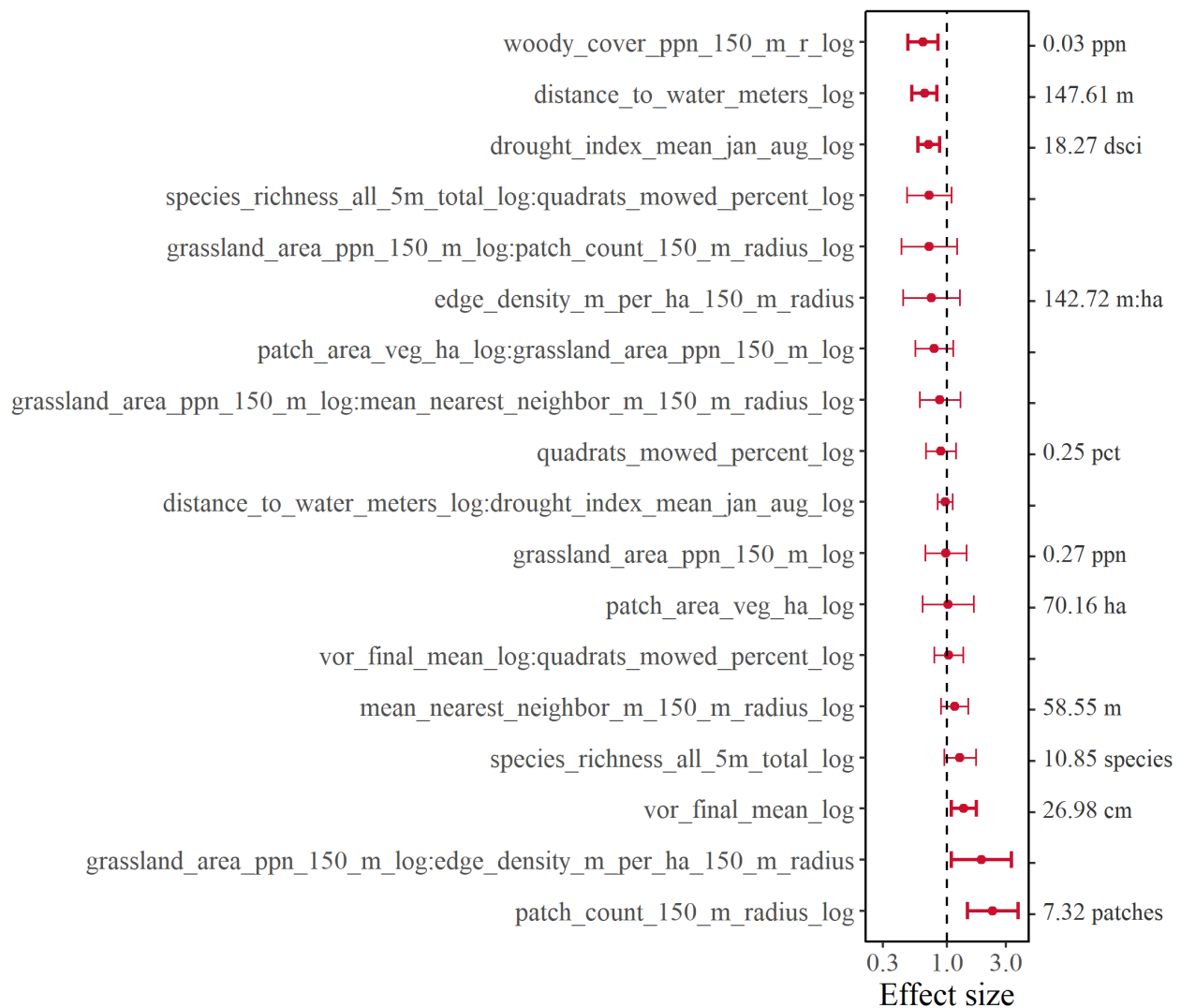


Figure 2-7. Red-winged blackbird apparent nest density effect sizes and 95% confidence intervals derived from the global model, expressed as odds ratios. Predictor variables were centered and scaled, allowing direct comparison. A one standard deviation (right axis) change in

the predictor variable multiplies apparent nest density by the indicated odds. Variable descriptions are provided in Table 2-3.

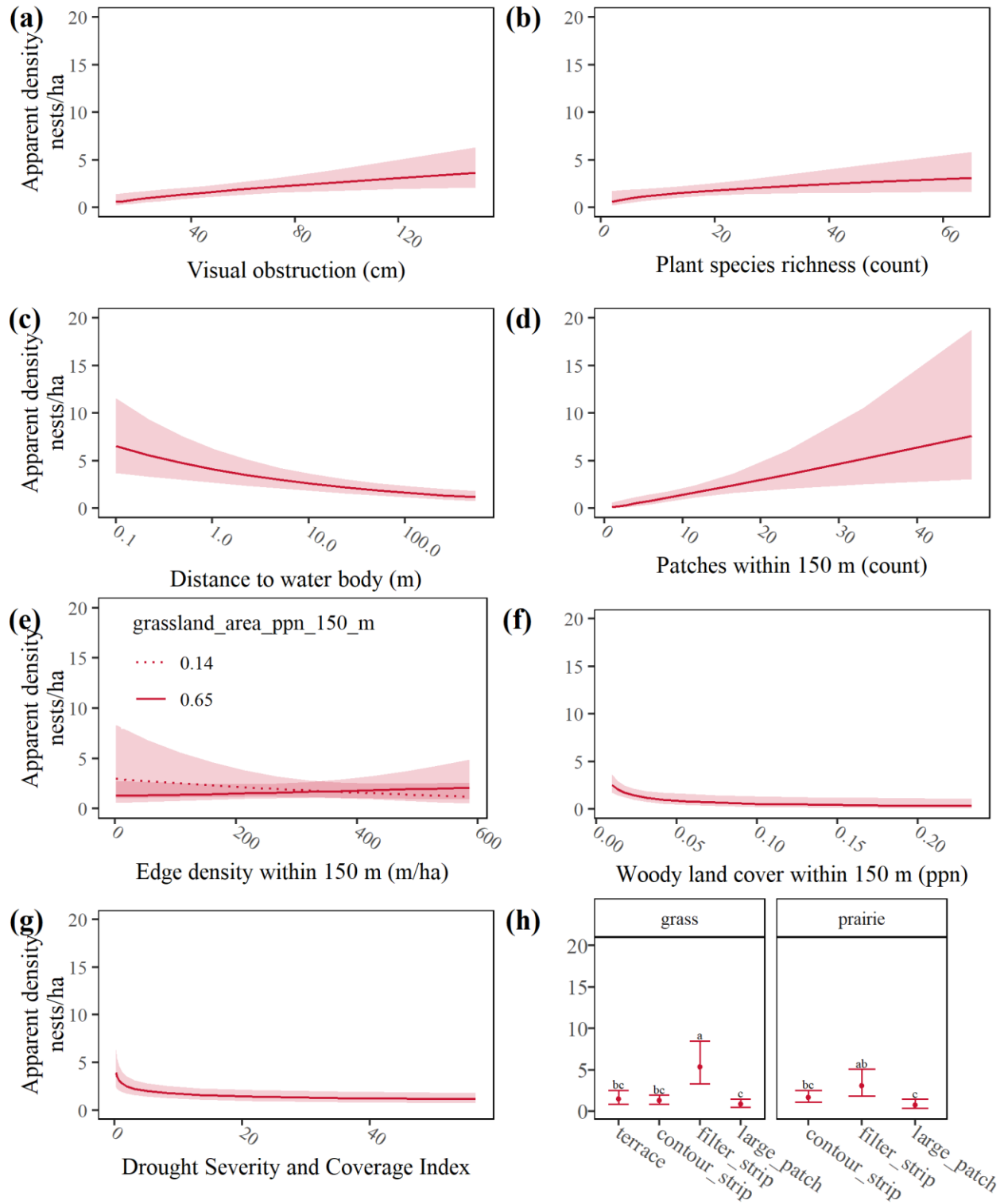


Figure 2-8. Red-winged blackbird apparent nest density predicted for each of 1059 models that represented 95% of the AICc model weight of all possible models. Mean predictions of nest

density by visual obstruction as a correlate of vegetation density (a), vegetation diversity (b), distance to water body (c), landscape patch count (d), landscape edge density with a grassland habitat amount interaction (e), landscape woody cover amount (f), annual drought severity and coverage index (Jan-Aug, g) and by conservation practice (h) categorized by vegetation diversity, patch shape, and slope position. 95% prediction intervals are indicated by the shaded area (a-g) and whiskers (h). Significance groups are indicated by letters (h). Groups that do not share letters are significantly different.

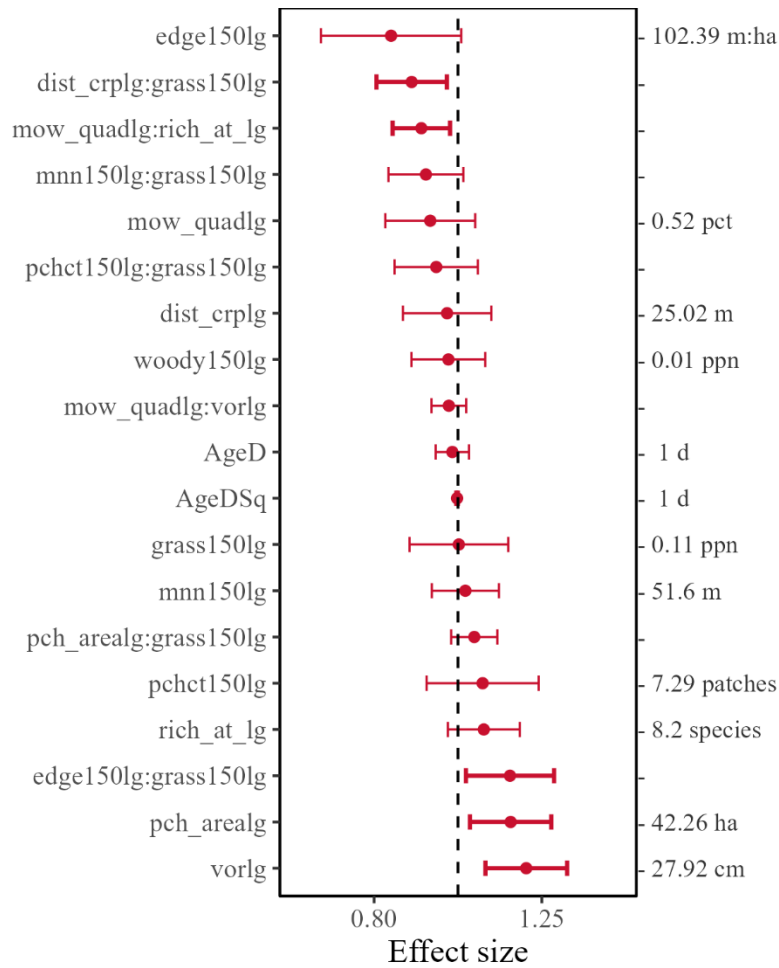


Figure 2-9. Effect sizes for nest survival global model for Red-winged blackbirds with 95% confidence intervals, expressed as odds ratios. Predictor variables (with the exception of Age) were centered and scaled, allowing direct comparison. A one standard deviation (right axis) change in the predictor variable multiplies daily survival rate by the indicated amount. Variable descriptions are provided in Table 2-4.



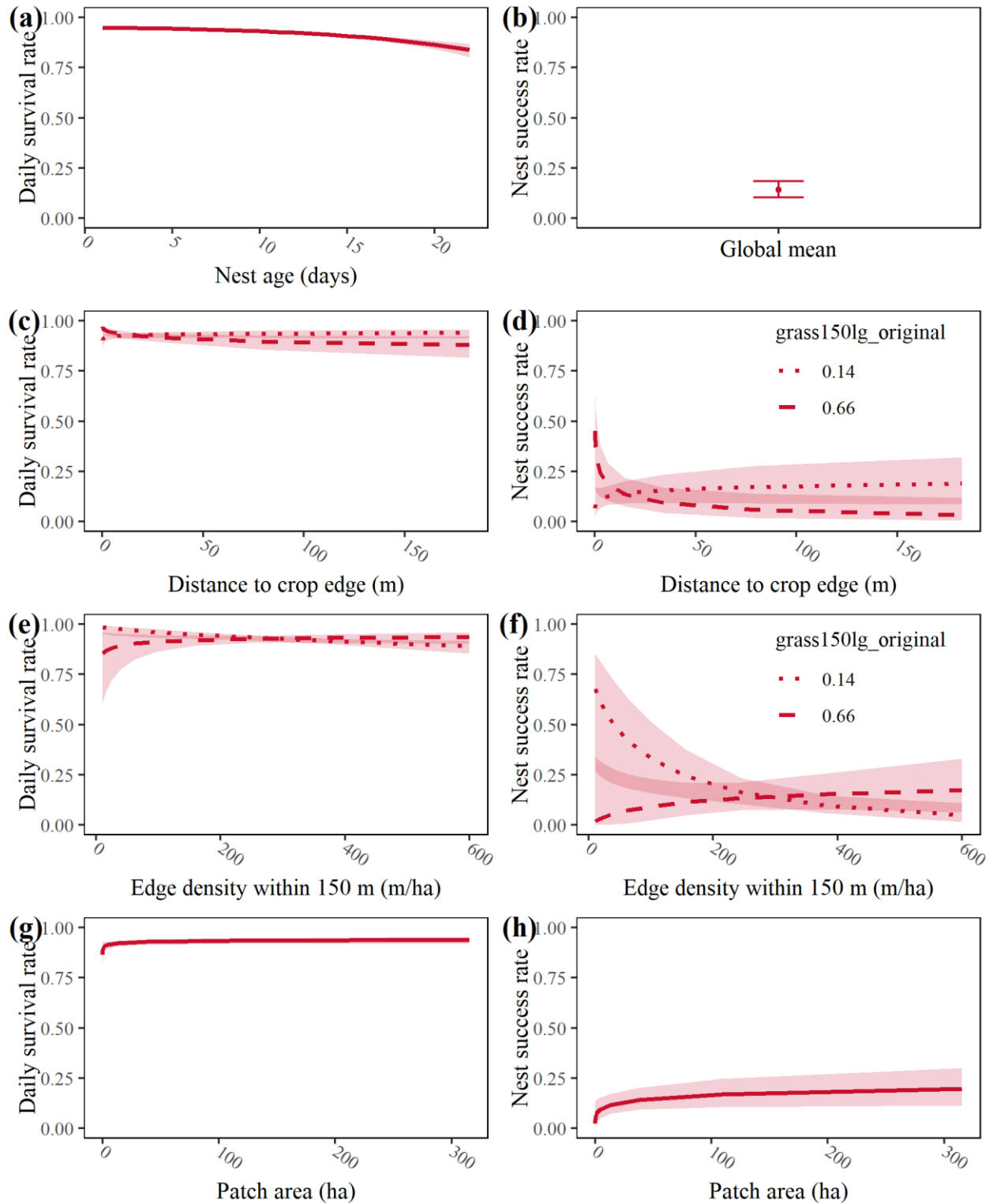


Figure 2-10. Red-winged blackbird nest daily survival rate (DSR) and overall success predicted for each of 465 models that represented 95% of the AICc model weight of all possible models.

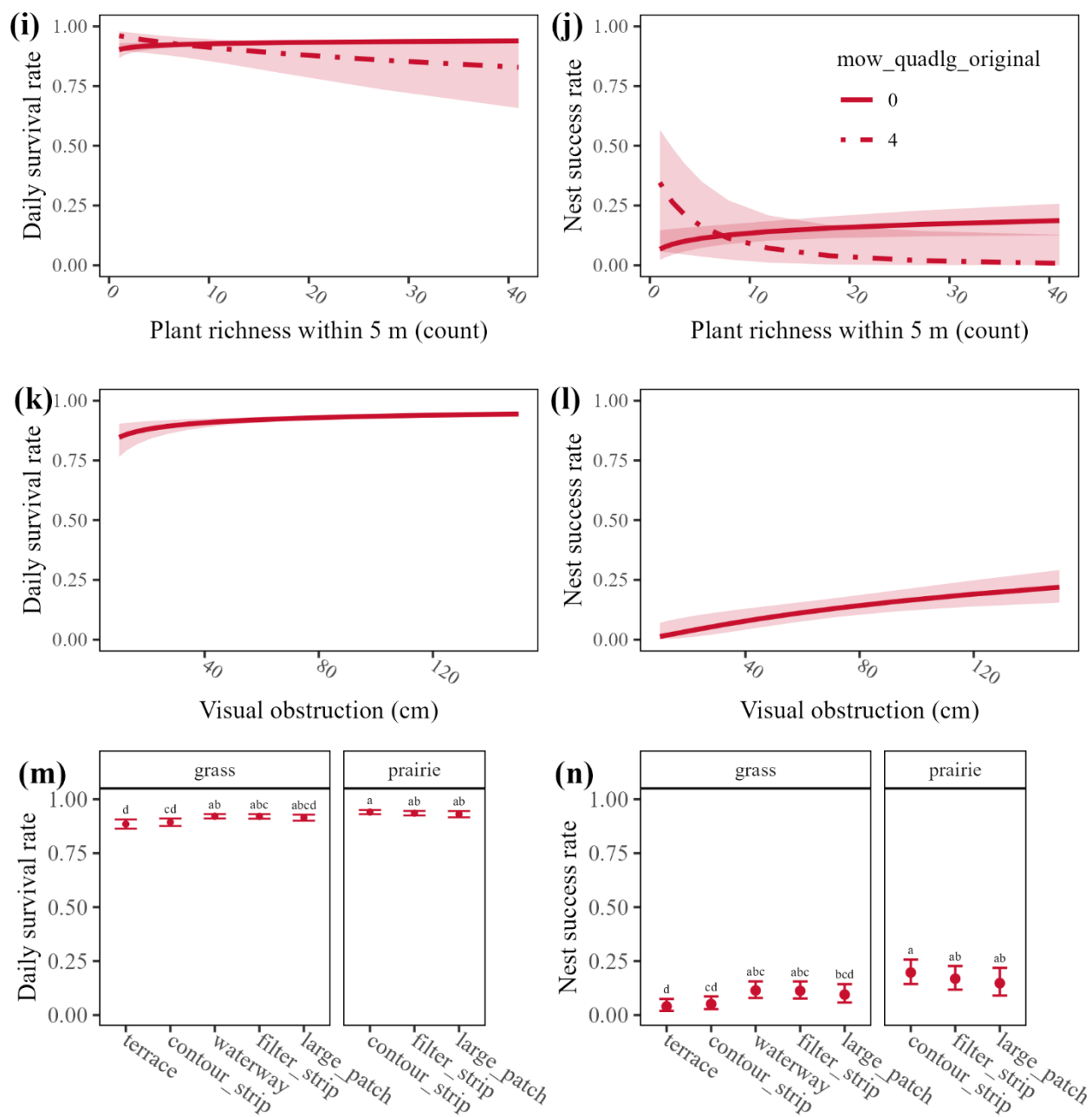


Figure 2-10 continued. Mean predictions of DSR and nest success by nest age (a), the global mean overall success rate (b), distance to crop edge (c, d), edge density within 150 m (e, f), patch area (g, h), plant species richness (i, j), visual obstruction as a correlate of vegetation density (k, l), and conservation practice (m, n). Daily survival rates are presented on the left and likelihood of surviving 24 days is on the right. Predictions with interaction terms include the smallest and

largest observed values. Shaded areas indicate the 95% prediction interval and conservation practices that do not share a letter are significantly different.

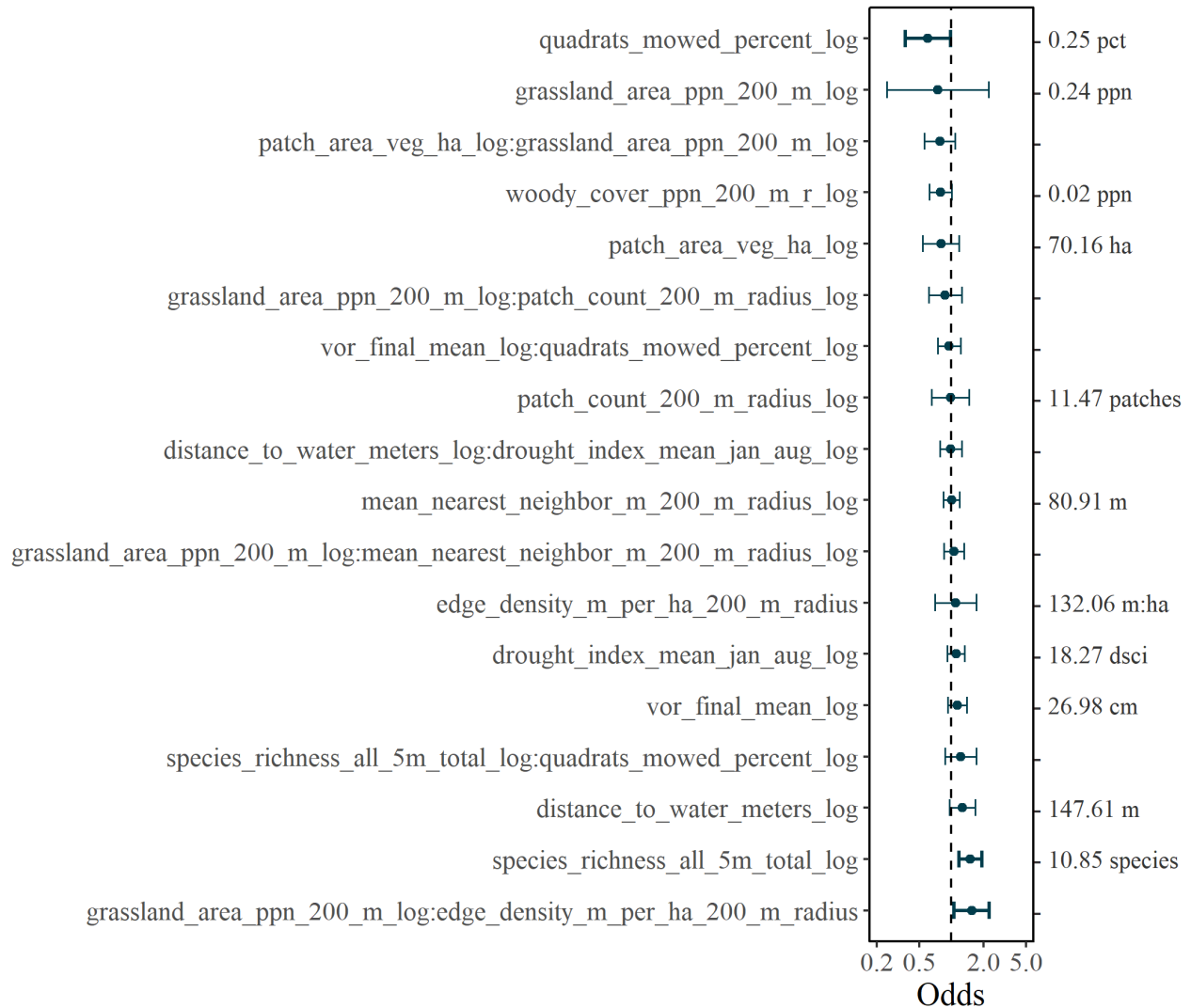


Figure 2-11. Effect sizes for the Dickcissel apparent nest density global model and 90% confidence intervals expressed as odds ratios. Predictor variables were centered and scaled, allowing direct comparison. One standard deviation (right axis) change in the predictor variable multiplies apparent nest density by the indicated amount. Variable descriptions are provided in Table 2-3.

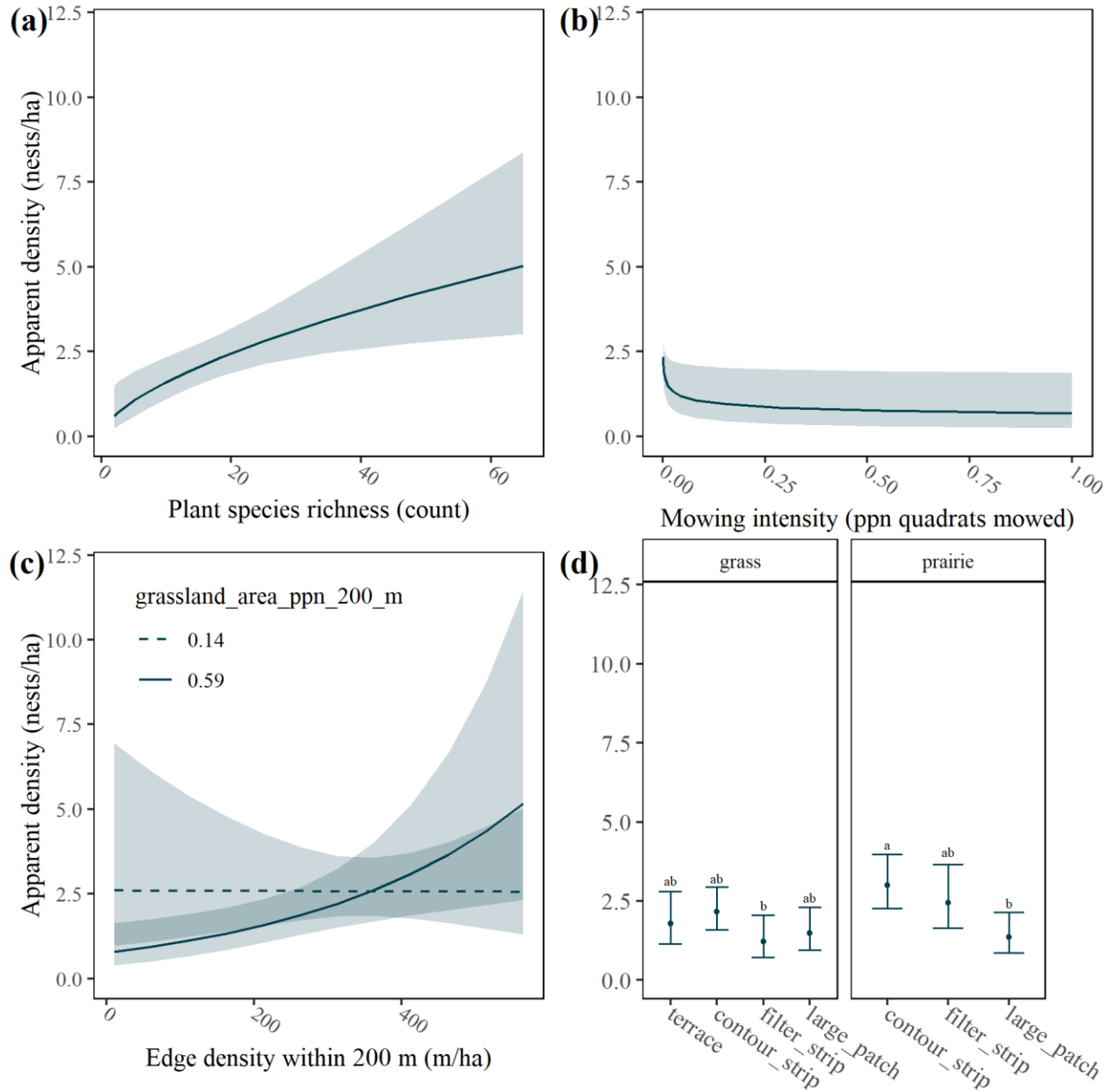


Figure 2-12. Dickcissel apparent nest density predicted for each of 4720 models that represented 95% of the AICc model weight of all possible models. Mean predictions of nest density by vegetation diversity (a), mowing intensity (b), landscape edge density with a grassland habitat amount interaction (c), and by conservation practice (d) categorized by vegetation diversity, patch shape, and slope position. 90% prediction intervals are indicated by the shaded area (a-c) and whiskers (d). Groups that do not share letters are significantly different at  $\alpha = 0.1$  (d).

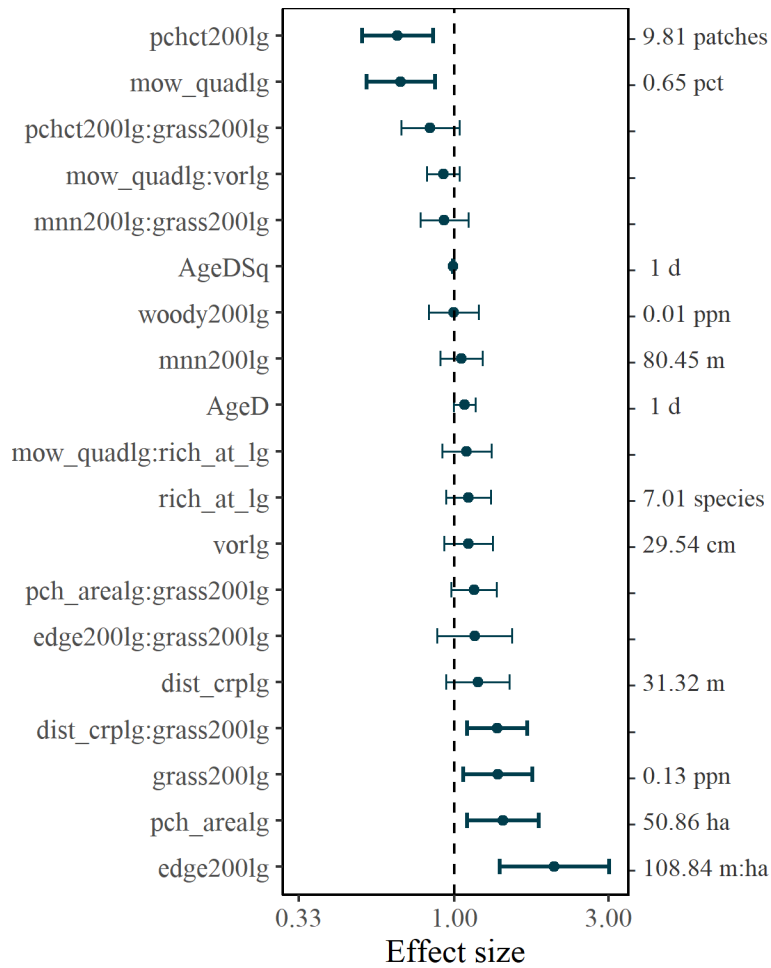


Figure 2-13. Effect sizes for the Dickcissel nest survival global model and 95% confidence intervals expressed as odds ratios. Predictor variables (with the exception of Age) were centered and scaled, allowing direct comparison. One standard deviation (right axis) change in the predictor variable multiplies apparent nest density by the indicated amount. Variable descriptions are given in Table 2-4.

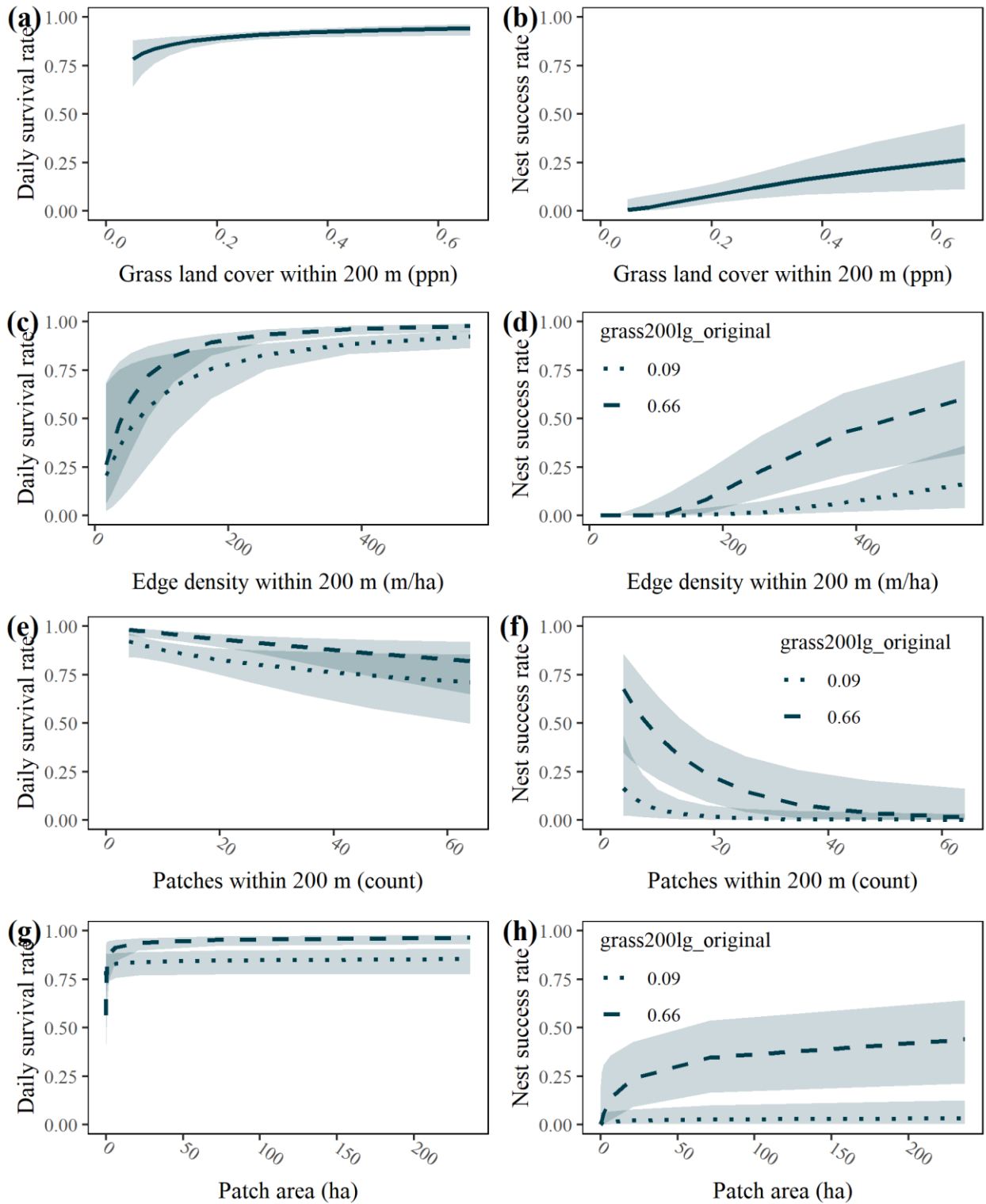


Figure 2-14. Dickcissel nest daily survival rate (DSR) and overall success predicted for each of 716 models that represented 95% of the AICc model weight of all possible models.

