

Behavioral and reproductive consequences of predator activity to grassland birds

THESIS

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## Abstract

Grassland birds are declining at greater rates than any other habitat guild in North America, yet conservation remains difficult due to extensive habitat loss and fragmentation throughout the urbanizing Midwest. Although urban green spaces can contribute to habitat conservation, fragmentation and high land acquisition costs typically limit these spaces to small fragments subjected to strong external pressure from humans. Human presence is often associated with non-native predators (e.g., cats) and anthropogenic food sources, which collectively can promote high densities of nest predators in urban landscapes. From a conservation perspective, high densities of nest predators are a concern because predation is the leading source of nest failure. Behavioral responses to predators may further diminish the value of urban habitats if birds avoid areas with high levels of predator activity, which could result in lower occupancy rates or densities of birds in urban habitat patches. In my research, I examined how habitat heterogeneity and variation in the predator community influenced the breeding ecology of grassland and early successional birds in urban parks. To understand these relationships, I asked two broad questions: (1) how do birds respond behaviorally (e.g. territory and nest-site selection) to abundance and activity of predators in urban natural areas? (2) to what extent is avian reproductive success linked to predator

communities and/or activity at plot and site scales? To answer these questions, I collected data on avian density, nest placement, and reproductive success of grassland birds within 46 2-ha plots at seven urban parks (sites) near Chicago, Illinois, during 2009 and 2010. Focal species included Common Yellowthroat (*Geothlypis trichas*), Field Sparrow (*Spizella pusilla*), Song Sparrow (*Melospiza melodia*), Savannah Sparrow (*Passerculus sandwichensis*), Henslow's Sparrow (*Ammodramus henslowii*), Bobolink (*Dolichonyx oryzivorus*), Eastern Meadowlark (*Sturnella magna*), and Dickcissel (*Spiza americana*). Relative abundance and activity levels of potential nest predator species, including mesopredators (e.g., northern raccoons [*Procyon lotor*], domestic cats [*Felis catus*]), small mammals, snakes, and avian predators, were estimated for each plot during surveys and as part of a collaborative study.

I found that, in general, territory densities were negatively related to predator activity within 2-ha plots, though associations varied across species. As capture rates of small mammals increased, territory densities of Field Sparrow, Common Yellowthroat, and Savannah Sparrow declined, but density of Song Sparrow rose. Mesopredator capture rates were negatively associated with Common Yellowthroat and Savannah Sparrow densities within 2-ha plots, as well as Eastern Meadowlark and total territory density at the site level. Whereas small mammal and mesopredator capture rates explained some of the observed variation in territory density, daily nest survival of both Field and Song Sparrows was best explained by numbers of snakes observed within plots. Interestingly, snake activity was positively associated with nest survival of Field Sparrows, though negatively associated with that of Song Sparrows. At large scales,

vegetation characteristics best predicted nest survival of both species, with nest survival of Field Sparrow improving as density of groundcover increased and nest survival of Song Sparrow improving as structural complexity increased. While the structural complexity of vegetation at nest sites was not explained by predator activity, Song Sparrows selected nest sites with lower groundcover density than available as activity of Brown-headed Cowbird (*Molothrus ater*) increased. As a whole, these results provide evidence that breeding grassland and early successional birds respond to both habitat structure and activity of potential predators at different scales. I also found that behavioral (e.g., territory selection) and demographic (e.g., nest survival) associations with predators do not necessarily match. For example, snakes had the strongest, though sometimes counterintuitive, relationship with nest success of Field and Song Sparrows, yet appeared to elicit no response during territory or nest site selection. My results are also consistent with other studies demonstrating the importance of vegetation structure to both settlement and reproductive success. Consequently, the best management practices in urban parks will both maintain vegetation structure that promotes successful nesting and discourage activities that promote high abundances of predators.

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## Dedication

To my parents, who encouraged outdoor learning of all kinds, and to my aunt Terri McCarthy, who has extended countless opportunities to expand my knowledge and experiences in the field.



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## Fields of Study

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## Table of Contents

<b>Abstract.....</b>	<b>ii</b>
<b>Acknowledgements .....</b>	<b>v</b>
<b>Dedication .....</b>	<b>vii</b>
<b>Vita .....</b>	<b>viii</b>
<b>Table of Contents .....</b>	<b>x</b>
<b>List of Tables .....</b>	<b>xiii</b>
<b>List of Figures.....</b>	<b>xv</b>
<b>Chapter 1: Behavioral and demographic responses of birds to predators: literature review .....</b>	<b>1</b>
Introduction .....	1
Objectives.....	3
Thesis format.....	4
Background .....	4
Avian responses to predators.....	4
Predators of grassland birds.....	7
Cats as a mesopredator of concern .....	18
Literature Cited .....	23
<b>Chapter 2: Linking grassland bird density to predator activity in urban parks.....</b>	<b>42</b>

Abstract .....	42
Introduction .....	43
Methods.....	46
Analysis .....	50
Results .....	56
Discussion .....	59
Literature Cited .....	80
<b>Chapter 3: Behavioral and demographic responses of breeding openland birds to predator activity and vegetation.....</b>	<b>88</b>
Abstract .....	88
Introduction .....	89
Methods.....	92
Analysis .....	96
Results .....	105
Discussion .....	107
Literature Cited .....	123
Bibliography.....	130
Appendix A: Study site maps and layout description .....	155

Appendix B: Results from principal components analysis on randomly available vegetation characteristics .....	163
Appendix C: Summary of vegetation characteristics at both randomly located and nest sites .....	166
Appendix D: Summary of avian species observed on surveys at each site.....	171
Appendix E: Summary of predator activity observed at each plot.....	177
Appendix F: Territory density models at the plot level for the five most common species .....	181
Appendix G: Territory density models at the site level for the five most common species .....	185
Appendix H: Daily survival rate models of the Field Sparrow and Song Sparrow at the plot level .....	189
Appendix I: Daily survival rate models of the Field Sparrow and Song Sparrow at the site level.....	192

## List of Tables

Table 2.1. Summary of study sites.....	65
Table 2.2. Plot-level results for principal components analysis performed on vegetation characteristics measured at random locations, including eigenvalues, proportion of variance, and loadings for the first two principal components. ....	66
Table 2.3. Constructing the base model, stage one.....	67
Table 2.4. Constructing the base model, stage two.....	68
Table 2.5. Proportion of species comprising each predator guild at each site.....	69
Table 2.6. Correlation matrix of predators and plot and site scale .....	70
Table 2.7. Summary of mean ( $\mu$ ) and standard error (SE) of avian territory densities at each site for the eight focal species.....	711
Table 2.8. Territory density models for plot-level densities of the five most common species in the study system .....	73
Table 2.9. Territory density models for site-level densities of the five most common species in the study system.. .....	74
Table 3.1. Creation of the base model for ranking daily survival rates at the plot and site level.....	113
Table 3.2. Eigenvalues, proportion of variance, and loadings for the first two principal components on nest site and random vegetation at the plot level. ....	114

Table 3.3. Creation of the base model for ranking the difference between random and nest groundcover density for Field Sparrow and Song Sparrow.....	115
Table 3.4. Summary of the number of nests found on each plot during 2009 and 2010, including daily survival rates (DSR) for plots with at least two nests.....	116
Table 3.5. Daily survival rate (DSR) models for DSR of Field Sparrow and Song Sparrow at both the plot and site scales. ....	117
Table 3.6. Nest site selection models for predicting the difference between density of available groundcover and groundcover at nest sites. ....	118
Table 3.7. Nest site selection models for predicting the difference between structural complexity at random locations and complexity at nest sites. ....	119

## List of Figures

Figure 2.1. Overview of site locations in Cook, Kane, and McHenry counties, IL.....	75
Figure 2.2. Example of results from interpolating capture rates at Glacial Park.....	76
Figure 2.3. Interpreting principal components at the plot scale: (a) biplot of first two principal components as originally calculated and (b) illustration of the habitat gradient represented by the first two components, after transforming (i.e. reversing) PC2 (groundcover density) loadings.....	77
Figure 2.4. Graph of plot-level relationships between territory density and predator activity for which confidence intervals do not overlap zero.....	78
Figure 2.5. Graph of site-level relationships between territory density and predator activity for which confidence intervals do not overlap zero.....	79
Figure 3.1. Results of principal components analysis conducted on vegetation characteristics from both randomly located and nest sites.....	120
Figure 3.2. Graph shows how random groundcover density and groundcover density at Field Sparrow nest sites change with increasing mesopredator capture rates. ....	121
Figure 3.3. Graph shows how random structural complexity and structural complexity at Song Sparrow nest sites change with increasing cowbird encounter rates, i.e. activity..	122



## CHAPTER 1

### **Introduction**

Grassland bird populations have been declining for over three decades (Peterjohn and Sauer 1999). As habitat loss is a major contributor to their declines (Brennan and Kuvlesky 2005), the current expansion of cities into natural areas threatens our ability to conserve these imperiled species. Urban green spaces therefore have the potential to be important contributors to habitat conservation (Schwartz 1999, Miller and Hobbs 2002). Often, however, fragmented landscapes and high costs of land acquisition limit conservation to relatively small areas (Miller and Hobbs 2002). Ecosystem dynamics within these small fragments are driven to a great extent by external pressure from human activities that modify the mosaic of land uses surrounding fragments, alter resource availability, introduce non-native species, and change species interactions (Janzen 1983, Saunders *et al.* 1991). Collectively, these human actions alter wildlife communities in ways that can seriously impact breeding birds (Baker *et al.* 2005, Beckerman *et al.* 2007).

Breeding birds may be strongly affected by human activities that promote high densities of nest predators, particularly of mesopredators that represent the mid-ranking predators within a food chain (Prugh *et al.* 2009). Mesopredators might rise in numbers if apex predators are eliminated from the system, which can release mesopredators from competition and/or predation (Prugh *et al.* 2009, Ritchie and Johnson 2009, Letnic *et al.*

2011). Despite limited empirical evidence, this “mesopredator release” has been implicated as the driver of reduced nest success (Sovada *et al.* 1995, Rogers and Caro 1998), lower species richness (Crooks and Soulè 1999), and even local extinctions of prey shared by apex and mesopredators (Courchamp *et al.* 1999). Humans also can promote high numbers of mesopredators by introducing non-native species (e.g., cats, *Felis catus*) and by provisioning resources that may support high densities of mesopredators (e.g., Prange *et al.* 2003, Chace and Walsh 2006, Withey and Marzluff 2009). Many common nest predators, such as northern raccoon (*Procyon lotor*), American Crow (*Corvus brachyrhynchos*), Blue Jay (*Cyanocitta cristata*), tree squirrels (*Sciurus* sp.) and ground squirrels (*Spermophilus tridecemlineatus*), are omnivorous generalists that regularly consume anthropogenic food sources (Bailey 1923, Bowers and Breland 1996, Marzluff and Neatherlin 2006, Bozek *et al.* 2007). Numerous studies have demonstrated that urban areas support greater densities of many generalist species known to be important avian nest predators, especially cats, raccoons, and corvids (e.g., Haskell *et al.* 2001, Sorace 2002, Chace and Walsh 2006, Rodewald *et al.* 2011).

High densities of nest predators are a legitimate conservation concern because avian reproductive success frequently declines as abundance and/or activity of nest predators rises, as shown in many non-urban landscapes (e.g., Andrén 1992, Cooper and Ginnett 2000, Zarette and Jenkins 2000, Weidinger 2002, but see Rodewald *et al.* 2011). In particular, cat predation on birds can be strong (Churcher and Lawton 1987, Coleman and Temple 1996), and numbers of cats have been linked to both population level (e.g., decreased reproductive productivity; Weggler and Leu 2001, Beckerman *et al.* 2007) and

community level (e.g., declines in bird species richness; Crooks and Soulé 1999, Hawkins *et al.* 1999, Sims *et al.* 2008) consequences. Abundant predators also can have behavioral consequences. Birds can respond directly to predation pressure by altering parental behavior, such as reducing feeding rates or increasing nest defense (Marzluff 1985, Wheelwright and Dorsey 1991), or by avoiding risky areas when selecting territories or nest sites (Forstmeier and Weiss 2004, Fontaine and Martin 2006a). However, the relationship between predator activity and avian breeding ecology within urban systems is only recently being explored. Moreover, virtually no research has experimentally examined relationships between grassland birds and their nest predators in urban systems where food is deliberately provisioned to mesopredators.

## **Objectives**

I examined how human-mediated changes in the predator community might affect interactions between grassland breeding birds and their predators in urban parks. Specifically, I asked: (1) How do birds respond behaviorally (e.g. territory and nest-site selection) to differences in predator abundance and activity in urban natural areas? (2) To what extent is avian reproductive success linked to both activity and/or communities of predators and vegetation characteristics at plot and site scales? I predicted that as numbers or activity of predators increased, I would detect corresponding declines in density of avian territories, as birds would avoid those areas; structural complexity of vegetation at nests, as birds would avoid areas with woody vegetation frequented by many predators; and nest success, as predation rates would rise.

## **Thesis Format**

In the current chapter, I provide a review of behavioral and demographic responses of birds to potential predators. Specifically, I emphasize the relationships that exist in urbanizing landscapes, and examine the role that high densities of mesopredators in urban areas play in altering ecological interactions between birds and their predators. Chapter 2 explores the extent to which predators in urban parks influence territory selection of eight grassland and early successional bird species. The work summarized in Chapter 3 examines how two focal early successional species respond to both habitat structure and the predator community at small (plot) and large (site) scales.

## **Background**

### *Avian responses to predators*

Birds respond to predators over evolutionary and contemporary time scales. High risk of predation can influence life history evolution, resulting in smaller clutch sizes, smaller eggs, (Eggers *et al.* 2006, Fontaine and Martin 2006b, Thomson *et al.* 2006a), or the ability to forgo breeding if risk of predation is too high (Spaans *et al.* 1998, Quakenbush *et al.* 2004). In addition, high nest predation is also associated with a greater number of broods per season and shorter nestling period (Martin 1995).

Behavioral antipredator strategies also develop over evolutionary and contemporary time scales. Given that predation accounts for most nest failures (Ricklefs 1969, Martin 1993a), choice of nesting substrates and placement of nests are expected to

reflect predation pressure (Martin 1993b, Blanco and Bertellotti 2002). Individually, birds also can assess predation risk via visual, olfactory, and auditory cues, and use this information in territory and nest site selection (Hakkarainen *et al.* 2001, Peluc *et al.* 2008, Amo *et al.* 2008). Information can take the form of direct assessments of predator activity, presence of conspecifics, presence of fledglings observed during post-breeding prospecting efforts, and environmental attributes known to reduce risk of predation (Fontaine and Martin 2006a, Nocera 2006, Parejo *et al.* 2007, Chalfoun and Martin 2009, Harrison *et al.* 2009). Empirical studies have shown that birds will choose territories with lower predator activity or abundance than nearby sites (Schmidt *et al.* 2006, Fontaine and Martin 2006a, Morosinotto *et al.* 2010). Birds also may select safer nest sites where perceived predation risk is high; these nests may be at different heights, distances to woody vegetation, or in different cover types than nests in low-risk areas, depending upon the predator type and plasticity of the bird species (Wiebe and Martin 1998, Forstmeier and Weiss 2004, Eggers *et al.* 2006). Additionally, birds respond directly to nesting success. Adults experiencing nest depredation may respond by selecting a different nesting site within the season (Dow and Fredga 1983, Greig-Smith 1982) or a different territory altogether the following year (Gavin and Bollinger 1988, Haas 1998, Doligez *et al.* 1999). In addition, actual or perceived nesting success of conspecifics may influence territory selection, as demonstrated experimentally with Prothonotary Warblers (*Protonotaria citrea*, Hoover 2003) and Black-throated Blue Warblers (*Dendroica caerulescens*, Betts *et al.* 2008).

Predation risk can also affect parental behavior. Interspecific variation in passerine incubation likely reflects vulnerability to predation over evolutionary scales, whereby species that are exposed to higher predation take longer bouts on and off the nest to avoid drawing a predator's attention (Conway and Martin 2000). At an individual level, birds may adjust their own parental behavior based on perceived risk of predation. Where predation risk is high, incubating adults may respond by spending more time on the nest, thereby keeping the nest concealed and reducing activity that could attract attention of predators (Weathers and Sullivan 1989, Sasvari and Hegyi 2000), or spend more time defending or foraging close to the nest (Martindale 1982, Marzluff 1985). Adults also might make fewer trips to the nest to feed nestlings, and can terminate feeding nestlings sooner where predation risk is high (Wheelwright and Dorsey 1991, Velando and Marquez 2002). These shifts in parental behavior can have consequences to young. For example, young that fledge from nests under high predation risk are lighter than those fledged from safer nests, likely in part as a result of these reduced feeding rates (Scheuerlein and Gwinner 2006, Thomson *et al.* 2006b).