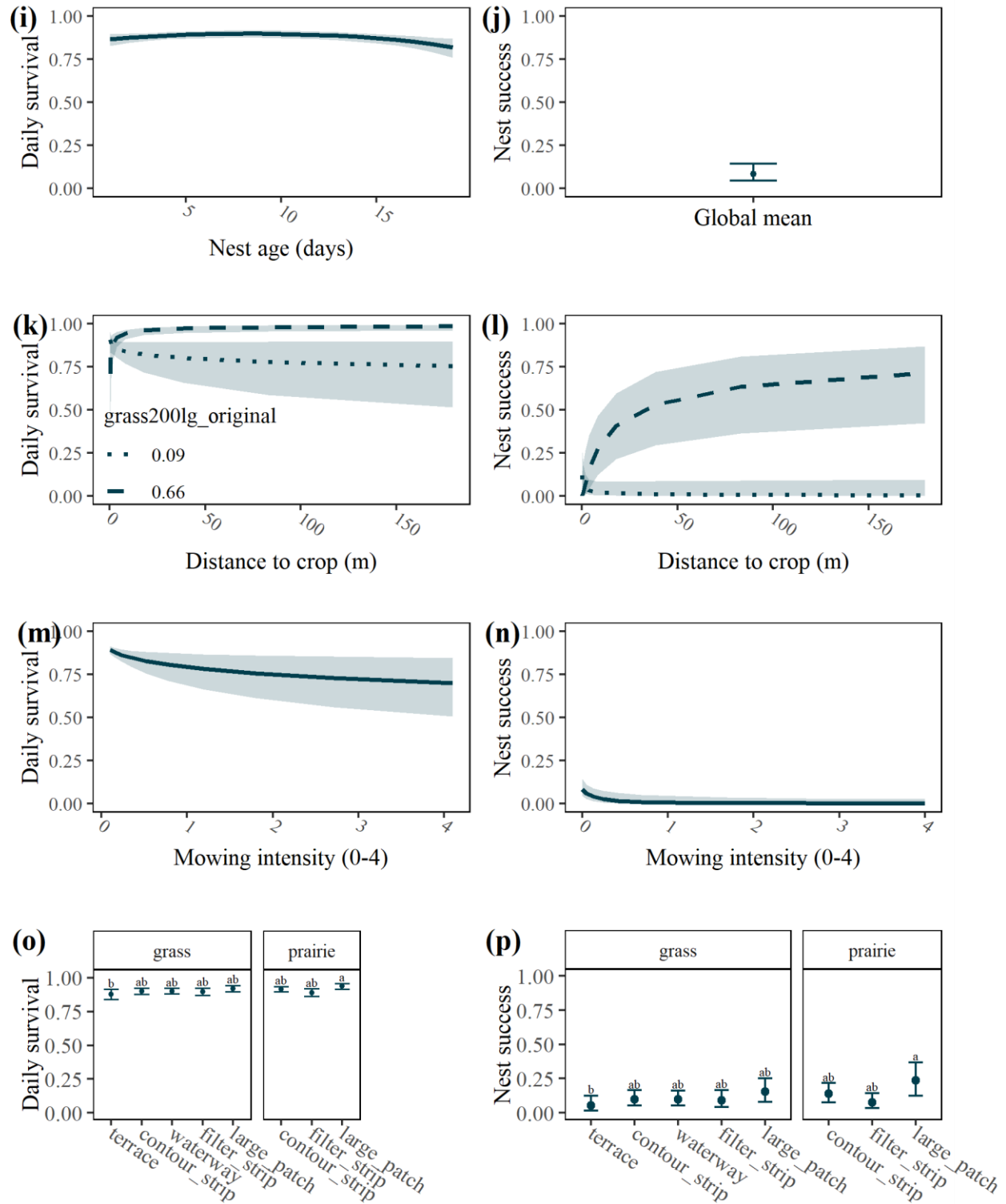


Figure 2-14 continued. Mean predictions of DSR and nest success by grass land cover within 200 m (a, b), edge density within 200 m (c, d), patch count within 200 m (e, f), patch area (g, h), nest

age (i), the global mean success rate (j), distance to crop edge (k, l), mowing intensity (m, n), and conservation practice (o, p). Daily survival rates are presented on the left and likelihood of surviving 21 days is on the right. Predictions with interaction terms include the smallest and largest observed values. Shaded areas indicate the 95% prediction interval and conservation practices that do not share a letter are significantly different.

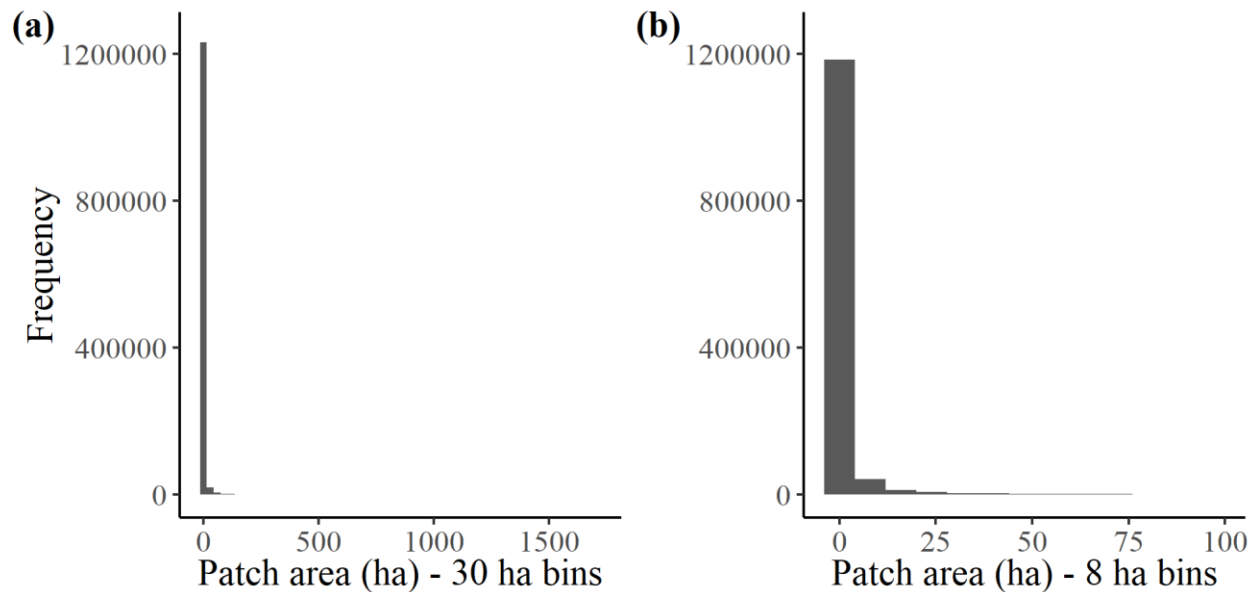


Figure 2-15. Grassland patch sizes in Iowa, 2021. Full range of patch sizes with 30 ha bins (a) and truncated to the smallest patch sizes with 8 ha bins (b). 8 ha was the cutoff we used to delineate “large” patches. Minimum patch area was 0.9 ha (1 pixel), median area was 0.18 ha, mean area was 1.94 ha, and the largest patch was 1704.15 ha. Data sourced from CropScape (USDA National Agricultural Statistics Service Cropland Data Layer) in 30 m resolution. Grassland defined as lumped perennial grassy land cover classes: (#176) grass/pasture, (#37) other hay/non-alfalfa, (#58) clover/wildflowers, and (#60) switchgrass.



## **Appendix S1. Hypotheses**

### **Ecological traps**

ET-1. Prairie strips are not population sinks for grassland nesting birds because the benefits of diverse native vegetation outweigh possible negative effects of their small, isolated nature. This will be supported by higher nest survival and number of chicks fledged in prairie strips compared to other on-farm habitat and equal to that in larger restored prairies.

ET-2. Prairie strips are not ecological traps for grassland-nesting birds because while they are attractive relative to the surrounding habitat, there is also a fitness benefit associated with them. This will be supported by higher nest densities, higher nest survival, more chicks fledged-per nest, and more chicks fledged per unit-area in prairie strips relative to other on-farm habitat.

### **Vegetation diversity**

VD-1. Nest density will be higher in areas of higher vegetation diversity because higher vegetation diversity results in more abundant suitable nest locations. This will be supported by higher nest densities and higher percentages of preferred plants in plots with higher vegetation diversity.

VD-2. Nest density will be higher in prairie strips than in surrounding on-farm habitat because higher vegetation diversity results in more abundant food resources (McIntyre and Thompson 2003). This will be supported by higher nest densities in plots with higher vegetation diversity and successful nests within those plots fledging more chicks.

VD-3. Nest survival will be higher in areas of higher vegetation diversity because more abundant suitable nest locations forces predators to search more locations, reducing their hunting efficiency. This will be supported by higher nest survival in more diverse patches and those with higher percentage of preferred plants.

VD-4. Nest survival will be higher in areas of higher vegetation diversity because more plant diversity offers a larger variety of physical locations to build nests and allows birds to choose more structurally suitable micro-habitats. This will be supported by higher nest survival during high-wind events for nests built in preferred plants and those with higher percentages of preferred plants nearby.

VD-5. Nest survival will be higher in areas of higher vegetation diversity because increased food resources allows parent birds to spend more time and energy on nest obfuscation and defense. This will be supported by areas with higher vegetation diversity having higher nest survival, a greater number of chicks fledged from successful nests, and parents present at a greater proportion of nest-checks.

VD-6. Fledglings produced per nest will be higher in areas of higher vegetation diversity because increased food resources allow females to produce more eggs and the parents to provision larger broods. This will be supported by larger clutch sizes and more birds fledged per successful nest in areas of higher vegetation diversity.

VD-7. Breeding bird diversity will be higher in areas of higher vegetation diversity because vegetation diversity creates a heterogeneous landscape with more nesting niches available. This will be supported by higher breeding bird alpha diversity in areas with higher vegetation diversity.

### **Vegetation structure**

VS-1. Nest density will be higher in areas of higher vegetation density because more physical plant mass has more potential nest locations that allow birds to make better concealed nests. This will be supported by higher nest densities and a higher average nest-concealment in plots with more dense vegetation.

VS-2. Nest survival will be higher in areas of higher vegetation density because dense vegetation increases the concealment of nests, making them harder for avian and mammalian predators to locate. This will be supported by higher nest concealment and nest survival in areas of more dense vegetation.

VS-3. Nest survival will be higher in areas of higher vegetation density because more plant material offers more physical locations to build nests and allows birds to choose more structurally suitable micro-habitats. This will be supported by higher nest survival and less high-wind impact on nest survival in areas of higher vegetation density.

VS-4. Nest survival will be higher in areas of higher vegetation density because dense vegetation is harder for meso-mammal predators to move through, lowering their search efficiency. This will be supported by higher nest survival and lower patch-interior meso-mammal detection probability in areas with higher vegetation density.

VS-5. Breeding bird diversity will be higher in areas of mixed vegetation density because heterogeneous vegetation structure provides more niches for breeding birds. This will be supported by plots with more variation in vegetation density having a higher alpha diversity of breeding birds.

### **Habitat area**

HA-1. Meso-predator release (Soulé et al. 1988, Rogers and Caro 1998, Crooks and Soulé 1999) will function in landscapes with intermediate areas of habitat, with medium-sized predators doing well in intermediate-area landscapes, prey animals doing better in small- and large-area landscapes than intermediate-area landscapes, and large predators having a minimum threshold habitat area below which they are uncommon. This will be supported by:

1. Lower nest survival in intermediate-area landscapes.

2. Equal or greater nest density in intermediate-area landscapes compared to small-area landscapes.

HA-2. Bird nest density will be lower in landscapes with greater habitat area due to a fixed meta-population of birds being able to spread out across more habitat. This will be supported by lower patch nest densities in landscapes with greater habitat area but total nest numbers similar across total landscape habitat and non-habitat areas.

HA-3. Grassland breeding birds have a threshold habitat area amount on the landscape below which they can support nesting territories, but their predators cannot support a year-round home range. This will be supported by a logarithmic relationship between landscape habitat area and nest survival and a logarithmic relationship between meso-mammal and large snake occupancy, colonization, and extinction rates.

HA-4. Breeding bird diversity will be higher in landscapes with more habitat area because increasing area also increases the number of habitat niches available. This will be supported by equal patch-level alpha diversity of breeding birds, but higher landscape-level beta and gamma diversity.

### **Habitat configuration**

#### **Number of patches**

PN-1. Environmental stochasticity will be higher in landscapes with more patches when controlled for total habitat area. This will be supported by landscapes with more patches having higher extinction rates of nesting species.

PN-2. Bird nest density will be higher in landscapes with more patches because territorial birds use distinct patch edges as territorial edges, resulting in territories-per-patch trending toward one as an equal amount of habitat is divided into multiple patches. This will be supported

by higher patch nest density in landscapes with more patches once controlled for habitat area and lower average distance-to-edge measurements for nests.

PN-3. Bird nest survival will not be affected by the number of patches on the landscape because predator behavior is hypothesized to be affected by patch size, isolation, and edge exposure and not patch count. This will be supported by no difference in nest survival in landscapes with varying numbers of patches, after controlling for habitat area.

PN-4. Breeding bird diversity will be higher in landscapes with many patches because differential habitat management among patches creates a more heterogeneous habitat mosaic, outweighing the effects of area-sensitivity on breeding bird diversity. This will be demonstrated by landscapes with several-small-patches having even plot-level alpha diversities of breeding birds with single-large-patch landscapes, but higher beta and gamma diversities after controlling for landscape habitat area.

### **Patch size**

PS-1. Meso-predator release (Rogers and Caro 1998) will function in intermediate-sized patches, with medium-sized predators doing well in intermediate-sized patches, prey animals doing better in small and large patches than intermediate-sized patches, and large predators having a minimum threshold patch size below which they are uncommon. This will be supported by:

1. Lower nest survival in intermediate-sized patches.
2. Equal or greater nest density in intermediate-sized patches compared to small patches.

PS-2. Bird nest density will be higher in smaller patches because increased competition for limited resources will shrink territory sizes. This will be supported by higher patch nest density in smaller patches after controlling for landscape habitat area.

PS-3. Patch-level breeding bird diversity will be lower in smaller patches due to there being fewer niches to fill. This will be supported by lower alpha diversity of breeding birds in smaller patches after controlling for landscape habitat area. Landscape-level diversity regarding patch size is predicted in the patch number subsection.

PS-4. Patch-level breeding bird diversity will be lower in smaller patches due to avoidance by area-sensitive species not being offset by attraction of other species. This will be supported by lower alpha diversity of breeding birds in smaller patches after controlling for habitat area and lower occupancy rates of these species (Ribic et al. 2009): Dickcissel, Grasshopper Sparrow, Meadowlark, Upland Sandpiper and Vesper Sparrow, and higher occupancy rates of Brown-headed cowbirds in smaller patches.

### **Patch isolation**

PI-1. Patch isolation is not important to grassland-nesting birds because efficient flight reduces barriers to travel experienced by other taxa. This will be supported by no difference in nest density in regard to patch isolation after landscape habitat area is accounted for.

PI-2. Patch isolation is attractive to grassland-nesting birds because the functional isolation is greater for their predators than themselves. This will be supported by higher densities of nests in more isolated patches and lower meso-mammal and large snake occupancy, and colonization and higher extinction in more isolated patches after correcting for landscape habitat area.

PI-3. Breeding bird diversity is not affected by patch isolation because efficient flight removes barriers to travel through the matrix experienced by other taxa. This will be supported by no difference in alpha, beta, or gamma diversity in landscapes of differing isolation, after landscape habitat area is accounted for.

### **Edge effects**

EE-1. Off-ground grassland bird nest density will be higher in patches with greater perimeter-edge ratio because the crop matrix does not contain suitable nesting substrates but is still considered by male birds when considering territory size. Therefore, a territory set up to include a small amount of a vegetated patch and a large amount of crop ground will increase the nest density within the patch, but not at the landscape scale. This will be supported by higher above-ground-nest densities in patches with greater perimeter-area ratio at the patch scale, but landscapes with higher perimeter-area ratios will have the same overall nest densities. Further, species that nest both in vegetated patches and in crop ground such as the Vesper Sparrow will have no difference in nest density related to perimeter-edge ratio because a territory that contains both vegetated and crop habitat could have the nest placed in either so there is no incentive to crowd.

EE-2. Bird nest survival is not affected by crop edge proximity because crop matrices do not consistently contain predators that might cross an edge to predate nests, but they are affected by tree edge proximity because patches of trees do contain predators that will cross the edge to hunt. This will be supported by distance-to-crop having no effect on nest survival and distance-to-tree having a negative effect on nest survival, after correcting for area of crops and trees on the landscape.

EE-3. Bird nest survival is lower in more linear patches because they are easier for predators to search efficiently. This will be supported by lower nest survival in patches with narrower widths and higher perimeter-edge ratio and meso-mammal interior-patch detection probability higher in patches with narrower widths and higher perimeter-edge ratios after controlling for landscape habitat area.

EE-4. Breeding bird diversity will not be affected by distance to crop edge because the number of species attracted to grassland-crop edge will be balanced by those repelled by it. This will be supported by no difference in alpha diversity of breeding birds in relation to crop perimeter-edge ratio after landscape habitat area is controlled for.

EE-5. Breeding bird diversity will increase near tree edges due to more nesting species being attracted by grassland-tree edges than repelled by them. This will be supported by higher breeding bird alpha diversity in relation to tree perimeter-edge ratio after landscape habitat area is controlled for.

EE-6. Fledgling production per-unit-area for species able to cope with nest parasitism will be unaffected by perimeter-edge ratios, but lower for species less able to cope because nest density is higher with no loss of nest survival due to predation so the major limit to fledgling production is cowbird parasitism. This will be supported by higher parasitism incidence and intensity in patches with higher perimeter to area ratio, no difference in fledgling production per-unit-area for Red-winged blackbirds and lower production for Dickcissels and Common Yellowthroats in relation to perimeter-edge ratio after controlling for landscape habitat area.



### Appendix S2. Supplementary Tables

Table S2-1. Nest search plot count by land cover and site. Grass large patch plots at SMI were delineated as prairie large patch but did not meet the minimum definition of prairie. SMI was the only site available with prairie strips adjacent to a water body.

|                       | KAL | MCC | NIR | WHI | SMI | GUT | INH | RHO | WOR | SPI | TER |
|-----------------------|-----|-----|-----|-----|-----|-----|-----|-----|-----|-----|-----|
| grass_contour_strip   | 20  | 9   | 8   | 11  | -   | -   | -   | -   | -   | -   | -   |
| grass_filter_strip    | 6   | -   | 9   | -   | 15  | -   | -   | -   | -   | -   | -   |
| grass_large_patch     | -   | -   | -   | -   | 3   | -   | -   | -   | -   | -   | -   |
| grass_terrace         | 3   | 6   | 23  | 2   | -   | -   | -   | -   | -   | -   | -   |
| prairie_contour_strip | -   | -   | -   | 25  | 9   | 6   | 11  | 6   | 2   | -   | -   |
| prairie_filter_strip  | -   | -   | -   | -   | 11  | -   | -   | -   | -   | -   | -   |
| prairie_large_patch   | -   | -   | -   | -   | -   | -   | 4   | -   | -   | 22  | 11  |

Table S2-2. Descriptions of land cover classifications. Land covers were manually digitized based primarily on NAIP aerial imagery and versioned annually, with the exception of 2017 for which there was no imagery flown. LiDAR imagery was used to distinguish land covers that involve sharp differences in elevation. All land covers within ownership boundaries of study sites and unusual land cover classes outside of ownership boundaries were verified in-person.

| Land cover class    | Lumped class | Description  |
|---------------------|--------------|--|
| alfalfa             | grassland    | Cultivated alfalfa field. Always verified in-person.   |
| amaranth            | crop         | Cultivated amaranth field. Always verified in-person.  |
| beans               | crop         | Cultivated soybean field without a cover crop. Distinguished from corn by color and texture on aerial imagery.   |
| beans_cc            | crop         | Cultivated soybean field with a cover crop, typically cereal rye. Cover crop terminated prior to growth of main crop, typically by herbicide application. Distinguished from corn by color and texture on aerial imagery. Presence of cover crop verified in-person. |
| brushy_waterway     | woody        | Superseded by waterway_woody land cover class.   |
| contour_strip       | grassland    | Linear low-diversity grass patch oriented with hill contour. Distinguished from prairie strip by greener, more homogenous texture on aerial imagery.   |
| contour_strip_woody | woody        | Linear low-diversity grass patch oriented with hill contour with individual shrubs visible on aerial imagery.  |
| corn                | crop         | Cultivated corn field without a cover crop. Distinguished from soy by color and texture on aerial imagery.   |
| corn_cc             | crop         | Cultivated corn field with a cover crop, typically cereal rye. Cover crop terminated prior to growth of main crop, typically by herbicide application. Distinguished from soy by color and texture on aerial imagery. Presence of cover crop verified in-person.     |
| crop                | crop         | Corn or soybean field unable to be distinguished by color or texture on aerial imagery and not able to be verified in-person.  |
| developed           | building     | Human structures large enough to be distinguished on aerial imagery and LiDAR not including roads or driveways. Mowed lawn areas had a separate classification   |
| disturbed           | crop         | Soil and vegetation disturbed, usually by cultivation, excavation, or and/or herbicide application.  |
| ditch               | grassland    | Roadside ditch encompassing all herbaceous vegetation from road edge to fence or field edge.   |
| ditch_woody         | woody        | Roadside ditch encompassing all woody vegetation from road edge to fence or field edge. Distinguished from herbaceous vegetation by color and texture on aerial imagery.   |
| diverse_block       | grassland    | Non-linear prairie vegetation larger than 8 ha. Distinguished from low-diversity grass by browner, more heterogenous texture on aerial imagery and always verified in-person.  |
| diverse_block_woody | woody        | Woody vegetation distinguishable on aerial imagery embedded within diverse_block land cover.   |
| filter_strip        | grassland    | Linear low diversity grass patches bordered by permeant water on one side and corn or soy on the other.  |

Table S2-2 continued

| Land cover class    | Lumped class | Description  |
|---------------------|--------------|--|
| filter_strip_woody  | woody        | Woody vegetation distinguishable on aerial imagery embedded within filter_strip land cover.  |
| grass_block         | grassland    | Non-linear low-diversity grass dominated patch larger than 8 ha. Distinguished from prairie by greener, more homogenous texture on aerial imagery.   |
| grass_block_woody   | woody        | Woody vegetation distinguishable on aerial imagery embedded within grass_block land cover.   |
| hay                 | grassland    | Low-diversity grass mowed at least annually. Distinguished from other low-diversity grass land covers by browner, homogenous but striped texture and the presence of hay bales or dead spots left by hay bales.  |
| high_diversity      | grassland    | Superseded by diverse_block and prairie_strip land cover classes.  |
| little_bluestem     | grassland    | Little bluestem monoculture for seed production. Verified in-person.   |
| low_diversity       | grassland    | Superseded by grass_block, contour_strip, and other low-diversity land cover classes.  |
| mowed_lawn          | building     | Short grass adjacent to developed land cover mowed multiple times annually. Does not include other classes of mowed grass such as hay or occasional maintenance mowing.  |
| pasture             | grassland    | Non-linear, short, low-diversity grass distinguished on aerial imagery by presence of cattle infrastructure and cow paths.   |
| pond                | water        | Lentic permeant water body.  |
| prairie_strip       | grassland    | Linear high-diversity herbaceous land cover oriented along the slope. Distinguished from low-diversity vegetation by browner, more heterogeneous color on aerial imagery and always verified in-person.  |
| prairie_strip_woody | woody        | Woody vegetation distinguishable on aerial imagery embedded within prairie_strip land cover.   |
| road                | road         | Public roads and private driveways. Typically gravel, but a few paved.   |
| root_crop           | crop         | Miscellaneous root crops including beets, carrots, garlic, etc. Verified in person.  |
| small_grains        | crop         | Small grain crops such as oat and cereal rye. Distinguished from cover crops by being left in place until harvest.   |
| stream              | water        | Lotic permanent water body. Borders delineated by tracing banks using LiDAR imagery.   |
| terrace             | grassland    | Superseded by terrace_grassy and terrace_woody. A large enough percentage of terraces were wooded to necessitate explicitly distinguishing the two communities.  |
| terrace_grassy      | grassland    | Conservation practice consisting of an earthen embankment along the slope. Planted to cool season exotic grasses at establishment, but frequently over-sprayed by herbicide and may be dominated by annual weeds. Distinguished from contour strips by confirming the embankment on LiDAR imagery. |
| terrace_woody       | woody        | Conservation practice consisting of an earthen embankment along the slope. Planted to cool season exotic grasses at establishment, but frequently over-sprayed by herbicide and now dominated by woody species. Distinguished from contour strips by confirming the embankment on LiDAR imagery.   |
| tree_shrub          | woody        | Woody vegetation that doesn't have a separate "_woody" land cover class. Woody vegetation distinguished from surrounding land cover by color and texture on aerial imagery.  |
| trees               | woody        | Patches containing large mature trees. Land cover classes with "_woody" designations given priority unless the patch contains many large trees.  |
| water               | water        | Superseded by pond, stream, and wetland land cover classes.  |

Table S2-2 continued

| Land cover class  | Lumped class | Description   |
|-------------------|--------------|---|
| waterway          | grassland    | Linear low-diversity grass conservation practice running against the hill contour at the bottom of sub-watersheds.  |
| waterway_driveway | grassland    | Linear low-diversity grass conservation practice typically arranged across the contour mowed without collecting hay for the purpose of vehicle field access. Often situated at field edges. |
| waterway_woody    | woody        | Woody vegetation within linear low-diversity grass conservation practice running against the hill contour at the bottom of sub-watersheds.  |
| wetland           | grassland    | Emergent vegetation zone of shallow semi-permanent lotic water body.  |

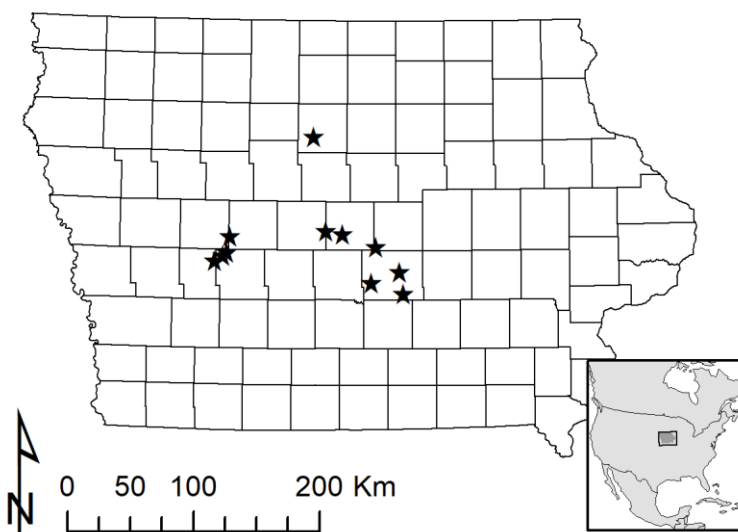
**Appendix S3. Supplementary Figures**

Figure S2-1. Study sites located in central Iowa, United States.

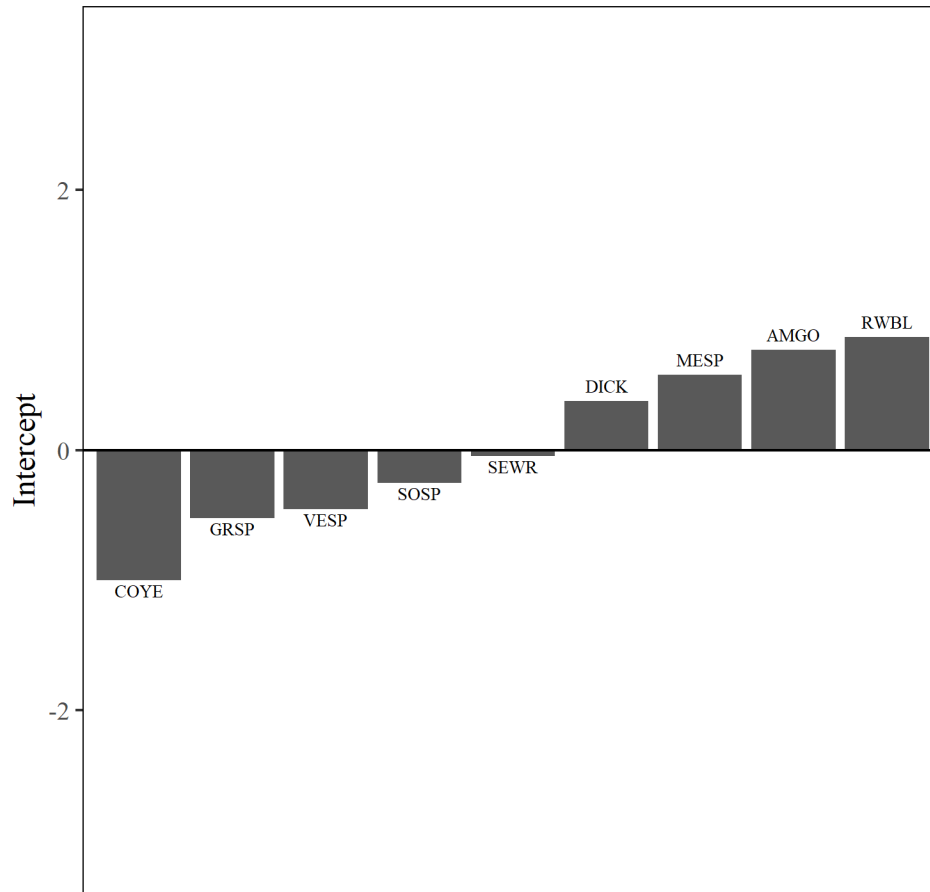


Figure S2-2. Intercepts for species random effect in the nest detection global model. The overall standard deviation for species was 0.86 ( $n = 9$ ). Abbreviations are four-letter species codes published by the American Ornithological Union.

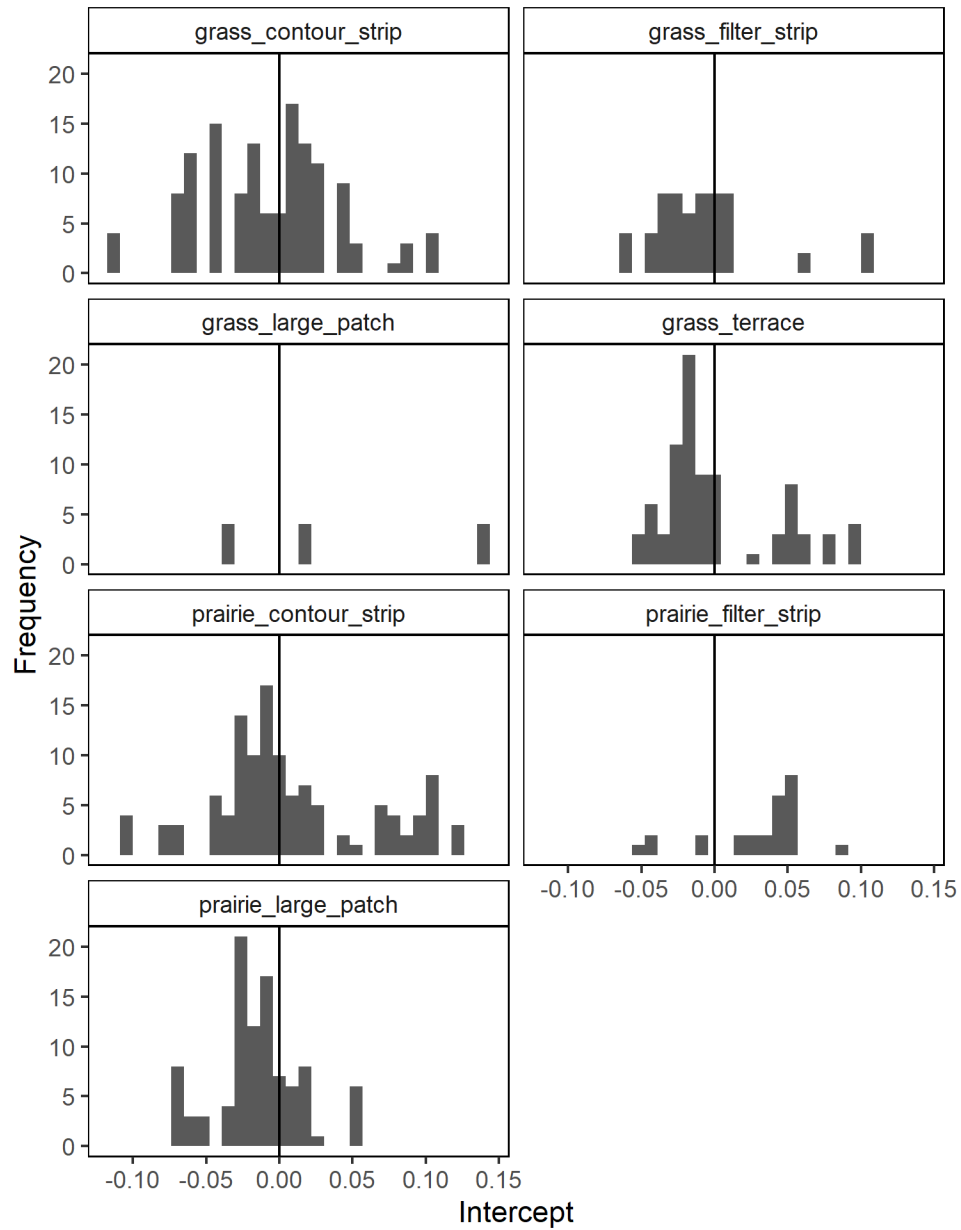


Figure S2-3. Distributions of intercepts of random effects from the grassland bird functional group nest density global model by conservation practice. There were 222 plots with an overall standard deviation of 0.100.