Avoidance of predators can have repercussions at the community level. For example, lower densities of songbirds and songbird nests are frequently observed where predator densities are high (e.g. Tryjanowski *et al.* 2002, Schmidt *et al.* 2006), and higher densities of breeding birds have been found where predator numbers have been experimentally reduced (Finney *et al.* 2003, Fontaine and Martin 2006a). Changes in bird communities also can occur near centers of predator activity, regardless of predator abundance. Lower abundance and densities of prey species are often recorded near avian

predator nests (e.g. Norrdahl and Korpimaki 1998, Forsman *et al.* 2001, Monkkonen *et al.* 2007, van der Vliet *et al.* 2008), and similar patterns of avoidance occur near centers of mammalian predator activity. Tryjanowski *et al.* (2002) recorded lower densities of avian prey species near active fox dens, while Hawkins *et al.* (1999) found lower abundance of native and ground-feeding birds at sites with high cat activity.

### *Predators of Grassland Birds*

Ground and shrub-nesting birds experience high nest-predation (Martin 1993a) from a diverse suite of predators (Renfrew and Ribic 2003, Thompson and Burhans 2003, Cervantes-Cornihis 2009). Predator abundance varies spatially, creating a matrix with varying levels of predation risk (Heske 1995, Schmidt *et al.* 2006). It is not surprising, then, that the top nest predators in grasslands and shrublands differ among studies. Regular nest predators include snakes (Morrison and Bolger 2002, Thompson and Burhans 2003, Klug *et al.* 2010), small mammals (e.g., thirteen-lined ground squirrel [*Peromyscus sp.*], Eastern chipmunk [*Tamias striatus*]) (Tewksbury *et al.* 1998, Schmidt and Ostfeld 2003, Renfrew *et al.* 2005), birds (e.g. Red-tailed hawk [*Buteo jamaicensis*], Cooper's hawk [*Accipiter cooperii*], Brown-headed Cowbird [*Molothrus ater*]) (Renfrew and Ribic 2003, Stake and Cimprich 2003), and mesopredators (e.g. raccoon, striped skunk [*Mephitis mephitis*], Virginia opossum [*Didelphis virginiana*], cat) (Donovan *et al.* 1997, Dijak and Thompson 2000).

*Snakes.* Snakes are often the most frequently observed predators of grassland and shrubland bird nests (Morrison and Bolger 2002, Thompson and Burhans 2003). Snakes

may account for up to 90% of recorded nest predation events in some systems (Morrison and Bolger 2002), while other studies reveal moderate (50-70%; Thompson and Dijk 1999, Stake and Cimprich 2003, Thompson and Burhans 2003) or low rates of snake predation (<5%; Rodewald and Kearns *in press*). In addition to taking eggs and nestlings, snakes have also been observed preying upon incubating females (Stake and Cimprich 2003, Augustine and Sandercock 2011), further illustrating their ability to limit reproductive success. As snake activity and abundance has been linked to grassland bird nest success (Patten and Bolger 2003, Sperry *et al.* 2008), investigating snake behavior and habitat preferences becomes important in understanding nest predation (Weatherhead and Blouin-Demers 2004).

Habitat use and activity patterns differ among snake species that depredate grassland nests (Patten and Bolger 2003, Weatherhead *et al.* 2003). The eastern yellowbelly racer (*Coluber constrictor flaviventris*) and Great Plains rat snake (*Ptherophis emoryi*) preferentially utilize shrubby habitat, using the cover as protection from predators or climbing shrubs to aid in thermoregulation (Wilgers and Horne 2007, Klug *et al.* 2010). Daily nest survival rates for several grassland species are lower near shrubby areas, demonstrating the increased risk of predation near centers of snake activity (Klug *et al.* 2010). Black rat snakes (*Elaphe obsoleta obsoleta*) use open areas more frequently as the season progresses (Durner and Gates 1993), whereas the milk snake (*Lampropeltis triangulum*), fox snake (*Elaphe vulpina vulpine*) and blue racer (*Coluber constrictor foxii*) show a consistent preference for open habitats throughout the spring, summer, and autumn (Keller and Heske 2000, Row and Blouin-Demers 2006).



Most grassland snakes are generalist predators for which birds are a small part of their diet (Klimstra 1959, Rossman *et al.* 1996, Weatherhead *et al.* 2003), but greater predation may occur mid-summer when activity levels peak, increasing the likelihood of encountering nests (Row and Blouin-Demers 2006, Sperry *et al.* 2008).

Grassland-nesting birds encounter a changing community of snake predators across urbanizing landscapes as snakes respond to patch size and edges. Kjos and Litvaitis (2001) examined snake assemblages in a human-dominated landscape and found greater species richness and abundance in large patches. Patches <1.5 ha in size were likely to be devoid of snakes or only contain the generalist garter snake. Snakes in the family Colubridae, constrictors that frequently depredate ground nests, have been found in greater numbers in the interior of reserves than near the edges (Durner and Gates 1993, Patten and Bolger 2003). However, other studies including a wider variety of species show no edge effect in these predators (Keller and Heske 2000, Sullivan 2000, Morrison and Bolger 2002). The hypothesis that the black rat snake and racer, both common nest predators, are drawn to edges by higher abundance of mammalian prey has not been supported (Carfagno *et al.* 2006). Instead, they may utilize edges for thermoregulatory purposes or for the presence of alternative prey, such as bird nests (Blouin-Demers and Weatherhead 2001).

Populations of snakes that prey on birds are not likely to be directly influenced by human-provisioned food because their diets are primarily comprised of amphibians, small mammals, avian prey, and insects, rather than food that would be provisioned to wildlife (e.g. corn at deer feeders, dry cat food at cat colonies) (Klimstra 1959, Rossman *et*

*al.* 1996, Weatherhead *et al.* 2003),. Instead, because small mammals comprise a large proportion of the diet of many grassland snakes (Klimstra 1959, Fitch and Fleet 1970, Fitch 1978, Weatherhead *et al.* 2003), these snakes could respond positively to an increase in small mammals feeding on such food. However, evidence that snakes utilize habitat based on small mammal abundance is weak (Carfagno *et al.* 2006, Sperry and Weatherhead 2009). Alternatively, densities of mesopredators (e.g. feral cat) may increase near anthropogenic food sources (Schmidt *et al.* 2007), potentially resulting increased mortality of snakes, as cats are opportunistic hunters that continue to kill prey even when provided with alternative food (Pearre and Maass 1998).

*Small mammals.* Small mammals also frequently depredate grassland and shrubland nests (Thompson and Burhans 2003, Renfrew and Ribic 2003, Cervantes-Cornhis 2009). Despite that small mammals are largely incidental nest predators (Schmidt *et al.* 2001), they can be dominant predators in these habitats (Pietz and Granfors 2000, Renfrew and Ribic 2003, Grant *et al.* 2006). Mice, weasels, and voles will consume both eggs and nestlings (Bures 1997, Pietz and Grandfors 2000, Bradley and Marzluff 2003), while thirteen-lined ground squirrels have been recorded taking eggs, nestlings, and adult passerines (Pietz and Granfors 2000, Renfrew and Ribic 2003). Predation by small mammals has likely been underestimated historically (Bradley and Marzluff 2003), but its importance is becoming more clearly understood as nest-monitoring cameras allow for accurate identification of diurnal and nocturnal predators.

Small mammal communities vary spatially and temporally (Grant and Birney 1979). Species composition is dominated by microtines (voles, lemmings) in the east and

heteromyids (mice, kangaroo rats) in the west (Grant and Birney 1979), and can exhibit high variability among sites (Heske 1995). Small mammal populations can fluctuate considerably from year to year (Boonstra *et al.* 1998, Oli and Dobson 2001, Brady and Slade 2004), posing a significantly different predation risk from one breeding season to the next. In addition, many small mammals are most active during their spring and summer breeding season (Foster and Gaines 1991), potentially increasing their encounters with nesting birds.

Small mammal assemblages in grasslands are also influenced by vegetation structure and patch size. Shortgrass prairies are characterized by a high biomass and high diversity of small mammals, whereas tallgrass prairies also have a high biomass, but low diversity, of small mammals (Grant and Birney 1979). Thirteen-lined ground squirrels and meadow voles (*Microtus pennsylvanicus*) are habitat specialists found almost exclusively in grassland interiors (Bellows *et al.* 2001, Grant *et al.* 2006). Mice (*Peromyscus spp.*), on the other hand, are generalists often found in old fields and grasslands (Buckner and Shure 1985, Brady and Slade 2004), but exhibit a preference for shrubby areas with reduced meadow vole abundance (Ostfeld *et al.* 1997). Small mammal densities are highest in small patches, and minimal thresholds differ by body size of the mammal (Foster and Gaines 1991). As fragmentation of grasslands continues, interior specialists are likely to decline, while habitat generalists, such as *Peromyscus spp.*, benefit by exploiting increased edge habitat (Bender *et al.* 1998, Bellows *et al.* 2001).

Grassland small mammals are largely herbivorous or granivorous (Lindroth and Batzli 1984, Batzli and Pitelka 1971, Cole and Batzli 1979, Sealy 1982), and therefore may consume supplemental sources of dry food provided to mesopredators. Additionally, an increase in abundance of mesopredators drawn to the food source could impact interactions among nest predator guilds. For example, because small mammals make up approximately 75-96% of an outdoor cat's diet (Baker *et al.* 2005, Turner and Bateson 2000, Biro *et al.* 2005), high local abundance of feral cats could depress numbers of small mammals (George 1974, Baker *et al.* 2003). Raptors and generalist predators have been shown to respond to reduced rodent abundance by including more bird prey in their diets, thereby reducing nest success (Beintema and Muskens 1987, Schmidt and Ostfeld 2003). Even if the rate of nest success remains the same near a supplemental food source, small mammals may be responsible for more predation. For example, Jones *et al.* (2002) supplied mesopredators with food, but compensatory predation by small mammals and raptors resulted in similar nest success on control and experimental plots.

*Birds.* Common avian predators of grassland and shrubland birds include raptors, owls, corvids, and Brown-headed Cowbirds (Soderstrom *et al.* 1998, Pietz and Granfors 2000, Renfrew and Ribic 2003, Stake and Cimprich 2003). In studies monitoring real grassland nests, predation by birds accounts for approximately 15% of predation events (Thompson and Dijak 1999, Pietz and Granfors 2000, Renfrew and Ribic 2003). Nests at both the egg and nestling stages are susceptible to avian predation; however, some studies suggest that predation by raptors is more likely to occur at the nestling stage (Thompson and Dijak 1999, Liebezeit and George 2002, Sergio *et al.* 2003).

Urbanization and the associated fragmentation strongly influence avian predator communities. Large expanses of grassland are more likely to support raptors with large home range requirements or specialist diets, such as the Prairie Falcon (*Falco mexicanus*), Rough-legged hawk (*Buteo lagopus*), or Golden eagle (*Aquila chrysaetos*) (Phillips *et al.* 1984, Berry *et al.* 1998). As fragmentation and urbanization increase, the abundance of generalist raptors (e.g. Red-tailed Hawk, American Kestrel (*Falco sparverius*)) and corvids (e.g. American Crow, Blue Jay) increases (Berry *et al.* 1998, Vigallon and Marzluff 2005, Marzluff *et al.* 2007, Bosakowski and Smith 1997). The presence of forested edges in urban areas can also influence avian predator communities, as the American Crow and Brown-headed Cowbird respond positively to forest edge in some systems (Smith 2004, Howell *et al.* 2007), but not all (Donovan *et al.* 1997, Withey and Marzluff 2009).

Though not “conventional” nest predators, Brown-headed Cowbirds can have predator-like consequences to passerine nests (Zanette *et al.* 2007). Cowbirds can cause nest failure by destroying all eggs or nestlings (e.g. Elliott 1999, Stake and Cimprich 2004), or by removing enough eggs to cause hosts to abandon (Rothstein 1982). Brood parasitism by cowbirds has been linked to increased nest predation, likely due to the tendency of cowbirds to remove host eggs or destroy nests that are too far along to parasitize in an attempt to initiate renesting by the potential host (Arcese *et al.* 1996). Hauber (2000) found that non-parasitized nests were most likely to fail during the incubation stage, although whether this is a result of cowbirds causing failure or selecting safe nests to parasitize remains to be tested. In addition, predation rates have been found

to be lower in years with few or no cowbirds (Arcese *et al.* 1996). Positive responses of cowbirds to either fragmentation or structural complexity of vegetation may thus result in increased nest predation rates.

The presence of avian predators can elicit avoidance responses in animals (Brown *et al.* 1999), resulting in a change in bird communities near centers of predator activity. Certain avian predators, such as accipiters, may indirectly offer a level of nest protection by evicting or preying upon other nest predators (e.g. Norrdahl *et al.* 1995, Quinn *et al.* 2003, Halme *et al.* 2004), while still providing a direct threat to adults (Meese and Fuller 1989, Holthuijzen 1990, Korpimaki and Norrdahl 1991). This often results in a peak abundance of prey species mid-distance from a predator's nest as birds trade off the risk of their own safety with that of their nests (e.g. Sodhi *et al.* 1990, Quinn and Kokorev 2002, Monkkonen *et al.* 2007).

Avian predators can also directly affect bird populations, reducing nest success (Miller *et al.* 2006) and increasing adult mortality rates (Thirgood *et al.* 2000) in open lands; however, corvids are the most significant avian nest predator many fragmented landscapes (Wilcove 1985, Angelstam 1986, Andren 1992). Corvid abundance has been negatively linked to nest success in both grassland (Manzer and Hannon 2005) and forested landscapes (Haskell *et al.* 2001, Luginbuhl *et al.* 2001). Soderstrom *et al.* (1998) found that corvids depredated significantly more shrub nests at grassland-forest interfaces than any other guild of predator, and nests deeper within the grassland were less likely to be depredated by corvids. In contrast, ground nests were relatively safe from avian depredation. In grassland landscapes fragmented by agricultural crops, prairie

grouse nests were eight times less likely to successfully fledge young if they were in areas with high corvid densities (Manzer and Hannon 2005). Nests in small urban reserves may be at similar risk of elevated predation, as avian predators can be more abundant at urban sites than rural counterparts (Sorace 2002, Marzluff and Neatherlin 2006), though this is not always the case (Gering and Blair 1999, Jokimaki *et al.* 2005). In addition, corvids consume supplemental food provisioned to wildlife (Jones *et al.* 2002), which may result in hotspots of predator activity (Buechner and Sauvajot 1996).

*Mesopredators.* Mesopredators are frequent raiders of grassland nests (Vickery *et al.* 1992b, Bollinger and Peak 1995, Staller *et al.* 2005), and sometimes comprise the majority of nest predators (Renfrew and Ribic 2003). Raccoons, cats, opossums, and skunks will consume both eggs and nestlings (van Aarden 1980, Crabtree and Wolfe 1988, Donovan 1997, Thompson and Dijak. 1999, Greenwood *et al.* 1999, Reidy 2009, Stevens *et al.* 2008). Grassland nest depredation by mesopredators is largely incidental (Vickery *et al.* 1992b, Newbury and Nelson 2007), but avian prey still occurs in large proportions of raccoon (49%, Greenwood 1981) and skunk (58%, Greenwood *et al.* 1999) diets in some habitats.

Depredation by mid-sized mammals is widely regarded as a growing threat to passerines as populations of mesopredators increase. The absence of apex predators (Soulè *et al.* 1988, Courchamp 1999) and availability of anthropogenic food sources (Prange and Gehrt 2004) are the main causes for increased abundance and density of mesopredators in urbanizing areas. Fragmentation and hunting have severely reduced the abundance of top predators, resulting in reduced predation pressure and increased habitat

availability for mesopredators (Ritchie and Johnson 2009). In addition, anthropogenic sources of food are abundant at both urban and rural sites of human activity (DeLap and Knight 2004, Bozek *et al.* 2007). Skunks and opossums do not utilize garbage sites to the same extent as raccoons (Prange and Gehrt 2004), but they do regularly consume food left for wildlife (Hawkins 1999, Cooper and Ginnet 2000, Jones *et al.* 2002).

Supplemental food can lead to healthier animals, potentially increasing survival and reproduction of these nest predators (Prange *et al.* 2003).