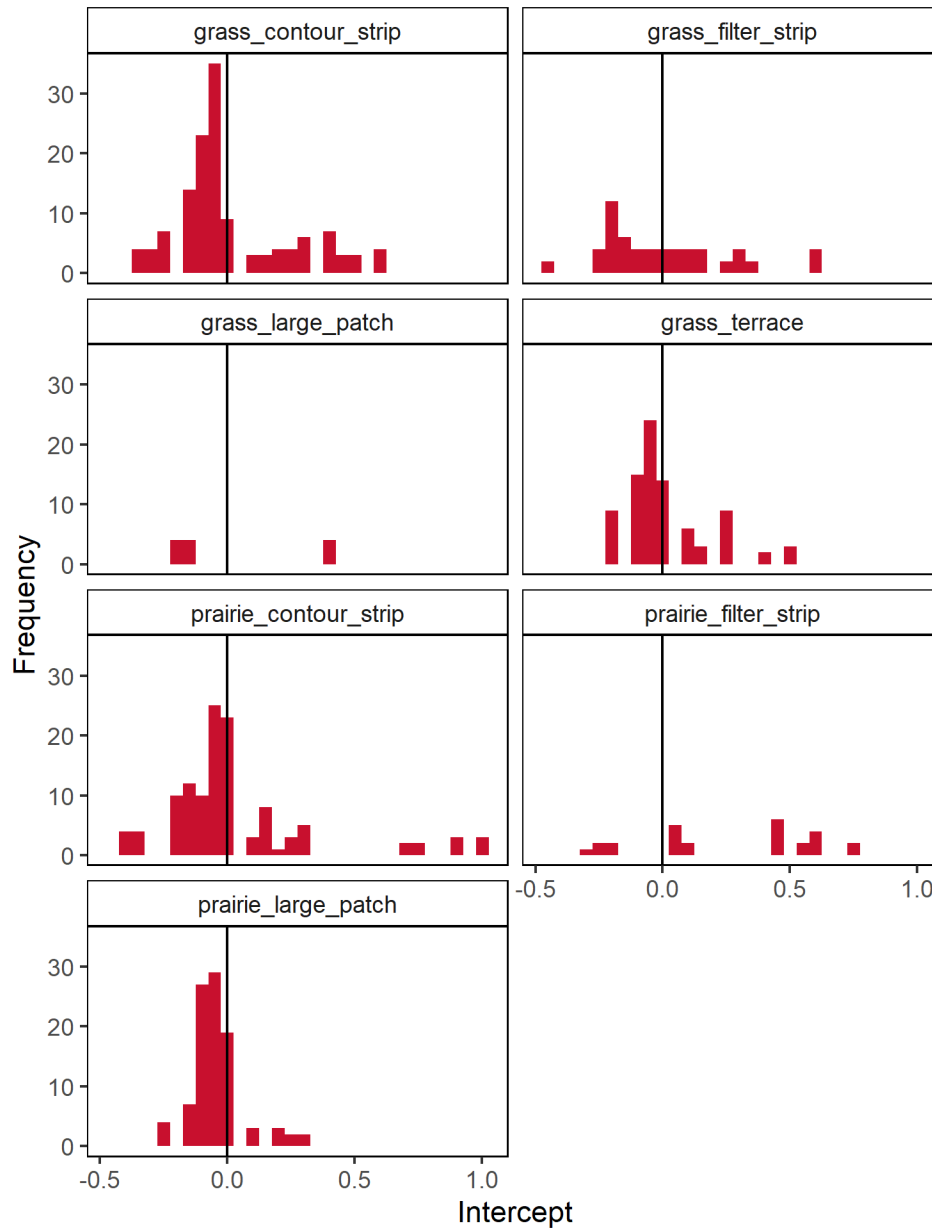


Figure S2-4. Distributions of 'plot\_name' random effect intercepts by conservation practice from the Red-winged blackbird nest density global model. There were 222 plots with an overall standard deviation of 0.585.



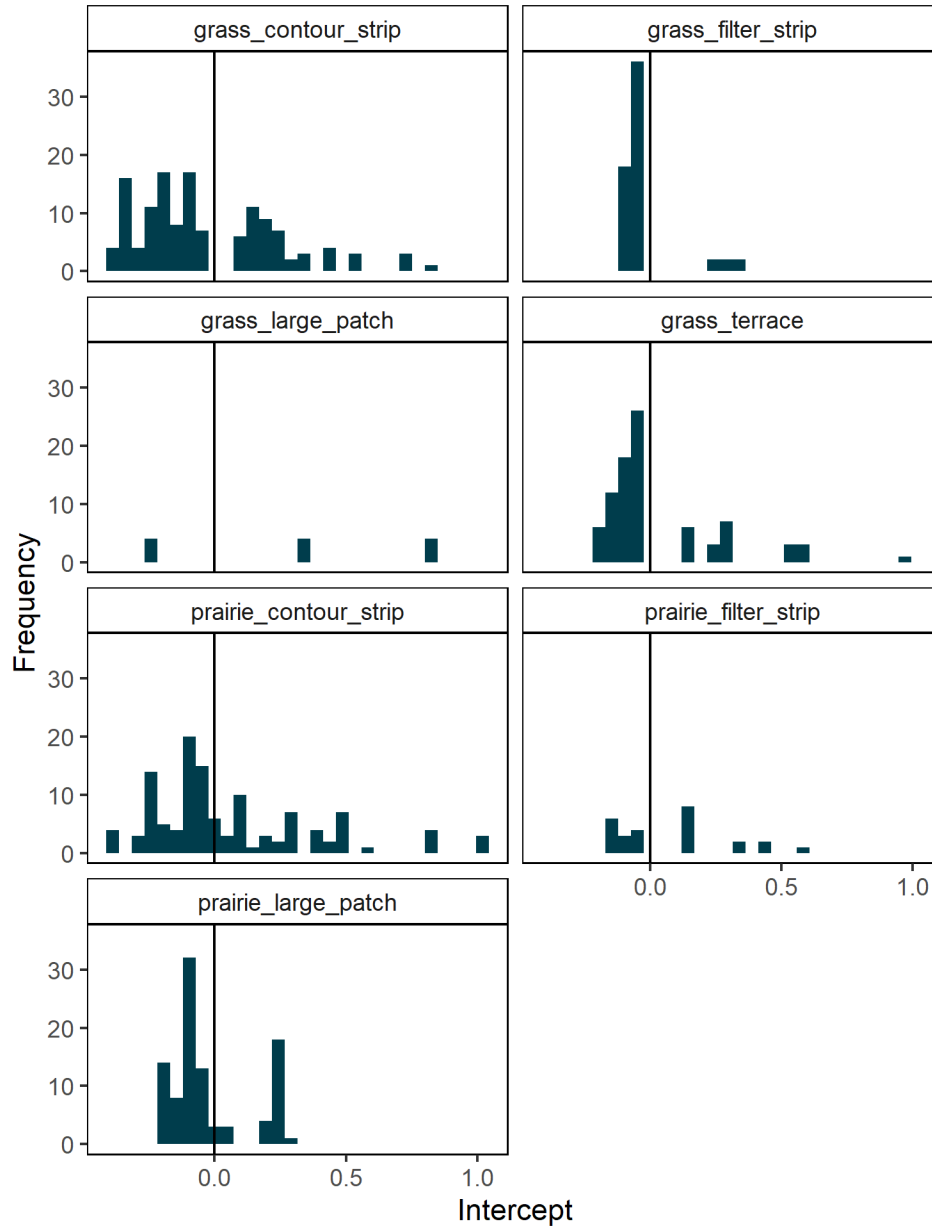
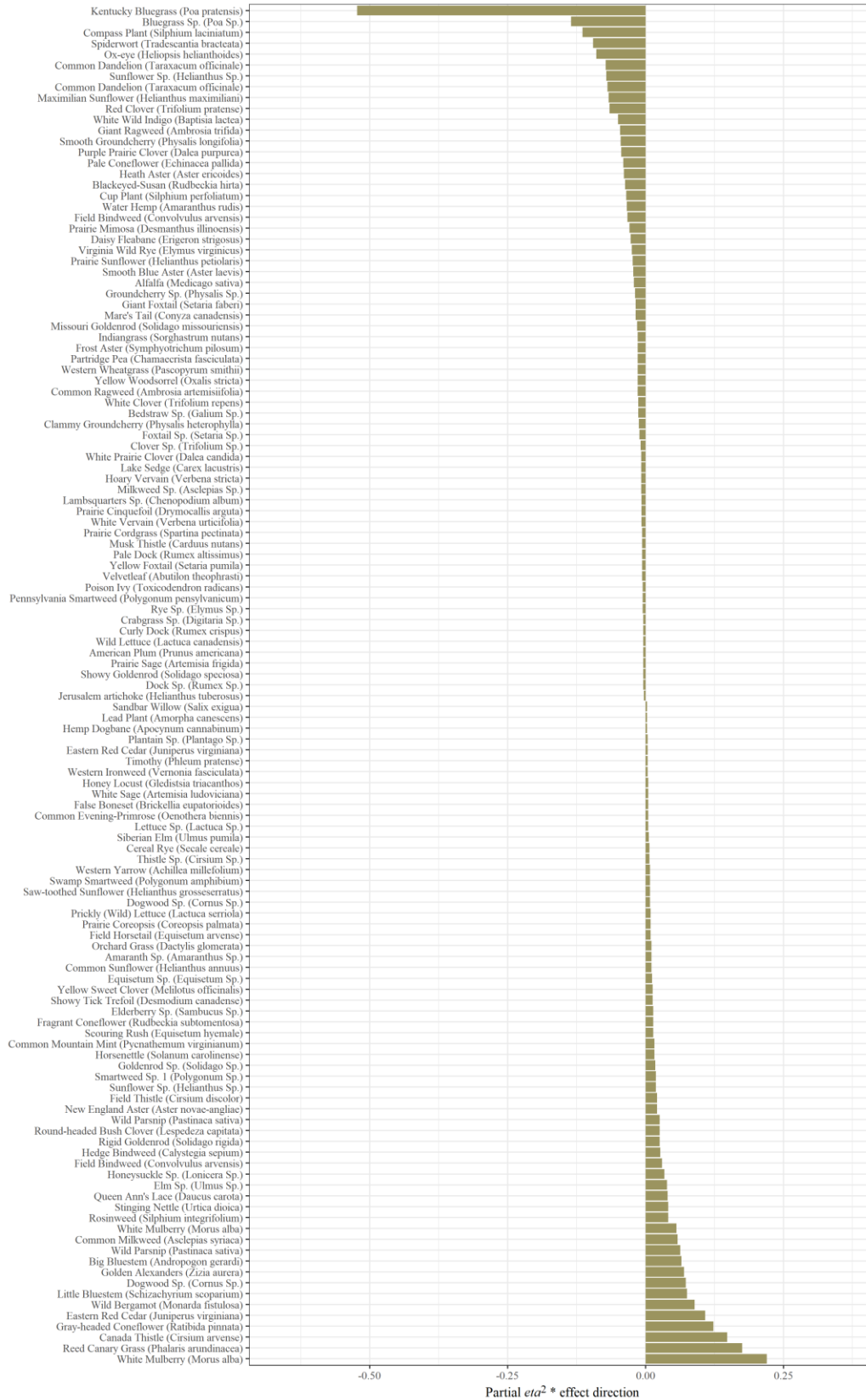


Figure S2-5. Distributions of 'plot\_name' random effect intercepts by conservation practice from the Dickcissel nest density global model. There were 222 plots with an overall standard deviation of 0.612.

Figure S2-6. Significant nest-plant associations at  $\alpha = 0.05$ .

### CHAPTER 3. HABITAT AMOUNT AND EDGE EFFECTS, NOT PERCH PROXIMITY, NEST EXPOSURE, OR VEGETATION DIVERSITY AFFECT COWBIRD PARASITISM IN AGRICULTURAL LANDSCAPES

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#### Abstract

#### Context

Prior research has documented positive relationships between brown-headed cowbird (*Molothrus ater*) brood parasitism and edge effects, proximity of cowbird perches, and nest exposure. Those relationships have not yet been compared in agroecosystems containing extremes of fragmentation and vegetation diversity. The extensively fragmented character of vegetative conservation practices on commercial-scale row crop farms, combined with variation in vegetation diversity between those practices makes it difficult to predict cowbird brood parasitism in these highly anthropogenic landscapes.

#### Objectives

Our goal was to compare three existing hypotheses on how cowbirds locate host nests

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with two new hypotheses regarding habitat amount and vegetation diversity to determine how the configuration and location of agricultural conservation practices affect grassland bird nest parasitism rates and to compare predicted rates for eight common conservation practices.

## **Methods**

We assessed cowbird parasitism of grassland bird nests on corn and soy farms in Iowa, USA, and measured variables related to perch proximity, nest exposure, edge effects, habitat amount, native vegetation diversity, and expert opinion hypotheses for each nest. We fit a global generalized linear mixed effects model containing all variables of interest and compared relative importance of model parameters using odds ratios. We predicted parasitism likelihood for every subset model and averaged the predictions from the cumulative 95% AICc weight models to explore individual effects.

## **Conclusions**

The variables that most influenced parasitism rates included main effects for nest initiation day-of-season ( $OR = 0.71$ ,  $CI_{95} = 0.60 - 0.84$ ) and the landscape variables of distance to nearest crop edge ( $0.63$ ,  $0.51 - 0.76$ ) and proportion of nearby grass land cover within 660 m ( $0.75$ ,  $0.57 - 1.00$ ). In contrast to previous research, we found little support for variables measuring perch proximity or nest exposure and little evidence that native vegetation diversity affects parasitism. We also assessed parasitism likelihood by conservation practice and found no significant differences, but parasitism rates trended higher in the narrower practices. Our results provide evidence to support the edge effect and habitat amount hypotheses, but not the nest exposure, native vegetation diversity, or perch proximity hypotheses.

## Keywords

Brood parasitism, Brown-headed cowbird, *Molothrus ater*, Conservation Reserve Program, grassland passerines, habitat amount hypothesis, Iowa USA, prairie strips

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## Introduction

Ecologists have long been interested in nest parasitism by brown-headed cowbirds (*Molothrus ater*) (Bendire 1895, Friedmann 1929, Soler 2017) for reasons both theoretical (e.g., Widmann 1897) and practical (e.g., Peer et al. 2020). Brood parasitism as a breeding strategy is interesting in its own right, but also has important effects on host species, including species of greatest conservation need. Parasitism by brown-headed cowbirds often reduces the success of the host species' nest and young, lowering fecundity and putting negative pressure on the host species' population growth rate (Schmidt and Whelan 1999, Jensen and Cully 2005, Forehead 2019). The ecology of brown-headed cowbird nest parasitism is therefore of broad interest to ecologists, including those managing grassland songbird populations.

The reproductive success of brood parasites is contingent upon their ability to locate host nests at the appropriate time in the egg-laying cycle as well as the density of host nests within a brood parasite's home range (Payne 1977, Rothstein 1990, Russo and Hauber 2000). Many hypotheses regarding cowbirds' ability to locate and parasitize host nests have been posited. The

‘perch proximity’ hypothesis asserts that host nests located near tall perches experience a higher likelihood of being parasitized, as perches offer a vantage point for female cowbirds as they observe host targets (Russo and Hauber 2000, Jensen and Cully 2005, Patten et al. 2011). The ‘nest exposure’ hypothesis predicts that concealment factors into brood parasitism likelihood by reducing the chances of a female cowbird incidentally discovering a nest (Barber and Martin 1997, Clotfelter 1998, Burhans and Thompson 1998, Patten et al. 2011). The ‘edge effect’ hypothesis states that the frequency of parasitized host nests increases near habitat edges, potentially due to increased host nest density and availability of perches near forested edges (Winter et al. 2000, Jensen and Finck 2004, Jensen and Cully 2005, Patten et al. 2006, 2011). Prospective grassland host species have been exposed to brood parasitism for millennia, however, and have evolved methods for mitigating its effects (Hosoi and Rothstein 2000, Shaffer et al. 2003, Yasukawa et al. 2016, Peer et al. 2018). For example, Dickcissels (*Spiza americana*) preferentially feed their own young over cowbird young (Hatch 1983) and Red-winged blackbirds (*Agelaius phoeniceus*) act with increased aggression toward cowbirds near active nests (Yasukawa et al. 2016).

Despite the considerable attention given to brood parasitism, there remains a lack of research addressing the extremes of fragmentation present in agroecosystems. Extensive agricultural production is often located in areas that historically comprised core breeding range of grassland birds, a guild in steep population decline (Rosenberg et al. 2019). North American grassland bird population declines from the pre-Columbian to the early 20<sup>th</sup> century have been attributed primarily to land-use changes (Gaston et al. 2003), including the conversion of historical prairie vegetation to row-crop agriculture in the U.S. Midwest region (Reif 2013, Hill et al. 2014). More recent declines (Rosenberg et al. 2019) have been attributed to agricultural

practices such as pesticide use, further habitat loss and alteration, and mowing/harvesting (Reif 2013, Hill et al. 2014, Stanton et al. 2018).

In landscapes dominated by extensive annual row-crop agriculture, such as those of the U.S. Midwest, grassland birds may be forced to use vegetative cover that is historically novel compared to their evolutionary plant community, and may be particularly attracted to patches that have more of those native species (Conover et al. 2011, Monroe et al. 2016). Within such agricultural landscapes, more-natural vegetation cover is often established for conservation purposes; usually the need to mitigate soil erosion, but also to address agriculture's typically adverse impacts to water quality and wildlife (McGranahan et al. 2013). The effect of vegetation diversity on brood parasitism has received little study, but we hypothesize that higher diversity habitat may decrease parasitism rates by providing a greater number of suitable nest microhabitats that are situated in more dense cover, thus decreasing nest exposure.

Fragmented landscapes that force birds to breed in a limited number of patches of suitable vegetation could result in population sinks, or ecological traps if birds do not select safer available patches, through exposure to increased parasitism or predation (Schlaepfer et al. 2002, Robertson and Hutto 2006, Hale and Swearer 2016). Landscapes with few, small, or isolated grassland patches have often been found to be low quality habitat (Stephens et al. 2003, Ries and Sisk 2004, Fletcher et al. 2018). However, in a review that challenged prevailing viewpoints, Fahrig (2017) found the majority of reported wildlife responses to fragmentation were positive, although that assertion has been challenged (Haddad et al. 2017, Fletcher et al. 2018). In the 'habitat amount hypothesis', Fahrig (2003) argued that patch size and isolation were correlated with overall habitat amount and that effects attributed to configuration were really driven by lower habitat amounts. Among other responses (Martin 2018), Villard (2014) argued that while

habitat amount is always important, configuration has the potential to mitigate the effects of habitat loss. To the best of our knowledge, the ‘habitat amount hypothesis’ has yet to be tested in a brood parasitism system.

We expect the relative importance of factors affecting brood parasitism to vary with species and the degree of alteration of the landscape (Turner et al. 2001, Tschamtkke et al. 2012). Our goal was thus to compare effects of established nest parasitism hypotheses and a possible effect of vegetation diversity and habitat amount on brood parasitism in agricultural landscapes dominated by extensive row crop production. We hypothesized that parasitism of grassland bird host nests will be positively associated with 1) proximity to suitable perches, 2) nest exposure, and 3) edge effects, and be negatively associated with 4) habitat amount and 5) vegetation diversity. Given significant population declines across most grassland bird species, we also seek to inform grassland bird conservation by identifying how agricultural landscape management, specifically the design and location of agricultural conservation practices, affects brood parasitism among grassland birds, especially in systems managed by many individual private landowners (Shaffer et al. 2022).

### Study Area

Our study sites were located on monocultural row-crop farms growing corn (*Zea mays* Gaertn.) and soybeans (*Glycine max* L.) within 100 km of Ames, Iowa, USA. Between 2015-2019, we surveyed 11 sites for 2-5 years each. We selected sites based on the presence of prairie contour strip, grass contour strip, or large patch prairie conservation practices. Most sites contained multiple conservation practices, which we defined by plant diversity, shape, and slope position (Table 3-1). Plant species within the non-prairie conservation features were dominated by cool-season exotic species such as smooth brome (*Bromus inermis*) and reed canary grass (*Phalaris arundinacea*). Prairie strips and large patch prairies included warm- and cool-season



grasses and forbs native to eastern tallgrass prairies, such as big bluestem (*Andropogon gerardi*), little bluestem (*Schizachyrium scoparium*), wild bergamot (*Monarda fistulosa*), and gray-headed coneflower (*Ratibida pinnata*). Older conservation practices typically contained some woody species such as eastern red cedar (*Juniperus virginiana*), mulberry (*Morus* sp.), and Siberian elm (*Ulmus pumila*); however, shrub height did not typically exceed 1 m due to periodic mowing, except within grassed terraces, which were typically not accessible for mowing. Most sites contained high-diversity prairie strips ranging from 0-12 years in age. Landscapes surrounding farm sites were characterized by many small, isolated, low-diversity grassland patches (e.g., ditches, grassed waterways, grass contour or filter strips). The land cover within 1 km of our sites averaged 63.1% row crop (28.6-84.8%), 25.2% grassland (11.1-51.1%), 7.7% woody (0.9-15.6%), 3.1% developed (1.2-6.1%), and 0.9% water (0.16-2.7%) and landscapes had average patch sizes of 1-7 ha. Because sites with uncorrelated habitat fragmentation and amount were not available, we controlled for differing amounts of habitat area at our study sites by including interaction terms with habitat area to isolate effects of configuration, per recommendations in the ‘habitat amount hypothesis’ (Fahrig 2013).

## Methods

### Data collection

We searched areas of perennial vegetation for grassland bird nests from mid-May to mid-August 2015-2019. We searched for nests both systemically in pre-determined plots and opportunistically in appropriate habitat. We recorded nest locations using Garmin eTrex 10 devices (~2-5 m accuracy, Garmin Ltd., Olathe, KS) in 2015 and Trimble Geo7X devices (< 1 m accuracy, Trimble Inc., Sunnyvale, CA) in subsequent years. We installed miniature temperature data-logging devices (iButton Thermochron DS1921G, Maxim Integrated, San Jose, California, USA) within the cups of most nests to monitor incubation activity (Hartman and Oring 2006,

Stephenson et al. 2021). We visited nests every 3-4 days to determine the nest status and presence of cowbird eggs and young (Clotfelter 1998, Russo and Hauber 2000, Jensen and Cully 2005, Patten et al. 2011).

### **Habitat configuration and amount**

To minimize trampling of vegetation, we visually estimated the distance from each nest to the nearest clearly distinguishable habitat edge (between grass and crop or trees) in the field if it was within 5 m, or measured it using a geographic information system if the distance was greater than 5 m. We created land cover maps by manually digitizing land cover polygons using aerial imagery from the National Agriculture Imagery Program (Farm Service Agency 2021) for each year of the study, using ArcMap (ESRI, Redlands, CA, version 10.3). We calculated proportions of land cover classifications and converted the native polygon layer to a 3 m pixel raster layer to calculate patch-scale metrics. A 3 m pixel size was chosen to balance capturing very small patches while still allowing very narrow linear features to serve as break points between patches to avoid a single, lace-like patch comprising all the grass within the section bordered by roads. We classified land cover as crop, developed, ditch, water, trees, grass contour or filter strips, grassed terraces, grassed waterways, grass large patch grasslands, prairie contour or filter strips, or prairie large patch grasslands based on patch shape, width, and slope position, and color and texture of vegetation in aerial images. Unusual land covers (i.e., prairie) were confirmed in-person.

### **Perch proximity**

We defined a suitable cowbird perch as an object that a cowbird would be capable of perching on that would allow a clear view of nearby habitat. We manually digitized locations of cowbird perches (large shrubs, trees, powerlines, and fences) visible in the NAIP and Light

Detection And Ranging imagery (Iowa LiDAR Consortium 2021), augmented with personal observations from researchers and reviewed with Google Maps Street View to the extent possible (Google LLC, Mountain View, CA).

### **Nest exposure**

We measured nest cup concealment, vegetation density, and native plant richness to estimate nest exposure. To normalize vegetation growth relative to nest stage and to reduce disturbance near active nests, we made vegetation-related measurements on or near the predicted fledge date when the nest was no longer active (McConnell et al. 2017). We used a circular 6.3 – 7.6 cm visual obstruction disk, separated into eight equal alternating black-and-white sections, to measure how visible the cup of the nest was from 1 m above the nest and 1 m from each of the cardinal directions at nest discovery and again near the predicted fledge date (Davis and Sealy 2000). Because nest concealment may be correlated with vegetation growth through the season, we used the concealment measured near the predicted fledge date when possible, but used the initial discovery measurement when a nest was destroyed and unavailable for measurement after the predicted fledge date. In a few cases, the nest was not accessible for the visual obstruction disk and an un-aided ocular estimation of the percent nest concealment was used instead. We measured vegetation density near the nest using the Robel method, with measurements taken approximately 5 m from the nest in each of the cardinal directions and viewed from approximately 1 m off the ground (Robel et al. 1970). We identified all plants found within 1 m<sup>2</sup> quadrats at the nest and 5 m away in each of 0°, 120°, and 240° azimuthal directions. We identified to species where possible, otherwise to genus, and classified them as either native or introduced according to the USDA Plants Database (National Plant Data Team et al. 2019). We recorded mowing activity at the quadrat locations to partition the variation that mowing

introduced in plant identification and density measurements but found it did not have a strong effect on these metrics and subsequently removed it from consideration to reduce the number of models.

### **Statistical analysis**

We modeled predictors of cowbird parasitism using a generalized linear mixed-effects model (GLMM) framework in R version 4.1.1 (R Core Team 2017) using the package ‘glmmTMB’ version 1.7.22 (Brooks et al. 2017) and package ‘MuMIn’ version 1.44 (Barton 2022). We used a binary response variable (parasitized/not parasitized) and included site and host species as random effects to account for local differences in cowbird abundance (Herkert et al. 2003) and for differences in host nest characteristics and anti-parasitic behaviors (Clotfelter 1998). We also included nest initiation day-of-season as an ‘expert opinion’ fixed effect to mitigate temporal autocorrelation. We initially included an indicator for miniature data logger use to allow for an effect from the device’s presence on cowbird nest preference and other related behaviors; however, the indicator variable was later removed to reduce the number of models after preliminary analyses did not show evidence of an effect on cowbird nest selection. We analyzed the nests of species that both were known acceptors of cowbird eggs (Lowther 2020) and that nest in grasslands with no shrubs (Billerman et al. 2020).

Prior to conducting model selection, we performed a series of tests to ensure our data met model assumptions (Zuur et al. 2010). First, we inspected the response variable and all predictor variables for outliers to limit overdispersion. We corrected datapoints found to be verifiable errors and left other datapoints as recorded (Hilbe 2007). We considered potential interactions between predictor variables by examining a panel of scatterplots with linear regression lines and variables that showed noticeable differences in slopes between groups were considered for an

interaction term (Zuur et al. 2010). Variables with a small percentage of missing records were replaced with mean values by site, year, and/or land cover classification.

We then assembled a provisional global model to test statistical assumptions regarding model fit. We assessed overdispersion and zero-inflation using functions provided by the package ‘DHARMA’ version 0.4.5 (Hartig 2020). We examined predictor variable multicollinearity by calculating the Variance Inflation Factor (VIF) for each variable in the model and sequentially dropping the variable with the highest VIF until all VIFs were under a pre-defined threshold ( $VIF < 7$ ) (Montgomery and Peck 1992). To meet the assumption of normally distributed residuals, we examined plots of the normalized/Pearson residuals versus fitted values as well as residuals versus each explanatory variable using the package ‘DHARMA’ (Hartig 2020) and transformed and removed variables or interactions from the provisional global model to achieve an approximately normal residual distribution. We centered and standardized all variables to increase the chances of model convergence (Hartig 2020) and to allow comparison between odds ratios (Rita and Komonen 2008). We checked the provisional global model for temporal and spatial autocorrelation with the package ‘DHARMA’ (Hartig 2020) using Moran's I test (Moran 1948) and the Durbin-Watson test (Durbin and Watson 1950) to confirm that autocorrelation in the residuals was not significant at  $\alpha = 0.05$ . After making the above adjustments to improve distribution or correlation issues, the provisional global model was accepted as the final global model.

Explanatory variables were grouped by hypothesis: perch proximity, nest exposure, vegetation diversity, edge effect, habitat amount, or expert opinion (Table 3-2). We selected a 660-m radius around each host nest for landscape measurements to encompass a distance five times an average Midwest cowbird home range's radius (Shaffer et al. 2003) to capture effects

occurring at the local population level (one circular cowbird territory surrounded with two ranks of adjacent territories). We defined grassland as cover that contained perennial grasses and forbs excluding mowed lawns and patches of shrubs distinguishable on aerial imagery.

To compare variable importance, we fit the final global model and exponentiated the beta parameters to give odds ratios (Rita and Komonen 2008) so that a one standard deviation change in the predictor variable indicated an [odds]-fold change in the likelihood of parasitism. We assessed model fit as  $R^2_{\text{GLMM}}$  using the delta method (Nakagawa and Schielzeth 2013, Nakagawa et al. 2017) implemented through function ‘r.squaredGLMM’ in package ‘MuMIn’. Then, to demonstrate the importance of individual variables, we predicted parasitism likelihood for each of the subset models across the range of observed values for each variable of interest. We used an all-subsets model averaging approach to produce precise, unbiased predictions of parasitism rates based on *a priori* single-variable hypotheses while avoiding inflated Type I error rates associated with stepwise model building approaches (Doherty et al. 2010, Lukacs et al. 2010, Cade 2015). We predicted parasitism likelihood by conservation practice and compared prediction intervals to determine if there were significant difference between practices.

## Results

We monitored 1,602 nests of 30 bird species over a 5-year period between 2015-2019. Of these, 1,192 nests belonged to grass-nesting passerine species known to accept cowbird eggs (Billerman et al. 2020). A total of 398 (33.4%) monitored nests were parasitized and eight species met our criteria for analysis and had at least one parasitism event (Table 3-3). The largest Pearson correlation coefficients between habitat configuration and amount variables were between patch\_area\_veg\_ha and distance\_to\_crop\_meters ( $r = 0.50$ ) and grassland\_660\_m\_r\_ppn ( $r = 0.48$ ).

The fixed effects within the global model explained 8.1% of the observation-level

variance ( $R^2_{\text{GLMM\_marginal}}$ ), while 26.3% of the variance was explained by the fixed and random effects together ( $R^2_{\text{GLMM\_conditional}}$ ). Of the 4,480 subset models of the global model, 937 models accounted for 95% of the AICc model weight (Table 3-4). Nest initiation day-of-season (Figure 3-1, Figure 3-2a), distance to nearest crop edge (Figure 3-1, Figure 3-2b), and grass land cover amount (Figure 3-1, Figure 3-2c) had the largest effects on the odds of parasitism in the global model (Figure 3-1). Distance to crop was included in 100% of the models in the 95% model weight set, grassland area appeared in 94.1% of models, and nest initiation day-of-season was included in 100% of models (Table 3-4). When other variables were held at mean values (Table S3-1), nests whose eggs were laid on May 2 had a 3.8-times higher likelihood of being parasitized than those laid on Aug. 14 (Figure 3-2a). Holding other variables at their means, an increase in the distance to the nearest crop edge from 0 to 222 m resulted in a 6.4-times lower likelihood of parasitism (Figure 3-2b) with a 1.9-times decrease in the first 3.2 m from crop edge. An increase in the percentage of grass land cover within 660 m of the host nest from 4.5% to 47.9% resulted in a 2.7-times lower likelihood of parasitism (Figure 3-2c). We found no significant differences in parasitism rates between conservation practices at  $\alpha = 0.05$ , however the smallest conservation practices trended toward higher parasitism likelihoods with largely overlapping prediction intervals (Figure 3-2d).

## Discussion

We hypothesized that parasitism of grassland bird host nests by Brown-headed cowbirds would be positively associated with 1) proximity to suitable perches, 2) nest exposure, and 3) edge effects, and negatively associated with 4) habitat amount and 5) vegetation diversity. We evaluated these hypotheses based on nest data from eight grassland bird species (Table 3-3) in the highly anthropogenic landscape of Iowa, USA, which contains extremes of landscape

fragmentation and vegetation diversity.