Mesopredator densities are often greater in urban and suburban areas than rural areas, which could result in elevated predation pressure on grassland nests in these landscapes (Clarke and Pacin 2002). Raccoon populations can be several times more dense in urban landscapes (Rosatte 2000, Prange 2003), reaching as high as 333 raccoons/km<sup>2</sup> (Riley *et al.* 1998). High densities are a result of smaller home ranges due to high resource abundance and shifts in social structure of urban raccoons (Gehrt and Fritzell 1998, Prange and Gehrt 2004). Rural raccoon home ranges average 28 to 2,560ha (Shirer and Fitch 1970, Fritzell 1978, Pedlar *et al.* 1997), while suburban raccoon home ranges have averaged as small as 5.1ha (Hoffmann and Gottschang 1977). Opossums are often more abundant in small patches with high proportions of edge (Crooks 2002, Disney 2008), but results are not consistent (Matthiae and Stearns 1981). Prange and Gehrt (2004) did not find support for increased densities of striped skunk in urban northeastern Illinois; however, average skunk home ranges are often smaller at urbanized sites (Weissinger *et al.* 2009).



Increases in mesopredator abundance have been linked to declines in avian nest success. Rogers and Caro (1999) found low Song Sparrow (*Melospiza melodia*) nest success in years with high mesopredator abundance. Alternatively, as coyote abundance increased over their study years, mesopredator abundance decreased, resulting in higher nest success. Similar results were found in an experiment involving artificial turkey nests in Texas; high concentrations of raccoons, skunks, and opossums at deer feeders resulted in higher nest predation rates near feeders than at control plots (Cooper and Ginnett 2000). Raccoons may have a particularly strong impact on nest success; Schmidt (2003) examined population trends for raccoon-vulnerable (low-nesting) and raccoon-invulnerable (high-nesting) shrub- and woodland songbird species in Illinois and found significantly greater nest mortality for raccoon-vulnerable species.

Though removal of mesopredators has increased nest success among many waterfowl and game species (e.g. Greenwood 1986, Sargeant *et al.* 1995, Garrettson and Rohwer 2001, Pieron and Rohwer 2010), positive responses of songbird nest success to experimental mesopredator reductions are lacking. Two years of raccoon, striped skunk, and red fox removal in North Dakota had no significant impact on survival of natural or artificial songbird nests (Dion *et al.* 1999). Although mesopredators depredated fewer nests at removal plots, compensatory predation by ground squirrels resulted in similar survival rates. In a Georgia field study, neither daily nest survival nor predator assemblage was affected by mesopredator removal and exclusion, but mesopredators were not significant nest predators in that system (Conner *et al.* 2010).

Decreased avian species richness has also been linked to increases in mesopredator presence. Crooks and Soulè (1999) linked a decline in California sage-scrub bird diversity to the high abundance of mesopredators caused by the absence of a top predator, the coyote. Between 1979 and 2001, richness of raccoon-vulnerable species on Breeding Bird Survey routes in Illinois significantly declined, while richness of raccoon-invulnerable species dramatically increased (Schmidt 2003).

Notably, most experimental studies involving relationships among nest success, species richness, and mesopredator abundance have entailed predator removal. However, supplemental food left for wildlife (e.g. feral cats) has the potential to draw mesopredators to the area (Hawkins 1998, Cooper and Ginnett 2000). Because supplemented mesopredators do not rely on natural prey abundance to support their populations, these animals can continue to prey on bird species even when the bird species populations are low (Churcher and Lawton 1987). This eliminates the natural rise and fall of predator-prey cycle, allowing predator abundance to continue to increase at the expense, and potentially extinction, of a prey species (Crooks and Soulè 1999, Courchamp 1999). Further study is therefore required to understand how these consequences relate to avian nest success.

#### *Cats as a Mesopredator of Concern*

Cat populations have been increasing for decades (Turner and Bateson 2000), and the total U.S. cat population exceeds 100 million (Clarke and Pacin 2002), 10-50 million of which are unowned (Patronek and Rowan 1995, Mahlow and Slater 1996). The

provisioning of food to unowned, free-roaming cats is becoming an increasingly common practice, often supported by well-funded activist organizations (Clarke and Pacin 2002). These organizations (e.g. Alley Cat Allies, Cat Network) often provide financial support for TTVAR (trap, test, vaccinate, alter, release) programs, with the intent of stabilizing or reducing feral cat populations without the use of euthanasia (Clarke and Pacin 2002). After alteration, cats are released near a food source that is maintained by volunteers, thus becoming a part of an established “cat colony.”

Although some cat colonies exist in urban setting such as abandoned lots or buildings, many are established in or near parks and nature reserves. For example, managed colonies have existed on or near natural areas and reserves for over a decade in California, Florida, and Hawaii (Clarke and Pacin 2002, HCF Sanctuary 2010), posing a threat for sensitive wildlife (Forys and Humphreys 1999). For birds living within urban reserves, which already are subject to strong external pressures (Saunders *et al.* 1991), cat colonies present yet another risk that can undermine the value of urban habitats to bird populations.

Even where colonies are not officially managed, the presence of a stable food source can result in high, localized densities of cats, concentrating predation impacts near the source (Schmidt *et al.* 2007). Because of the abundance of food sources, cats in urban areas have smaller home ranges with more overlap than rural cats (Page *et al.* 1992, Hall *et al.* 2000, Biro *et al.* 2004, Molsher *et al.* 2005). In addition, cats provided with supplemental food have higher survival and fecundity (Scott *et al.* 2002, Schmidt *et al.* 2007). Free-roaming cats are able to breed throughout the year, and average 1.6 litters

of 4.4 kittens annually (Warner 1985). Cat populations can therefore increase dramatically despite high kitten mortality (75%, Nutter *et al.* 2004) and short life spans (3-5 years, Warner 1985). Hence, provisioning of food to free-ranging cats in urbanizing landscapes may have severe impacts on surrounding wildlife via the increased concentration and abundance of these predators.

Although there are relatively few estimates of the specific amount of avian mortality that is attributable to cats, the fact remains that cats are non-native mesopredators that have the potential to threaten avian populations (Coleman *et al.* 1997, Baker *et al.* 2005). Cats exist today on a gradient of dependency upon humans; however, even when well-fed, cats continue to hunt (Soulè 1988). Cats are opportunistic hunters, taking prey whether hungry or not (Adamec 1976). In addition, they hunt both during day and night, and unlike native predators such as the raccoon and skunk, cats regularly stalk and kill healthy adult birds (Fiore and Sullivan 2000, Dauphine and Cooper 2009). Studies of fecal samples, stomach contents, and prey returned to owners show that birds make up approximately 20% of feral and domestic cat diet (Turner and Bateson 2000). Because cats are subsidized hunters, they may continue to hunt species with small populations that would otherwise not support a wild, unsubsidized predator (George 1974, Baker *et al.* 2005).

Public and scientific opinions are divided over the impact these millions of cats have on bird populations, and the extent to which that predation is additive or compensatory. Estimates of the numbers of birds cats take vary widely; 2 million rural cats in Wisconsin are estimated to kill between 7.3 and 219 million birds per year

(Coleman and Temple 1996), while the British population of 9 million cats is estimated to capture 27 million birds in the course of five months (Woods *et al.* 2003). Because many studies estimate wildlife mortality due to cats based on prey that is returned to the cat's owner (e.g. Lepczyk 2004, Woods *et al.* 2003, Baker *et al.* 2008), the actual number may be much higher; Dauphine and Cooper (2009) conservatively estimate one billion birds killed by cats annually in the United States. Baker *et al.* (2008) found that birds killed by cats were in significantly poorer condition, suggesting compensatory predation, but other studies report that cat predation has a large impact on bird populations (Churcher and Lawton 1987, Coleman and Temple 1997, Woods *et al.* 2003). Cats may also affect populations by taking large amounts of hatch year birds and turning population sources into sinks (Weggler and Leu 2001, Balogh *et al.* 2011).

In addition to taking adult and fledgling birds, cats will depredate nests at the egg and nestling stages (VanAarden 1980, Renfrew and Ribic 2003, Stevens *et al.* 2008), potentially affecting nest success. In Italy, artificial ground nest predation was positively associated with cat abundance (Jokimaki *et al.* 2005). Smith *et al.* (2002) found significantly lower nest survival for Wedge-tailed Shearwaters (*Puffinus pacificus*) nesting at sites where feral cats were regularly fed by the public. The presence of cats may also increase nest abandonment rates; Common terns (*Sterna hirundo*) nesting in Ohio were more likely to abandon nests at sites where cats were frequently observed (Shields and Townsend 1985). In a recent study using time-lapse video at nests, >70% of depredations of urban Northern Mockingbird nests were attributed to cats (Stracey 2010).

There is also growing evidence that cat density and activity influence avian community composition. A negative relationship exists between cat density and bird species richness, and sensitive bird species are often more rare or absent where cats are abundant (Crooks and Soulè 1999, Hawkins *et al.* 1999, Sims *et al.* 2008). In the western US, native scrub bird diversity decreases where cats are abundant (Crooks and Soulè 1999, Maestas *et al.* 2003). Hawkins *et al.* (1999) found fewer ground-foraging species in California where subsidized populations of cats persisted, and the ground-feeding California quail (*Callipepla californica*) and California thrasher (*Toxostoma redivivum*) were completely absent in these areas, yet abundant in cat-free sites. Ground-nesters and ground-feeders are often found to be at greater risk to predation by cats (Mead 1982, Dunn and Tessalia 1994, Fiore and Sullivan 2000), stressing the need to understand how cats may affect grassland bird species.

While many observational studies link cat abundance to avian population and community level consequences, experimental evidence is severely lacking. In addition, much research has been conducted on the diet of cats, but little is known about how the presence of a cat colony and its associated anthropogenic food source affect avian territory establishment and nest success. No study has thoroughly investigated the changes in predator community that accompany the deliberate provisioning of food to mesopredators, and how those changes may influence bird behavior. Clearly, a greater understanding of the complex interactions between predators and prey involved in a system of supplemental food is required before provisioning food to mesopredators on a large scale.

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## CHAPTER 2

### Linking grassland bird density to predator activity in urban parks

#### **Abstract**

The proximity of urban green spaces to anthropogenic food sources can promote high densities of predators that can negatively affect breeding birds. Not only can high numbers of predators depress reproduction and survival, but birds may behaviorally respond by avoiding those patches, which diminishes the value of urban habitats. From 2009-2010, I examined relationships between avian territory density and activity of nest predators, including mesopredators, snakes, small mammals, and avian predators, in 49 2-ha plots in seven urban grassland parks (sites) near Chicago, Illinois. In general, territory densities were negatively related to predator activity within 2-ha plots, though associations varied across species and sometimes were counterintuitive (e.g., density of Song Sparrow (*Melospiza melodia*) was positively related to small mammal numbers at plot and site levels). Density of Field Sparrow (*Spizella pusilla*), Common Yellowthroat (*Geothlypis trichas*), and Savannah Sparrow (*Passerculus sandwichensis*) were negatively related to captures of small mammals. Common Yellowthroat and Savannah Sparrow densities within 2-ha plots, as well as Eastern Meadowlark (*Sturnella magna*) and all species combined at the site level, were negatively related to mesopredator

capture rates. At the site scale, densities of Song Sparrow, Common Yellowthroat, and Savannah Sparrow were better explained by habitat characteristics than activity of predators. These results provide evidence that grassland and early successional birds not only respond to habitat structure, but also to activity of potential predators. Thus, in addition to providing suitable habitat, managers need to consider how human activities that promote activity of predators may undermine the conservation value of urban parks to birds.

## **Introduction**

With less than 1% of native North American grassland remaining (Samson and Knopf 1994) and continued habitat loss and fragmentation due to shifts in land use practices (Askins *et al.* 2007), restored and managed grassland preserves play a central role in conservation of grassland birds, which are declining at a greater rate than any other guild in North America (Peterjohn and Sauer 1999). Given the accelerating rates of residential encroachment into undeveloped lands, preserves are frequently limited to small fragments in urban parks. This situation is especially likely for grassland habitats, which are now uncommon in many parts of the Midwest (Iverson 1988, Herkert 1994). Urban grasslands have the potential to be important contributors to habitat conservation despite their small size and high edge-to-interior ratio (Schwartz 1999, Miller and Hobbs 2002). However, pressures from human activity both within and beyond park boundaries may compromise the ability of urban parks to support sensitive grassland species.

Grasslands within urban landscapes have the potential to be affected by diverse and widely available anthropogenic resources, such as garbage dumps (Prange and Gehrt 2004) or litter at recreational sites (DeLap and Knight 2004). Anthropogenic resources can promote high densities of generalist predators due to reduced territory size, high recruitment, or increased survival (Prange *et al.* 2003). Indeed, many studies confirm that urban areas support greater abundances (Haskell *et al.* 2000, Rodewald *et al.* 2011) or densities (Sorace 2002) of both native predators and non-native feral cats (*Felus catus*) and dogs (*Canis lupus familiaris*) (Maestas *et al.* 2003, Marks *et al.* 2009) than do rural areas. An increasingly common source of anthropogenic resources to wildlife in urban areas is the deliberate provisioning of food at feeding stations for feral cats (i.e. cat colonies; Clarke and Pacin 2002). Although cats associated with colonies may be food-subsidized, they often hunt regardless of hunger level (Adamec 1976). As subsidized hunters, cats may continue to take prey from declining populations that would otherwise not support a wild, unsubsidized predator (George 1974, Baker *et al.* 2005). In addition to cats, a wide variety of generalist predators, including American Crow (*Corvus brachyrhynchos*), northern raccoon (*Procyon lotor*), and Virginia opossum (*Didelphis virginiana*) may be attracted to food provisioned to wildlife (Hawkins *et al.* 1999, Cooper and Ginnet 2000, Jones *et al.* 2002). Although urban parks are likely to support high numbers and/or activity of predators, our understanding of the behavioral and population responses of birds to predators in urbanizing landscapes remains poor.

In addition to potentially increasing rates of nest predation (e.g. Cooper and Ginnet 2000, Cain *et al.* 2003, but see Rodewald *et al.* 2011), high densities of generalist

predators can elicit behavioral responses such that birds avoid sites with high perceived risk of predation. Birds assess habitat quality before selecting a territory for the breeding season by evaluating patch size (Ribic *et al.* 2009), food availability (Crampton *et al.* 2011), vegetation structure (Michel 2010), and risk of predation (Fontaine and Martin 2006). Cues used to assess territories and nesting sites can be visual (Ekner and Tryjanowski 2008), auditory (Peluc *et al.* 2008), or olfactory (Amo *et al.* 2008). Sites with high risk of predation can thereby be avoided by birds, resulting in lower densities (e.g. Norrdahl and Korpimaki 1998, van der Vliet *et al.* 2008) or changes in species composition (e.g. Forsman *et al.* 2001). Important feedbacks between demography and behavior can also occur. For example, low rates of nest success could negatively impact territory settlement because birds also use public cues related to nest success, such as number of fledglings produced (Doligez *et al.* 1999, Parejo *et al.* 2007) or song associated with successful nesting attempts (Betts *et al.* 2008), when prospecting for future territories in the post-breeding season.

I examined relationships between breeding birds and their predators within urban parks near mesopredator feeding stations. Specifically, I evaluated relationships between predator activity in grassland and early successional habitats, and territory selection of eight species of grassland and early successional songbirds. A large body of literature shows that birds may actively settle in areas that minimize risk of predation, but few studies have examined how individual grassland bird species respond to the entire suite of nest predators (Chalfoun *et al.* 2002). Therefore, I predicted that territory density

would be negatively related to activity of predators, but the strength of relationships would be species-specific.

## **Methods**

### *Site selection*

As part of a larger study of mesocarnivore dynamics near supplemental food stations managed by Max McGraw Wildlife Foundation (hereafter termed “McGraw study”), seven sites were selected in Cook, Kane, and McHenry Counties in northeastern Illinois (Figure 2.1). Site selection was based on isolation from the public, permission for mesopredator food provisioning, and habitat characteristics (i.e., comprised primarily of open grassland, early successional tree and shrub species [e.g., boxelder (*Acer negundo*), gray dogwood (*Cornus racemosa*)], or restored oak savannah). Study sites were located within managed public parks and separated by a minimum of 3.5 km (range: 3.5 – 20.8 km). Park size ranged from 178 to 1738 ha (Table 2.1) with at least 90% of the area managed as natural habitat. Other land uses within the parks included paved and/or unpaved recreational trails, picnic and parking areas, crop rows, and a visitor center at two sites.

At each site, 2-ha plots were established along two transects, with each transect containing a 2-ha plot 100m, 300m, and 500m away from an anthropogenic food source made accessible to mesocarnivores as part of the McGraw study. An additional plot was located at least 1 km from the food source, for a total of seven 2-ha plots per site. Study plots were maintained as grassland or early successional habitat through either mowing

(Crabtree, Poplar Creek Central, Living Lands) or burning (Glacial Park, Prairieview), or were not maintained (Poplar Creek Northwest).