In comparing the nest parasitism rates we recorded to other studies, we found that Red-winged blackbird nests in our study were parasitized (PR = 26.2%) at rates within the range reported by other studies in Iowa (PR = 11-22%, 39%, 46%) (Camp and Best 1994, Hultquist and Best 2001, Henningsen and Best 2005) as well as those reported in Kansas (PR = 21.9%) (Rivers et al. 2010). We observed parasitism rates for Dickcissels (PR = 55.2%) that were on the high end of the range reported by other studies in Iowa agricultural landscape (PR = 19%, 21%, 33%, 53.3%, 68%) (Frawley and Best 1991, Patterson and Best 1996, Fletcher et al. 2006, Maresh Nelson et al. 2018, Shaffer et al. 2022), and within the range of those reported in Kansas (PR = 43-47%, 69.6%) (Rahmig et al. 2009, Rivers et al. 2010). Published estimates of brood parasitism for Common yellowthroat nests were less common, but the parasitism rate we observed (PR = 29.8%) was higher than those reported in Iowa switchgrass fields (17%) (Murray and Best 2014) but lower than those for nests found in Michigan and Minnesota (PR = 38%, 45%) (Stewart 1953, Hofslund 1957). The parasitism rate we observed for Vesper sparrows (PR = 22%) was higher than reported by studies in Iowa in similar landscapes (PR = 0%, 11%) (Rodenhouse and Best 1983, Frawley and Best 1991). Comparison rates for the other four species are not presented because together they comprise 3% of the sample ( $n = 36$ ).

### **Edge effect hypothesis**

We found that the proximity to a crop edge was one of the strongest effects on brown-headed cowbird nest parasitism, congruent with previous research on female cowbird behavior (Maresh Nelson et al. 2018, Thompson and Dijak 2021). Previous studies have associated landscape fragmentation in grassland systems with higher densities of host species and therefore increased density of cowbirds and incidence of parasitism (Tewksbury et al. 1999, Davis and



Sealy 2000, Koford et al. 2000). Because female cowbirds spend their afternoons feeding in grassland, hayfields, and cropland (Thompson and Dijak 2021) and fly directly to a potential host nest to lay an egg as soon as it is light enough to fly (Neudorf and Sealy 1994), it is possible that they may discover nests near grassland edges while feeding that they then parasitize the following morning (Davis and Sealy 2000).

We did not find distance to tree edge to be an influential variable. In a review, Cavitt and Martin (2002) found the relationship between brood parasitism and forest fragmentation was only detectable in the Eastern US and was absent west of the Rocky Mountains, which they attributed to heterogeneous landscapes in the West. Similarly, it is possible that cowbirds display different host targeting behaviors in ecoregions dominated by agricultural grasslands with very few trees. Alternatively, Pietz et al. (2009) found a *negative* relationship between brood parasitism and percentage of landscape in tree land cover within 2 km for four grassland bird species on Sheyenne National Grassland, North Dakota. This supports the idea that cowbirds may preferentially target nests in forest patches (Robinson et al. 1999), reducing parasitism pressure on grassland nesting birds in those landscapes. Our study landscapes had small proportions of tree land cover ( $\bar{x} = 1.7\%$ ,  $SD = 0.025$ ) and our finding of no effect of distance to trees could also be due to a threshold or non-linear effect that was rare on our landscapes. In a tallgrass prairie system in Kansas, Jensen and Finck (2004) found a negative effect of distance to wooded edge on brood parasitism but no effect from distance to crop edge. We were unable to locate any other studies comparing the two edge types.

### **Habitat amount hypothesis**

We found that when we included habitat amount, measured at a scale relevant to cowbird behavior, patch size and isolation were not significant in the global model (Figure 3-1) and were

included in only a modest number of all-subsets models (Table 3-3), providing evidence to support an extension of the ‘habitat amount hypothesis’ to a nest parasite system. Fahrig (2013) argues with the ‘habitat amount hypothesis’ that landscape habitat amount and not patch size or isolation was responsible for patterns observed in biodiversity through the sample area effect. While the sample area effect is less relevant to demographic parameters, strong correlations between habitat fragmentation metrics and total habitat amount (Table S3-2) could have led to incorrect attribution of effects of habitat amount to fragmentation in previous studies (Winter et al. 2000, Jensen and Finck 2004, Jensen and Cully 2005, Patten et al. 2006, 2011) . Correct attribution of landscape effects for population-level demographic parameters is important because those disparate demographic parameters ultimately lead to community level phenomena such as biodiversity.

### **Nest exposure hypothesis**

Our results did not support nest concealment or vegetation density as being influential in predicting the likelihood of parasitism. While there have been numerous studies on nest concealment and exposure in relation to parasitism, there has been little support when compared directly to other hypotheses (Patten et al. 2011). Female cowbirds appear to strongly rely on host activity (i.e., nest building, flushing, aggression) to locate active nests (Thompson and Gottfried 1981, Patten et al. 2011). However, cowbird egg-laying in inactive nests was documented in this study and in previous studies (Norman and Robertson 1975), indicating that female cowbirds do not rely solely on host activity for locating nests. Differences in methodology may explain differences in our findings from previous studies (Barber and Martin 1997, Clotfelter 1998, Burhans and Thompson 1998). For instance, while this study and others (Davis and Sealy 2000, Russo and Hauber 2000) measured only overhead nest concealment, other brood parasitism studies accounted for the visibility of the entire nest structure from several directions (Burhans

and Thompson 1998, Patten et al. 2011). If cowbirds do rely partially on nest exposure, it is unclear which part of the nest structure is most relevant to this locating strategy. We also accounted for the vegetation density in the area immediately surrounding the nest as a measure of concealment; however, vegetation density was weakly correlated with overhead nest cup concealment ( $r = 0.13$ ).

### **Vegetation diversity hypothesis**

We hypothesized that increased plant species richness should provide more, higher quality nesting microhabitats, requiring cowbird females to search more locations and be more likely to overlook better concealed nests. In a concurrent study (Chapter 2), we found that vegetation species richness predicted higher densities of host nests, which suggested more suitable nesting micro-habits were present, but also confounded the prediction of higher incidence of parasitism through the presence of more host nests for (presumably) the same number of cowbirds, potentially lowering overall parasitism rates by flooding female cowbirds with target nests. We were thus surprised that native vegetation richness was not an important variable in our models (Figure 3-1, Table 3-3). However, we also found that native vegetation richness was not strongly correlated with nest concealment ( $r = -0.03$ ) or with vegetation density ( $r = 0.09$ ), providing evidence against our hypothesized mechanism of host nests being better concealed in higher-diversity conservation practices. Overall, our results suggest that the richness of native plant species surrounding a host nest does not influence the likelihood of it being parasitized.

### **Perch proximity hypothesis**

Our data did not support the perch proximity hypothesis for this study system, contrary to our expectations based on previous research (Clotfelter 1998, Russo and Hauber 2000, Jensen and Cully 2005, Patten et al. 2011). Perch abundance, rather than not distance to closest perch, may have been a more important factor in parasitism likelihood. While we did not measure perch

abundance, it is possible there may have been fewer elevated ( $> 2$  m) perches available compared to other study systems, due to shrub management and fewer trees on the landscape. Fewer elevated perches paired with high densities of Red-winged blackbirds may have led to strong competition for tall perches (Clotfelter 1998). Red-winged blackbirds rely on aggression as an anti-parasitism behavior (Clotfelter 1998, Yasukawa et al. 2016), and we frequently observed male blackbirds successfully defending the sparse elevated perches available at our study sites, forcing cowbirds to switch nest-finding strategies and removing perch proximity as an important factor. Alternatively, our strategy of relying on remote-sensing approaches to quantify perches excluded tall, stiff-stemmed forb species (e.g., compass plant [*Silphium laciniatum*]), which may provide adequate perches for female cowbirds. We rarely witnessed this behavior, however, and typically encountered cowbirds on the ground in row crop fields.

### **Conservation practices**

We found that the likelihood of parasitism trended higher in the narrower conservation practices, but the differences were not significant (Figure 3-2d). This may have been because distance to crop and grass land cover proportion were the most important predictors of parasitism, but conservation practice width and nearby habitat amount varied within and overlapped between conservation practices.

### **Conclusions**

We provide evidence supporting the ‘edge effect’ hypothesis and an extension of the ‘habitat amount hypothesis’ to demographic parameters such as cowbird parasitism, but do not find support for the ‘perch proximity’, ‘nest exposure’, or ‘vegetation diversity’ hypotheses. Because our global model only accounted for 26.3% of the variance present in the data, it is likely that we did not capture all the ecological interactions affecting cowbird parasitism. Including a term for host nest density within the patch (Strausberger 2001) and directly

estimating local cowbird abundance (Patten et al. 2011) likely would have improved our models. As our study was exploratory and thus inference is limited, we suggest that replicated studies be conducted in other landscapes of interest to further test the relationships we present for agricultural landscapes with extremes of fragmentation and vegetation diversity.

In this study we established a strong relationship between time of year, distance to crop edges, and the nearby habitat amount with the likelihood of a host nest being parasitized. We did not find a difference in parasitism likelihood between categorical classifications of conservation practices, although nests in smaller conservation practices tended to have higher predicted rates of parasitism. We did not find support for perch proximity, nest exposure, or vegetation diversity as important factors within our agricultural study system. Instead, our study supports the edge effect hypothesis and an extension of the habitat amount hypothesis to nest parasitism in agricultural landscapes.

### **Statements and Declarations**

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#### **Author contributions**

KY conceived the idea for the study using methods and data provided by MS. MS and KY collected the data, MS lead the statistical analysis with advice from Jarad Niemi, and both MS and KY contributed substantially to the analysis and writing. LAS and RK oversaw the research and edited the manuscript. LAS secured funding for the research program.

### **Data availability**

The data and code to replicate the analyses presented in this study will be published at Iowa State University's DataShare open research data repository.

### **Compliance with Ethical Standards**

This study was conducted under IACUC log # 2-15-7960-Q. Any mention of trade, product, or firm names is for descriptive purposes only, and does not imply endorsement by the U.S. Government.

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## Tables

Table 3-1. Conservation practice descriptions based on patch shape, slope position, and vegetation diversity. Cost share program designations were archetypical; actual enrollment in a cost share program was not verified or required for inclusion in study.

| Conservation practice | Example cost share program                              | Description  |
|-----------------------|---|--|
| Grass contour strip   | CP-15A  | Linear strip (3-100 m wide, typically ~10 m) of low diversity grass planted along a contour within a field. Often planted to exotic cool-season grass species such as smooth brome ( <i>Bromus inermis</i> ).  |
| Grassed terrace       | IA-600 grassed backslope terraces, narrow base terraces | Linear earthen berm (2-5 m wide) along a contour within a field, typically planted to cool-season exotic grasses (e.g., smooth brome) when established, but were frequently affected by herbicide drift and filled with annual weeds and woody species.  |
| Grass filter strip    | CP-21   | Linear strips (3-30 m wide, typically ~10 m) of low diversity grass planted at toe slope position adjacent to a permeant water body. Typically planted to cool-season exotic grasses such as reed canary grass ( <i>Phalaris arundinacea</i> ).  |
| Grassed waterway      | CP-8A   | Linear strips of variable width (typically ~10 m) of low diversity grass planted along drainage paths to conduct surface water off fields. Typically planted with exotic cool-season grasses such as smooth brome.   |
| Grass large patch     | CP-1, CP-4D   | Low diversity grass planted in larger patches (9 - 315 ha) such as field corners, areas isolated by streams, or entire fields. Plantings contained exotic or native warm or cool season grasses.   |
| Prairie contour strip | CP-43   | Linear strips (3-100 m wide, typically ~10 m) of medium-high diversity native grasses and forbs planted along a contour within a field. Common species included big bluestem ( <i>Andropogon gerardi</i> ), little bluestem ( <i>Schizachyrium scoparium</i> ), Canada wild rye ( <i>Elymus canadensis</i> ), gray coneflower ( <i>Ratibida pinnata</i> ), wild bergamot ( <i>Monarda fistulosa</i> ), rattlesnake master ( <i>Eryngium yuccifolium</i> ), ox-eye ( <i>Heliopsis helianthoides</i> ), etc. |
| Prairie filter strip  | CP-43   | Linear strips (3-30 m wide, typically ~10 m) of medium-high diversity native grasses and forbs planted along permeant water bodies with plant communities similar to prairie contour strips.   |
| Prairie large patch   | CP-33, CP-38, CP-42                                     | Medium-high diversity native grasses and forbs planted in larger patches (9 - 315 ha) such as field corners, strips wider than 100 m, or whole fields.   |

Table 3-2. Variables included in the final global model estimating parasitism as a binary response in a generalized linear mixed model, categorized by hypothesis. Random effects for host species and study site were also included. Nests belonging to grassland birds were monitored from 2015-2019 in central Iowa.

| Hypothesis           | Variable                                  | Description   |
|----------------------|---|---|
| Perch proximity      | distance_to_trees_meters_log              | Distance to nearest tree cover (m)  |
| Perch proximity      | distance_to_fence_meters_log              | Distance to nearest fence (m)   |
| Perch proximity      | distance_to_powerlines_meters_log         | Distance to nearest powerline (m)   |
| Nest exposure        | conceal_log                               | % Concealment measured 1 m above nest rim at time of nest completion      |
| Nest exposure        | vor_final_mean_log                        | Visual obstruction reading taken 5 m away at time of nest completion (cm) |
| Vegetation diversity | species_richness_native_quadrats_mean_log | Native vegetation species richness within 5 m of nest                     |
| Edge effect          | distance_to_crop_meters_log               | Distance to nearest crop body (m)   |
| Habitat amount       | grassland_660_m_r_ppn_log                 | Proportion of grassland cover within 660 m radius of nest                 |
| Habitat amount       | patch_area_veg_ha_log                     | Area of nest patch (ha)   |
| Habitat amount       | mean_nearest_neighbor_m_660_m_radius_log  | Mean distance to nearest neighboring patch within 660 m radius of nest    |
| Expert opinion       | nest_initiation_day_of_season             | Days since start of field season (Apr 1)                                  |

Table 3-3. Grassland bird nests by species and observed parasitism rates 2015-2019 in central Iowa.

| Common name          | Scientific name               | Sample size | Parasitized | Rate parasitized |
|----------------------|-------------------------------|-------------|-------------|------------------|
| American goldfinch   | <i>Spinus tristis</i>         | 15          | 1           | 6.7%             |
| Grasshopper sparrow  | <i>Ammodrammus savannarum</i> | 6           | 2           | 33.3%            |
| Lark sparrow         | <i>Chondestes grammacus</i>   | 1           | 1           | 100.0%           |
| Vesper sparrow       | <i>Pooecetes grammacus</i>    | 41          | 19          | 22.0%            |
| Song sparrow         | <i>Melospiza melodia</i>      | 14          | 6           | 42.9%            |
| Red-winged blackbird | <i>Agelaius phoeniceus</i>    | 772         | 202         | 26.2%            |
| Common yellowthroat  | <i>Geothlypis trichas</i>     | 47          | 14          | 29.8%            |
| Dickcissel           | <i>Spiza Americana</i>        | 297         | 164         | 55.2%            |
| Overall              |                               | 1192        | 398         | 33.4%            |

Table 3-4. All-subset model variables by hypothesis and representation in the 95% of the AICc model weight list (N = 937 of 4480 total models). All models also contained random effects for host species and study site.

| Hypothesis           | Variable                                  | 95% Cum.<br>wt. count | 95% Cum.<br>wt. ppn. |
|----------------------|---|-----------------------|----------------------|
| Perch proximity      | distance_to_trees_meters_log              | 370                   | 0.395                |
| Perch proximity      | distance_to_fence_meters_log              | 411                   | 0.439                |
| Perch proximity      | distance_to_powerlines_meters_log         | 430                   | 0.459                |
| Nest exposure        | conceal_log                               | 441                   | 0.471                |
| Nest exposure        | vor_final_mean_log                        | 386                   | 0.412                |
| Vegetation diversity | species_richness_native_quadrats_mean_log | 377                   | 0.402                |
| Edge effect          | distance_to_crop_meters_log               | 937                   | 1.00                 |
| Habitat amount       | grassland_660_m_r_ppn_log                 | 882                   | 0.941                |
| Habitat amount       | patch_area_veg_ha_log                     | 604                   | 0.645                |
| Habitat amount       | mean_nearest_neighbor_m_660_m_radius_log  | 579                   | 0.618                |
| Expert opinion       | nest_initiation_day_of_season             | 937                   | 1.00                 |

## Figures

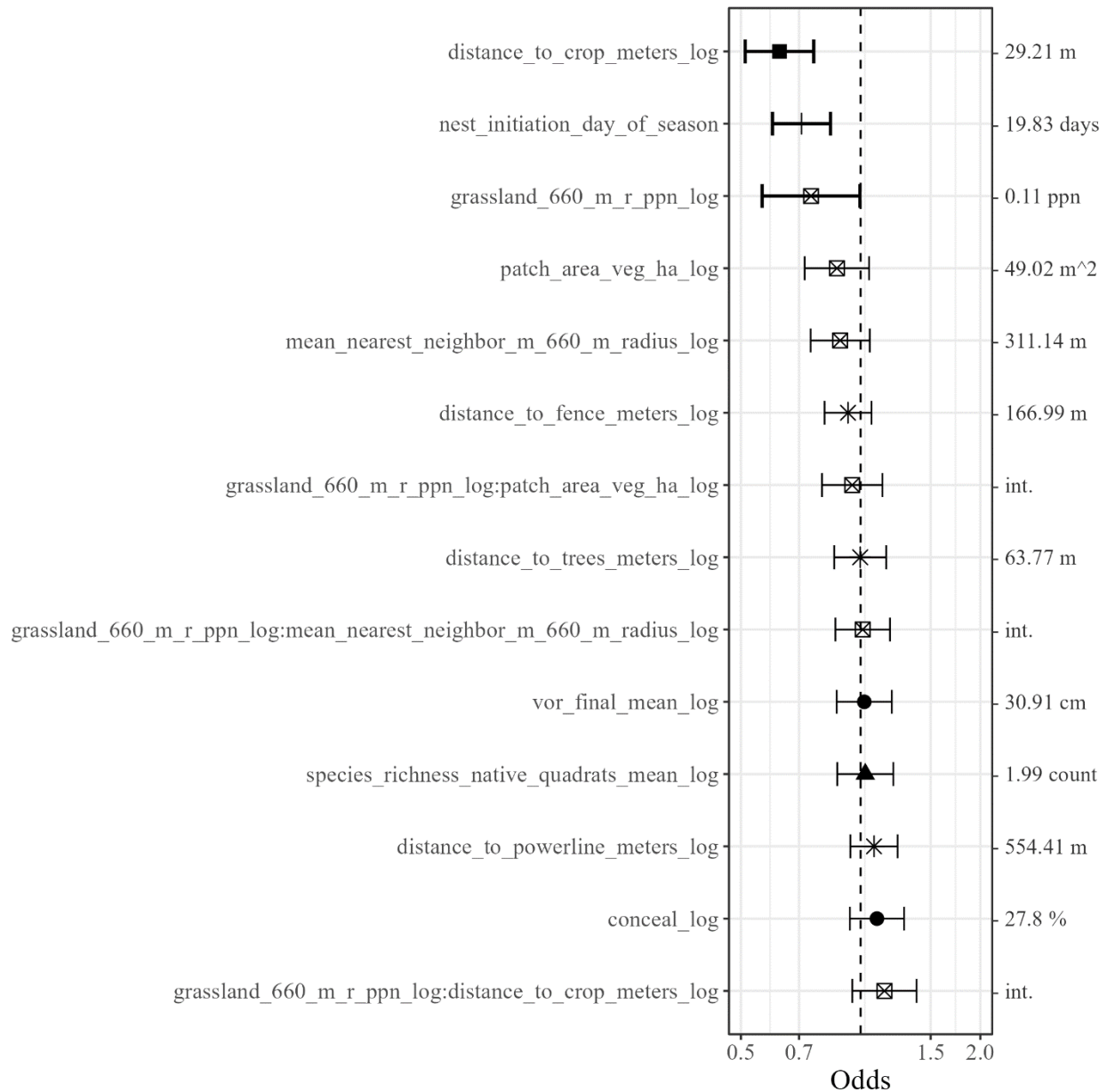


Figure 3-1. Odds ratios (OR) of a parasitism event for each parameter in the global model with 95% confidence intervals. Bold confidence intervals are statistically significant. Variables whose point estimates are represented with an asterisk (\*) were related to perch proximity, circles (●) were related to nest exposure, triangles (▲) were related to vegetation diversity, closed squares (■) were related to edge effects, open squares (□) were related to habitat amount, and the tick

mark symbol ( | ) was an expert opinion variable. Standard deviations (SD) are listed on the right axis. Interaction terms (“int.”) do not have their own SD. For every SD change in the predictor variable, the odds of parasitism changed [odds]-fold. An OR of one indicates no effect on the odds of parasitism event,  $OR > 1.0$  indicates higher odds of a parasitism event, and  $OR < 1.0$  indicates reduced odds of a parasitism event.

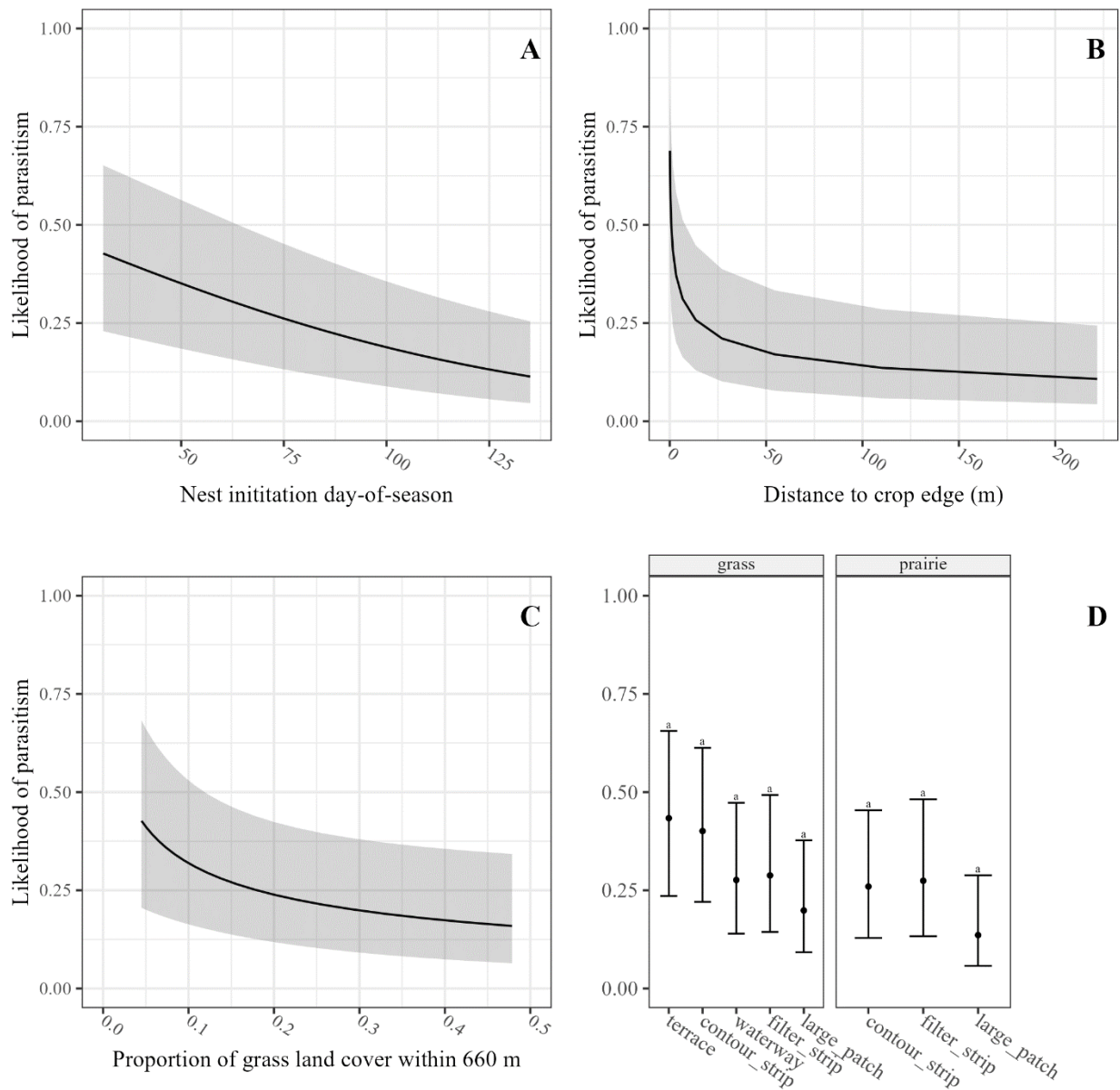


Figure 3-2. Predicted likelihood of parasitism by (A) nest initiation day-of-season, (B) distance to crop edge, (C) grass land cover within 660 m, and (D) conservation practice. Predictions were made across the range of observed values for the variable of interest, or at mean observed values for conservation practices (D). Conservation practices that share a letter were not significantly different at  $\alpha = 0.05$ .

## Appendix

Table S3-1. Summary statistics of variables concerning the nest exposure, perch, and fragmentation hypotheses measured at each grassland bird nest monitored from 2015-2019 in central Iowa, USA. Mean, S.D., and median are presented in non-transformed units for ease of interpretation. Patches that had no neighbors within 660 m were assigned a mean\_nearest\_neighbor\_m\_660\_m\_radius value of 660.

| Hypothesis           | Variable                                  | Mean  | S.D.  | Median | Unit  |
|----------------------|---|-------|-------|--------|-------|
| Perch proximity      | distance_to_trees_meters_log              | 62.0  | 63.8  | 41.2   | m     |
| Perch proximity      | distance_to_fence_meters_log              | 185.7 | 167.0 | 142.2  | m     |
| Perch proximity      | distance_to_powerlines_meters_log         | 544.5 | 554.4 | 388.5  | m     |
| Nest exposure        | conceal_log                               | 58.2  | 27.8  | 61     | %     |
| Nest exposure        | vor_final_mean_log                        | 78.1  | 30.9  | 77.5   | cm    |
| Vegetation diversity | species_richness_native_quadrats_mean_log | 3.0   | 2.0   | 2.4    | count |
| Edge effect          | distance_to_crop_meters_log               | 22.8  | 29.2  | 13.6   | m     |
| Habitat amount       | grassland_660_m_r_ppn_log                 | 0.18  | 0.11  | 0.13   | ppn   |
| Habitat amount       | patch_area_veg_ha_log                     | 51.7  | 49.0  | 44.1   | ha    |
| Habitat amount       | mean_nearest_neighbor_m_660_m_radius_log  | 395.2 | 311.1 | 660    | m     |
| Expert opinion       | nest_initiation_day_of_season             | 72.6  | 19.8  | 72     | day   |



Table S3-2. Pearson correlation coefficients for habitat amount and fragmentation metrics for 1192 nests of 8 species of grass-nesting birds monitored from 2015-2019 in Iowa, USA.

|                                      | grassland_660_m_r_ppn | patch_area_veg_ha | mean_nearest_neighbor_m_660_m_radius | distance_to_crop_meters | distance_to_trees_meters |
|--------------------------------------|-----------------------|-------------------|--------------------------------------|-------------------------|--------------------------|
| grassland_660_m_r_ppn                | 1.00                  |                   |                                      |                         |                          |
| patch_area_veg_ha                    | 0.48                  | 1.00              |                                      |                         |                          |
| mean_nearest_neighbor_m_660_m_radius | -0.20                 | -0.38             | 1.00                                 |                         |                          |
| distance_to_crop_meters              | 0.22                  | 0.50              | -0.05                                | 1.00                    |                          |
| distance_to_trees_meters             | 0.00                  | -0.05             | 0.10                                 | -0.01                   | 1.00                     |

## CHAPTER 4. THE RELATIVE CONTRIBUTIONS OF HABITAT AREA, CONFIGURATION, AND VEGETATIVE DIVERSITY ON SNAKE AND LIZARD PRESENCE IN AGRICULTURAL LANDSCAPES

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### Abstract

Worldwide, nearly one in five reptile species is at risk of extinction, and loss of grassland habitat has contributed to reptile declines in the US Midwest. Loss of habitat area, fragmentation of the remaining habitat, and altered diversity of grassland vegetation all have the potential to affect habitat use, but their relative importance has rarely been studied.

From 2015-2020 we monitored 695 cover board artificial cover objects at 15 sites in agricultural landscapes in Iowa, US for the presence of snakes and skinks. We visited cover boards 16,441 times and found very low species-wise single-visit encounter rates, including common garter snake (*Thamnophis sirtalis*;  $r = 0.012$ ), western fox snake (*Pantherophis ramspotti*;  $r = 0.0068$ ), prairie ringneck snake (*Diadophis punctatus*;  $r = 0.0066$ ), prairie skink (*Plestiodon septentrionalis*;  $r = 0.0063$ ), brown snake (*Storeria dekayi*;  $r = 0.0057$ ), plains garter snake (*Thamnophis radix*;  $r = 0.0035$ ), and lower rates for five additional snake species. Nine of 11 species encountered, and 54.2% of total encounters, were Species of Greatest Conservation Need in Iowa. Rarefied snake and lizard species richness was highest for large prairie and grass patches (5.5 – 6), lowest in grass terraces (1.7), and intermediary in other conservation practices (2.1 – 3.2) after 381 board checks.

Mean detection-corrected occupancy estimates by patch for common garter snakes was 0.18 (0.03 – 0.79, SD = 0.13). Occupancy models were not informative for any other single species, but for all snake species combined occupancy was 0.45 (0.23 – 0.90, SD = 0.12). We found that naïve presence of all snake species combined was best explained by survey effort, vegetation diversity and density, developed and woody land cover proportion, and edge density and patch size interacting with grassland land cover proportion. While most effect sizes were very weak, edge density, patch area, vegetation diversity, and survey effort had biologically meaningful effects. Common garter snake naïve presence was influenced by survey effort, vegetation density and diversity, distance to water, edge density and its interaction with grassland land cover amount, and woody land cover proportion on the landscape; edge density, grassland land cover proportion on the landscape, and survey effort had biologically meaningful effects on presence. Large patch prairie conservation practices were more likely to contain snakes than any other conservation practice, and more likely to contain common garter snakes than prairie contour strips, grass contour strips, grass waterways, or grass terraces.

Overall, we found that the richness and presence of reptile species in highly agricultural Midwestern landscapes was low, but many species with urgent conservation need were present. Due to much higher occurrence rates in large patches, conservation planners should work to include more large core nature reserves in these low habitat amount, fragmented landscapes.

### **Introduction**

Worldwide, nearly one in five reptile species is at risk of extinction from effects of habitat loss, agricultural operations, urban development, and other modifications of natural systems (Böhm et al. 2013). North American grassland snakes appear to be undergoing declines (Busby and Parmelee 1996, Brodman et al. 2002, Cagle 2008), although systematic review is lacking. The grassland systems that many snakes depend on have also experienced significant

declines (White et al. 2000, Samson and Knopf 2006, Gallant et al. 2011, Sylvester et al. 2013, Wright and Wimberly 2013), including in the US, where 71.2% of the tallgrass prairie that existed at the time of Euro-American settlement has been converted to cropland (White et al. 2000).

Most contemporary grasslands in the US Midwest are privately owned, and many were re-planted back into cropped landscapes under government conservation programs, resulting in landscapes configured with many small, isolated patches often dominated by cool-season exotic grasses such as smooth brome (*Bromus inermis*) and reed canary grass (*Phalaris arundinacea*). These small, isolated, low-diversity grassland patches now represent a considerable percentage of the grassland habitat in the Midwest, yet little is known about their habitat value to snakes (but see Knoot and Best 2011).

The process by which large areas of contiguous habitat becomes fragmented can be described through five mechanisms (Fahrig 2003): habitat loss, decreased patch size, increased patch isolation, increased number of patches, and an increase in perimeter to area ratio (i.e. “increase in edge”). Small total habitat area can negatively affect average fitness in a population through a lack of suitable space for territories, basking sites, or access to other required resources. Small areas of suitable space may trigger negative density-dependent effects such as greater conspecific competition, higher chances of predation, and reduction in per capita resource availability, as well as use of non-suitable spaces, until the population declines to the carrying capacity of the habitat area or becomes a persistent drag on the metapopulation (Lande 1987, Andrén 1994). In the Habitat Amount Hypothesis, Fahrig (2013) argued that reduced species richness attributed to habitat fragmentation was fundamentally due to reduced habitat area and all other metrics of fragmentation were unnecessary. In a contemporaneous paper, Villard and

Metzger (2014) made the case that habitat amount was always important, but habitat configuration had the potential to reduce the impacts of habitat loss. After further review, Fahrig (2017) maintained that 76% of ecological responses to indicators of fragmentation tested independently of habitat area were positive, including other responses beyond species diversity, but those claims have been contested (Hanski 2015, Haddad et al. 2017, Fletcher et al. 2018). We propose that if biodiversity is affected by habitat amount on the landscape, then the occurrence rates of individual species should be similarly affected, since species occurrence summed across a community forms the higher-order measures of biodiversity.

Habitat amount on the landscape has been demonstrated to be important for grassland snakes. Pernetta (2009) found that percentage of grassland in the landscape surrounding heath patches were among the best predictors of the presence of the smooth snake (*Coronella austriaca*) in the UK, and Kapfer et al. (2010) found that home range sizes of bullsnakes (*Pituophis catenifer sayi*) increased as the amount of habitat on the landscape decreased in Wisconsin, USA.

The effect of habitat configuration on snake occurrence or habitat preference has been investigated by several authors. For example, small nature reserves were inadequate by themselves for large-ranging snakes who must venture outside of small patches to forage or look for mates (Driscoll 2004, Nordberg et al. 2021) and for habitat specialists restricted from immigrating due to an inability to cross the matrix between isolated patches (Pernetta et al. 2011). Importantly, Pernetta (Pernetta 2009) found that patch size and habitat amount on the landscape were both predictive of snake presence, demonstrating a habitat amount effect at multiple scales simultaneously. We were unable to locate any studies investigating the effect of patch number on snake occurrence or habitat preference, but edge effects have been

demonstrated to be important to snake habitat use. Carfagno and Weatherhead (2006) found that forest edges were preferred for rat snakes (*Elaphe obsoleta*) and racers (*Coluber constrictor*) in some regions, but not others. Studies on grassland snake use of edge habitat is less common, but DeGregorio et al. (2011) showed that eastern Massasauga rattlesnakes (*Sistrurus catenatus*) and eastern fox snakes (*Pantherophis gloydi*) were both associated with forest-grassland edge habitats using different selection analysis techniques. Whatever the specific mechanism, the process of fragmentation is typically viewed as detrimental to habitat quality, with the resulting small, isolated patches suspected as population sinks or ecological traps (Robertson and Hutto 2006), although these processes are still active areas of research.