### *Predator activity*

The activity of four guilds of predators (i.e., snakes, small mammals, mesocarnivores, and avian predators) was monitored in two ways. First, all detections of avian predators were recorded. Raptors, corvids, and owls were counted only if they were utilizing the habitat (e.g. scan the ground for prey, perch, attack prey); flyovers above 50m were omitted. All detections of Brown-headed Cowbirds (*Molothrus ater*) were recorded separately.

Second, as part of the McGraw study, predators were surveyed using traps and coverboards on each 2-ha plot. Small mammals were trapped at each site for five to six nights in summer (June and July) and again in fall (September and October) using Sherman live traps deployed at 5m intervals on a 25mx25m grid centered within the plot. Traps were baited with peanut butter and bird seed, left overnight, and checked every morning for 5-6 days depending on capture rates. Mammals were identified to species, ear-tagged with a unique ID number, weighed, and sexed.

To survey snakes, four 1x1m coverboards (1 rubber, 3 wood) were placed at stratified random locations within each 2-ha plot. Coverboards were checked weekly and all snakes were identified to species and released.

Mesocarnivores were trapped annually to estimate abundance of raccoon, skunk (*Mephitis mephitis*), cat, and opossum. A 500m buffer encircling the supplemental food

location was divided into 50m x 50m grid cells, and one trap (81 x 25 x 30 cm, model 108, Tomahawk Live Trap Co., Tomahawk, Wisconsin) was placed in every other cell to reach a total of 25 traps. Traps were baited with canned cat food, left overnight, and checked every morning for 5-6 days depending on capture rates. Cats and raccoons were sedated with Telazol® (Elkins-Sinn, Incorporated, Cherry Hill, NJ, USA) prior to handling. Morphometric measurements and blood samples were taken on all captured mesopredators, and raccoons, skunks, and opossums were tagged with a uniquely identifiable ear tag. All cats and a subsample of raccoons and skunks were radio-collared as part of the McGraw study.

Canids were not monitored as predators for this study. Dog-leash laws were enforced at all parks, and study sites were isolated from public use with the exception of a single trail at one site. Additionally, though density of coyotes in the study system occurred at some of the highest levels recorded (Gehrt and Riley 2010), avian prey generally comprises less than one percent of a coyote's diet (see Korschgen 1957 for review, but see also Litvaitis and Shaw 1980) and studies of nest predation in grasslands and shrublands rarely record predation by canids (Thompson and Burhans 1999, Renfrew *et al.* 2003, Schaefer 2004).

### *Vegetation Surveys*

Using modified BBIRD Grassland Protocol (Martin *et al.* 1997), I measured vegetation characteristics within 11.3-m-r circular plots. Vegetation measurements were collected at four stratified random points within each 2-ha plot. Within each random



vegetation plot, all trees were recorded by species and placed within one of four size classes based on diameter-breast-height (dbh): small (8-23cm dbh), small/medium (>23-38cm dbh), medium (38-64cm dbh), and large (>64cm dbh). Tree, shrub and non-woody stems <8cm dbh were counted within 5m of the center as a measure of stem density. Where counts exceeded 100 stems, only those within 1m of the center were counted. Height of groundcover was recorded in each cardinal direction at 5, 3, and 1m from the center and at the center. A Robel pole marked every 0.25m was placed at 5, 3, 1, and 0m from the center in each cardinal direction, and the lowest visible section was recorded to estimate groundcover density. The circular plot was divided into quarters along cardinal directions, and within each quarter, distance to the nearest tree and shrub was measured, and species, height, and diameter at breast height (or width for shrubs) recorded. I also estimated percent of ground covered by living vegetation, grasses, forbs, shrubs, marsh vegetation, bare ground, rock, standing water, and leaf litter within 5m of the plot center. Measurements were collected once at each random location during the course of the study.

### *Bird surveys*

Each site was surveyed for territorial and breeding activity of Common Yellowthroat (*Geothlypis trichas*), Field Sparrow (*Spizella pusilla*), Song Sparrow (*Melospiza melodia*), Savannah Sparrow (*Passerculus sandwichensis*), Henslow's Sparrow (*Ammodramus henslowii*), Bobolink (*Dolichonyx oryzivorus*), Eastern Meadowlark (*Sturnella magna*), and Dickcissel (*Spiza Americana*) seven to eight times

during the breeding seasons of 2009, and 10-11 times during 2010. Surveys occurred every six to eight days between April 12 and July 17 in both years. Surveys began within twenty minutes after sunrise with the exception of several weather-related delays, and were completed within approximately 3.5 hours. Standard spot-mapping protocol was followed (Bibby *et al.* 1992). During a survey, a single observer systematically walked each 2-ha plot following a pre-defined route and recorded the location, sex (where possible), and territorial (e.g. singing, aggressive encounter) or reproductive (e.g. mate-guarding, nest-building) behavior of all target study species on a map of the plot. Starting points for surveys were rotated among three designated points each week to avoid bias. Records of avian activity across all visits were compiled onto separate maps for each species, and number of territories was determined using standardized protocol as outlined by Bibby *et al.* (1992). Territories in which at least 50% of the observations fell within the 2-ha plot were included in analysis.

## **Analysis**

### *Predator activity at two scales*

I examined associations between avian reproductive success and predator activity at both local (2-ha plot) and landscape (site) scales. For small mammals, I calculated capture rate by dividing the number of animals captured at each plot by the number of trap nights (i.e., one trap deployed for one night = one trap night) in a given year.

Because I was interested in small mammal activity (i.e., movement and likelihood of encountering a nest) rather than actual density of small mammals, I used total capture

rates at the plot scale (i.e. number of captures per trap night) to estimate small mammal activity. Although *Microtus ochrogaster* and *M. pennsylvanicus* are primarily herbivorous and insectivorous (Cole and Batzli 1979, Lindroth and Batzli 1984; but see Maxson and Oring 1978, Sealy 1982, Bures 1997, Forstmeier and Weiss 2004 for reports of depredation of songbird nests), I did not expect birds to discriminate among small mammal species in terms of territory selection, and all species of small mammals were pooled for analysis.

Mesopredator traps were located within random 50mx50m grid cells across the site, and did not necessarily fall within our 2ha study plots; therefore, I interpolated capture rates across the site using a kriging method in ArcGIS 9.0. Kriging was selected over inverse distance weighting because it makes no assumptions about spatial autocorrelation, and because it allows for values outside the range of the actual observations (Mantaay and Zeigler 2006). First, I calculated the capture rate for each mesopredator trap separately for each year (total number of animals captured by a given trap divided by the number of nights that trap was set) with all species pooled. These capture data were then kriged separately for 2009 and 2010 to obtain capture rates for each year. Capture rates could not be interpolated for the 1 km plots because their locations exceeded the bounds of the furthest data point (i.e. furthest trap) at each site. I used a fixed-radius search, whereby the capture rates of all traps within 225m of a given point were used to calculate the interpolated capture rate. This distance allowed 2-5 traps to be considered for each point. With the resulting layer, I created an output raster containing 10mx10m cells, whereby each 2-ha plot contained approximately 200 cells. I

reclassified this output layer into 10 equal intervals (0.1 intervals) and then averaged the interpolated capture rates of all 200 grid cells within a plot to obtain the final mesopredator capture rate for the given year at each plot (Figure 2.2).

For avian predators, Brown-headed Cowbirds, and snakes, I generated encounter rates by separately calculating the mean number of individuals observed on all standardized surveys in a plot for each year. Similar to capture rates of small mammals and mesopredators, the encounter rates for avian predators, cowbirds, and snakes provided an estimate of predator activity at the plot scale.

I obtained site-level predator data by averaging predator capture or encounter rates from all plots at a site separately for each year. For example, the encounter rate of snakes at each of the seven plots at Glacial Park during 2009 were summed and divided by seven; this was repeated for 2010.

### *Constructing habitat variables*

To reduce redundancy among vegetation variables, I performed a principal components analysis on the following subset of 10 plot-level measurements: minimum distance to shrub, minimum distance to tree, stem density, percent grass, forb, shrub, and marsh within 5m radius, number of trees within 11.3m radius, average groundcover height, and average groundcover density (as measured with Robel pole).

At the plot level, the first two principal components explained 30.2% and 26.9% of the total variation in vegetation characteristics, respectively; the third component only explained an additional 11% (Table 2.2, Figure 2.3). The first component loaded most

heavily on decreasing distance to the nearest shrub and tree, and increasing tree density and shrub cover, and was interpreted as increasing structural complexity of the habitat (hereafter, “structural complexity”). The second component was positively associated with percent of ground covered by grass and negatively associated with height and density of groundcover. This was interpreted to reflect a gradient from tall, dense groundcover to open, grassy groundcover. To aid in interpretation, I transformed this second principal component by reversing the direction of the gradient. I multiplied each component score by -1, and therefore this second component described the gradient from low groundcover density to high groundcover density (hereafter, “groundcover density”). Structural complexity and groundcover density at the site level were obtained by averaging the component scores of all plots at each site separately.

### *Territory density*

Avian territory density was obtained at each plot separately for each year. I used the average number of territories at each plot as a measure of site-level territory density. Site-level density was calculated separately for each species and separately by year. I restricted analysis to species that had at least 10 territories observed during the two year period.

In all analyses, territory density was used as a response variable and linear models were fit using either a Poisson distribution for plot-level data or normal distribution for site-level data. I used an information-theoretic approach with Akaike’s Information Criteria corrected for small sample sizes ( $AIC_c$ ) to compare the relative support for

alternative models (Burnham and Anderson 1998). In this way, the most parsimonious model that best fits the data was selected, and the probability that each model was the best model was calculated ( $\omega_i$ ). Alternative models were evaluated based on the difference between the model's  $AIC_c$  and the  $AIC_c$  of the best model ( $\Delta AIC_c$ ). Models with  $\Delta AIC_c < 2$  were considered competitive with the best model. I used a staged analysis whereby I initially constructed a base model that accounted for spatial and temporal variability in territory density, and then evaluated support for models relating density to predator activity.

#### *Constructing the base/modified null model*

Avian territory densities are known to vary widely across years (e.g. Jones *et al.* 2003, Moynahan *et al.* 2007), and among sites with varying habitat heterogeneity (e.g. Rotenberry and Wiens 1980, Grant *et al.* 2004). Because my primary focus was on predator-prey relationships, I wanted to account for contributions of these spatio-temporal factors across all models rather than specifically compare them to predator models. Therefore, I developed a modified null, or “base,” model by first identifying the model that best accounted for variation among sites. When considering the contribution of site and year to variation in density, I considered five alternative base models (Table 2.3). The model containing the variables site and year was best supported ( $\omega_i = 0.899$ ) and no other models were competitive; therefore, this model was carried forward in the further development of the base model.

In stage two, I used  $AIC_c$  to rank 12 candidate models, each containing site and year, and also containing variables describing habitat heterogeneity (i.e., structural complexity, groundcover density), predator activity, or distance to supplemental food source. The same model set was run separately for each species, and all models were run with identical data sets. Variables describing habitat heterogeneity were in the top model set for all five species (Table 2.4), which is not surprising given that many studies have demonstrated that birds respond to habitat heterogeneity (e.g. Rotenberry and Wiens 1980, Delisle and Savidge 1997, Coppedge 2008). Because I was most interested in understanding responses of birds to predators, I accounted for habitat influences by including structural complexity and groundcover density in my base model, and this base model served conceptually as the null model throughout analyses. The use of this modified null model allowed me to focus on response of breeding birds to predators, while accounting for expected variation among site and year as well as response to habitat heterogeneity.

#### *Evaluating avian responses to predators*

I used  $AIC_c$  to rank eight candidate models containing the modified null model and predator covariates or distance to anthropogenic food source to determine what best explained territory density at the plot scale (Appendix F). To maintain consistency between plot and site level analysis, a modified null model accounting for variation among years and habitat heterogeneity was also used to evaluate support for six models at

the site scale (Appendix G). Analyses were conducted separately for each species using identical data sets.

## **Results**

### *Predator Activity*

Over the two year period, six avian, nine small mammal, eight snake, and four mesopredator species were recorded at sites (Table 2.5). The most common avian predator was the Blue Jay (40% of observations), followed by Red-tailed Hawk (30%) and American Crow (23%). *Microtus sp.* comprised the majority of small mammal captures (59%), and Common garter snake (*Thamnophis sirtalis*) was the most common snake encountered (80% of encounters). Northern raccoon was the mostly frequently captured mesopredator, comprising 58% of all captures. Captures of cats were low (6%), and therefore the relationship between cats and avian territory density was could not specifically be examined. Snakes and mesopredators were the most strongly correlated predator guilds at both plot (Pearson's  $r = -0.23$ ) and site (Pearson's  $r = -0.52$ ) levels.

### *Territory summary*

Across both years, I recorded 552 territories of eight focal species, with densities varying widely among plots (0 to 14 territories/plot). Overall density was great in 2010 (6.67 territories/2-ha) than 2009 (5.30 territories/2-ha), and densities of some species differed between years at the site level (Table 2.7). Territory density was positively associated with both structural heterogeneity ( $\beta = 0.380$ , SE = 0.179, 95% CI: 0.024,



0.735) and density of groundcover ( $\beta = 0.566$ ,  $SE = 0.185$ , 95% CI: 0.199, 0.933), and therefore the highest densities of territories were found in plots with the greatest structural complexity and densest vegetation.

### *Plot scale*

The null model was competitively ranked ( $\Delta AIC_c < 2$ ) for three of the five species with at least 10 territories (Table 2.8, Appendix F). Measures of predator activity were included in the top model set for four of five species and, in general, avian territories were negatively related to predator numbers. Densities of Field Sparrow increased with structural complexity ( $\beta = 0.148$ ;  $SE = 0.072$ ; 95% CI: 0.008, 0.289) and decreased with density of groundcover ( $\beta = -0.221$ ;  $SE = 0.092$ ; 95% CI: -0.400, -0.041) in the top model, and showed a weak negative association with small mammals and positive association with snakes in competitively-ranked models. Common Yellowthroat density was negatively related to activity of mesopredators (Figure 2.4a), but showed a weak positive association with small mammals. Savannah Sparrow density was best explained by and negatively associated with small mammal activity (Figure 2.4b). Only for the Eastern Meadowlark were no predator models included in the top set. Rather, Meadowlark territory density showed a weak negative association with structural complexity ( $\beta = -0.081$ ;  $SE = 0.367$ ; 95% CI: -0.801, 0.638) and weak negative association with density of groundcover ( $\beta = -0.371$ ;  $SE = 0.227$ ; 95% CI: -0.073, 0.815). Song Sparrow density increased with small mammal activity, though support for this

model was weak ( $w.AIC = 0.317$ ), as the confidence interval overlapped zero and the null model was equally competitive ( $\Delta AIC = 0.30$ ,  $w.AIC = 0.27$ ).

Not surprisingly, the null model best explained total territory density of all species combined ( $\omega_i = 0.400$ ) and no other models were competitive. Total territory density increased with increasing density of groundcover, but showed no significant association with structural complexity.

### *Site scale*

Evidence for site-level responses to predator activity was generally weak and varied across species (Table 2.9, Appendix G), which probably reflects influence from a variety of habitat and landscape factors that were not considered in my study.

Field Sparrow densities significantly increased with activity of snakes (Figure 2.5a). Both Savannah Sparrow and Song Sparrow densities were positively associated with small mammal activity in the top-ranked models, but this relationship was only significant for Savannah Sparrow (Figure 2.5b). Eastern Meadowlark territory density was best explained by and negatively associated with mesopredator capture rates (Figure 2.5c). Common Yellowthroat densities were best explained by the null model. Additionally, the density of all species grouped was negatively associated with mesopredator activity.

## Discussion

After accounting for variation among sites, years, and in habitat structure, I found that predator activity, particularly of small mammals and mesopredators, explained some of the variation in densities of several species in urban openland parks. Risk of predation, or perceived risk of predation, has been linked to anti-predator behaviors in breeding birds and includes reduced feeding rates (Wheelwright and Dorsey 1991, Dunn *et al.* 2010), shifts in incubation strategies (Conway and Martin 2000), and selection of attributes associated with safe nest sites (Wiebe and Martin 1998, Forstmeier and Weiss 2004) and safe territories (Schmidt *et al.* 2005, Fontaine and Martin 2006, Harrison *et al.* 2009). These anti-predator strategies develop over evolutionary and contemporary time scales and are shaped by the degree of actual or perceived risk a bird faces during breeding periods (Conway and Martin 2000). Risk of predation is evaluated through direct assessments of predator activity (Fontaine and Martin 2006), presence of conspecifics (Harrison *et al.* 2009), evidence of successful breeding during post-breeding prospecting efforts (Betts *et al.* 2008), individual breeding experience (Hoover 2003, Parejo *et al.* 2007), and environmental attributes known to reduce risk of predation (Nocera 2006, Chalfoun and Martin 2009). High actual or perceived risk of predation can depress avian abundance and species richness (Engels and Sexton 1994, Tomialojc 2006) as birds avoid those areas. Consistent with this idea, experimental reduction of predator populations has been shown elsewhere to prompt increases in abundance of breeding birds (Fontaine and Martin 2006).