Aside from habitat amount and configuration, vegetation diversity should also be an important aspect of habitat quality. This area requires more targeted study; however, especially for non-avian taxa. For snakes, habitat studies are typically conducted at the landscape scale and rarely consider non-categorical vegetation diversity. Two recent studies have investigated the effect vegetation diversity has on snake abundance. Glass and Eichholz (2022) found that the relative proportion of forbs to grass was an important predictor of snake relative abundance in Illinois grasslands. Mizsei et al. (2020) found that directly-measured Shannon diversity of vegetation had a negative relationship with abundance of meadow vipers (*Vipera ursinii*) and had no effect on three species of lizards in Hungary.

Iowa, USA, has some of the most extensively fragmented grasslands in North America (Smith 1998, Gallant et al. 2011, Wright and Wimberly 2013), with very little perennial vegetation and patch sizes ranging from thousandths to thousands of hectares. Previous work (Steen et al. 2012, Lawrence et al. 2018) has focused on more intact landscapes (but see Kjoss and Litvaitis 2001) or has not investigated effects of small patches (Cagle 2008), but Iowa

landscapes provide access to a spectrum of patch sizes. Agricultural grasslands in the region are furthermore dominated by cool season exotic plant species, with scattered patches containing high-diversity prairie reconstructions. These ranges of habitat amount, configuration, and vegetation diversity offer an opportunity to compare the relative importance of these three aspects of snake habitat quality.

Reptiles are the second most imperiled taxa in Iowa, with 83% of snake species and 100% of lizard species listed as state Species of Greatest Conservation Need (Iowa Department of Natural Resources 2015). Therefore, in addition to filling a gap in knowledge of the relative importance of habitat characteristics broadly, we were also interested in the relative habitat value of specific agricultural conservation practices to snakes in Iowa and the Midwestern US region. A variety of perennial vegetation conservation practices have been available to farmers for decades (Table 4-1), but relatively few studies of their habitat value for reptiles have been conducted (but see Kjoos and Litvaitis 2001, Knoot and Best 2011). Contour or buffer strips of prairie vegetation are a more recently available conservation practice and have been demonstrated to provide multiple ecological services (Schulte et al. 2017), including bird habitat, but no assessment has been made on their quality as reptile habitat. A better understanding of how snakes and lizards utilize new and existing conservation practices would improve wildlife managers' ability to conserve these species, which fill important roles in grassland ecosystems.

The goals of this study were to 1) compare the relative importance of habitat amount, habitat configuration, and vegetation diversity on reptile presence in agricultural landscapes and 2) determine relative usage of agricultural conservation practices by snakes and lizards in the Midwest. To accomplish these goals, we estimated reptile occupancy and presence across a range of landscape grassland amounts, configurations, and vegetative diversities in small

conservation practices (0.05 – 8 ha) on commercial-scale corn and soy farms and on larger grassland restorations (8 – 60 ha) designed explicitly as nature reserves. We developed multiple competing hypotheses (Chamberlin 1890) with mechanistic predictions on how habitat amount, configuration, and vegetative diversity would affect snake habitat use (Appendix S1), meeting the call for such predictions presented in Fletcher et al. (2018).

## Methods

### Study sites

Our study sites were located within 100 km of Ames, Iowa, USA (Figure S4-1) on row-crop farms growing corn (*Zea mays* Gaertn.) and soybeans (*Glycine max* L.) in monocultures for commercial production, using conventional practices for the region. Access to study sites required permission from the farm managers. Study sites were selected for presence of prairie strips, contour grass strips, or large patch grasslands and most contained multiple conservation practices (Table 4-1). We defined conservation practices as prairie if they averaged at least 15 native plant species in more than half of vegetation surveys. Prairie areas contained plant species such as big bluestem (*Andropogon gerardi*), little bluestem (*Schizachyrium scoparium*), wild bergamot (*Monarda fistulosa*), gray-headed coneflower (*Ratibida pinnata*), and golden alexanders (*Zizia aurea*) and non-prairie grasslands were dominated by cool-season exotic species such as smooth brome (*Bromus inermis*), reed canary grass (*Phalaris arundinacea*), Timothy grass (*Phleum pratense*) and Kentucky bluestem (*Poa pratensis*). Each study site had at least two fields.

Landscapes surrounding farm sites were characterized by many small, low-diversity, isolated patches such as ditches, waterways, contour grass strips, grass filter strips, and grassed terraces, and most sites also contained high-diversity prairie strips ranging from 0 – 12 years in age. The land cover within 1 km of our sites averaged 63.1% row crop (28.6 – 84.8%), 25.2%



grassland (11.1 – 51.1%), 7.7% woody (0.9 – 15.6%), 3.1% developed (1.2 – 6.1%), and 0.9% water (0.16 – 2.7%) and landscapes had average patch sizes of 1 – 7 ha. Large patch grassland sites were more internally intact with mid-high diversity plantings of 40 – 60 ha, a typical size for private prairie restorations in Iowa, and were also situated in more intact landscapes with higher percentages of grassland or forest cover. Differing amounts of habitat area at our study sites were controlled for with interaction effects to isolate effects of configuration from the effect of habitat area. Data collection took place between 2015 – 2020. Sites were visited on 1 – 30 days per year (mean = 11.4, SD = 7.1, Table 4-2).

### **Sampling design**

All grassy areas of farms were included in stratified sampling frames to determine locations for cover board artificial cover objects. In 2015 the sampling frame consisted of all grassy areas in a crop field, within which we randomly placed 12 cover boards. This resulted in unequal sampling effort per conservation practice; thus, in 2016 we re-located cover boards using individual conservation practices as the sampling frame, locating three cover boards in each conservation practice. Conservation practices were defined by vegetation community, management history, conservation purpose (Table 4-1) and edges with non-habitat areas (crop, roads, and water bodies). Monolithic conservation practices such as full-field restorations or large filter strips were broken into equal area sampling frames no larger than 8 ha (approximately the size of the largest non-partitioned conservation practice).

We rebalanced our sites in 2017 because we lost access to one private farm (MCC) and establishment-phase mowing of prairie strips continued longer than anticipated on other farms (GUT, RHO, WHI, WOR; Table 4-2). We added one site (INH) that contained a large prairie strip that would not be mowed and a large site (NIR) that contained many grassed terraces, which were limited at our existing sites. In 2018 a second prairie large patch site with ponds

(TER) was added to improve our distribution of the plot distance-to-water configuration metric and help mitigate potential site effects.

### **Field methods**

Cover boards were made from 1.27 cm thick 3-ply plywood or ordinated-strand board. The large majority were 0.6 m by 1.2 m with a few boards 0.85 m by 0.85 m, but all with the same area of 0.72 m<sup>2</sup>. From 2016 – 2020 cover board locations were not altered, with boards replaced in the spring every 2 – 4 years. Cover boards were turned when researchers were on-site between April – November 2015 – 2019 and all coverboards were turned weekly in 2020.

When a board was turned, all reptiles present were counted and captured when possible to record age, sex, total length, snout-vent length, and mass. Snakes could generally be identified to species without capture, with the exception of some garter snakes which were recorded to genus (*Thamnophis sp.*) when not captured. Snakes displaying clinical symptoms of Snake Fungal Disease (Clark et al. 2011, Allender et al. 2015) were discovered at multiple sites in 2016, so starting in 2017 any gear that touched snakes was sanitized with 99.8% isopropyl alcohol wipes between captures and hands were sanitized with 70% ethanol liquid hand sanitizer (Purell® Advanced Hand Sanitizer, GOJO Industries, Inc., Akron, Ohio, USA).

We collected vegetation data in the first year a site was used and in 2019 or the last year a site was used. We placed a 1 m<sup>2</sup> quadrat by each cover board directly next to the least trampled long edge and estimated coverages of each plant species present and repeated 5 m away in the 0°, 120°, and 240° azimuthal directions. We also estimated vegetation visual obstruction as a correlate to vegetation density using the Robel method (Robel et al. 1970) from approximately 1 m off the ground in four directions 5 m away.

Weather data were summarized from raw data downloaded from the Automated Surface Observing System (National Weather Service 2022). Cover board check times were matched to

the nearest weather station that gathered data for that timeframe, with mean site-to-station distance of 65.5 km (SD = 21.9).

### **Statistical methods**

All analyses were conducted in R version 4.0 – 4.2 (R Foundation for Statistical Computing 2020). To compare reptile diversity while accounting for unequal sampling effort, we calculated a spatially explicit richness rarefaction curve (Chiarucci et al. 2009, Chao et al. 2014) using package ‘Rarefy’ (Thouvenai et al. 2021) where each sample was one cover board visit and grouped output by conservation practice.

All spatial data were curated in ArcGIS Desktop 10.6 (ESRI, Redlands, CA) and spatial analyses were conducted in R with packages ‘landscapemetrics’, ‘rgeos’, and ‘raster’ (Bivand et al. 2017, Hesselbarth et al. 2019, Hijmans et al. 2022). A categorical land cover map was hand-digitized for each site based on high-resolution National Agricultural Imagery Program aerial imagery (Farm Service Agency 2021), LiDAR (Iowa LiDAR Consortium 2021), and field-checked. Land cover maps were digitized to 1 km surrounding cover boards and versioned annually to reflect changes in land cover. Land cover classes (Table S4-11) were distinguished by differences in color, texture, shape, slope, and landscape position. All land covers within or visible from a site were verified in-person and unusual land covers (e.g., prairie) were also verified in person. To make patch and habitat area measurements, we rasterized the land cover map by sampling the polygon layers with a 3 m pixel size. A 3-m pixel size was chosen because it allowed very narrow grass features to serve as break points between patches, avoiding landscapes with a single lace-like patch of grass land cover broken only by roads.

Patch-level detection and occupancy were estimated using a maximum-likelihood framework (MacKenzie et al. 2002) in package ‘unmarked’ (Fiske and Chandler 2011). Primary periods were years (2015 – 2020), and secondary periods were weeks within the year. Each line

of data ( $n = 1$ ) represented a single conservation practice or a portion of a conservation practice larger than 8 ha for a single year.

We developed our variable list (Table 4-3) by additively combining all variables from our list of hypotheses with expert opinion variables thought to be important to occupancy but not of direct interest, with the goal of reducing un-modeled variation and improving our ability to resolve the relationships outlined in our hypotheses. Detection covariates included effort (number of board-turns), time of year, mean temperature, cloudiness, and total precipitation. Covariates on occupancy and naïve presence included vegetation composition, landscape configuration, and habitat area variables. Vegetation composition variables included vegetation richness and density. Covariates on habitat amount and configuration were measured at ecologically relevant radii based on published home ranges (Fahrig 2017). Habitat area variables included the proportion of the landscape in grassy, woody, and developed land cover. Habitat configuration variables included patch area, patch nearest neighbor, edge density, number of patches, and interactions of the previous with grass habitat amount. For common garter snakes we used 650 m as the radius of interest to include a mean home range of 5.2 ha, plus one rank of neighboring 5.2 ha home ranges (Macartney et al. 1988). We also used a 650 m radius for all snakes as a group, as common garter snakes were the most frequently encountered species and the second and third most commonly encountered species (western fox snake and prairie ringneck snake) had home ranges sizes larger and smaller, respectively.

We also estimated naïve presence for each board-year using a generalized linear mixed model in package ‘glmmTMB’ (Brooks et al. 2017) where presence was modeled as a binary response variable (presence/absence). Each line of data ( $n = 1$ ) represented a single board-year.

Covariates on presence were the same as those on in the occupancy model. To control for spatial autocorrelation, we included random effects for site and cover board.

For both modeling approaches we developed a fully parameterized global model and created a list of covariates of interest, expert opinion variables, and interactions to control for habitat amount and vetted them against model assumptions (after Zuur et al. 2010), removing or transforming variables as needed. Log transformations were used for all explanatory variables unless residuals indicated a lack-of-fit.

We examined the variables of interest for outliers by viewing their distributions as box plots and any extreme observations that could be verified as errors (e.g., data entry errors) were censored. Interactions between variables of interest were considered based on stated hypotheses or expert knowledge. Missing values were typically caused by missed vegetation surveys and were replaced with means by site, conservation practice, and year. All continuous response variables were centered and scaled to improve the likelihood of model convergence and interpretation of the coefficients.

We limited multicollinearity by calculating the Variance Inflation Factor (VIF) (Zuur et al. 2010, Freckleton 2011) for each explanatory variable using R package ``performance`` (Lüdecke et al. 2020) and sequentially removed the variable with the highest VIF score until no variables had a score higher than 7 (Quinn and Keough 2002), excepting interaction and polynomial terms. We also tested for spatial and temporal autocorrelation in the GLMM using Moran's I test (Moran 1948) and the Durbin-Watson test (Durbin and Watson 1950), respectively, implemented in package ``DHARMA`` (Hartig 2020), to confirm autocorrelation in the residuals was not significant at  $\alpha = 0.05$ . To meet model assumptions we also tested for homogeneity of variance by viewing residuals plotted by observed versus expected for the global

model (Hartig 2020) and also viewed plots of standardized residuals versus predicted values for each variable (Hartig 2020). We also viewed a histogram of error term residuals to confirm the global model met the assumption of normally distributed residuals. Goodness of fit for the single-season occupancy global model was assessed with a parametric bootstrap implemented in ‘unmarked’ (Fiske and Chandler 2011) and the naïve presence global model was assessed as  $R^2_{\text{GLMM}}$  using the delta method (Nakagawa et al. 2017).

After vetting the preferred global model, some variables were eliminated to reduce overall variable count and to keep the all-subsets model list within computational limits. Variables were eliminated if they were expert opinion variables that did not improve model AICc or if they were variables of interest but were correlated with other variables ( $|r| > 0.7$ ). To compare the effect sizes of variables on parameters of interest, we exponentiated the beta parameter estimates of the global model and their 95% confidence intervals to give odds ratios. Because all variables were centered and scaled, their effect sizes were then compared directly (Schielzeth 2010).

To predict occupancy and presence across conservation practices and other variables of interest, we then developed a model list of all possible subsets of the global model, fit each model, and calculated an AICc value (Burnham and Anderson 2002). To reduce the number of models and improve computation time, we then trimmed the all-subsets model list to those models comprising 95% of the cumulative AICc model. Using this model list, we predicted the parameter of interest (and associated standard error) for each model at the observed mean values for each conservation practice. We then calculated weighted averages of the predictions using AICc model weight and made predictions across the range of observed values for variables of interest.

We were able to make meaningful estimates of presence for all snakes as a functional group and for the largest single-species capture group (common garter snake). Although the predictions were less informative, we also include results for western fox snake (Figure S4-2, Figure S4-3), ringneck snake (Figure S4-4, Figure S4-5), DeKay's brown snake (Figure S4-6, Figure S4-7), and the only lizard whose range includes all our study sites, the prairie skink (Figure S4-8, Figure S4-9) as baseline data. We present 90% confidence intervals on presence estimates due to the large variability in the data.

## Results

We flipped 695 cover boards at 15 sites a total of 16,441 times from 2015 – 2020. Because all our sites were privately owned, we present summary statistics by site code or county to protect the owners' identity. We encountered nine species of snake and one species of lizard, but encounter rates were very low (Table 4-4), with non-zero species-by-county board flip encounter rates ranging from 0.0002 – 0.12. Global encounter rates were lowest for bullsnakes, smooth green snakes, and western ribbon snakes with a single capture each (0.0001) and highest for common garter snakes (0.012) followed by western fox snakes (0.0069). Seven of the 10 species of snakes and the only lizard species we encountered (Table 4-4) were Iowa Species of Greatest Conservation Need (Iowa Department of Natural Resources 2015) and comprised 54.2% of encounters.

Uncorrected richness varied from 1 – 7 species per county and species richness per 100 board-flips varied from 0.15 – 1.78 (4713 – 338 board flips). We used a richness rarefaction curve to correct for unequal sampling effort (Figure 4-1a) and found that large patches of prairie and grass had the highest species richness (5.5 – 6) after 381 visits, grass terraces had the lowest richness (1.7), and prairie contour strips, and grass contour strips, filter strips, and waterways had intermediary (2.1 – 3.2) species richness (Figure 4-1b) and the same relationships held at more

than double the number of board visits (Figure 4-1c). Species accumulation leveled off after 4,000 board visits (Figure 4-1a) for the conservation practice with the most board visits (grassed waterway), but did not clearly do so for the other conservation practices (grass terraces, grass filter strips, large grass patches), suggesting we may have found more species with greater sampling effort.

### **Single-season occupancy**

We used the same single season occupancy global model (Equation 4-1) for snakes as a group and common garter snakes. The mean predicted occupancy rates from the global model were 0.46 (Prediction Interval 95% = 0.33 – 0.59) for snakes as a group and 0.18 ( $PI_{95} = 0.08 - 0.34$ ) for common garter snakes. Mean detection rates predicted from the global model were 0.12 ( $PI_{95} = 0.09 - 0.16$ ) for snakes as a group and 0.08 ( $PI_{95} = 0.05 - 0.14$ ) for common garter snakes. When we attempted to fit all the subset models for both snakes as a group and for common garter snakes, many combinations of variables failed to estimate well due to low detection rates (Steen 2010, Durso et al. 2011). Because of this, we limited our exploration of detection-corrected occupancy to the global model and simplified our approach for making individual covariate predictions to naïve presence using a GLMM to allow variable importance to factor into effect sizes. We present implications of this choice in the discussion.

### **Snakes as a group**

We encountered at least one snake in 241 of 851 patch-years and at every site. The global model for snakes as a group fit the data well ( $p_{tb>t0} = 0.56$ ) and predictions made from the global model using the input data produced mean occupancy estimates by patch for all snake species combined of 0.45 (range = 0.23 – 0.90, SD = 0.12). The global model contained two significant covariates: patch nearest neighbor and amount of developed land cover nearby (Figure 4-2). The



only significant predictor of detection probability was number of board flips per week (Figure 4-2).

### **Common garter snake**

We encountered common garter snakes in 76 of 851 patch-years and at 13 of 15 sites. The global model for snakes as a group fit the data well ( $p_{tb>t0} = 0.47$ ) and predictions made from the global model using the input data produced mean occupancy estimates by patch for all snake species combined of 0.18 (range = 0.03 – 0.79, SD = 0.13). Important covariates on occupancy in the global model included woody cover within 650 m and patch count within 650 m interacting with grass land cover amount in the same area (Figure 4-3). The only important predictor of detection probability was number of board flips per week (Figure 4-3).

### **Predicted presence**

#### **Snakes as a group**

We encountered at least one species of snake in 336 of 2845 board-years and at every site. Random effect standard deviations were 0.79 (site\_abbreviation) and 0.23 (coverboardID) with individual intercepts for the site ranging from -1.3 (SMI) – 1.2 (WOR) (Figure S4-10). The global model fixed effects explained 10.6% (marginal) and 18.6% (conditional) of the variance in the data. After fitting all possible subset models of the global model, we trimmed the model list to only the 454 models containing the top 95% of the AICc model weight.

There were several significant covariates in the global model (Figure 4-4). Edge density (Figure 4-5a, b) and patch area (Figure 4-5c) interacting with grassland habitat amount (Figure 4-5b), developed land cover within 650 m (Figure 4-5d), vegetation visual obstruction (Figure 4-5e) and diversity (Figure 4-5f) and survey effort (Figure 4-5g) were all significant at  $\alpha = 0.1$ , although the predicted change in probability of presence was minimal for several (Figure 4-5).

Large prairie patch conservation practices were more likely to have snakes present (0.29,  $CI_{90\%} = 0.19 - 0.42$ ; Figure 4-5h) than other conservation practices, which were all approximately equally as likely (0.07 – 0.13,  $CI_{90\%\_total} = 0.04 - 0.19$ ) to have snakes present under an average board in a given year.

### **Common garter snake**

We encountered at least one common garter snake in 116 of 2845 board-years and in every county except Linn and Audubon. Random effect standard deviations were 0.77 (site\_abbreviation) and 0.0001 (coverboardID) with individual intercepts for the site ranging from -1.0 (SMI) – 1.1 (TER) (Figure S4-11). The global model fixed effects explained 6.8% (marginal) and 10.4% (conditional) of the variance in the data. After fitting all possible subset models of the global model, we trimmed the model list to only the 1240 models containing the top 95% of the AICc model weight.

There were several significant terms in the global model (Figure 4-6). Edge density interacting with grassland amount (Figure 4-7a), grassland amount interacting with edge density (Figure 4-7b), patch area interacting with grassland amount (Figure 4-7c), developed land cover within 650 m (Figure 4-7d), vegetation visual obstruction (Figure 4-7e) and diversity (Figure 4-7f) and survey effort (Figure 4-7g) were all significant at  $\alpha = 0.1$ , although the predicted change in probability of presence was minimal for several (Figure 4-7).

Large prairie patch conservation practices were more likely to have common garter snakes present (0.10,  $CI_{90\%} = 0.05 - 0.21$ ) than prairie contour strips (0.03,  $CI_{90\%} = 0.02 - 0.06$ ), grass waterways (0.02,  $CI_{90\%} = 0.01 - 0.03$ ), contour strips (0.02,  $CI_{90\%} = 0.01 - 0.03$ ), or terraces (0.01,  $CI_{90\%} = 0.006 - 0.029$ ), but had similar probabilities of presence as large patch grasslands (0.06,  $CI_{90\%} = 0.03 - 0.10$ ) and grass filter strips (0.04,  $CI_{90\%} = 0.02 - 0.08$ ) (Figure 4-7h).

## Discussion

We found that occurrence of snakes and lizards was very low in perennial conservation practices in extensively cropped landscapes in Iowa, US with only 45% of patches containing any snakes in a given year after accounting for imperfect detection. Diversity was also low, with an estimated 1.7 – 3.2 species found after turning a given cover board more than 800 times. Larger prairie reconstructions seemed to be the core snake habitat at sites we surveyed. Snake presence was significantly higher in large prairie reconstructions than in smaller, more fragmented conservation practices, as was species richness.

We found fewer snakes in grass waterways than Knoot and Best (2011), who estimated a 77% occupancy rate for snakes as a group and 58% occupancy for common garter snakes in one southeastern Iowa county. Since our study regions did not overlap it is difficult to say if the difference was due to sampling methods or a genuine difference in presence on the landscape. Glass and Eichholz (2022) found detection-corrected occupancy rates of 0.12 – 0.86 for eight snake species in southern Illinois, USA. Their study landscape was substantially different, however, being conducted on a single 1,824 ha state wildlife management area with up to 75% trees within 400 m.

One explanation for why snake presence was low in conservation practices could be that patches with no hibernacula either were not colonized or underwent annual extinctions. Harvey et al. (2006) found that for eastern Massasaugas in Ontario, Canada, microhabitat features such as refugia and hibernacula were better at describing habitat selection than were landscape-scale habitat variables. Within-patch woody cover was the best predictor of snake presence in a study in southern Illinois (Glass and Eichholz 2022). This suggests that if conservation practices do not contain necessary microhabitats they may either not be colonized or undergo extinction when reptiles leave in search of suitable hibernacula every year. Intentional meso-filter conservation

strategies to restore or preserve critical life-stage microhabitats may be needed in these landscapes (Hunter 2005).

While we did not collect data on potential hibernacula, such an effect could be compounded by a reluctance among snakes and lizards to cross barren crop ground in the spring, resulting in low recolonization rates. We found that our isolation metric, patch nearest neighbor, was a significant predictor of detection-corrected occupancy for snakes as a group and common garter snakes, although the 90% odds ratio confidence interval for common garter snakes did barely cross 1.0. This trend was less clear in our simple presence analysis, with a non-significant positive effect on presence for snakes as a group and a weak effect with broadly overlapping confidence intervals for common garter snakes. An unwillingness to cross a hostile matrix has been proposed as a driver of snake occupancy. For example, Pernetta et al. (2011) found evidence of genetic isolation of the smooth snake (*Coronella austriaca*) in southern England, indicating a persistent inability to cross modest (< 6 km) distances of non-habitat; however, a prior patch occupancy study (Pernetta 2009) found that patch size and habitat amount were more important than isolation. In an exhaustive meta-analysis, Prugh et al. (2008) found that patch size and isolation were generally poor predictors of species' presence, although they did find that the type of land cover in the intervening matrix had a strong effect on the sensitivity of species to patch isolation.

We did not find a strong effect of grassland habitat amount on snake occupancy or presence (Fahrig 2013), but we did consistently see a strong interaction effect between grassland habitat amount and edge density within the focal landscape. We expect that having large amounts of habitat or low-edge density landscapes were not enough separately; snakes in our study landscapes needed both high habitat amounts and low edge densities to be present at higher

rates. This result could be another indication that snakes strongly avoided barren crop ground. We also found statistically significant but very weak positive effects of woody land cover amount and similarly weak negative effects of developed land cover proportion on snake presence, although not significantly so for common garter snakes. These trends were also present in our detection-corrected occupancy analysis and generally agreed with Glass and Eichholz (2022), who found snake relative abundance increased with the amount of woody and grass cover within 400 m.

We encountered snakes more frequently in high grass land cover landscapes that had larger patches of prairie or grass cover, but patch size did not have a biologically-meaningful effect in low grass land cover landscapes. There was no biologically meaningful effect of patch size on common garter snake presence. Patch area also had a weakly positive, but not statistically significant, effect for snakes as a group and common garter snakes in our detection-corrected occupancy models. Our finding of patch area as a modest predictor of snake occupancy agreed with similar studies on snakes (Kjoss and Litvaitis 2001, Pernetta 2009), but not a larger meta-analysis including many taxa (including 50 species of lizard), but no snakes (Prugh et al. 2008).

We found that vegetation richness was a significant positive predictor of presence for snakes as a group and common garter snakes, with a modest effect size for snakes and lizards as a group and a weak effect for common garter snakes. Vegetation richness was not a significant variable in our global model for detection-corrected occupancy. We could only locate one other test of directly measured plant species richness on the presence or abundance of snakes or lizards, although other studies have hinted at such an effect. Mizsei et al. (2020) found that plant Shannon diversity negatively predicted the presence of meadow vipers (*Vipera ursinii*) in Europe but was not predictive for three species of lizards. Glass and Eichholz (2022) found that snake

relative abundance decreased with forb percent cover, which could be correlated with vegetation diversity.

Our ability to fit subset models of our occupancy global model was hampered by low detection rates (Steen 2010, Durso et al. 2011), despite considerable survey effort, limiting our ability to examine collinear habitat variables in isolation from one another. To maintain our ability to tease apart collinear effects, we chose to examine individual variables in a simple presence framework. While this limited our ability to observe variation due to detection probability, the occupancy global model fit the data well with detection covariates on only survey effort and weather. Weather was unbiased toward any of our predictor variables, and we included survey effort as a variable in our presence model to account for unequal sampling effort.

In addition to low detection rates, the rarity of individual species also caused us to analyze all snakes as a single taxonomic group rather than as individual species, with the exception of common garter snakes, the most common species we encountered. This decision was validated by an improved model fit for snakes as a group compared to our largest single-species group, indicating that lumping species together gained more in sample size than it sacrificed in noise due to differences between species (Smith et al. 2019). We expect the results of our analysis on presence of snakes as a taxonomic group to be useful to conservation planners specifically because it is broad (Norton 1998). The results provided by such a combined study highlight the commonalities between species that are more similar to one another in physiology, dispersal, and life-history requirements than they are to other taxonomic groups that are more common conservation foci (Smith et al. 2019).

Many of the species we encountered have historically been locally abundant over a large geographic range in several habitats (Rabinowitz 1981, Iowa Department of Natural Resources 2015). Their relative absence from our study sites is indicative of the degree of habitat alteration, and their inability to adapt to the novel, highly fragmented, low habitat amount landscape.

Future studies would benefit from higher detection rates, perhaps from locating study sites in landscapes expected to have larger snake and lizard populations, or by integrating multiple survey protocols such as drift fences, metal artificial cover objects, or visual encounter surveys. Using multiple survey techniques would also increase the likelihood of finding species that rarely use cover boards or other artificial cover objects.

### **Conclusions and recommendations**

In this study we provide evidence that snakes and lizards occur in agricultural conservation practices at low rates compared to larger patches of restored prairie. We encountered snakes at higher rates in landscapes with more grass land cover, lower edge densities, larger patch sizes, and higher diversity vegetation. Conservation planners should consider important microhabitats such as refugia and hibernacula, even when endotherms are not the highest conservation priority. Over half the encounters we had with snakes or lizards were with a Species of Greatest Conservation Need, indicating that at-risk species still use these landscapes, presenting a pressing conservation need and a valuable opportunity to conserve declining species. To preserve the presence of rare and declining terrestrial reptiles, larger core nature reserves will be necessary in low habitat amount, highly fragmented agricultural landscapes.