My results suggest that behavioral responses of birds to small mammal activity may vary widely among species and across spatial scales. Whereas Song Sparrow density was positively associated with small mammal activity at both scales, Field Sparrow densities were negatively associated with small mammals in all competitively-ranked models. Likewise, Savannah Sparrow density was negatively associated with small mammal activity at the plot scale, but the relationship was reversed at the larger site scale. Though research on behavioral responses of birds to small mammals is limited, a growing body of evidence suggests that birds can assess small mammal activity when selecting territories and nest sites. Dusky Warbler (*Phylloscopus fuscatus*) females in eastern Russia preferentially select mates on territories with low chipmunk density, and shift to higher nest sites when chipmunk populations are high (Forstmeier and Weiss 2004). Schmidt *et al.* (2006) showed that Veeries (*Catharus fuscescens*) were more likely to select nest sites in areas of below-average mouse activity. After experimental removal of the nest predator black rat (*Rattus rattus*), both territory density and productivity of Modesto Song Sparrow (*M. melodia maillardi*) increased more on removal plots than control plots (Hammond 2008). However, Engels and Sexton (1994) found no relationship between the presence of Golden-cheeked warblers (*Dendroica chrysoparia*) and the predatory eastern fox squirrel (*Sciurus niger*).

The positive correlation between densities of Song and Savannah Sparrows and activity of small mammals may have occurred if, contrary to expected, these birds associated small mammal activity with safety. Small mammals are the primary food for the Red-tailed hawk (Marti and Kochert 1995), which was the most common raptor

observed on surveys, and are taken in greater quantities than avian prey by several snake species in the system (Conant 1938, Tuttle and Gregory 2009). Studies have demonstrated that small mammals respond to risk of predation through avoidance (Fulk 1972, Jacob and Brown 2000) or reduced activity (Wolff *et al.* 1999). High small mammal activity, then, could indicate areas with low risk of predation by raptors and snakes. Additionally, if predation risk is lower where small mammal activity is high, a resulting increase in nest success could promote high site fidelity (Dow and Fredga 1983, Gavin and Bolinger 1988, Doligez *et al.* 1999), and ultimately, high territory density. Habitat selection and dietary preferences of small mammals, particularly *Microtus sp.*, may also play a role in the observed positive relationship between small mammal activity and avian territory density. Voles in prairie habitats regularly consume insects and seeds (Cole and Batzli 1979), both of which may indicate high quality habitat for insectivorous or granivorous breeding birds, especially where nestlings are fed primarily insects (Best 1977). Voles also feed preferentially upon forbs such as clover (*Trifolium sp.*), goldenrod (*Solidago sp.*), and ragweed (*Ambrosia sp.*) (Cole and Batzli 1979, Lindroth and Batzli 1984), which were positively associated with density of groundcover in this study. *M. pennsylvanicus* also preferentially selects habitat with high amounts of groundcover (Zimmerman 1965), and notably, Common Yellowthroat and Song Sparrow densities were positively associated with both density of groundcover and small mammals.

Results indicated that density of grassland specialists, in particular, declined with increasing mesopredator activity. This inverse relationship between territory density and mesopredator activity was evident in all competitively ranked models that included a

measure of mesopredator activity. Consequently, my study suggests that human activities that are likely to attract mesopredators (e.g., provisioning food to wildlife at cat colonies) may lead to declines in grassland bird abundance either as a consequence of predation by mesopredators or avoidance of areas with high mesopredator activity. In a study comparing avian abundance at California parks with and without maintained feral cat colonies, Hawkins (1998) attributed low abundance of ground feeding birds to direct predation by cats. Additionally, Crooks and Soule (1999) suggested that in fragmented California sage-scrub habitats lacking apex predators, cats reached densities that resulted in unsustainably high predation on sensitive bird species. Cat depredation of birds occurs regularly (Turner and Bateson 2000, Bonnaud *et al.* 2007), and impacts can be especially strong on ground feeders and ground nesters (e.g. Woods *et al.* 2003, Baker *et al.* 2005). My study suggests that, even if cats and other mesopredators do not directly kill birds, they may reduce avian abundance by eliciting avoidance responses from birds. For example, Tryjanowski *et al.* (2002) showed that reduced avian densities near dens of the nest predator red fox (*Vulpes vulpes*) were a result of avoidance, not predation, because the red fox did not consume adult birds. The mechanism underlying the negative relationship between mesopredator activity and territory density in my study remains poorly understood, underscoring the need to further understand these interactions.

I also found that apparent responses of birds to predators at large (i.e., site) scales was species-specific. Mesopredators were negatively related to both density of Eastern Meadowlarks and density of all species grouped at the site scale. Moreover, densities of Song Sparrow, Field Sparrow, Savannah Sparrow, and Common Yellowthroat tended to

decrease as mesopredator activity increased, although none of these relationships were strong. Density of Field Sparrows was strongly positively associated with snake activity, and density of Savannah Sparrows increased as small mammals increased, but no other species showed significant associations with either of these predators. Such species-specific responses to predators at large scales have been recorded in other studies.

Marzluff *et al.* (2007) demonstrated that while abundance of several species of songbird was negatively related to total predator abundance at multiple scales, equally as many were positively associated with predators. Moreover, the relationship between songbirds and individual species of predators often was not consistent across scales. This trend has also been described in urban parks in Italy, where densities of several bird species are higher in urban parks than the countryside, despite a greater abundance of predators in urban parks (Sorace 2002). The authors suggested that high bird densities were a result of increased food availability in urban parks. Tomialojc (2006) found that the abundance of several bird species responded positively to the absence of two major predators in urban parks in Poland, but the degree of response varied: while Eurasian Blackbird (*Turdus merula*) numbers tripled, Collared dove (*Streptopelia decaocto*) abundance increased ten-fold.

As expected, grassland birds in my study area were sensitive to habitat structure at both plot and site scales. Dense groundcover (e.g. tall vegetation, low visibility, high forb cover) and high structural complexity are often linked to high densities or abundance of birds (e.g. Martin *et al.* 2011, Castillo-Guerro *et al.* 2009, Kath *et al.* 2009), including in grassland and early successional habitats (e.g. Comer *et al.* 2011, Grant *et al.* 2010,

Negus *et al.* 2010). High densities may occur in these habitats because of increased food availability (Klute 1994) or lower predator abundance (Klug *et al.* 2009), both of which may increase nests success. Groundcover density has been positively linked to nest success of grassland birds (Best and Stauffer 1980, Camp and Best 1994, Kershner and Bollinger 1996) and, as previously noted, high reproductive success can positively influence territory settlement. Indeed, a concurrent study in this system showed that daily nest survival rates were positively linked to the availability of dense groundcover (Chapter 3).

Overall, my research provides a cautionary tale to managers of urban parks, which typically contain a variety of resources that are attractive to predators. If parks inadvertently facilitate use by predators, high predator activity may elicit avoidance behavior from birds and ultimately reduce the conservation value of habitat remnants. Urban parks already are challenged by factors such as edge effects (e.g. Renfrew *et al.* 2005) and small patch size (e.g. Davis *et al.* 2006, Vos and Ribic 2011) that can limit the amount of high quality of habitat available to grassland birds. These results show that certain grassland specialists may avoid areas with high activity of mesopredators, but further research is needed to examine how other rare and/or sensitive grassland species respond to such activity, and how long-term provisioning of food could alter these relationships.



Site	County	Area (ha)	Latitude	Longitude
Crabtree Nature Center	Cook	659	42° 7' 12.37"	88° 8' 42.85"
Glacial Park	McHenry	1324	42° 25' 47.35"	88° 19' 26.86"
Living Lands	McHenry	178	42° 13' 38.43"	88° 12' 42.59"
Max McGraw Wildlife Foundation	Kane	495	42° 5' 5.82"	88° 15' 5.68"
Poplar Creek (Northwest)	Cook	1738	42° 3' 39.87"	88° 11' 59.01"
Poplar Creek (Central)	Cook	1738	42° 2' 51.27"	88° 9' 51.00"
Prairieview Education center	McHenry	340	42° 15' 26.79"	88° 13' 26.10"

Table 2.1. Summary of site names, areas, and locations.

	Structural complexity	Groundcover density (original)	Groundcover density (transformed)
<b><i>Eigenvalue</i></b>	3.023	2.695	3.185
<b><i>Proportion of variance</i></b>	0.302	0.269	0.318
Shrub.Distance	-0.435	-0.027	0.027
Tree.Distance	-0.462	0.023	-0.023
Stem.Density	0.353	-0.157	0.157
Grass	0.104	0.417	-0.417
Forb	0.120	-0.363	0.363
Shrub	0.409	-0.213	0.213
Marsh	-0.320	-0.278	0.278
Tree.Count	0.395	-0.138	0.138
Veg.Height	-0.099	-0.531	0.531
Veg.Density	-0.110	-0.494	0.494

Table 2.2. Plot-level results for principal components analysis performed on vegetation characteristics measured at random locations, including eigenvalues, proportion of variance, and loadings for the first two principal components. Loadings of PC2 (groundcover density) were transformed (i.e., multiplied by -1) for analysis, in order to maintain the gradient from low groundcover density to high.

Model	k	AIC	AIC <sub>C</sub>	ΔAIC <sub>C</sub>	ω <sub>i</sub>
Site + Year	8	330.14	332.54	0.00	0.899
Site	7	335.84	337.68	5.14	0.069
Site * Year	14	331.46	339.24	6.70	0.032
Year	2	357.61	357.79	25.25	<0.001
Null	1	359.06	359.12	26.58	<0.001

Table 2.3. Constructing the base model, stage one: Candidate models include only spatio-temporal factors for explaining density of grassland and early successional birds, as ranked using Akaike Information Criterion

Model	k	AIC	AIC <sub>c</sub>	ΔAIC <sub>c</sub>	ω <sub>i</sub>
<i>Field sparrow</i>					
Structural complexity + Groundcover density	10	172.51	176.31	0.00	0.377
Groundcover density	9	174.92	177.97	1.66	0.164
<i>Song sparrow</i>					
Groundcover density	9	236.44	239.49	0.00	0.419
Small mammals	9	237.97	241.02	1.53	0.195
<i>Common yellowthroat</i>					
Groundcover density	9	209.67	212.72	0.00	0.507
Structural complexity + Groundcover density	10	209.43	213.23	0.51	0.393
<i>Eastern meadowlark</i>					
Groundcover density	9	70.81	73.86	0.00	0.323
Null	8	72.47	74.87	1.01	0.195
<i>Savannah sparrow</i>					
Snakes + Small mammals + Avian predator + Mesopredator	12	79.76	85.34	0.00	0.254
Small mammal	9	82.67	85.72	0.38	0.210
Structural complexity + Groundcover density	10	82.09	85.88	0.54	0.194
Mesopredator	9	83.13	86.18	0.84	0.167
Structural complexity	9	84.16	87.21	1.87	0.100

Table 2.4. Constructing the base model, stage two: Competitively ranked models ( $\Delta AIC_c < 2$ ) explaining territory density of Field Sparrow, Song Sparrow, Common Yellowthroat, Eastern Meadowlark, and Savannah Sparrow. All models contain site and year in the modified null model and additional covariates related to habitat, predator activity, or distance to anthropogenic food source.

Common name	Scientific name	CT	GP	LL	MM	NW	PC	PV	Total
<b>Avian predators</b>									
Cooper's Hawk	<i>Accipiter cooperii</i>	0.000	0.000	0.000	0.000	0.429	0.000	0.000	0.061
Red-tailed Hawk	<i>Buteo jamaicensis</i>	0.471	0.333	0.500	0.526	0.143	0.000	0.129	0.300
Northern Harrier	<i>Circus cyaneus</i>	0.000	0.000	0.000	0.000	0.000	0.000	0.032	0.005
American Crow	<i>Corvus brachyrhynchos</i>	0.176	0.667	0.500	0.053	0.000	0.000	0.226	0.232
Blue Jay	<i>Cyanocitta cristata</i>	0.353	0.000	0.000	0.421	0.429	1.000	0.613	0.402
<b>Small mammals</b>									
Short-tailed shrew	<i>Blarina brevicauda</i>	0.000	0.060	0.043	0.003	0.000	0.017	0.097	0.031
Vole sp.	<i>Microtus sp.</i>	0.502	0.725	0.879	0.651	0.466	0.502	0.392	0.588
Weasel sp.	<i>Mustela sp.</i>	0.000	0.000	0.000	0.000	0.000	0.000	0.006	0.001
Mouse sp.	<i>Peromyscus sp.</i>	0.470	0.158	0.050	0.303	0.507	0.390	0.257	0.305
Shrew sp.	<i>Shrew sp.</i>	0.000	0.000	0.000	0.009	0.000	0.003	0.000	0.002
Masked shrew	<i>Sorex cinereus</i>	0.022	0.021	0.000	0.005	0.004	0.028	0.063	0.020
Thirteen-lined ground squirrel	<i>Spermophilus tridecemlineatus</i>	0.000	0.013	0.014	0.009	0.000	0.047	0.122	0.029
Eastern chipmunk	<i>Tamias striatus</i>	0.007	0.000	0.007	0.016	0.000	0.003	0.041	0.011
Jumping mouse	<i>Zapus hudsonius</i>	0.000	0.023	0.007	0.004	0.023	0.011	0.022	0.013
<b>Snakes</b>									
Western fox snake	<i>Elaphe vulpina</i>	0.000	0.027	0.075	0.000	0.000	0.000	0.024	0.018
Milk snake	<i>Lampropeltis</i>	0.000	0.006	0.053	0.000	0.000	0.000	0.004	0.009
Smooth green snake	<i>Liochlorophis vernalis</i>	0.004	0.000	0.016	0.000	0.000	0.000	0.004	0.003
Northern	<i>Nerodia sipedon</i>	0.000	0.002	0.011	0.000	0.000	0.000	0.024	0.005
Northern brown	<i>Storeria dekayi</i>	0.000	0.006	0.027	0.000	0.004	0.000	0.118	0.022
Red-belly snake	<i>Storeria occipitomaculata</i>	0.000	0.004	0.000	0.000	0.000	0.000	0.000	0.001
Plains garter snake	<i>Thamnophis radix</i>	0.213	0.056	0.011	0.000	0.146	0.423	0.089	0.134
Ribbon snake	<i>Thamnophis sauritus</i>	0.004	0.000	0.000	0.000	0.000	0.000	0.000	0.001
Common garter snake	<i>Thamnophis sirtalis</i>	0.743	0.895	0.807	1.000	0.850	0.577	0.736	0.801
Garter snake, sp. unknown	<i>Thamnophis sp.</i>	0.037	0.004	0.000	0.000	0.000	0.000	0.000	0.006
<b>Mesopredators</b>									
Virginia opossum	<i>Didelphis virginiana</i>	0.258	0.280	0.267	0.179	0.485	0.250	0.279	0.285
Domestic cat	<i>Felis catus</i>	0.097	0.000	0.000	0.143	0.000	0.156	0.023	0.060
Striped skunk	<i>Mephitis mephitis</i>	0.000	0.480	0.000	0.000	0.030	0.000	0.000	0.073
Northern raccoon	<i>Procyon lotor</i>	0.645	0.240	0.733	0.679	0.485	0.594	0.698	0.582

Table 2.5. Proportion of species comprising each predator guild at each site.

(a)

	<b>Snake</b>	<b>Small mammal</b>	<b>Avian</b>	<b>Mesopredator</b>
<b>Snake</b> [81]	1.00			
<b>Small mammal</b> [90]	-0.11	1.00		
<b>Avian</b> [92]	-0.24	-0.07	1.00	
<b>Mesopredator</b> [69]	-0.23	-0.05	0.07	1.00
<b>Cowbird</b> [92]	-0.06	-0.03	0.01	0.02

(b)

	<b>Snake</b>	<b>Small mammal</b>	<b>Avian</b>	<b>Mesopredator</b>
<b>Snake</b> [13]	1.00			
<b>Small mammal</b> [14]	-0.33	1.00		
<b>Avian</b> [14]	-0.49	-0.33	1.00	
<b>Mesopredator</b> [12]	-0.52	-0.25	0.34	1.00
<b>Cowbird</b> [14]	-0.2	-0.14	0.14	-0.22

Table 2.6. Correlation matrix, including sample size [n] and Pearson's  $r$ , for predator guild activity at (a) plot, and (b) site scale

Site	2009		2010	
	$\mu$	SE	$\mu$	SE
<i>All species</i>				
Crabtree	7.14	1.22	9.43	1.25
Glacial Park	0.22	0.86	8.00	1.07
Living Lands	3.25	0.85	3.25	0.85
Max McGraw	5.00	0.44	4.71	0.68
Northwest Poplar	6.29	0.81	7.43	1.02
Poplar Creek	6.57	1.07	7.43	0.92
Prairieview	3.86	1.20	5.00	1.38
All sites	5.30	0.40	6.67	0.48
<i>Field sparrow</i>				
Crabtree	2.71	1.22	3.00	1.25
Glacial Park	0.00	0.00	0.00	0.00
Living Lands	0.00	0.00	0.50	0.29
Max McGraw	0.00	0.00	0.00	0.00
Northwest Poplar	2.57	0.72	3.71	0.92
Poplar Creek	0.57	0.30	2.00	0.38
Prairieview	0.86	0.26	0.86	0.26
All sites	1.02	0.24	1.50	0.26
<i>Song sparrow</i>				
Crabtree	3.00	0.69	4.29	0.61
Glacial Park	0.86	0.34	1.85	0.46
Living Lands	0.50	0.30	0.75	0.27
Max McGraw	0.68	-	0.61	-
Northwest Poplar	2.86	0.51	2.86	0.26
Poplar Creek	3.29	0.92	3.00	0.98
Prairieview	1.14	0.55	1.57	0.61
All sites	2.39	0.30	2.65	0.27
<i>Common yellowthroat</i>				
Crabtree	1.43	0.61	2.14	0.55
Glacial Park	2.00	0.53	4.86	1.03
Living Lands	1.25	0.20	1.00	0.34
Max McGraw	0.14	0.14	0.14	0.14
Northwest Poplar	0.57	0.43	0.43	0.20
Poplar Creek	1.57	0.61	0.71	0.36
Prairieview	1.43	0.57	2.29	1.04
All sites	1.20	0.20	1.70	0.34

continued

Table 2.7. Summary of mean ( $\mu$ ) and standard error (SE) of avian territory densities at each site for the eight focal species.

Table 2.7 continued

Site	2009		2010	
	$\mu$	SE	$\mu$	SE
<i>Savannah sparrow</i>				
Crabtree	0.00	-	0.00	-
Glacial Park	0.00	-	0.00	-
Living Lands	0.25	0.25	0.25	0.25
Max McGraw	0.57	0.37	1.00	0.72
Northwest Poplar	0.29	0.29	0.29	0.18
Poplar Creek	1.00	0.44	1.14	0.55
Prairieview	0.00	-	0.00	-
All sites	0.30	0.11	0.39	0.15
<i>Eastern meadowlark</i>				
Crabtree	0.00	-	0.00	-
Glacial Park	0.29	0.18	0.43	0.30
Living Lands	0.50	0.29	0.25	0.25
Max McGraw	0.00	-	0.00	-
Northwest Poplar	0.00	-	0.14	0.14
Poplar Creek	0.14	0.14	0.29	0.18
Prairieview	0.29	0.18	0.29	0.18
All sites	0.15	0.05	0.20	0.07
<i>Henslow's sparrow</i>				
Crabtree	0.00	-	0.00	-
Glacial Park	0.14	0.14	0.00	-
Living Lands	0.25	0.25	0.25	0.25
Max McGraw	0.00	-	0.00	-
Northwest Poplar	0.00	-	0.00	-
Poplar Creek	0.00	-	0.14	0.14
Prairieview	0.14	0.14	0.00	-
All sites	0.07	0.04	0.04	0.03
<i>Bobolink</i>				
Crabtree	0.00	-	0.00	-
Glacial Park	0.43	0.30	0.86	0.59
Living Lands	0.50	0.29	0.25	0.25
Max McGraw	0.00	-	0.00	-
Northwest Poplar	0.00	-	0.00	-
Poplar Creek	0.00	-	0.14	0.14
Prairieview	0.00	-	0.00	-
All sites	0.11	0.06	0.17	0.10
<i>Dickcissel</i>				
Crabtree	0.00	-	0.00	-
Glacial Park	0.43	0.43	0.00	0.00
Living Lands	0.00	-	0.00	-
Max McGraw	0.00	0.00	0.14	0.14
Northwest Poplar	0.00	-	0.00	-
Poplar Creek	0.00	-	0.00	-
Prairieview	0.00	-	0.00	-
All sites	0.07	0.07	0.02	0.02



Model	k	AIC	AIC <sub>C</sub>	ΔAIC <sub>C</sub>	ω <sub>i</sub>	β	β SE	95% CI	
<i>Field sparrow</i>									
Null	10	172.51	176.31	0.00	0.33	-	-	-	-
Small mammals	11	172.52	177.15	0.85	0.22	-1.503	1.072	-3.604	- 0.598836
Snakes	11	173.38	178.01	1.70	0.14	0.076	0.071	-0.063	- 0.215667
<i>Song sparrow</i>									
Small mammals	11	236.81	243.75	0.00	0.32	1.336	0.703	-0.042	- 2.714
Null	10	238.41	244.05	0.30	0.27	-	-	-	-
Distance	11	238.33	245.28	1.53	0.15	-0.001	0.001	-0.002	- 0.000
<i>Common yellowthroat</i>									
Mesopredators	11	206.56	211.19	0.00	0.41	-4.759	2.336	<b>-9.338</b>	- <b>-0.180</b>
Small mammals	11	208.13	212.77	1.57	0.19	1.493	0.824	-0.123	- 3.109
<i>Savannah sparrow</i>									
Small mammals	11	78.65	83.28	0.00	0.40	-5.009	2.409	<b>-9.731</b>	- <b>-0.287</b>
Mesopredators	11	78.99	83.62	0.34	0.34	-14.460	8.380	-30.885	- 1.965
<i>Eastern meadowlark</i>									
Null	10	72.76	76.56	0.00	0.43	-	-	-	-
<i>All species grouped</i>									
Null	10	328.97	332.76	0.00	0.40	-	-	-	-
Mesopredators	11	330.06	334.69	1.93	0.15	-0.855	0.907	-2.631	- 0.922

Table 2.8. Territory density models for plot-level densities of the five most common species in the study system. Modified null model includes site, year, structural complexity, and groundcover openness. Table includes, ω<sub>i</sub>, parameter estimates, standard errors of parameter estimates. **Boldface** denotes confidence intervals that do not overlap zero. Only competitively ranked models (ΔAIC<sub>C</sub> < 2) are shown.

Model	k	AIC	AIC <sub>C</sub>	ΔAIC <sub>C</sub>	ω <sub>i</sub>	β	β SE	95% CI		
<i>Field sparrow</i>										
Snakes	5	15.12	25.12	0.00	0.71	0.274	0.097	<b>0.083</b>	-	<b>0.465</b>
<i>Song sparrow</i>										
Null	4	37.28	42.99	0.00	0.62	-	-	-	-	-
Small mammals	5	34.55	44.55	1.55	0.29	6.415	3.486	-0.418	-	13.248
<i>Common yellowthroat</i>										
Null	4	41.43	47.15	0.00	0.78	-	-	-	-	-
<i>Savannah sparrow</i>										
Null	4	18.50	24.22	0.00	0.51	-	-	-	-	-
Small mammals	5	14.85	24.85	0.63	0.37	3.149	1.535	<b>0.142</b>	-	<b>6.157</b>
<i>Eastern meadowlark</i>										
Mesopredators	5	-17.51	-7.51	0.00	0.56	-1.956	0.810	<b>-3.543</b>	-	<b>-0.369</b>
Null	4	-12.23	-6.52	0.99	0.34	-	-	-	-	-
<i>All species grouped</i>										
Mesopredators	5	41.08	51.08	0.00	0.84	-28.010	9.301	<b>-46.240</b>	-	<b>-9.780</b>

74

Table 2.9. Territory density models for site-level densities of the five most common species in the study system. Base model includes year, structural complexity, and groundcover openness. Table includes, ω<sub>i</sub>, parameter estimates, standard errors of parameter estimates, and confidence intervals of parameter estimates. **Boldface** denotes confidence intervals that do not overlap zero. Only competitively ranked models (ΔAIC<sub>C</sub> < 2) are shown.

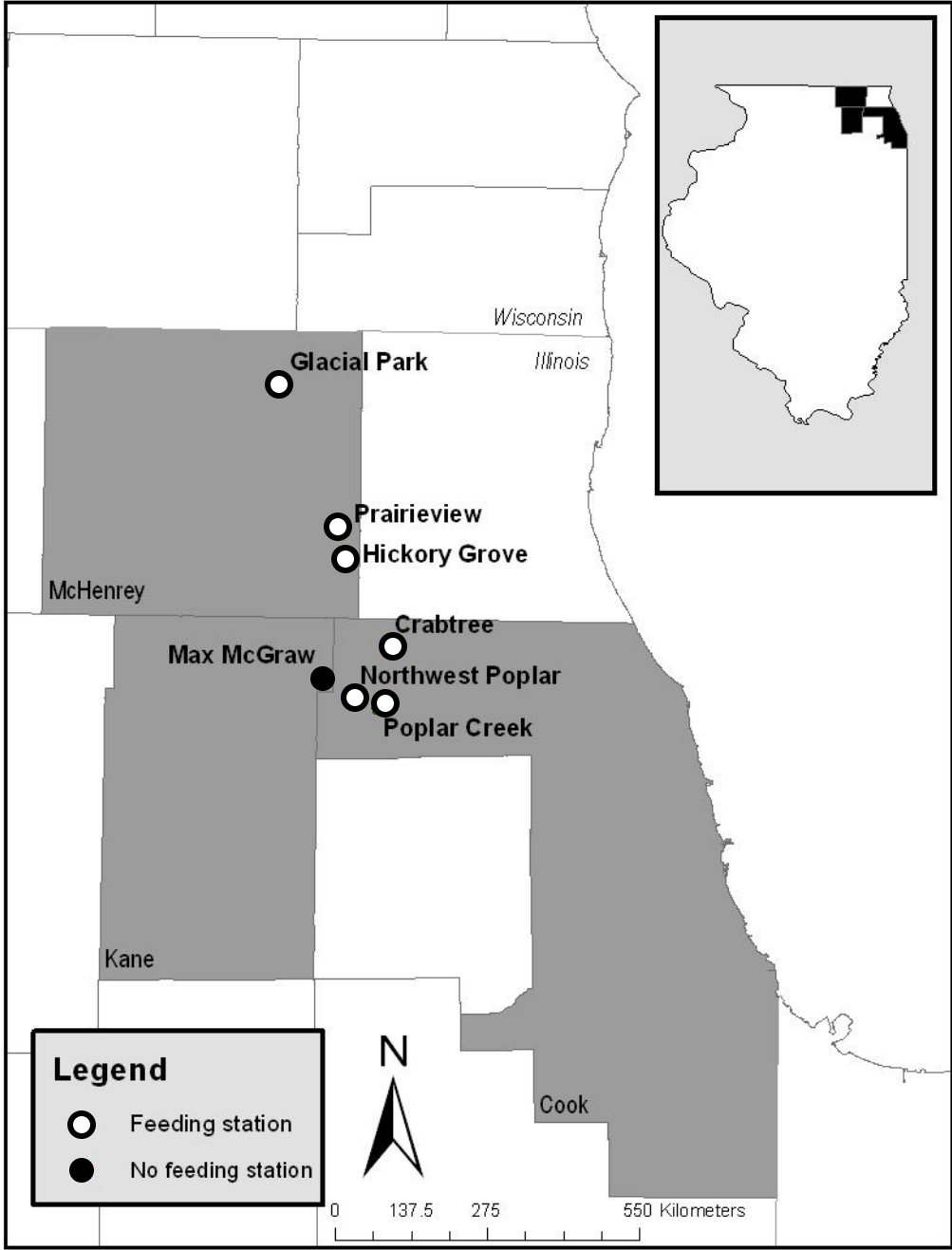


Figure 2.1. Overview of site locations in Cook, Kane, and McHenry counties, IL.

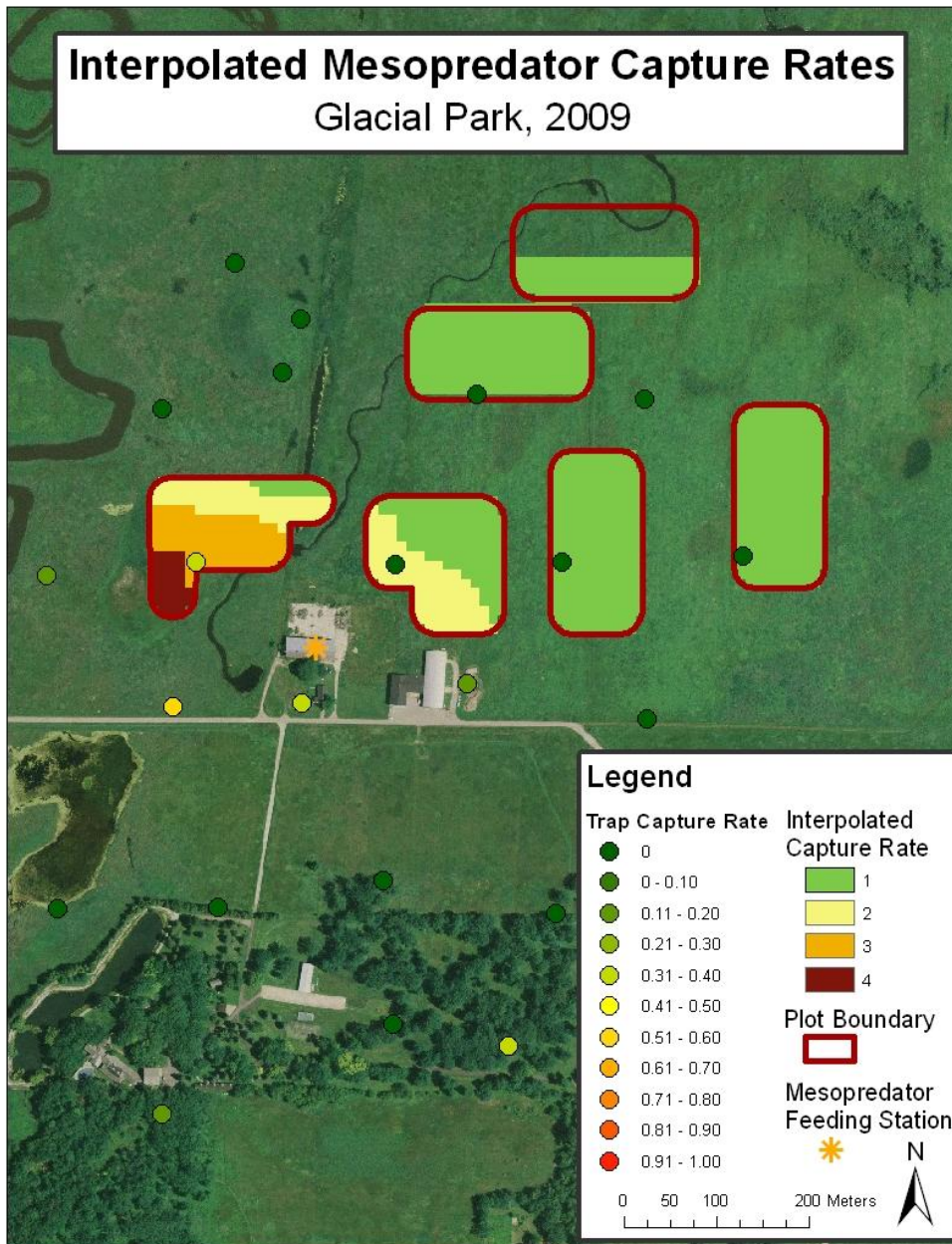
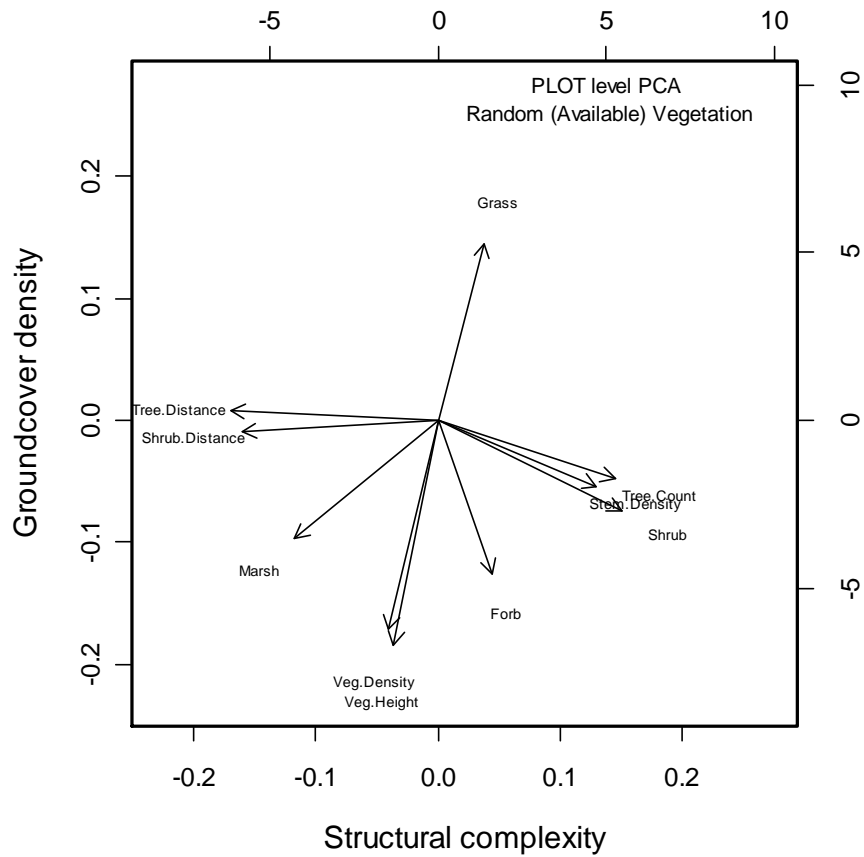
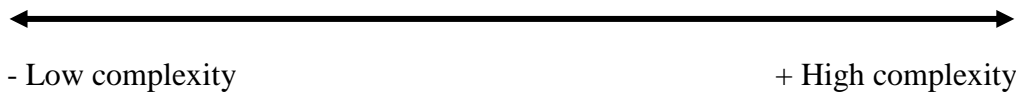


Figure 2.2. Example of results from interpolating capture rates at Glacial Park.