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### Equations

Equation 4-1. Global models for detection and single season occupancy for all cover boards in each conservation practice lumped over a year.

$$\begin{aligned}
 & \text{detection} \sim 1 + \text{visits} + \text{time} + \text{cloud\_cover\_percent\_daily\_mean} \\
 & \quad + \text{temperature\_fahrenheit\_daily\_mean} \\
 & \text{occupancy} \sim 1 + \text{vor\_final\_mean\_log} + \text{species\_richness\_all\_5m\_total\_mean\_log} \\
 & \quad + \text{patch\_nearest\_neighbor\_veg\_m\_log} \\
 & \quad + (\text{edge\_density\_m\_per\_ha\_}\#\#\text{m\_radius\_log} \\
 & \quad + \text{patch\_count\_}\#\#\text{m\_radius\_log} + \text{patch\_area\_veg\_ha\_log}) \\
 & \quad * \text{grassland\_area\_}\#\#\text{m\_r\_ppn\_log} + \text{woody\_cover\_}\#\#\text{m\_r\_ppn\_log} \\
 & \quad + \text{developed\_}\#\#\text{m\_r\_ppn\_log} + \text{distance\_to\_water\_meters\_log}
 \end{aligned}$$

Equation 4-2. Final global model for GLMM estimating snake presence at a cover board over the course of a year. Presence was a binomial present/absent (1/0) and random effects were included for site and coverboard.

$$\begin{aligned}
 & \text{presence} \sim 1 + \text{vor\_final\_mean\_log} + \text{species\_richness\_all\_5m\_total\_log} \\
 & \quad + \text{patch\_nearest\_neighbor\_veg\_m\_log} \\
 & \quad + (\text{edge\_density\_m\_per\_ha\_}\#\#\text{m\_radius\_log} \\
 & \quad + \text{patch\_count\_}\#\#\text{m\_radius\_log} + \text{patch\_area\_veg\_ha\_log}) \\
 & \quad * \text{grassland\_area\_}\#\#\text{m\_r\_ppn\_log} + \text{woody\_cover\_}\#\#\text{m\_r\_ppn\_log} \\
 & \quad + \text{developed\_}\#\#\text{m\_r\_ppn\_log} + \text{distance\_to\_water\_meters\_log} \\
 & \quad + \text{board\_flips} + (1|\text{site\_abbreviation}) + (1|\text{coverboardID})
 \end{aligned}$$

## Tables

Table 4-1. Conservation practice descriptions based on patch shape, slope position, and vegetation diversity. Cost share program designations were archetypical; actual enrollment in a cost share program was not required or verified.

| Conservation practice | Example cost share program                              | Description   |
|-----------------------|---|---|
| Grass contour strip   | CP-15A  | Linear strip (3 – 100 m wide, typically ~10 m) of low diversity grass planted along a contour within a field. Often planted to exotic cool-season grass species such as smooth brome ( <i>Bromus inermis</i> ).   |
| Grassed terrace       | IA-600 grassed backslope terraces, narrow base terraces | Linear earthen berm (2 – 5 m wide) along a contour within a field, typically planted to cool-season exotic grasses (e.g., smooth brome) when established, but were frequently affected by herbicide drift and filled with annual weeds and woody species.   |
| Grass filter strip    | CP-21   | Linear strips (3 – 30 m wide, typically ~10 m) of low diversity grass planted at toe slope position adjacent to a permeant water body. Typically planted to cool-season exotic grasses such as reed canary grass ( <i>Phalaris arundinacea</i> ).   |
| Grass waterway        | CP-8A   | Linear strips (3 – 20 m wide) of low diversity grass planted along drainage paths to conduct surface water off fields. Typically planted with exotic cool-season grasses such as smooth brome.  |
| Grass large patch     | CP-1, CP-4D   | Low diversity grass planted in larger patches (> 8 ha) such as field corners, areas isolated by streams, or entire fields. Plantings contained exotic or native warm or cool season grasses.  |
| Prairie contour strip | CP-43   | Linear strips (3 – 100 m wide, typically ~10 m) of medium-high diversity native grasses and forbs planted along a contour within a field. Common species included big bluestem ( <i>Andropogon gerardi</i> ), little bluestem ( <i>Schizachyrium scoparium</i> ), Canada wild rye ( <i>Elymus canadensis</i> ), gray coneflower ( <i>Ratibida pinnata</i> ), wild bergamot ( <i>Monarda fistulosa</i> ), rattlesnake master ( <i>Eryngium yuccifolium</i> ), oxeye ( <i>Heliopsis helianthoides</i> ), etc. |
| Prairie filter strip  | CP-43   | Linear strips (3 – 30 m wide, typically ~10 m) of medium-high diversity native grasses and forbs planted along permeant water bodies with plant communities similar to prairie contour strips.  |
| Prairie large patch   | CP-33, CP-38, CP-42                                     | Medium-high diversity native grasses and forbs planted in larger patches (> 8 ha) such as field corners, strips wider than 100 m, or whole fields.  |

Table 4-2. Cover board flips by site and year. Individual board flips were aggregated by conservation feature and week for the occupancy analysis and by year for the GLMM analysis.

| Site         | 2015 | 2016 | 2017 | 2018 | 2019 | 2020 | Total |
|--------------|------|------|------|------|------|------|-------|
| ARM          | 124  | 48   | 45   | 119  | 119  | 226  | 681   |
| EIA          | 26   | 54   | 43   | 64   | 0    | 0    | 187   |
| GUT          | 331  | 147  | 66   | 210  | 132  | 357  | 1243  |
| INH          | 0    | 0    | 30   | 115  | 80   | 78   | 303   |
| KAL          | 692  | 707  | 500  | 679  | 475  | 484  | 3537  |
| MCC          | 783  | 47   | 0    | 0    | 0    | 0    | 830   |
| MCN          | 230  | 75   | 65   | 110  | 135  | 0    | 615   |
| NIR          | 0    | 0    | 276  | 410  | 297  | 298  | 1281  |
| RHO          | 0    | 83   | 28   | 42   | 58   | 125  | 336   |
| SLO          | 70   | 39   | 43   | 71   | 89   | 181  | 493   |
| SMI          | 775  | 340  | 288  | 324  | 272  | 400  | 2399  |
| SPI          | 0    | 0    | 0    | 137  | 80   | 110  | 327   |
| TER          | 0    | 0    | 0    | 227  | 111  | 312  | 650   |
| WHI          | 0    | 524  | 424  | 520  | 357  | 763  | 2588  |
| WOR          | 556  | 52   | 0    | 97   | 85   | 322  | 1112  |
| <b>Total</b> | 3587 | 2116 | 1808 | 3125 | 2290 | 3656 | 16582 |

Table 4-3. Presence variables considered. Landscape variables used 650 m radius from cover board, denoted below as “##”. Bold text “transformations considered” indicates the final transformation. Interactions were included for grassland area with patch area, patch count, and edge density.

| Variable                                   | Description  | Native units  | Transformations considered              | Category                | Selected for final model list |
|--|--|---------------|---|-------------------------|-------------------------------|
| grassland_area_##_m_r_ppn                  | proportion of a ## m radius circle in grass land cover   | proportion    | linear, <b>log</b> , <b>interaction</b> | landscape: habitat area | yes                           |
| patch_area_veg_ha                          | area of patch using vegetation communities and 3 m pixels  | ha            | linear, <b>log</b> , <b>interaction</b> | landscape: patch size   | yes                           |
| patch_area_mean_##_m_radius                | mean area of patches within ## m distance to nearest similar-community patch   | ha            | linear, log, interaction                | landscape: patch size   | no                            |
| patch_nearest_neighbor_veg_m               | Mean distance to nearest similar-community patch   | m             | linear, <b>log</b> , interaction        | landscape: isolation    | yes                           |
| mean_nearest_neighbor_m_##_m_radius        | Mean distance to nearest similar-community patch within ## m   | m             | linear, log, interaction                | landscape: isolation    | no                            |
| patch_count_##_m_radius                    | count of distinct patches within ## m perimeter:area ratio of patch using vegetation community definition and 3 m pixels | count         | linear, <b>log</b> , <b>interaction</b> | landscape: patch count  | yes                           |
| perimeter_area_ratio_veg_m_per_sq_m        |  | m             | linear, log, interaction                | Landscape: edge effects | no                            |
| edge_density_m_per_ha_##_m_radius          | length of edge per unit area within ## m   | m/ha          | linear, <b>log</b> , <b>interaction</b> | landscape: edge effects | yes                           |
| vor_final_mean                             | visual obstruction around cover board measured with a Robel pole from 5 m (10-150)                                       | cm obscured   | linear, <b>log</b> , interaction        | vegetation: density     | yes                           |
| species_richness_all_5m_total              | plant species count within 5 m of cover board  | count         | linear, <b>log</b> , interaction        | vegetation: diversity   | yes                           |
| preferred_species_cover_grassland_mean_all | mean cover of preferred plant species within plot  | percent cover | linear, log, interaction                | vegetation: diversity   | no                            |

Table 4-3 continued

| Variable                        | Description  | Native units | Transformations considered                  | Category       | Selected for final model list |
|---------------------------------|--|--------------|---|----------------|-------------------------------|
| <i>Expert opinion variables</i> |  |              |   |                |                               |
| quadrats_mowed_percent          | percent of quadrats mowed                                  | percentage   | linear, log, interaction                    | confounding    | no                            |
| woody_cover_ppn_##_m_r          | proportion of a ## m radius circle in woody land cover     | proportion   | linear, quadratic, <b>log</b>               | life history   | yes                           |
| developed_##_m_r_ppn            | proportion of a ## m radius circle in developed land cover | proportion   | linear, quadratic, <b>log</b>               | life history   | yes                           |
| distance_to_water_meters        | distance to nearest water land cover                       | m            | linear, quadratic, <b>log</b> , interaction | life history   | yes                           |
| board_flips                     | number of cover board flips (visits) per year              | count        | <b>linear</b> , log                         | life history   | yes                           |
| coverboardID                    | individual cover board                                     | categorical  | none  | random effects | yes                           |
| sample_unit_areaID              | individual conservation practice                           | categorical  | none  | random effects | no                            |
| site_abbreviation               | Site   | categorical  | none  | random effects | yes                           |

Table 4-4. Percentage of the time a species was present when a cover board was flipped, by county in Iowa, US. Some counties had multiple sites. Sampling effort was unequal between sites and counties. Species designated with a ‘\*’ are Iowa Species of Greatest Conservation Need (Iowa Department of Natural Resources 2015).

|   | Audubon | Buch-<br>anan | Greene | Guthrie | Jasper | Linn | Lucas | Marshall | Pottawa-<br>ttamie | Story | Wright | Total |
|---|---------|---------------|--------|---------|--------|------|-------|----------|--------------------|-------|--------|-------|
| Brown snake ( <i>Storeria dekayi</i> )                      | 0.16    | 0.61          | 1.77   | 1.14    | 0.11   | 0    | 0.61  | 0.6      | 0.6                | 1.27  | 0.04   | 0.57  |
| Common garter snake ( <i>Thamnophis sirtalis</i> )          | 0       | 0.61          | 12.19  | 1.76    | 0.32   | 0    | 2.74  | 0.6      | 0.89               | 0.98  | 0.34   | 1.23  |
| Eastern yellow-bellied racer ( <i>Coluber constrictor</i> ) | 0       | 0             | 0      | 0       | 0.22   | 0    | 0     | 0        | 0.15               | 0     | 0      | 0.07  |
| *Gopher (bull) snake ( <i>Pituophis catenifer</i> )         | 0       | 0             | 0      | 0       | 0.02   | 0    | 0     | 0        | 0                  | 0     | 0      | 0.01  |
| *Lined snake ( <i>Tropidoclonion lineatum</i> )             | 0       | 0             | 0      | 0.62    | 0      | 0    | 0.15  | 0        | 1.04               | 0.04  | 0      | 0.16  |
| *Plains garter snake ( <i>Thamnophis radix</i> )            | 0       | 0             | 3.21   | 0.31    | 0.11   | 0.53 | 0     | 0.89     | 0                  | 0.64  | 0.21   | 0.35  |
| *Prairie skink ( <i>Plestiodon septentrionalis</i> )        | 0.72    | 0             | 7.36   | 0.34    | 0      | 0    | 0     | 0        | 1.91               | 0     | 1.04   | 0.63  |
| *Ringneck snake ( <i>Diadophis punctatus</i> )              | 0       | 0             | 0.15   | 3.58    | 0      | 0    | 0     | 0        | 0                  | 0     | 0.04   | 0.66  |
| *Smooth green snake ( <i>Opheodrys vernalis</i> )           | 0       | 0             | 0      | 0       | 0      | 0    | 0     | 0.3      | 0                  | 0     | 0      | 0.01  |
| Unidentified garter ( <i>Thamnophis sp.</i> )               | 0.08    | 0             | 1.45   | 0.14    | 0.02   | 0    | 1.83  | 0.6      | 0                  | 0.51  | 0      | 0.25  |
| *Western fox snake ( <i>Pantherophis ramspotti</i> )        | 0.16    | 1.42          | 0.48   | 0.14    | 1.1    | 0    | 0     | 0.3      | 0.45               | 1.78  | 0      | 0.68  |
| *Western ribbon snake ( <i>Thamnophis proximus</i> )        | 0       | 0             | 0      | 0       | 0      | 0    | 0     | 0        | 0                  | 0.04  | 0      | 0.01  |
| Snakes as a group   | 0.04    | 0.24          | 1.67   | 0.69    | 0.17   | 0.05 | 0.49  | 0.30     | 0.28               | 0.48  | 0.06   | 0.38  |

## Figures

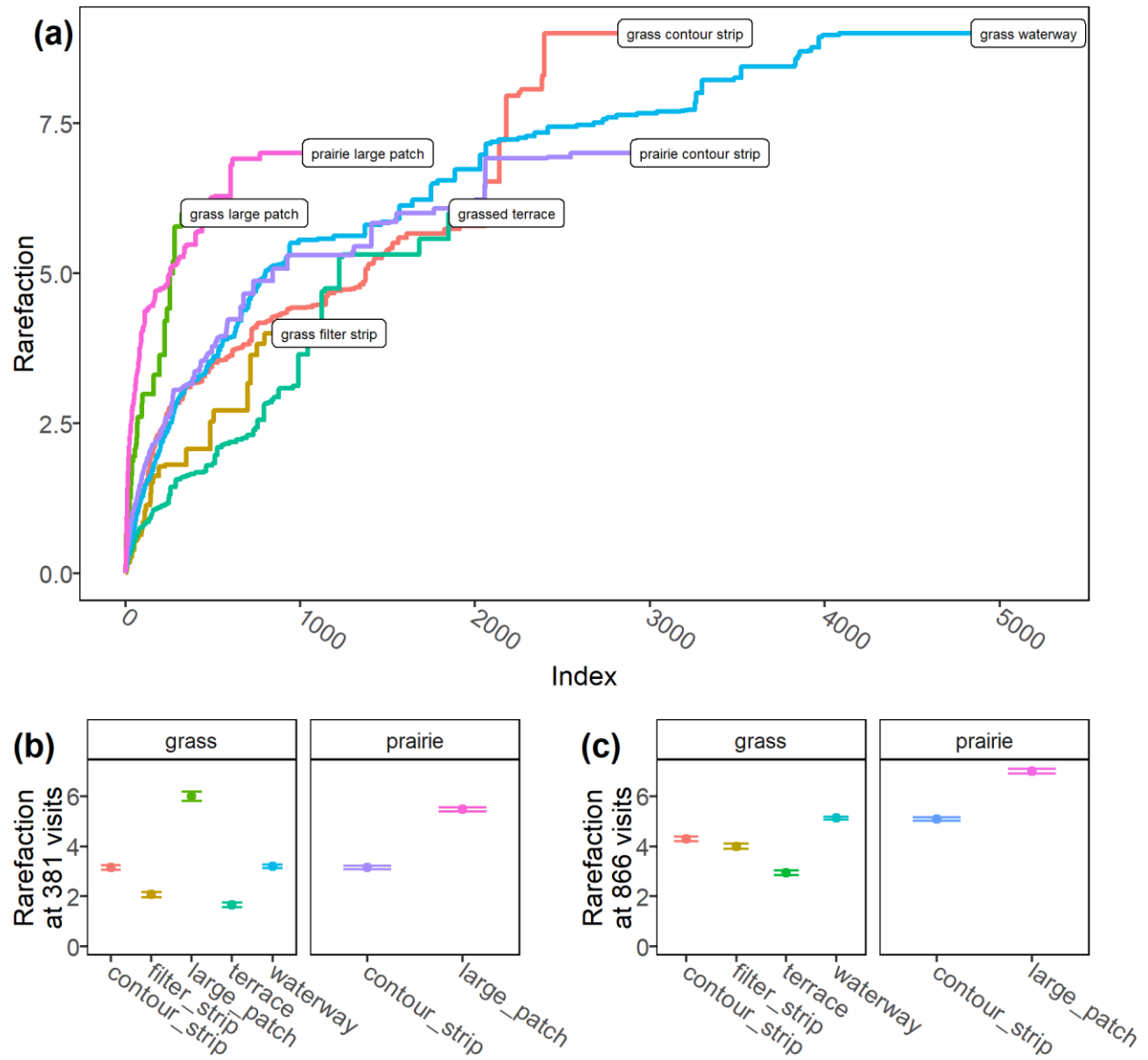


Figure 4-1. Rarefaction curve of reptile species richness by cover board and conservation practice where each sample is one cover board check. All conservation practices rarefied to their maximum number of board-turns (a) and equal-effort estimates of richness with 95% confidence intervals for the conservation practice with the lowest (b) and second-lowest (b) number of board-turns.

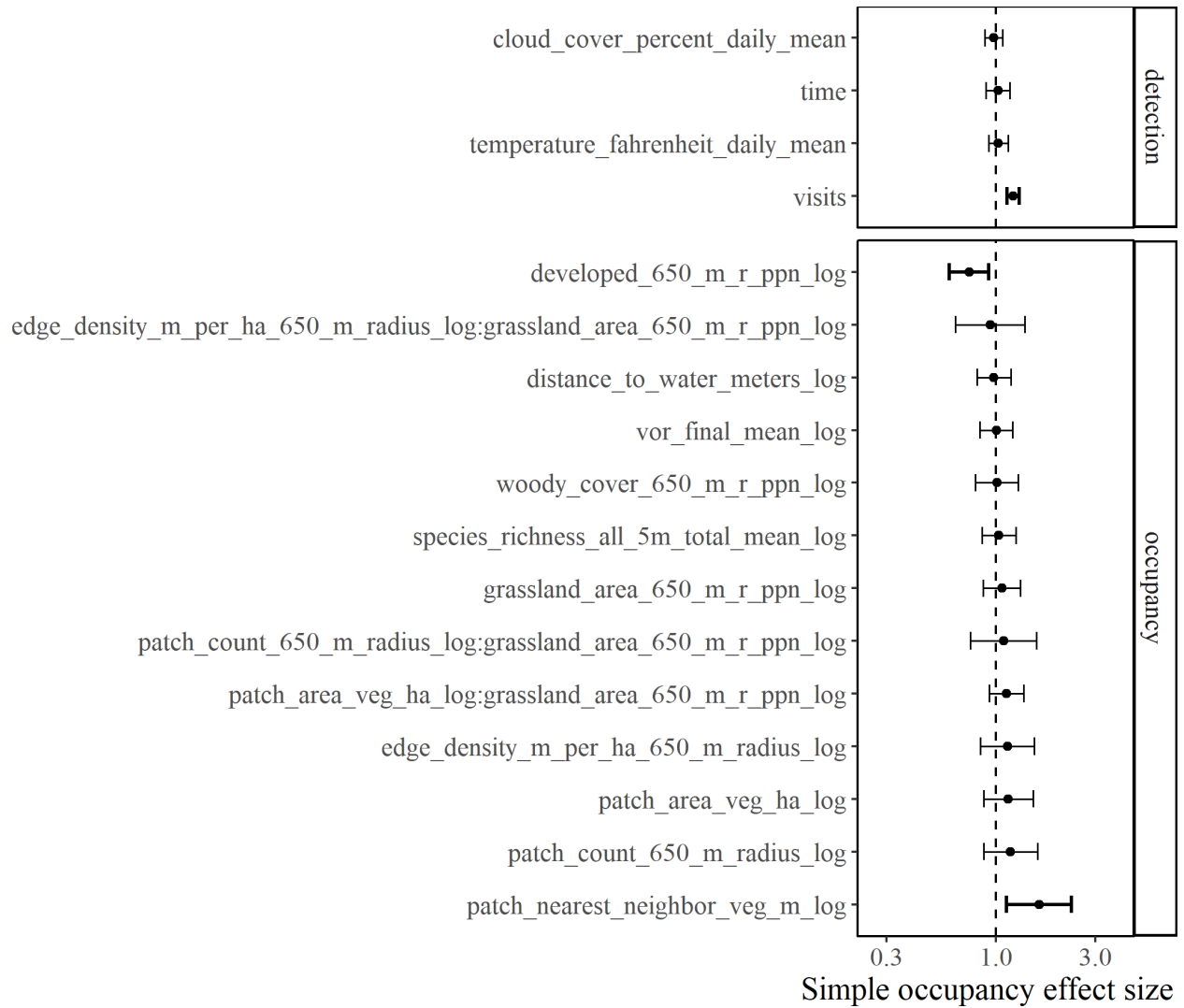


Figure 4-2. Snake suborder single-season detection and occupancy effect sizes expressed as odds ratios with 90% confidence intervals. Bolded confidence intervals do not cross one and are significant at  $\alpha = 0.1$ . Descriptions of variables are provided in Table 4-3.



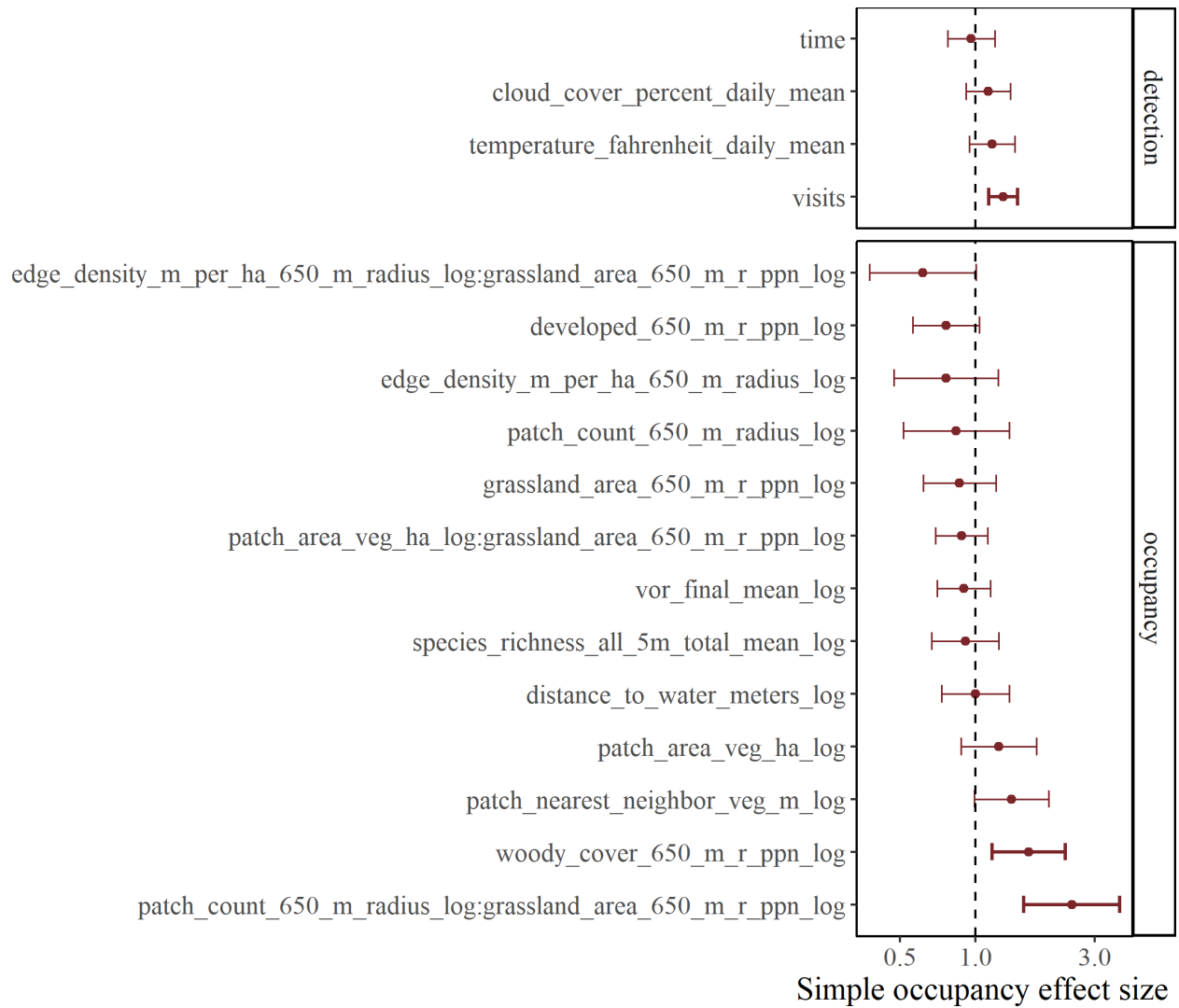


Figure 4-3. Common garter snake single-season detection and occupancy effect sizes expressed as odds ratios with 90% confidence intervals. Bolded confidence intervals do not cross one and are significant at  $\alpha = 0.1$ . Descriptions of variables are provided in Table 4-3.

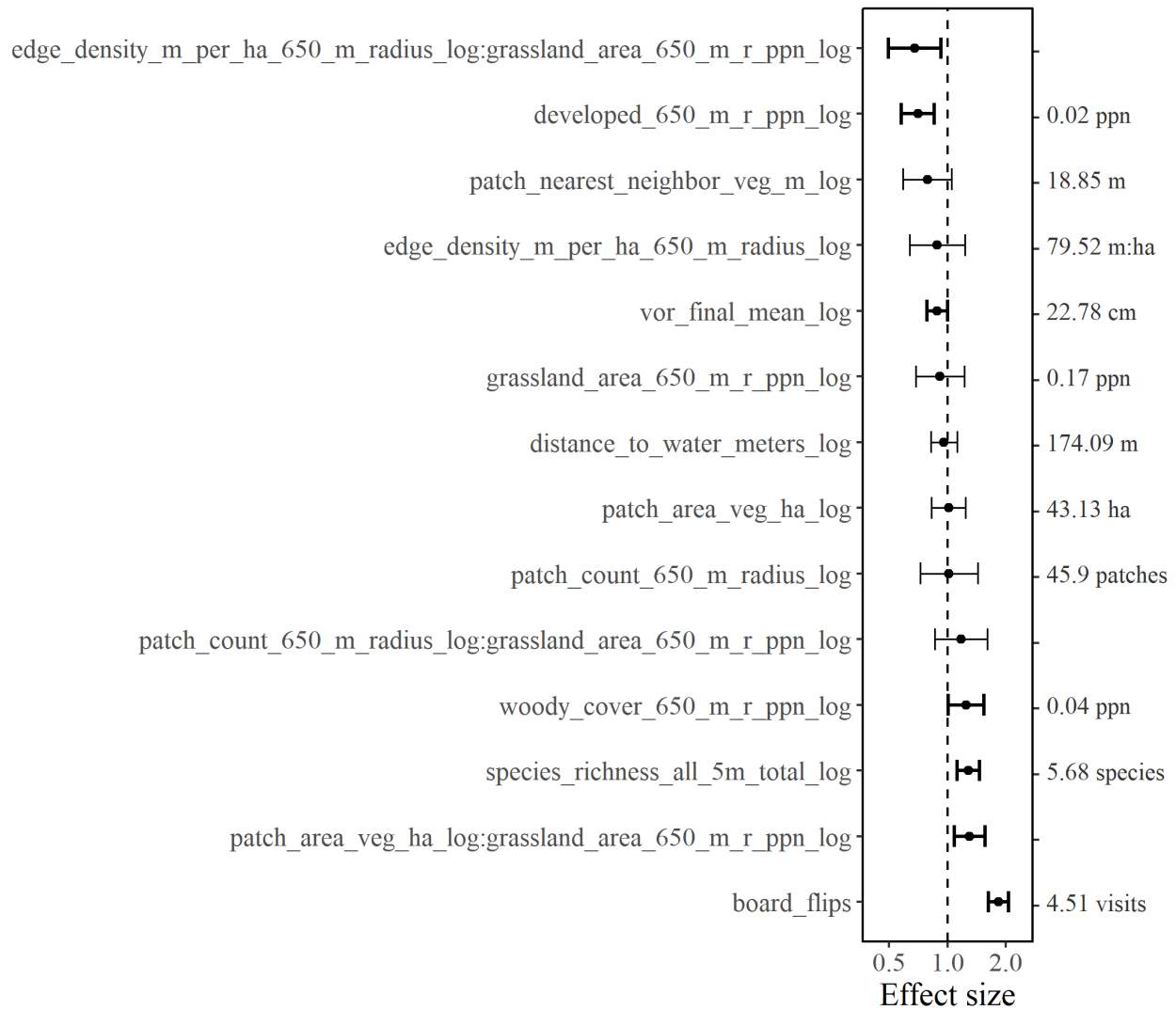


Figure 4-4. Snake suborder presence effect sizes expressed as odds ratios with 90% confidence intervals. Bolded confidence intervals do not cross one and are significant at  $\alpha = 0.1$ . A one standard deviation change (right axis) in the predictor variable multiplied the odds of apparent occupancy by the indicated amount. Standard deviations not listed for interaction terms.

Descriptions of variables are provided in Table 4-3.

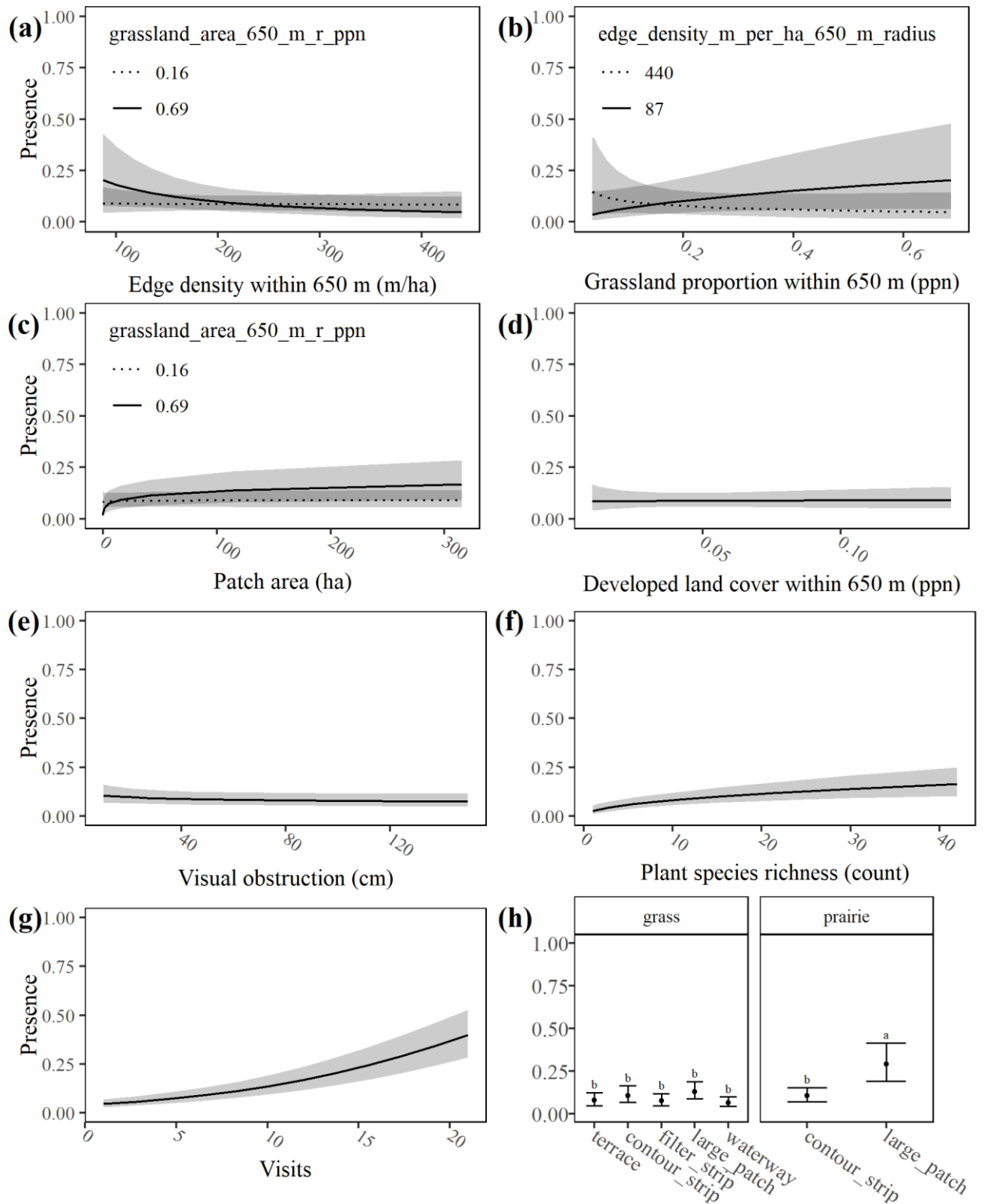


Figure 4-5. Snake suborder presence predicted by (a) edge density within 650, (b) patch area, (c) grassland habitat amount within 650 m, (d) developed land cover within 650 m, (e) visual

obstruction as a correlate of vegetation density, (f) plant species richness, (g) time of day, and (h) by conservation practice. 90% prediction intervals are indicated by the shaded area (a-g) and whiskers (h). Groups that do not share letters are significantly different at  $\alpha = 0.1$  (h).

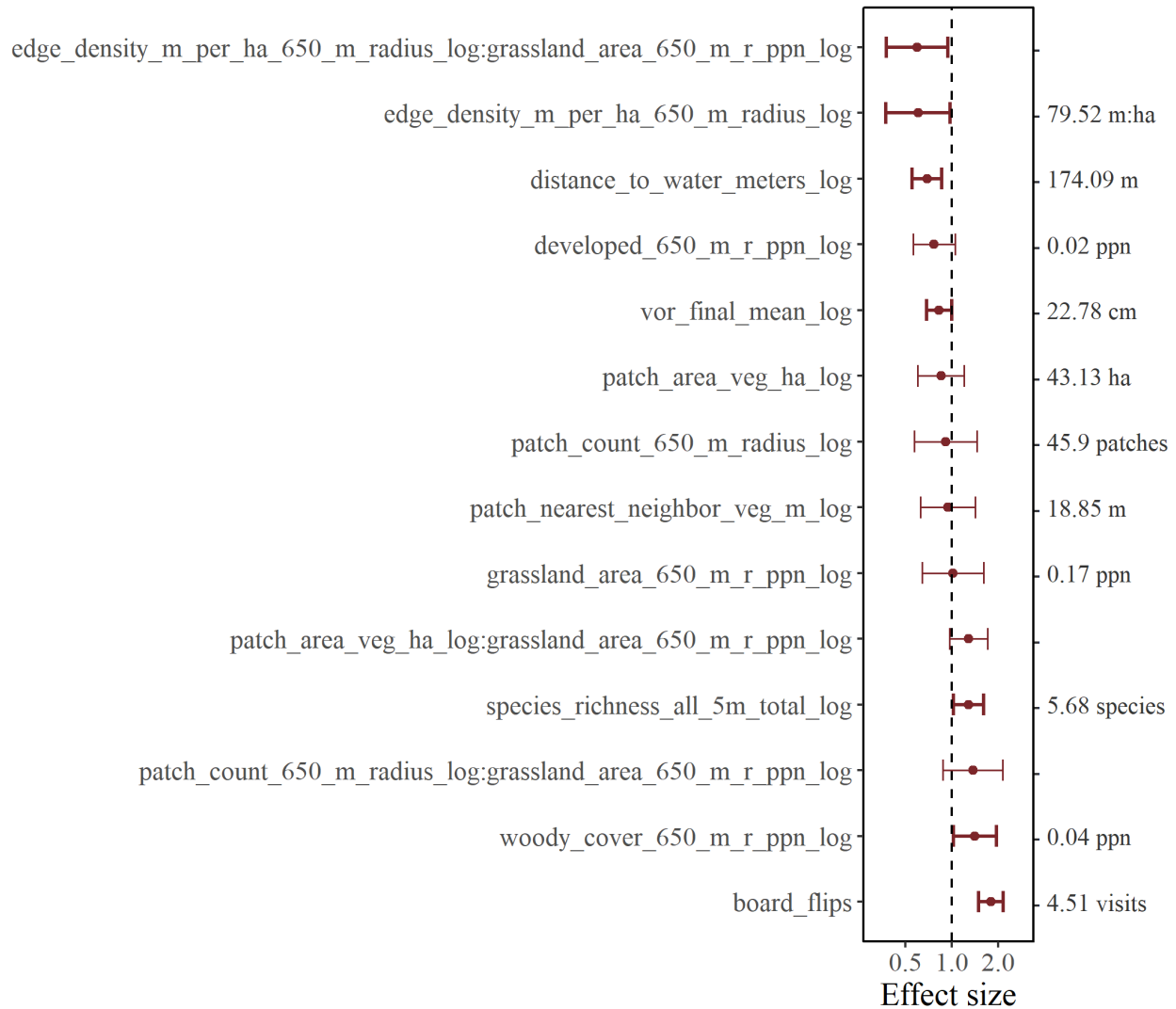


Figure 4-6. Common garter snake presence effect sizes expressed as odds ratios with 90% confidence intervals. Bolded confidence intervals do not cross one and are significant at  $\alpha = 0.1$ . A one standard deviation change (right axis) in the predictor variable multiplied the odds of apparent occupancy by the indicated amount. Standard deviations not listed for interaction terms. Descriptions of variables are provided in Table 4-3.