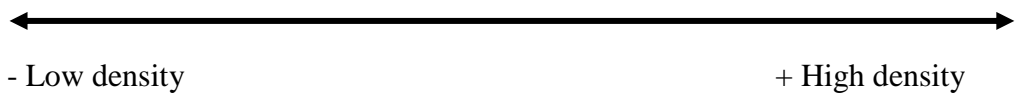


(a)

PC1: Increasing structural complexity



PC2: Increasing groundcover density



(b)

Figure 2.3. Interpreting principal components at the plot scale: (a) biplot of first two principal components as originally calculated and (b) illustration of the habitat gradient represented by the first two components, after transforming (i.e. reversing) PC2 (groundcover density) loadings.

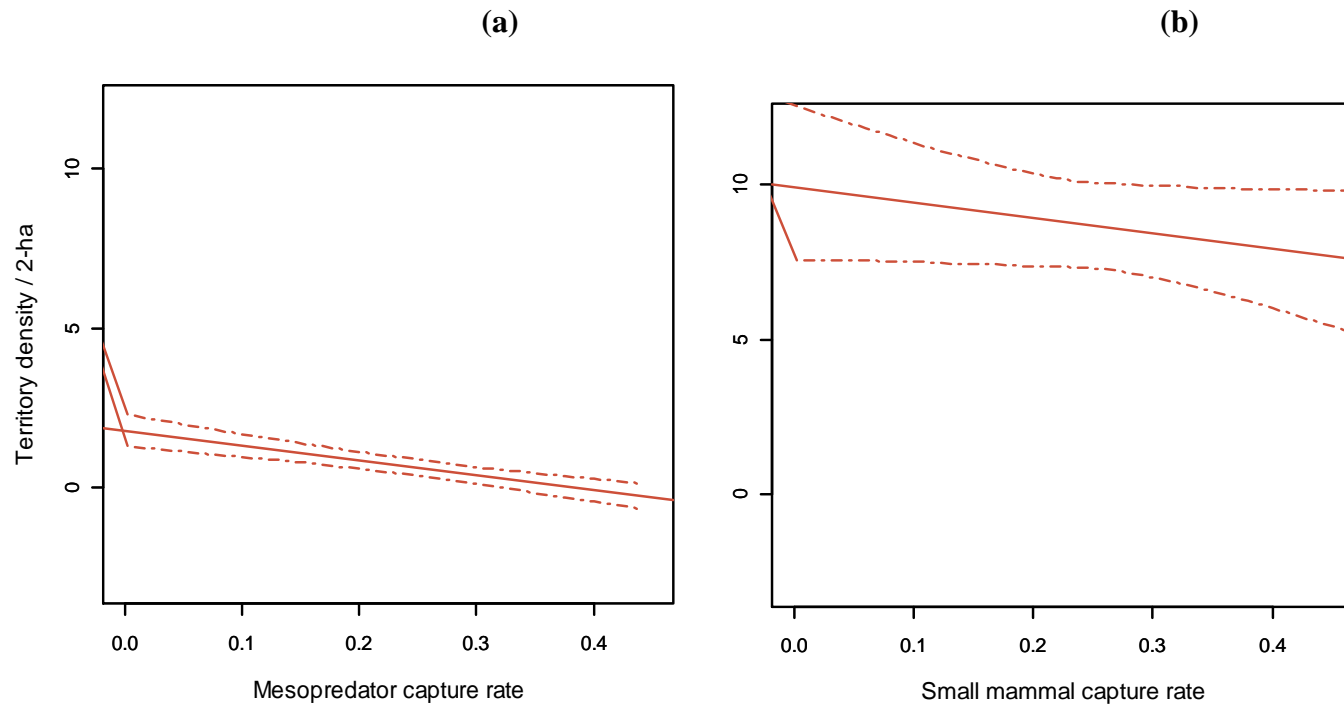


Figure 2.4. Plot-level relationships ( $\pm$  95% CI) between (a) Common Yellowthroat density and mesopredator capture rates and (b) Savannah Sparrow density and small mammal capture rates, with structural complexity held constant at low levels (component score = -4) and groundcover density held at moderate levels (component score = 2).

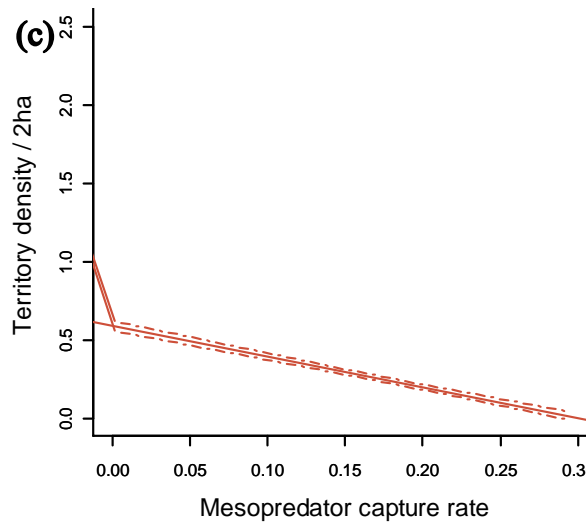
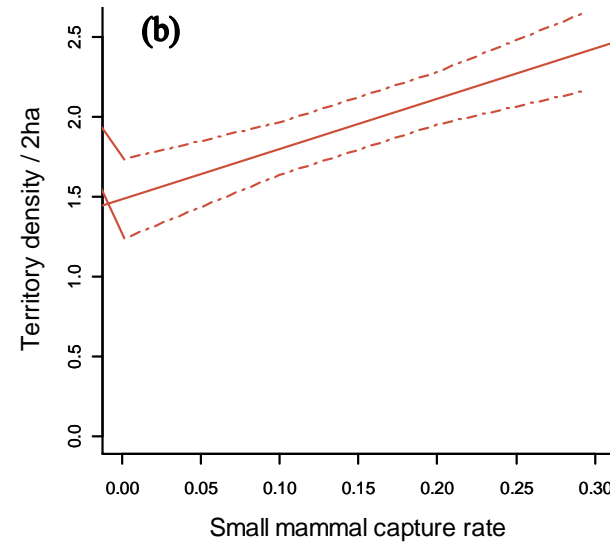
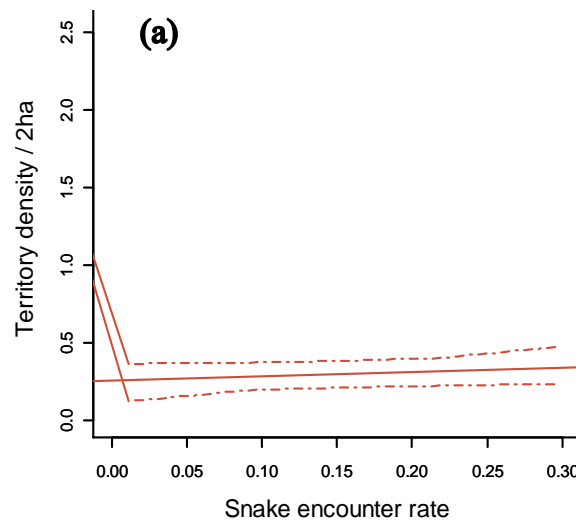


Figure 2.5. Relationship ( $\pm$  95% confidence interval) between (a) Field Sparrow and encounters (i.e. activity) of snakes, (b) Savannah Sparrow capture rates of small mammals, and (c) Eastern Meadowlark and capture rates of mesopredators, with structural complexity held constant at moderate levels (component score = 2) and groundcover density held constant at low levels (component score = -4).

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## CHAPTER 3

### Behavioral and demographic responses of breeding openland birds to predator activity and vegetation

#### **Abstract**

Although urban green spaces have the potential to provide valuable habitat to declining species of grassland and early successional birds, they often support greater abundance and diversity of predators than rural lands. High densities of predators may prompt behavioral and/or demographic responses from breeding birds that diminish the conservation value of urban parks, irrespective of how suitable the habitat may otherwise be (e.g., vegetation structure). Thus, understanding the relative importance of predators and vegetation attributes in urban preserves to avian behavior and demography is essential to effectively manage habitats. From 2009-2010, I examined relationships between nest success and nest site selection of Field Sparrow (*Spizella pusilla*) and Song Sparrow (*Melospiza melodia*), activity of nest predators (i.e., mesopredators, snakes, small mammals, and birds), and habitat heterogeneity in 28 2-ha plots in four urban grassland parks (sites) near Chicago, Illinois. Daily nest survival of both species was linked to snake activity at plot scales, though in opposite ways.



Snake activity was positively associated with nest survival of Field Sparrows, but negatively associated with that of Song Sparrows. At larger spatial scales (i.e., site), vegetation characteristics best predicted nest survival of both species. In terms of nest-site selection, birds did not apparently adjust nest placement relative to groundcover as predator activity changed. However, as activity of Brown-headed Cowbird (*Molothrus ater*) increased, Field Sparrows selected nest sites that were more structurally complex. As a whole, this study provides evidence that both habitat structure and predator activity influence reproductive activity of openland birds, with birds responding strongly to habitat structure at large scales and predator activity at small scales. Therefore, maintaining vegetation positively associated with nest survival at large scales could mitigate the negative effect of some predators at local scales, ultimately benefiting reproduction of birds in openland parks.

## **Introduction**

Habitat loss due to shifts in land-use practices and urban development is the primary cause of declines in grassland and early-successional bird abundance (Bollinger and Gavin 1992, Askins 2007). High costs of land acquisition coupled with fragmentation often limit conservation to small parcels of land in urban areas, but even small tracts of restored grassland can promote local increases in grassland bird abundance (Veech 2006). Management practices to improve breeding bird habitat can vary substantially among preserves, ranging from predator removal (see Smith *et al.* 2010 for review) to habitat management (e.g. Chandler *et al.* 2009). Both habitat

structure and predator communities can interact to influence avian nesting ecology (e.g. Li and Martin 1991, Dion *et al.* 2000, Liebezeit and George 2002); however, recent evidence suggests that high resource availability in urban landscapes may decouple predator-prey relationships (Rodewald *et al.* 2011). Hence, management techniques derived from traditional understanding of ecological relationships may not be effective in urban reserves, and a better understanding of these interactions in urban areas is therefore necessary to determine effective management decisions.

Small preserves are especially vulnerable to external pressures, such as the introduction of non-native species and changes in species interactions (Schwartz 1999, Miller and Hobbs 2002). In particular, the availability of anthropogenic food sources (e.g. Prange *et al.* 2003, Chace and Walsh 2006, Withey and Marzluff 2009) and the absence of apex predators (Crooks and Soule 1999, Ritchie and Johnson 2009) can promote high densities of generalist nest predators. Indeed, many studies confirm that urban parks support greater abundances (Haskell *et al.* 2000, Rodewald *et al.* 2011) or densities (Sorace 2002) of native nest predators and non-native feral cats (*Felis catus*) and dogs (*Canis lupus familiaris*) (Maestas *et al.* 2003, Marks 2009) than their rural counterparts. High densities of nest predators are a conservation concern because nest predation is the primary cause of nest failure in songbirds (Ricklefs 1969, Martin 1993a) and predation rates often rise with predator abundance (e.g. Cooper and Ginnett 2000, Weidinger 2002).

Nest predation can have important behavioral and demographic consequences for breeding birds. High predation rates can depress nest survival rates to the point

where populations act as sinks (Schmidt 2003). Predation, or perceived risk of predation, also can evoke behavioral responses. Prior to nesting, risk of predation may influence nest site selection. Where predators are abundant, birds may adjust nest location to reduce risk, depending upon the predator type and plasticity of the bird species (Wiebe and Martin 1998, Forstmeier and Weiss 2004, Eggers *et al.* 2006). Likewise, where predation risk is high, birds may respond by spending more time on the nest incubating (Weathers and Sullivan 1989, Sasvari and Hegyi 2000), increasing nest defense (Martindale 1982, Marzluff 1985), or decreasing number of trips to feed nestlings (e.g. Wheelwright and Dorsey 1991, Eggers *et al.* 2005). Nest success can also be influenced by habitat structure (Best and Stauffer 1980, Hughes 1996, Chalfoun and Martin 2009). Therefore, management decisions should not only consider the extent to which birds respond to predation risk, but also the consequences such responses can have when predators elicit shifts in nest site selection. Thus, a further understanding of the extent to which both vegetation structure and predator activity affect avian reproductive success is crucial to making effective management decisions in grasslands and shrublands.

I examined relationships between the reproductive strategies and success of early successional birds and their predators in urban parks. Specifically, I evaluated how daily nest survival and nest site selection of Field Sparrow and Song Sparrow responded to habitat characteristics and activity of four predator guilds. Empirical evidence shows that nest survival may be directly linked to both predator activity and habitat characteristics (e.g. Winter 1999, Sperry *et al.* 2008). However, predators may

also indirectly affect nest survival by eliciting shifts in nest site selection. I hypothesized that these focal species would alter nest site selection to avoid predators that were most strongly associated with reduced nest survival.

## **Methods**

### *Site selection*

As part of a larger study of mesocarnivore dynamics near supplemental food stations managed by Max McGraw Wildlife Foundation (hereafter termed “McGraw study”), seven sites were selected in Cook, Kane, and McHenry Counties in northeastern Illinois (Chapter 2, Figure 2.1). Site selection was based on isolation from the public, permission for mesopredator food provisioning, and habitat characteristics (i.e., comprised primarily of open grassland, early successional tree and shrub species [e.g., boxelder (*Acer negundo*), gray dogwood (*Cornus racemosa*)], or restored oak savannah). Study sites were located within managed public parks and separated by a minimum of 3.5 km (range: 3.5 – 20.8 km). Park size ranged from 178 to 1738 ha (Chapter 2, Table 2.1) with at least 90% of the area managed as natural habitat. Other land use within the parks included paved and/or unpaved recreational trails, picnic and parking areas, crop rows, and a visitor center at two sites.

At each site, 2-ha plots were established along two transects, with each transect containing a 2-ha plot 100 m, 300 m, and 500 m away from an anthropogenic food source made accessible to mesocarnivores as part of the McGraw study. An additional plot was located at least 1 km from the food source, for a total of seven 2-ha plots per

site. Study plots were maintained as grassland or early successional habitat through either mowing (Crabtree, Poplar Creek Central, Living Lands) or burning (Glacial Park, Prairieview), or were not maintained (Poplar Creek Northwest).

### *Predator activity*

The activity of four guilds of predators (i.e., snakes, small mammals, mesocarnivores, and avian predators) was monitored in two ways. First, all avian predators observed during spot-mapping surveys were recorded. Spot-map surveys lasted approximately two hours, resulting in equal sampling effort across sites. Raptors, corvids, and owls were counted only if they were utilizing the habitat (e.g. scan the ground for prey, perch, attack prey); flyovers above 50m were omitted. All cowbirds observed during the survey were recorded separately.