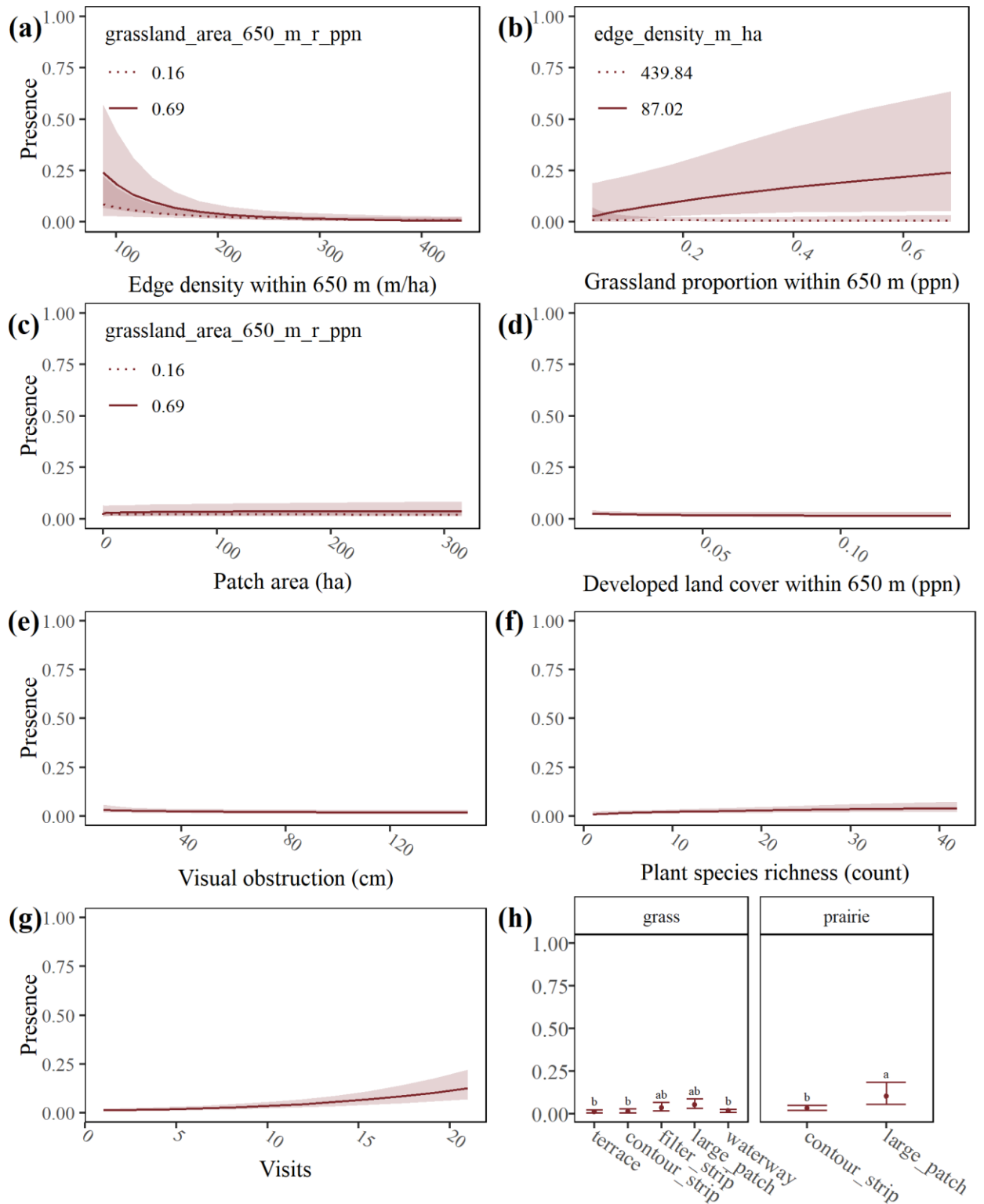


Figure 4-7. Common garter snake board-year presence predicted by (a) edge density within 650, (b) grassland habitat amount within 650 m, (c) patch size, (d) developed land cover within 650

m, (e) visual obstruction as a correlate of vegetation density, (f) plant species richness, (g) survey effort, and (h) by conservation practice. 90% prediction intervals are indicated by the shaded area (a-g) and whiskers (h). Groups that do not share letters are significantly different at  $\alpha = 0.1$  (h).

## **Appendix S1. Hypotheses**

### **Vegetation diversity**

VD-1 Snake occupancy will be higher in areas of higher vegetation diversity because greater diversity promotes more food resources, resulting in an increase of fitness for snakes. This will be supported by higher snake occupancy and colonization, lower snake extinction, and higher snake body condition indices in areas with more diverse vegetation.

VD-2 Large snake occupancy will be higher in areas of higher vegetation diversity because greater vegetation diversity increases bird nest density, providing more food resources and an increase in fitness. This will be supported by higher nest densities, higher large snake occupancy and colonization, lower large snake extinction, and higher large snake body condition index in areas with higher vegetation diversity.

VD-3 Snake and lizard diversity will be higher in areas of higher vegetation diversity because vegetation diversity creates a heterogeneous landscape with more available niches. This will be supported by higher reptile alpha diversity in areas with higher vegetation diversity.

### **Vegetation structure**

VS-1 Snake occupancy will be unaffected by vegetation density because it does not hamper their ability to travel or locate prey. This will be supported by no difference in occupancy, colonization, and extinction rates in areas of differing vegetation density.

VS-2 Snake occupancy will be higher in areas of higher vegetation density because dense vegetation provides more cover from predators. This will be supported by higher occupancy and colonization and lower extinction rates and detection probabilities, and greater percent covers of live grasses and forbs in areas with higher vegetation density.

VS-3 Snake occupancy will be higher in areas of lower vegetation density due to more sunlight reaching the ground and improving the thermal environment for reptiles. This will be

partially supported by higher snake occupancy and colonization and lower extinction rates in patches with lower vegetation density, but cannot be fully supported because we have no assessment of the thermal environment.

VS-4 Snake and lizard diversity will be higher in patches of mixed vegetation density because heterogeneous vegetation structure provides more niches. This will be supported by patches with more variation in vegetation density having a higher reptile alpha diversity.

### **Habitat area**

HA-1 Meso-predator release will function in landscapes with intermediate areas of habitat, with medium-sized predators doing well in intermediate-area landscapes, prey animals doing better in small- and large-area landscapes than intermediate-area landscapes, and large predators having a minimum threshold habitat area below which they are uncommon. This will be supported by (1) Lower small snake and lizard occupancy and colonization and higher extinction rates in intermediate-area landscapes compared to smaller- and larger-area landscapes and (2) Higher large snake occupancy and colonization, and lower extinction rates in intermediate-area landscapes compared to smaller- and larger-area landscapes.

HA-2 Snake and lizard occupancy will be higher in patches with more habitat on the landscape because the meta-population is better able to re-colonize patches after extinction events. This will be supported by higher occupancy and colonization rates, lower extinction rates, and colonization rates greater than or equal to extinction rates for patches within landscapes with more habitat area.

HA-3 Snake occupancy will be higher in patches with more habitat area on the landscape because the landscape is more likely to contain critical life-stage micro-habitats such as hibernacula. This will be partially supported by higher snake occupancy and colonization and



lower snake extinction rates in landscapes with greater habitat areas, but cannot be fully supported because we have no measure of availability of hibernacula.

HA-4 Snake occupancy has a lower threshold to habitat area on the landscape below which there is not enough warm-season prey and hibernacula to support a population. This will be supported by a logarithmic relationship between landscape habitat area and snake occupancy, colonization, and extinction.

HA-5 Snake and lizard diversity will be higher in landscapes with more habitat area because increasing area also increases the number of habitat niches available. This will be supported by equal patch-level alpha diversity, but higher landscape-level beta and gamma diversity.

## **Habitat configuration**

### **Number of patches**

PN-1 Environmental stochasticity will be higher in landscapes with more patches when controlled for total habitat area. This will be supported by landscapes with more patches having higher extinction rates of snakes and lizards.

PN-2 Demographic stochasticity will be lower in landscapes with more patches when controlled for total habitat area due to the Allee Effect. We are not able to test this hypothesis due to the timescales over which this process operates.

PN-3 Snake and lizard meta-populations will be less likely to go extinct on landscapes with more patches. This will be supported by higher reptile colonization rates at the patch level in landscapes with more patches, and lower reptile extinction rates at the landscape level, after controlling for habitat area.

PN-4 Snake and lizard diversity will be higher in landscapes with many patches because differential habitat management among patches creates a more heterogeneous habitat mosaic,

outweighing potential effects of area-sensitivity. This will be demonstrated by landscapes with several-small-patches having even patch-level alpha diversities of reptiles with single-large-patch landscapes, but higher beta and gamma diversities.

### **Patch size**

PS-1 Meso-predator release (Rogers and Caro 1998) will function in intermediate-sized patches, with medium-sized predators doing well in intermediate-sized patches, prey animals doing better in small and large patches than intermediate-sized patches, and large predators having a minimum threshold patch size below which they are uncommon. This will be supported by (1) Lower small snake and lizard occupancy and colonization and higher extinction rates in intermediate sized patches compared to smaller and larger patch sizes and (2) Higher large snake occupancy and colonization, and lower extinction rates in intermediate-sized patches compared to smaller and larger patch sizes.

PS-2 Snake occupancy has a lower threshold to patch size below which there is not enough prey to make occupying a patch worthwhile. This will be supported by a logarithmic relationship between patch size and snake occupancy, colonization, and extinction.

PS-3 Snake occupancy will be higher in larger patches because those patches are more likely to contain critical life-stage micro-habitats such as hibernacula. This will be partially supported by higher snake occupancy and colonization and lower snake extinction rates in larger patches after controlling for landscape habitat area, but cannot be fully supported because we have no measure of availability of hibernacula.

PS-4 Snake and lizard diversity will be higher in larger patches because increasing area also increases the number of habitat niches available. This will be supported by higher patch-level alpha diversity in larger patches after controlling for landscape habitat area.

### **Patch isolation**

PI-1 Patch isolation will reduce habitat use by snakes because they prefer not to cross a crop matrix. This will be supported by lower patch occupancy and colonization for more isolated patches after correcting for landscape habitat area.

PI-2 Patch isolation by a crop matrix will have no effect on mouse habitat use because mice are also utilizing food resources present in the matrix. This will be supported by no difference in patch occupancy, colonization, or extinction rates due to patch isolation after correcting for landscape habitat area.

### **Edge effects**

EE-1 Patches with more edge exposure are more likely to be colonized by terrestrial animals due to the increased likelihood of encountering the patch while traveling through the matrix. This will be supported by patches with higher perimeter-edge ratio having higher colonization rates for snakes after controlling for landscape habitat area.

EE-2 Habitat quality for reptiles is not affected by crop edge proximity because crop ground does not contain predators that might cross the edge to predate them. This will be supported by no affect from crop perimeter-edge ratio on snake occupancy or extinction rates once habitat area is corrected for.

EE-3 Reptile habitat quality is lower in more linear patches because they are easier for predators to search efficiently. This will be supported by lower reptile occupancy and higher extinction rates in patches with narrower widths and higher perimeter-edge ratio and meso-mammal interior-patch detection probability higher in patches with narrower widths and higher perimeter-edge ratios after controlling for landscape habitat area.

EE-4 Reptile diversity will not be affected by distance to crop edge because the number of species attracted to grassland-crop edge will be balanced by those repelled by it. This will be

supported by no difference in alpha diversity of reptiles in relation to perimeter-edge ratio after landscape habitat area is controlled for.

EE-13 Reptile diversity will increase near tree edges due to overlap of species that primarily use one habitat but will occasionally cross into the other. This will be supported by higher reptile alpha diversity in relation to tree perimeter-edge ratio after landscape habitat area is controlled for.

## Appendix S2. Supplementary Tables

Table S4-1. Descriptions of land cover classifications. Land covers were manually digitized based primarily on NAIP aerial imagery and versioned annually, with the exception of 2017 for which there was no imagery flown. LiDAR imagery was used to distinguish land covers that involve sharp differences in elevation. All land covers within ownership boundaries of study sites and unusual land cover classes outside of ownership boundaries were verified in-person.

| Land cover class    | Lumped class | Description  |
|---------------------|--------------|--|
| alfalfa             | grassland    | Cultivated alfalfa field. Always verified in-person.   |
| amaranth            | crop         | Cultivated amaranth field. Always verified in-person.  |
| beans               | crop         | Cultivated soybean field without a cover crop. Distinguished from corn by color and texture on aerial imagery.   |
| beans_cc            | crop         | Cultivated soybean field with a cover crop, typically cereal rye. Cover crop terminated prior to growth of main crop, typically by herbicide application. Distinguished from corn by color and texture on aerial imagery. Presence of cover crop verified in-person. |
| brushy_waterway     | woody        | Superseded by waterway_woody land cover class.   |
| contour_strip       | grassland    | Linear low-diversity grass patch oriented with hill contour. Distinguished from prairie strip by greener, more homogenous texture on aerial imagery.   |
| contour_strip_woody | woody        | Linear low-diversity grass patch oriented with hill contour with individual shrubs visible on aerial imagery.  |
| corn                | crop         | Cultivated corn field without a cover crop. Distinguished from soy by color and texture on aerial imagery.   |
| corn_cc             | crop         | Cultivated corn field with a cover crop, typically cereal rye. Cover crop terminated prior to growth of main crop, typically by herbicide application. Distinguished from soy by color and texture on aerial imagery. Presence of cover crop verified in-person.     |
| crop                | crop         | Corn or soybean field unable to be distinguished by color or texture on aerial imagery and not able to be verified in-person.  |
| developed           | building     | Human structures large enough to be distinguished on aerial imagery and LiDAR not including roads or driveways. Mowed lawn areas had a separate classification   |
| disturbed           | crop         | Soil and vegetation disturbed, usually by cultivation, excavation, or and/or herbicide application.  |
| ditch               | grassland    | Roadside ditch encompassing all herbaceous vegetation from road edge to fence or field edge.   |
| ditch_woody         | woody        | Roadside ditch encompassing all woody vegetation from road edge to fence or field edge. Distinguished from herbaceous vegetation by color and texture on aerial imagery.   |
| diverse_block       | grassland    | Non-linear prairie vegetation larger than 8 ha. Distinguished from low-diversity grass by browner, more heterogenous texture on aerial imagery and always verified in-person.  |
| diverse_block_woody | woody        | Woody vegetation distinguishable on aerial imagery embedded within diverse_block land cover.   |
| filter_strip        | grassland    | Linear low diversity grass patches bordered by permeant water on one side and corn or soy on the other.  |

Table S4-1 continued

| Land cover class    | Lumped class | Description  |
|---------------------|--------------|--|
| filter_strip_woody  | woody        | Woody vegetation distinguishable on aerial imagery embedded within filter_strip land cover.  |
| grass_block         | grassland    | Non-linear low-diversity grass dominated patch larger than 8 ha. Distinguished from prairie by greener, more homogenous texture on aerial imagery.   |
| grass_block_woody   | woody        | Woody vegetation distinguishable on aerial imagery embedded within grass_block land cover.   |
| hay                 | grassland    | Low-diversity grass mowed at least annually. Distinguished from other low-diversity grass land covers by browner, homogenous but striped texture and the presence of hay bales or dead spots left by hay bales.  |
| high_diversity      | grassland    | Superseded by diverse_block and prairie_strip land cover classes.  |
| little_bluestem     | grassland    | Little bluestem monoculture for seed production. Verified in-person.   |
| low_diversity       | grassland    | Superseded by grass_block, contour_strip, and other low-diversity land cover classes.  |
| mowed_lawn          | building     | Short grass adjacent to developed land cover mowed multiple times annually. Does not include other classes of mowed grass such as hay or occasional maintenance mowing.  |
| pasture             | grassland    | Non-linear, short, low-diversity grass distinguished on aerial imagery by presence of cattle infrastructure and cow paths.   |
| pond                | water        | Lentic permeant water body.  |
| prairie_strip       | grassland    | Linear high-diversity herbaceous land cover oriented along the slope. Distinguished from low-diversity vegetation by browner, more heterogeneous color on aerial imagery and always verified in-person.  |
| prairie_strip_woody | woody        | Woody vegetation distinguishable on aerial imagery embedded within prairie_strip land cover.   |
| road                | road         | Public roads and private driveways. Typically gravel, but a few paved.   |
| root_crop           | crop         | Miscellaneous root crops including beets, carrots, garlic, etc. Verified in person.  |
| small_grains        | crop         | Small grain crops such as oat and cereal rye. Distinguished from cover crops by being left in place until harvest.   |
| stream              | water        | Lotic permanent water body. Borders delineated by tracing banks using LiDAR imagery.   |
| terrace             | grassland    | Superseded by terrace_grassy and terrace_woody. A large enough percentage of terraces were wooded to necessitate explicitly distinguishing the two communities.  |
| terrace_grassy      | grassland    | Conservation practice consisting of an earthen embankment along the slope. Planted to cool season exotic grasses at establishment, but frequently over-sprayed by herbicide and may be dominated by annual weeds. Distinguished from contour strips by confirming the embankment on LiDAR imagery. |
| terrace_woody       | woody        | Conservation practice consisting of an earthen embankment along the slope. Planted to cool season exotic grasses at establishment, but frequently over-sprayed by herbicide and now dominated by woody species. Distinguished from contour strips by confirming the embankment on LiDAR imagery.   |
| tree_shrub          | woody        | Woody vegetation that doesn't have a separate "_woody" land cover class. Woody vegetation distinguished from surrounding land cover by color and texture on aerial imagery.  |
| trees               | woody        | Patches containing large mature trees. Land cover classes with "_woody" designations given priority unless the patch contains many large trees.  |
| water               | water        | Superseded by pond, stream, and wetland land cover classes.  |

Table S4-1 continued

| Land cover class  | Lumped class | Description   |
|-------------------|--------------|---|
| waterway          | grassland    | Linear low-diversity grass conservation practice running against the hill contour at the bottom of sub-watersheds.  |
| waterway_driveway | grassland    | Linear low-diversity grass conservation practice typically arranged across the contour mowed without collecting hay for the purpose of vehicle field access. Often situated at field edges. |
| waterway_woody    | woody        | Woody vegetation within linear low-diversity grass conservation practice running against the hill contour at the bottom of sub-watersheds.  |
| wetland           | grassland    | Emergent vegetation zone of shallow semi-permanent lotic water body.  |

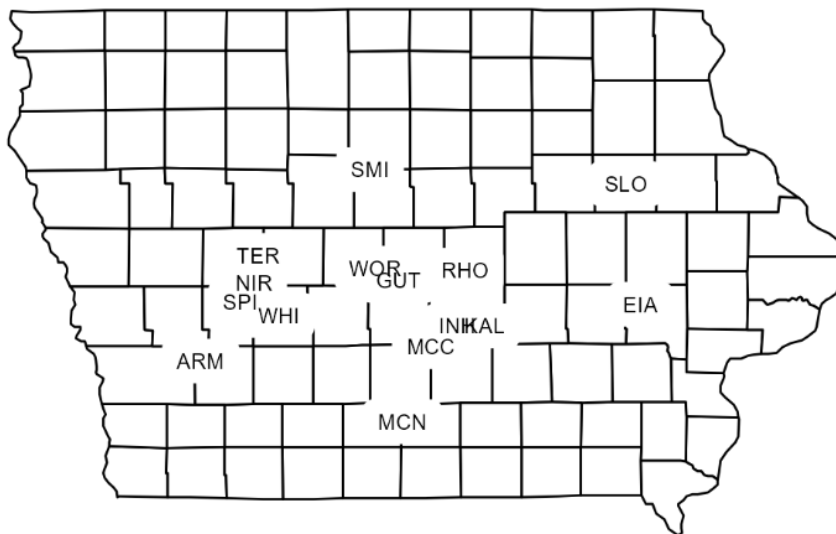
**Appendix S3. Supplementary Figures**

Figure S4-1. Study sites located in Iowa, USA. Exact locations have been jittered slightly for anonymity and labels may not be centered in their actual county.



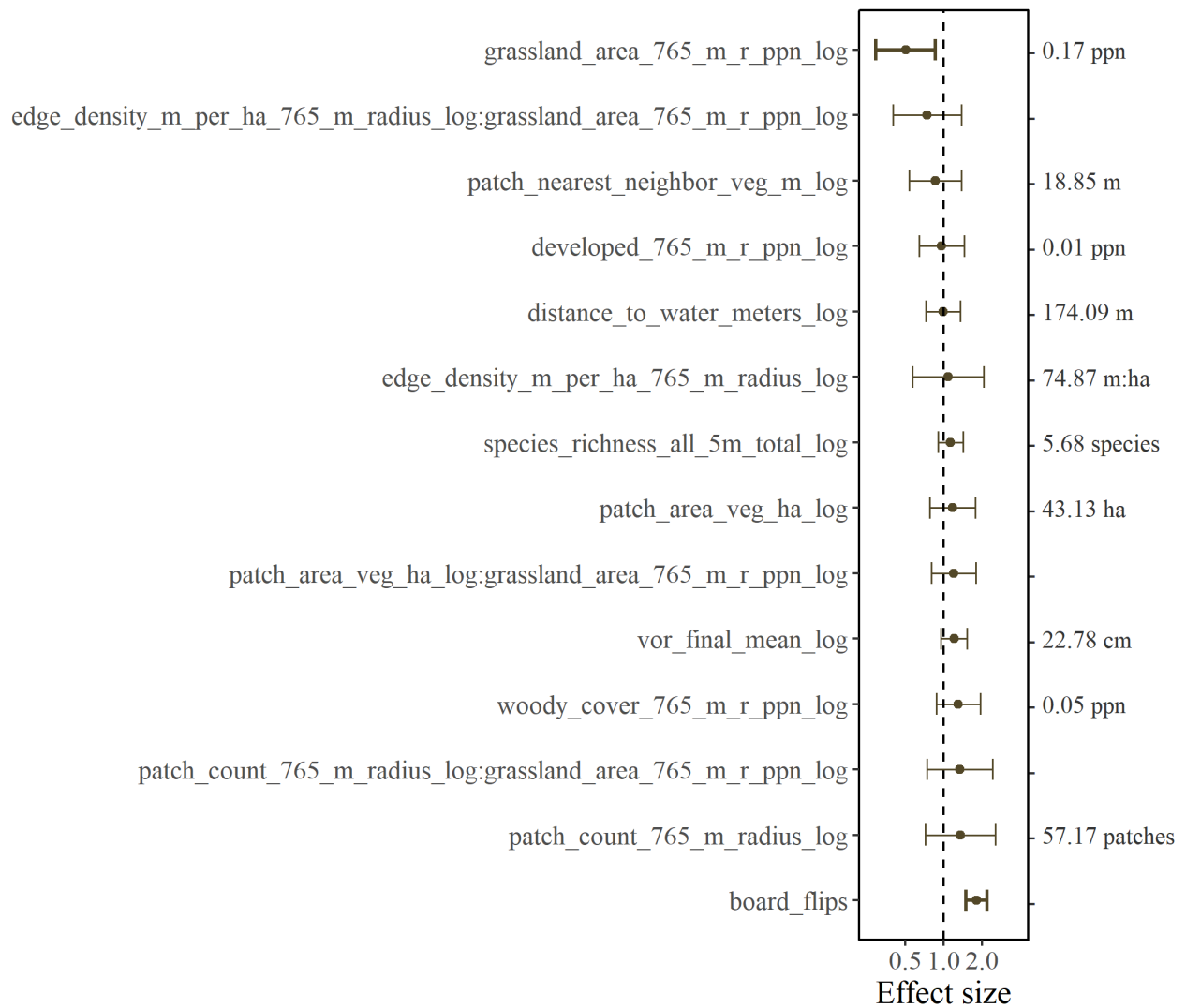


Figure S4-2. Western fox snake presence effect sizes expressed as odds ratios with 90% confidence intervals. Bolded confidence intervals do not cross one and are significant at  $\alpha = 0.1$ . A one standard deviation change (right axis) in the predictor variable multiplied the odds of apparent occupancy by the indicated amount. Standard deviations not listed for interaction terms. Descriptions of variables are provided in Table 4-3.

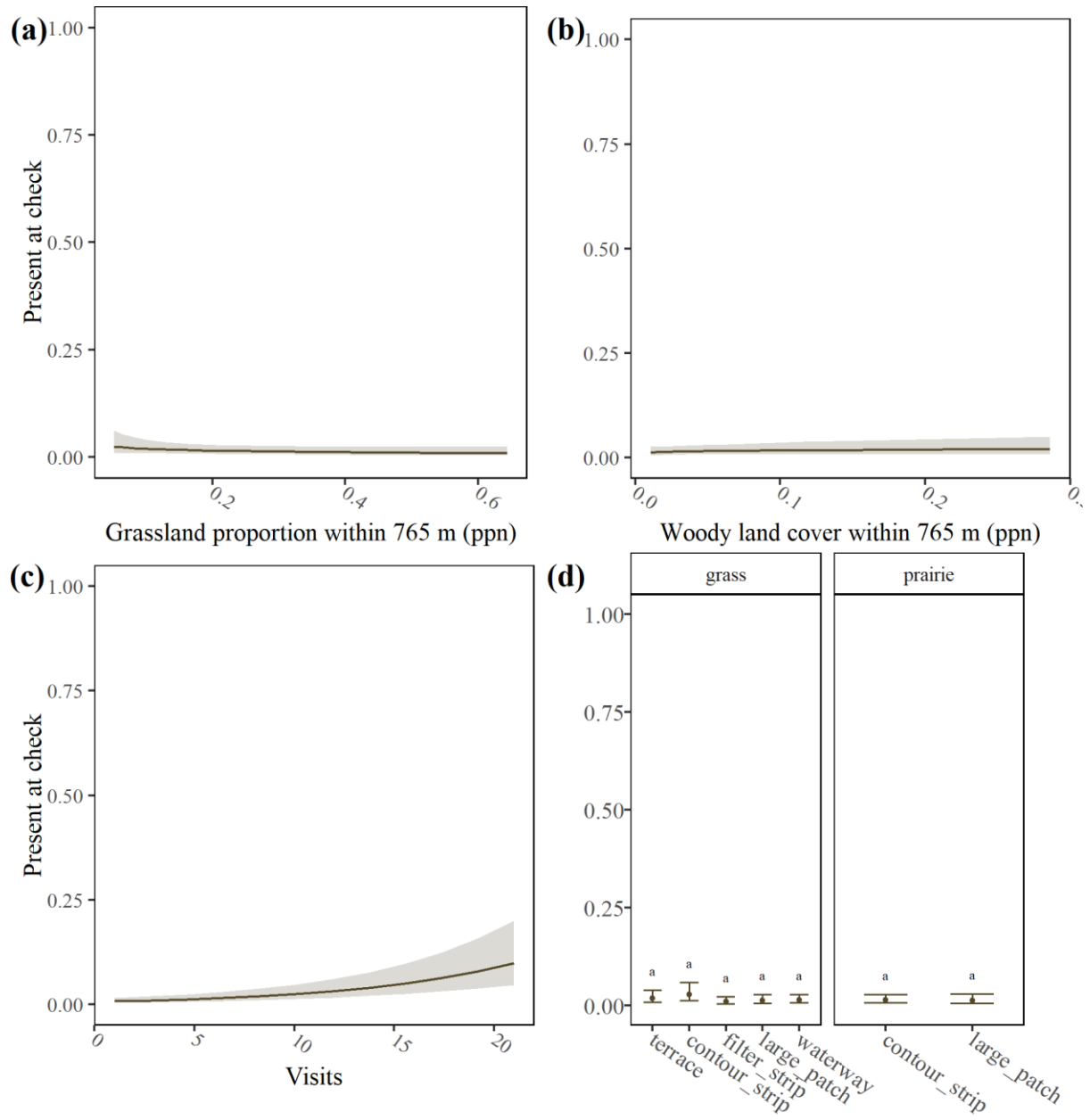


Figure S4-3. Western fox snake board-year presence predicted by (a) grass land cover within 765 m, (b) woody land cover within 765 m, (c) visual obstruction as a correlate of vegetation density, (d) plant species richness, (e) time of day, and (f) by conservation practice. 90% prediction intervals are indicated by the shaded area (a-e) and whiskers (f). Groups that do not share letters are significantly different at  $\alpha = 0.1$  (f).

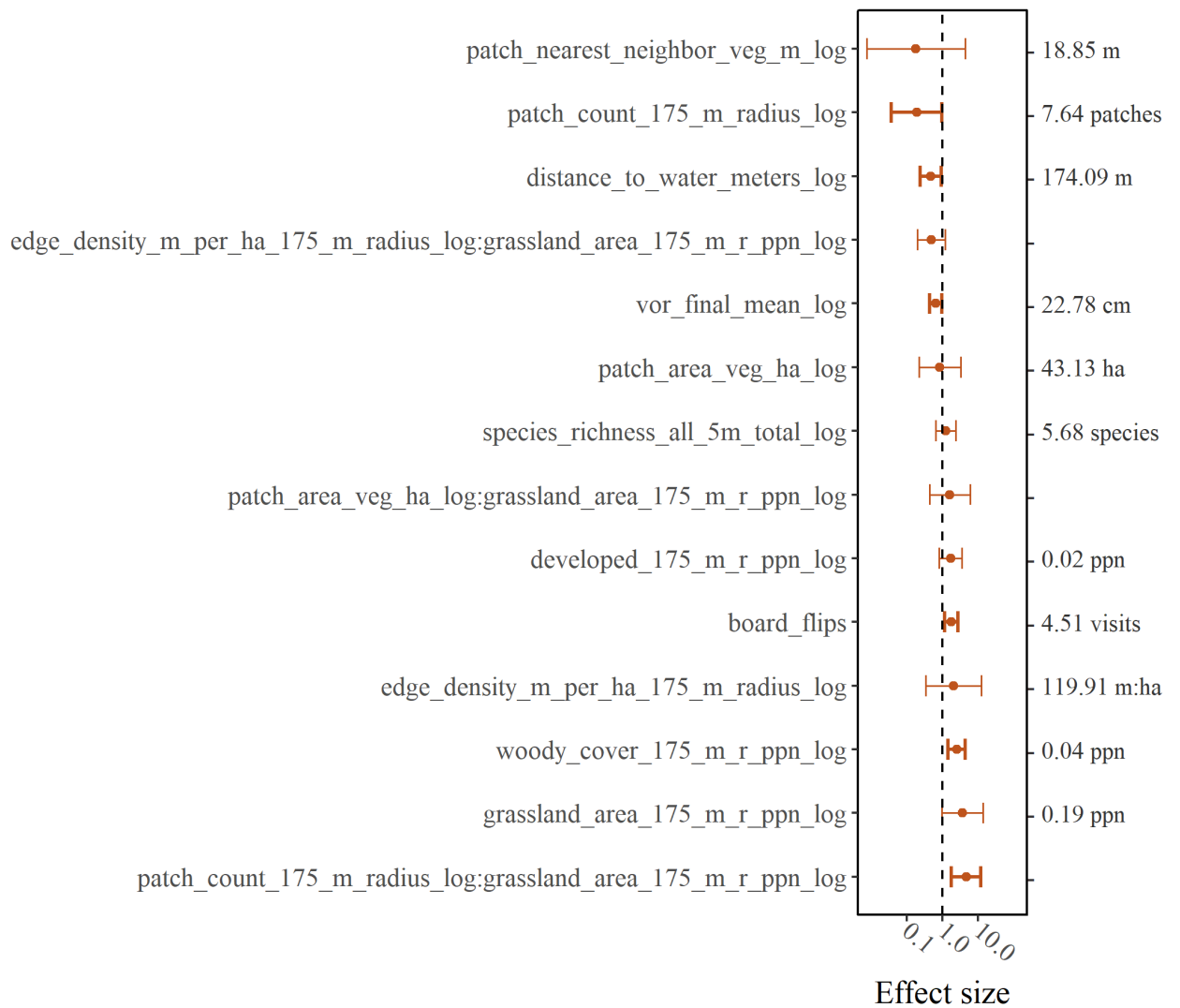


Figure S4-4. Ringneck snake presence effect sizes expressed as odds ratios with 90% confidence intervals. Bolded confidence intervals do not cross one and are significant at  $\alpha = 0.1$ . A one standard deviation change (right axis) in the predictor variable multiplied the odds of presence by the indicated amount. Standard deviations not listed for interaction terms. Descriptions of variables are provided in Table 4-3.

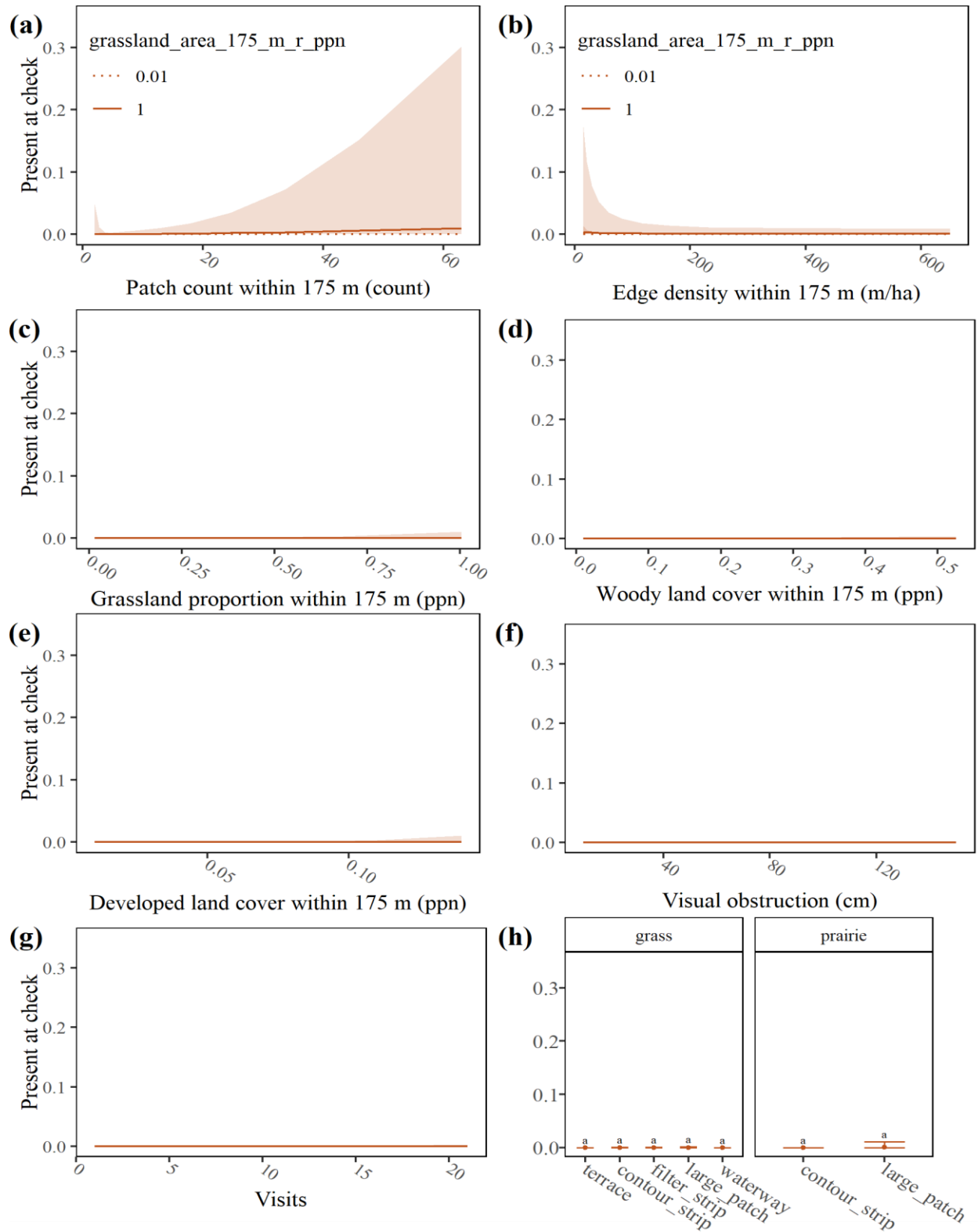


Figure S4-5. Ringneck snake board-year presence predicted by (a) patch count within 175 m, (b) edge density within 175 m, (c) grassland habitat amount within 175 m, (d) woody land cover

within 175 m, (e) developed land cover within 175 m, (f) visual obstruction as a correlate of vegetation density, (g) number of board visits, and (h) by conservation practice. 90% prediction intervals are indicated by the shaded area (a-g) and whiskers (h). Groups that do not share letters are significantly different at  $\alpha = 0.1$  (h).

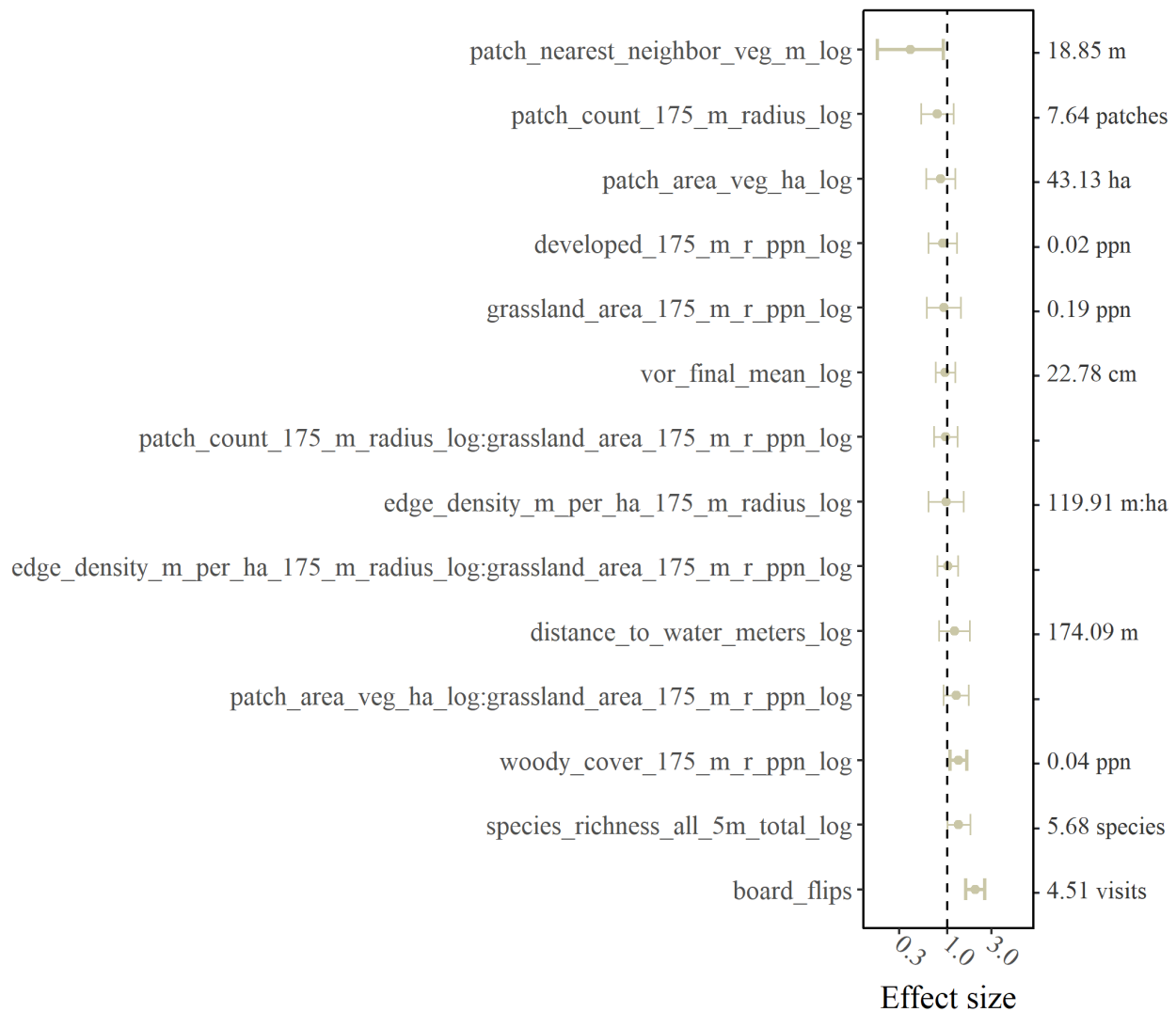


Figure S4-6. DeKay's brown snake presence effect sizes expressed as odds ratios with 90% confidence intervals. Bolded confidence intervals do not cross one and are significant at  $\alpha = 0.1$ . A one standard deviation change (right axis) in the predictor variable multiplied the odds of apparent occupancy by the indicated amount. Standard deviations not listed for interaction terms. Descriptions of variables are provided in Table 4-3.

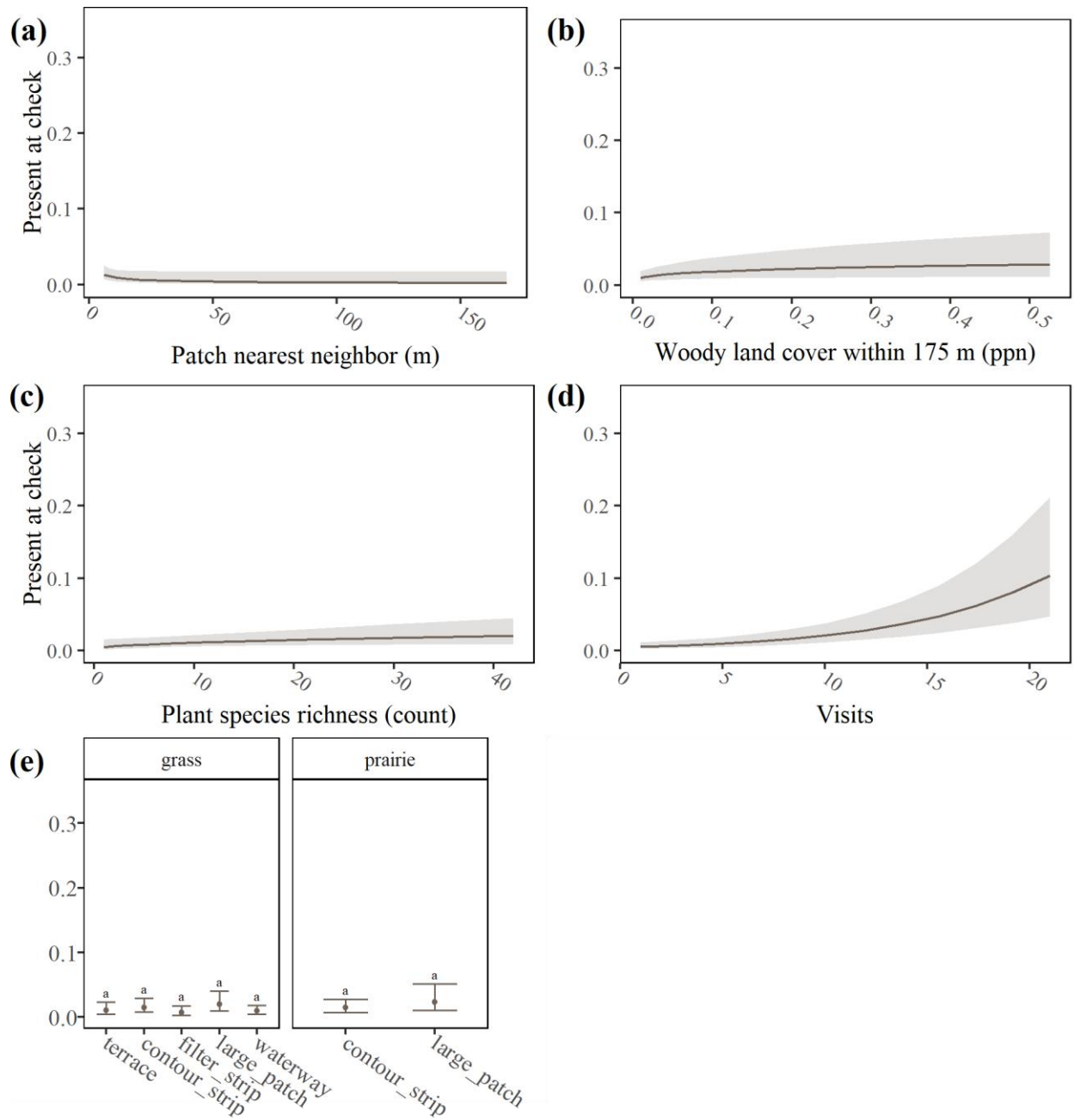


Figure S4-7. DeKay's brown snake board-year presence predicted by (a) patch nearest neighbor, (b) woody land cover within 175 m, (c) vegetation diversity, (d) number of board visits, and (e) by conservation practice. 90% prediction intervals are indicated by the shaded area (a-d) and whiskers (e). Groups that do not share letters are significantly different at  $\alpha = 0.1$  (e).

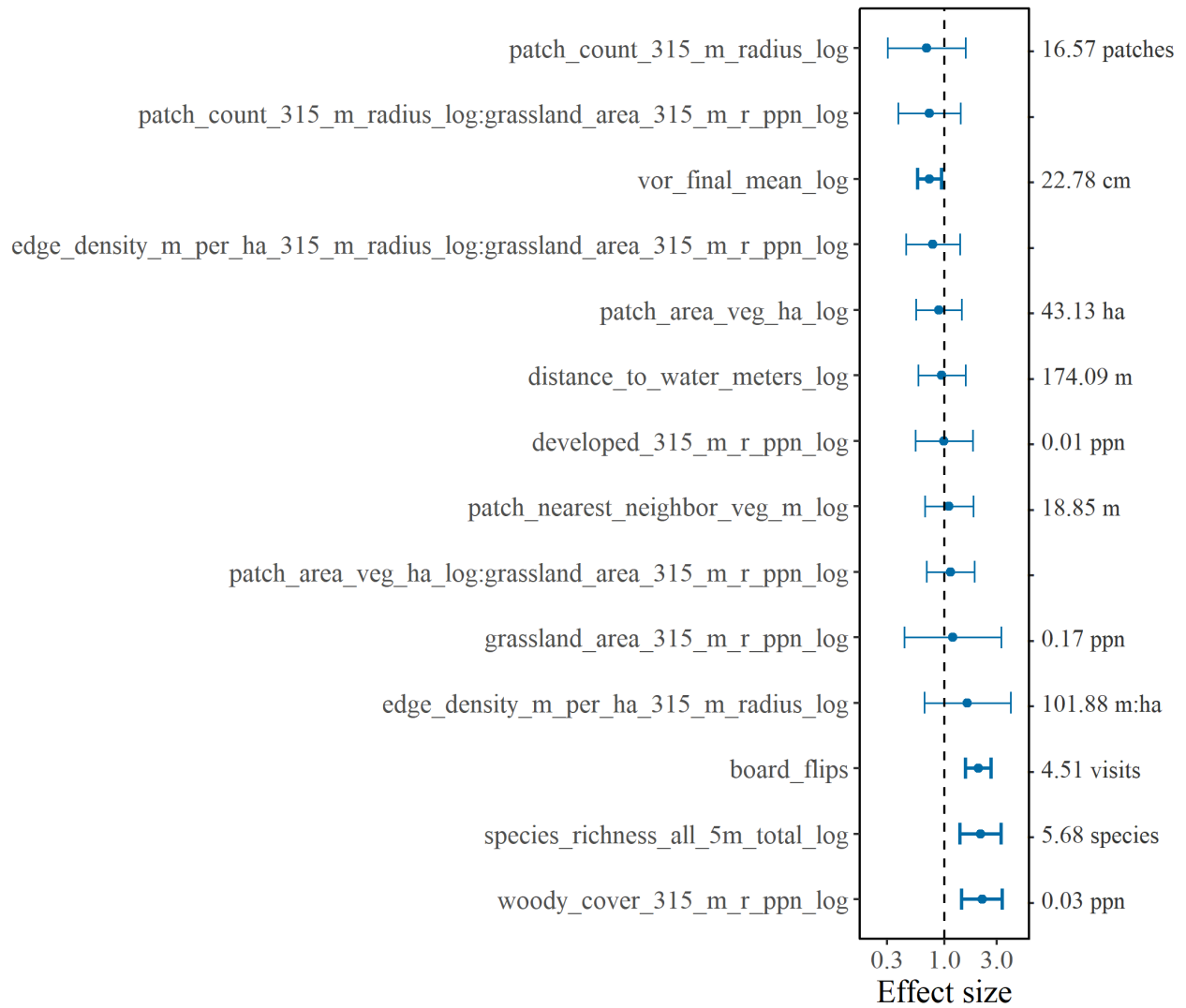


Figure S4-8. Prairie skink presence effect sizes expressed as odds ratios with 90% confidence intervals. Bolded confidence intervals do not cross one and are significant at  $\alpha = 0.1$ . A one standard deviation change (right axis) in the predictor variable multiplied the odds of apparent occupancy by the indicated amount. Standard deviations not listed for interaction terms.

Descriptions of variables are provided in Table 4-3.



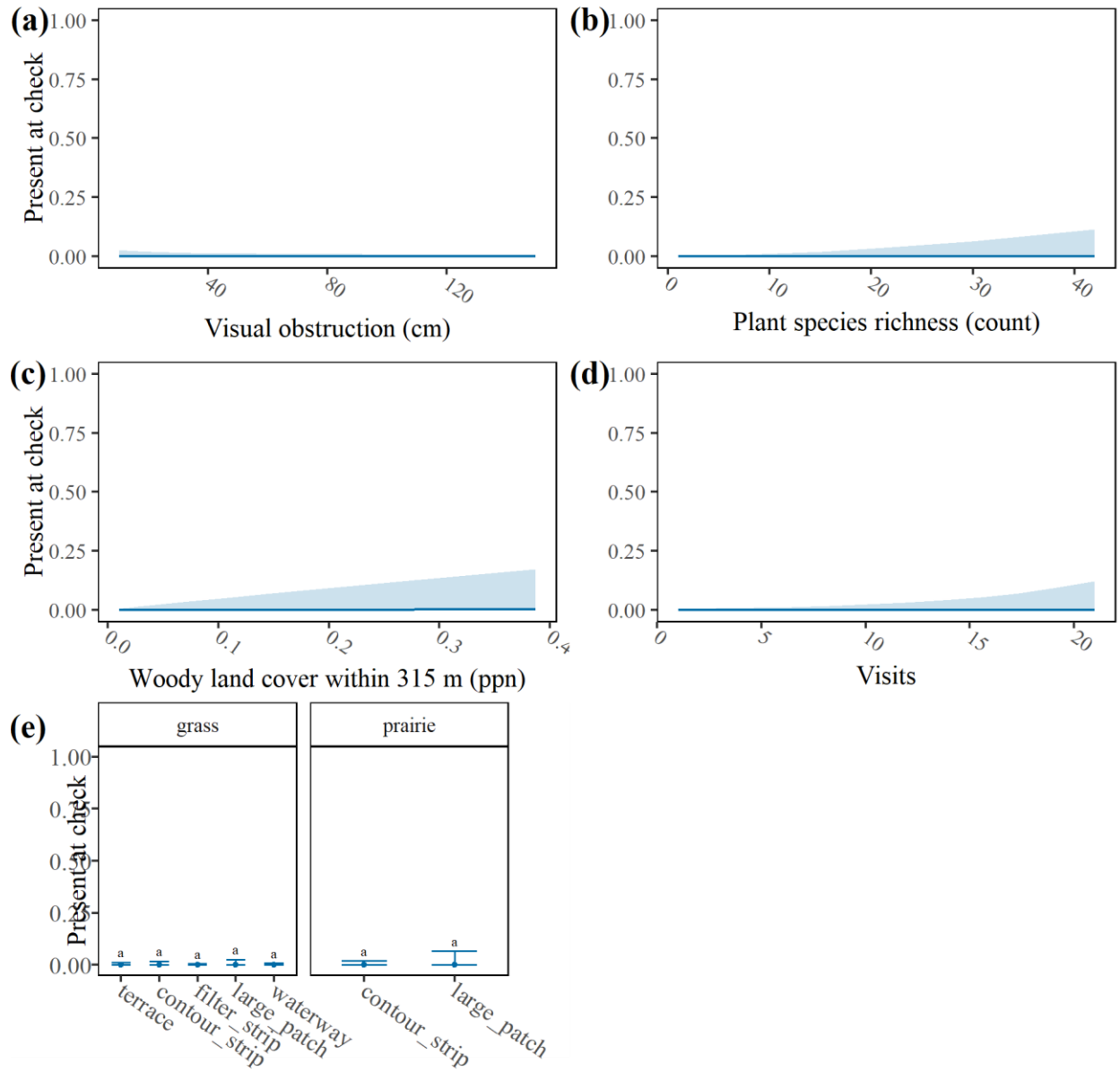


Figure S4-9. Prairie skink board-year presence predicted by (a) grass land cover within 315 m, (b) woody land cover within 315 m, (c) visual obstruction as a correlate of vegetation density, (d) plant species richness, (e) time of day, and (f) by conservation practice. 90% prediction intervals are indicated by the shaded area (a-e) and whiskers (f). Groups that do not share letters are significantly different at  $\alpha = 0.1$  (f).

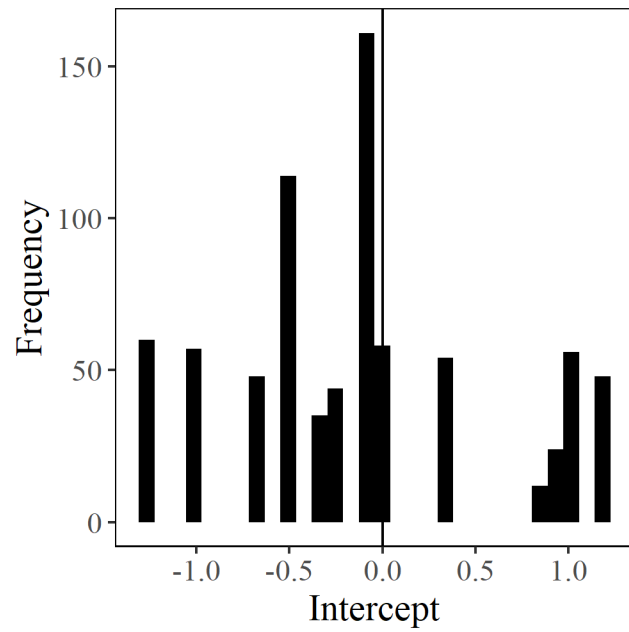


Figure S4-10. Distribution of residuals from 'site' random effect for snakes as a family.

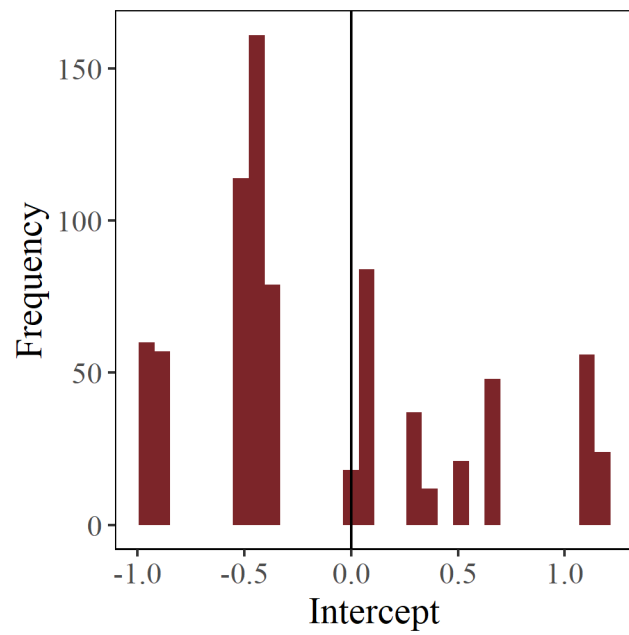


Figure S4-11. Distribution of residuals from 'site' random effect for common garter snakes.

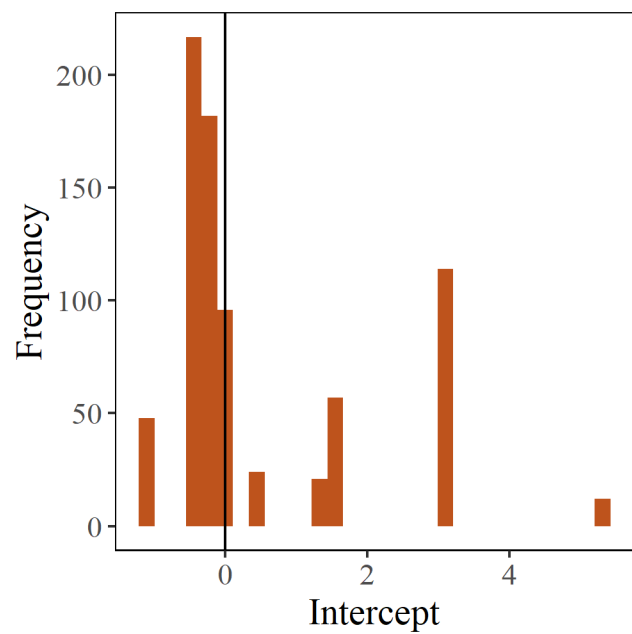


Figure S4-12. Distribution of residuals from 'site' random effect for prairie ringneck snakes.

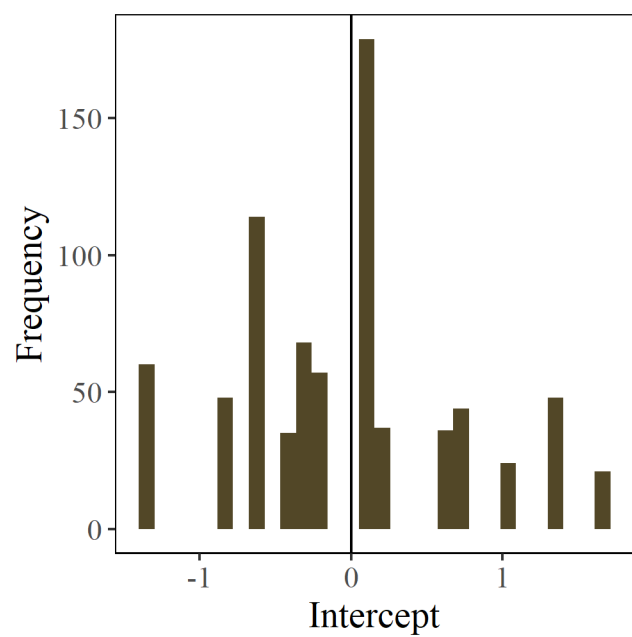


Figure S4-13. Distribution of residuals from 'site' random effect for western fox snakes.

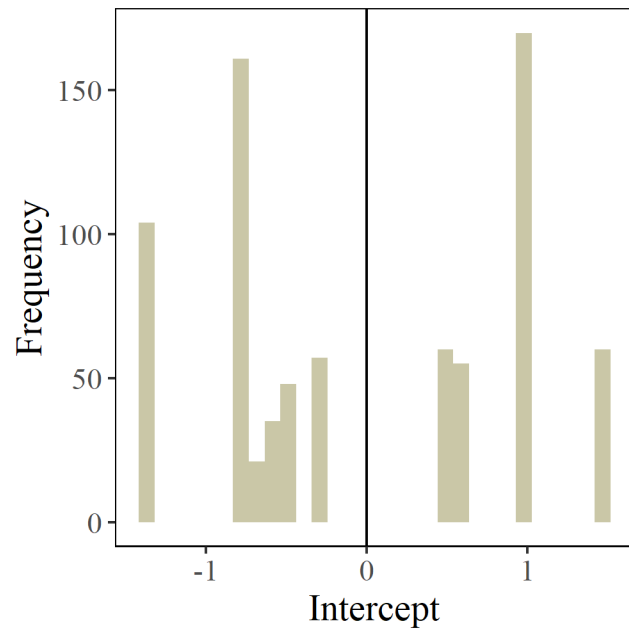


Figure S4-14. Distribution of residuals from 'site' random effect for DeKay's brown snakes.

## CHAPTER 5. GENERAL CONCLUSION

Grassland habitat and the species that depend on it have been undergoing major declines worldwide, including in North America. The North American tallgrass prairie produced deep, rich soil that supported highly productive crops, which led to a systematic conversion to agricultural land after Euro-American colonization. This land use change has contributed to population declines in 74% of grassland bird species and increased threat of extinction for 12% of Palearctic reptile species. There is a recent debate in landscape ecology about the relative importance of habitat area and configuration, and little is known about the contribution of vegetation diversity to habitat quality for vertebrates. In this dissertation I (1) tested an extension of the Habitat Amount Hypothesis to nest density and survival of grassland breeding passerines, (2) compared effect sizes of habitat area, habitat configuration, and vegetation diversity on habitat quality in agricultural landscapes, (3) evaluated three existing hypotheses and two new hypotheses to determine how the configuration and location of agricultural conservation practices affect grassland bird nest parasitism by brown-headed cowbirds (*Molothrus ater*), and (4) compared how habitat area, habitat configuration, and vegetation diversity affect the occupancy, presence, and biodiversity of snakes and lizards in agricultural landscapes in Iowa, USA.

Twenty-nine species of birds nested in the study landscapes, including species from order Passeriformes (n = 21), Charadriiformes (n = 3), Galliformes (n = 3), Anseriformes (n = 1), and Columbiformes (n = 1) and 10 species listed as Iowa Species of Greatest Conservation Need. We categorized species as grassland nesting (n = 18) or tree/shrub nesting (n = 11). Red-winged blackbird (*Agelaius phoeniceus*) nest density was predicted by amount of nearby woody land cover (–), distance from water body (–), annual drought conditions (–), landscape patch count

(+), and an interaction between grass land cover amount and landscape edge density (+). Nest survival was predicted by vegetation density (+), an interaction between mowing intensity and vegetation diversity (–), patch area (+), and interactions between grass land cover amount and landscape edge density (+) and distance to crop (–). Dickcissel (*Spiza americana*) nest density was predicted by mowing intensity (–), vegetation diversity (+), and grass land cover amount interacting with landscape edge density (+). Nest survival was predicted by mowing intensity (–), patch area (+), landscape patch count (–), landscape edge density (+), grass land cover amount (+), and an interaction between grass land cover amount and distance to crop (+). Nest density and survival estimates were not informative for any other single species, but for grassland passerines as a guild nest density was predicted (effect direction +/–) by amount of nearby woody land cover (–), number of patches on the landscape (+), vegetation density (+) and diversity (+), and an interaction between nearby grass land cover amount and landscape edge density (+). Nest survival was predicted by mowing (–), vegetation density (+) and diversity (+) with an interaction between diversity and mowing activity (–) and interactions between grass land cover amount and landscape patch count (–) and landscape edge density (+).

In contrast to the predictions I made extending the HAH to demographic parameters, after measuring fragmentation effects on the landscape scale and correcting for landscape habitat amount, configuration was still an important predictor of habitat quality. This study provides evidence that grassland bird nesting habitat is affected by vegetation diversity, habitat configuration, and habitat amount in agricultural landscapes.

The environmental variables that most influenced brown-headed cowbird nest parasitism rates included main effects for nest initiation day-of-season (–) and the landscape variables of distance to nearest crop edge (–) and proportion of nearby grass land cover (–). In contrast to

previous research, I found little support for variables measuring perch proximity or nest exposure and little evidence that native vegetation diversity affected parasitism. I also assessed nest parasitism likelihood by conservation practice and found no significant differences, but parasitism rates trended higher in the narrower practices. These results provide evidence to support the edge effect hypothesis and HAH, but not the nest exposure, native vegetation diversity, or perch proximity hypotheses.

We also monitored cover board artificial cover objects for the presence of snakes and lizards. We visited cover boards 16,441 times and found very low species-wise encounter rates. Nine of 11 species encountered were state Species of Greatest Conservation Need, comprising 54.2% of encounters. Rarefied snake and lizard species richness was highest for prairie and grass large patches, lowest in grass terraces, and intermediary in other conservation practices.

Mean detection-corrected occupancy estimates by patch for common garter snakes was 0.18 (0.03 – 0.79, SD = 0.13). Occupancy and naïve presence estimates were not well estimated for any other single species, but occupancy for all snake species combined was 0.45 (0.23 – 0.90, SD = 0.12). I found that naïve presence of all snake species combined was best explained by survey effort (+), vegetation diversity (+) and density (–), developed (–) and woody (–) land cover amount, and edge density (–) and patch size (+) interacting with grassland land cover proportion. However, most effect sizes were very weak and only edge density, patch area, vegetation diversity, and survey effort had biologically meaningful effects. Common garter snake naïve presence was influenced by survey effort (+), vegetation density (–) and diversity (+), distance from water (–), edge density (–) and its interaction with grassland land cover amount (–), and woody land cover amount on the landscape (+); however, only edge density, grassland land cover proportion on the landscape, and survey effort had biological meaningful

effects on presence. Large patch prairie conservation practices were more likely to contain snakes than any other conservation practice, and more likely to contain common garter snakes than prairie contour strips, grass contour strips, grass waterways, or grass terraces. Overall, I found that snake diversity and presence in highly agricultural Midwestern landscapes was low, but many species with urgent conservation need were present.

Together, these tests extending the HAH to demographic parameters and individual species occurrence consistently failed to show an effect of habitat amount in the absence of a habitat configuration variable. Each of my analyses included habitat amount interacting with habitat configuration and each time at least one of those interaction terms was an important predictor. This underscores the complexity of landscape ecological processes where configuration not only matters, but can have different effects depending on the amount of habitat on the landscape.

As outlined in previous chapters, the effect of vegetation diversity on demographic parameters has received little research attention. Somewhat surprisingly, then, I found that vegetation diversity was commonly among the best predictors of a species' presence, breeding density, or reproductive success. Additionally, vegetation diversity and density often had similar effect sizes to habitat amount and configuration, which have received orders of magnitude more research attention.

### **Management Implications**

When comparing demographic parameters between conservation practices, grass contour strips and grassed terraces had very low reproductive success rates for grassland nesting passerines that probably indicated they were population sinks and, in some landscapes, could also function as ecological traps when birds do not preferentially nest in higher-quality habitat. Additionally, I found that prairie contour strips appear to be of similar breeding habitat quality as



larger patches of restored prairie. When comparing the nest survival rates observed in prairie strips and large (40 – 60 ha) patches of prairie to published studies that attempted to determine at what nest survival rate a patch became a population sink, the highest rates we observed fell within a range where a population sink was possible. This is alarming, given the huge majority of grassland patches in Iowa are smaller and of lower vegetative diversity than the large prairie restorations we used as our benchmark. More studies of source-sink dynamics that provide benchmark demographic rates are needed to confidently assess source-sink habitat in regional landscapes comprised almost entirely of small, isolated, high-edge patches.

Because predation was the major cause of nest failure, it is probable that differences in predator species presence and/or behavior could account for differences in nest survival between conservation practices. For instance, snakes, including those that predate nests, were less common in high-edge landscapes such as those containing prairie strips, potentially removing one source of nest failure. The absence of large-bodied snakes may have then been offset by a relative increase in predation pressure from another guild of nest predators, given that nest survival in prairie strips was not higher than rates estimated for larger prairies. More study is needed on the composition and relative effectiveness of nest predators in these two landscapes.

Due to lower nest survival in low-diversity linear conservation practices, absence of area-sensitive birds in small conservation practices, and relative absence of snakes and lizards in small conservation practices, the most efficient wildlife conservation practice I studied was large-patch, high-diversity prairie restorations. In situations where landowners or conservation planners use linear conservation practices to meet other conservation goals, linear strips of prairie vegetation did not commonly host snakes, but did serve as suitable grassland passerine nesting habitat.