Second, as part of the McGraw study, predators were surveyed using traps and coverboards on each 2-ha plot. Small mammals were trapped at each site for one week in summer (June and July) and again in fall (September and October, 2009 only) using Sherman live traps deployed at 5m intervals on a 25mx25m grid centered within the plot. Traps were baited with peanut butter and bird seed, left overnight, and checked every morning for 5-6 days depending on capture rates. Mammals were identified to species, ear-tagged with a unique ID number, weighed, and sexed when possible.

To survey snakes, four 1x1m coverboards (1 rubber, 3 wood) were placed at stratified random locations within each 2-ha plot. Coverboards were checked weekly and all snakes were identified to species and released.

Mesocarnivores were trapped annually to estimate abundance of northern raccoon (*Procyon lotor*), striped skunk (*Mephitis mephitis*), domestic cat (*Felus catus*), and Virginia opossum (*Didelphis virginiana*). Sites were divided into 50mx50m grid cells and one trap (81 x 25 x 30 cm, model 108, Tomahawk Live Trap Co., Tomahawk, Wisconsin) was placed in every other cell to reach a total of 25 traps. Traps were baited with canned cat food, left overnight, and checked every morning for 5-6 days depending on capture rates. Cats and raccoons were sedated with Telazol® (Elkins-Sinn, Incorporated, Cherry Hill, NJ, USA) prior to handling. Morphometric measurements and blood samples were taken on all captured mesopredators, and raccoons, skunks, and opossums were tagged with a uniquely identifiable ear tag. All cats and a subsample of raccoons and skunks were radio-collared as part of the McGraw study.

Canids were not monitored as predators for this study. Dog-leash laws were enforced at all parks, and study sites were isolated from public use with the exception of a single trail at one site. Additionally, though density of coyotes in the study system occurred at some of the highest levels recorded (Gehrt *et al.* 2010), avian prey generally comprises less than one percent of a coyote's diet (see Korschgen 1957 for review, but see also Litvaitis and Shaw 1980) and studies of nest predation in grasslands and shrublands rarely record predation by canids (Thompson and Dijak 1999, Renfrew *et al.* 2003, Schaefer 2004).

### *Vegetation Surveys*

Using modified BBIRD Grassland Protocol (Martin *et al.* 1997), I measured vegetation characteristics within 11.3-m-r circular plots. Vegetation measurements were collected at four stratified random points within each 2-ha plot, and also at a random sub-sample of 100 nests at the end of each breeding season (late July). Measurements were collected once at each random location during the course of the study. Within each random vegetation plot, all trees were recorded by species and placed within one of four size classes based on diameter-breast-height (dbh): small (8-23cm dbh), small/medium (>23-38cm dbh), medium (38-64cm dbh), and large (>64cm dbh). Tree, shrub and non-woody stems <8cm dbh were counted within 5m of the center as a measure of stem density. Where counts exceeded 100 stems, only those within 1m of the center were counted. Height of groundcover was recorded in each cardinal direction at 5, 3, and 1m from the center and at the center. A Robel pole marked every 0.25m was placed at 5, 3, 1, and 0m from the center in each cardinal direction, and the lowest visible section was recorded to estimate groundcover density. The circular plot was divided into quarters along cardinal directions, and within each quarter, distance to the nearest tree and shrub was measured, and species, height, and diameter at breast height (or width for shrubs) recorded. I also estimated percent of ground covered by living vegetation, grasses, forbs, shrubs, marsh vegetation, bare ground, rock, standing water, and leaf litter within 5m of the plot center.

### *Nest Searches*

Each of four sites was searched at 2-4 day intervals for nests of Field Sparrow (*Spizella pusilla*), Song Sparrow (*Melospiza melodia*), Savannah Sparrow (*Passerculus sandwichensis*), and Eastern Meadowlark (*Sturnella magna*). Behavioral observations (e.g. carrying nest material or food, sounding alarm calls) and systematic searching (e.g walking through territories in an attempt to flush birds, looking in potential nest locations) were used to locate nests (Winter *et al.* 2003). Once located, nests were checked every 2-5 days until fate was determined. Because I was most interested in nest predation, nests fledging Brown-headed Cowbirds (*Molothrus ater*) were considered “successful,” as they had not been depredated. No attempt was made to identify nest predators from nest or egg remains, as nest predators cannot be reliably identified by these cues (Lariviere 1999).

### **Analysis**

#### *Predator activity at two scales*

I examined associations between avian reproductive success and predator activity at both local (2-ha plot) and landscape (site) scales. For small mammals, I calculated capture rate by dividing the number of animals captured at each plot by the number of trap nights (i.e., one trap deployed for one night = one trap night) in a given year. Because I was interested in small mammal activity (i.e., movement and likelihood of encountering a nest) rather than actual density of small mammals, I used total capture rates at the plot scale (i.e. number of captures per trap night) to estimate



small mammal activity. Estimates were calculated for (a) non-vole (*Microtus sp.*) small mammals, given that *M. ochrogaster* and *M. pennsylvanicus* are primarily herbivorous and insectivorous (Cole and Batzli 1979, Lindroth and Batzli 1984; but see Maxson and Oring 1978, Sealy 1982, Bures 1997, Forstmeier and Weiss 2004 for reports of depredation of songbird nests) and (b) all small mammals combined, as birds may not discriminate among small mammal species in terms of nest site selection.

Because mesopredator traps were located within random 50mx50m grid cells across the site, and did not necessarily fall within our 2ha study plots, I interpolated capture rates across the site using a kriging method in ArcGIS 9.0. Kriging was selected over inverse distance weighting because it makes no assumptions about spatial autocorrelation, and because it allows for values outside the range of the actual observations (Mantaay and Zeigler 2006). First, I calculated the capture rate for each mesopredator trap separately for each year (total number of animals captured by a given trap divided by the number of nights that trap was set) without adjusting for recaptures. Capture data were then kriged separately for 2009 and 2010 to obtain capture rates for each year. I used a fixed-radius search, whereby the capture rates of all traps within 225m of a given point were used to calculate the interpolated capture rate. This distance allowed 2-5 traps to be considered for each point. I chose to use a fixed-radius search as opposed to a search for a fixed number of traps so that information from the same size area was considered when interpolating each point. Capture rates could not be interpolated for the 1 km plots because their locations exceeded the bounds of the furthest data point (i.e. furthest trap) at each site. Next, I

created an output raster from kriging containing 10m x 10m cells, resulting in each 2-ha plot containing approximately 200 cells. I reclassified this output layer into 10 equal intervals (0.1 intervals) and then averaged the interpolated capture rates of all 200 grid cells within a plot to obtain the final mesopredator capture rate for the given year at each plot (Chapter 2, Figure 2.2).

For avian predators, Brown-headed Cowbirds, and snakes, I generated encounter rates by separately calculating the mean number of individuals observed on all standardized surveys in a plot for each year. Similar to capture rates of small mammals and mesopredators, the encounter rates for avian predators, cowbirds, and snakes provided an estimate of predator activity at the plot scale.

I obtained site-level predator data by averaging predator capture or encounter rates from all plots at a site separately for each year. For example, the encounter rate of snakes at each of the seven plots at Glacial Park during 2009 were summed and divided by seven; this was repeated for 2010.

#### *Constructing random habitat variables for DSR analysis*

Using only information from random vegetation surveys, I performed a principal components analysis (PCA) on the following subset of 10 variables: minimum distance to shrub, minimum distance to tree, stem density, percent grass, forb, shrub, and marsh within 5m radius, number of trees within 11.3m radius, average groundcover height, and average groundcover density (as measured with Robel pole). Only random vegetation surveys were included because I sought to describe the

available habitat at the plot scale. This is the most valuable level of information for management, as habitat can be manipulated at this level, but not necessarily at the nest-site level. The resulting components were used when ranking models to describe variation in daily nest survival rates.

At the plot level, the first two principal components explained 30.2% and 26.9% of the total variation in vegetation characteristics, respectively; the third component only explained an additional 11% (Chapter 2, Table 2.2, Figure 2.3). The first component loaded most heavily on decreasing distance to the nearest shrub and tree, and increasing tree density and shrub cover, and was interpreted as increasing structural complexity of the habitat (hereafter, “structural complexity”). The second component was positively associated with percent of ground covered by grass and negatively associated with height and density of groundcover. This was interpreted to reflect a gradient from tall, dense groundcover to open, grassy groundcover. To aid in interpretation, I transformed this second principal component by reversing the direction of the gradient. I multiplied each component score by -1, and therefore this second component described the gradient from low groundcover density to high groundcover density (hereafter, “groundcover density”). Structural complexity and groundcover density at the site level were obtained by averaging the component scores of all plots at each site separately.

### *Daily survival rates*

Daily survival rates (DSR) were calculated in SAS (PROC genmod, SAS Institute 2010) using logistic exposure models (Shaffer 2004). The logistic exposure model accounts for variation in nest-check intervals by estimating the probability of survival between visits. As a generalized linear model with binomial distribution and a link function adjusted for length of exposure for each nest, it can be applied using an information theoretic approach for multiple model analysis (Akaike's information criterion, Burnham and Anderson 2002). Survival rates were calculated for each species separately at the plot and site level. Daily survival rates of all four species grouped were also calculated at plot and site levels. This metric was used when examining spatial and temporal variation in DSR.

In all analyses of daily survival rates, DSR at the plot or site level was used as a response variable. Because the daily survival rates of Field Sparrows (Shapiro-Wilk  $W = 0.907$ ,  $p = 0.03$ ) were not normally distributed across plots, I arcsine-transformed this variable at the plot scale. Daily survival rates of Song Sparrow did not deviate from normal distribution (Shapiro-Wilk  $W = 0.925$ ,  $p = 0.18$ ). Linear models were then fit using a normal distribution. I used an information-theoretic approach with Akaike's Information Criteria corrected for small sample sizes ( $AIC_c$ ) to compare the relative support for alternative models. In this way, the most parsimonious model that best explained the variation in the data was ranked highest, and the probability that each model was the best model was calculated using Akaike weights ( $\omega_i$ ). Alternative models were evaluated based on the difference between the model's  $AIC_c$  and the

AIC<sub>c</sub> of the best model ( $\Delta\text{AIC}_c$ ). Models with  $\Delta\text{AIC}_c < 2$  are considered competitive with the best model. I limited analysis to plots with at least two nests. Multiple nests of Eastern Meadowlark and Savannah Sparrow were only found on two and four plots, respectively, and therefore these species were omitted from species-specific model ranking. I used a two-staged analysis whereby I initially constructed a base model that accounted for spatial and temporal variability in DSR, and then evaluated support for models relating DSR to predator activity and habitat characteristics.

#### *Constructing the base model for DSR*

Daily survival rate of nests often varies among sites (e.g. Rodewald and Shustack 2008, Husek *et al.* 2010), especially when management techniques differ, as they do on these sites (e.g. Churchwell *et al.* 2008, Rahmig *et al.* 2009). Daily survival rates can also vary among years (e.g. Chase *et al.* 2005). However, because this study sought to investigate the relative influence vegetation characteristics and predator communities on nesting ecology, I began my analysis by developing a base model to account for the background spatiotemporal variation in DSR.

At the plot level, I considered five alternative models containing site effect, year effect, the additive effect of site and year, the interaction between the two, and an intercept-only model. As the model containing site was ranked highest ( $\omega_i = 0.571$ , Table 3.1) and no other models were competitive, only site was used in the modified base model. The use of this modified base model, which served conceptually as the null model, allowed me to focus on the response in daily survival to both predators and

vegetation, while accounting for expected variation at the site level. At the site level, I examined support for a year effect on DSR by ranking a model containing year against the intercept-only model. Year was not supported ( $\Delta\text{AIC}_c = 3.64$ ,  $\omega_i = 0.139$ , Table 3.1) and therefore was not included in the base model at the site level.

*Evaluating responses of daily survival rates to predators and habitat heterogeneity*

At the plot level, I used AIC to rank 13 candidate models containing the modified base model and predator or randomly available vegetation. Because 1 km plots lacked mesopredator capture data, they were not included in AIC modeling. At the site level, I ranked the ability of 12 models containing predator or randomly available vegetation to explain daily survival rates. The same model set was run for Field and Song Sparrow at each spatial scale.

*Nest site selection*

To describe patterns in nest-site selection, I examined the extent to which vegetation surrounding nests differed from what was available in the plot and used this as an indicator of selection. First, I averaged (a) nest vegetation characteristics for each species within the plot and (b) vegetation characteristics at random locations. Plots with vegetation data for fewer than two nests of a given species were omitted from analysis.

Second, I performed a single principal components analysis on *both* nest and random vegetation characteristics at the plot scale. The first principal component

explained 30.0% of the total variance in vegetation characteristics (Table 3.2, Figure 3.1). The first component loaded positively with height and density of groundcover, and increasing percent of ground covered by forbs and shrubs. This was interpreted as the gradient from short, open groundcover to tall, dense, cover, and is hereafter termed “groundcover density.” The second principal component explained 21.8% of the variation in vegetation characteristics. Low stem density and number of trees, and increasing distance from trees weighed heavily into this second component, which was interpreted as decreasing structural complexity. To aid in interpretation and maintain consistency with variables used to examine daily nest survival rates, I transformed this component by multiplying the component scores by -1 in order to reverse the gradient. Therefore, this component described increasing structural complexity (hereafter, “structural complexity”). I restricted further analysis to these two components because they explained the majority of variation in habitat structure and allowed for a comparison to similar components used analysis of nest survival rates.

Third, I subtracted the component scores assigned to nest vegetation at a given plot from the value assigned to random vegetation at that same plot. For example, if groundcover density at Field Sparrow nests had a component score of 0.346 for a given plot, and groundcover density of randomly available vegetation in that same plot had a component score of 2.342 (i.e. more dense than nest sites), I subtracted 0.346 from 2.342. The difference represented the direction and extent to which nest site vegetation differed from randomly available habitat. For groundcover, positive differences indicated that nest sites were less dense than randomly available, whereas

negative differences indicated that nest sites were more dense than random. For structural complexity, a positive difference indicated selection of nest sites that were less structurally complex than available. In this way, I accounted for variation in vegetation among plots and determined the degree to which birds selected particular habitat features.

#### *Constructing the base/null model for nest site selection*

When examining patterns of nest-site selection, I analyzed groundcover density and structural complexity separately for Field Sparrow and Song Sparrow. As with daily nest survival, I used a staged analysis to examine how nest sites deviated from available habitat, whereby I first examined support for an effect of year on nest-site selection patterns, and then evaluated the ability of seven models containing measures of predator activity to explain how nest-site vegetation deviated from available. Linear models were fit using a normal distribution. Using identical datasets, these model sets were run separately for groundcover and structural complexity.

For the Field Sparrow, I found little evidence of temporal variation in nest-site selection for either groundcover (intercept-only model:  $\Delta AIC_c = 0$ , year model:  $\Delta AIC_c = 2.23$ ) or structural heterogeneity (intercept-only model:  $\Delta AIC_c = 0$ , null model:  $\Delta AIC_c = 2.17$ ), and therefore did not include “year” as a term in subsequent models (Table 3.3).

For the Song Sparrow, I found support for a year effect on both groundcover density (year model:  $\Delta AIC_c = 0$ , intercept-only model:  $\Delta AIC_c = 1.49$ ) and structural



complexity (year model:  $\Delta AIC_c = 0$ , intercept-only model:  $\Delta AIC_c = 1.55$ ) selection (Table 3.3). Thus, to account for this effect, year was included in the modified null model when examining how vegetation at Song Sparrow nests deviated from random in relation to predator activity.

#### *Evaluating nest site selection in relation to predator activity*

I used  $AIC_c$  to rank seven *a priori* candidate models containing the modified base model, where applicable, and predator covariates to determine what best explained the difference between random and nest site (a) groundcover density, and (b) structural complexity. Linear models with a normal distribution were used, and the same model set was run separately for Field and Song Sparrow.

## **Results**

### *Overview of daily survival*

A total of 215 nests were found during the two-year study period. Of those, 206 with known fates and non-weather related failures were considered for analysis (116 Field Sparrow, 70 Song Sparrow, 12 Savannah Sparrow, and 8 Eastern Meadowlark). Daily survival rates ranged from 0.734 +/- 0 SE to 1.0 +/- 0 SE across plots with at least two nests, and ranged from 0.939 +/- 4.37E-18 (Field Sparrow) to 0.966 +/- 9.66E-18 (Savannah Sparrow; Table 3.4) across species.

#### *Daily survival rates – plot scale*

After accounting for site-level variation, Field Sparrow daily survival rate was best explained by and positively associated with snake activity ( $\omega_i = 0.311$ , Table 3.5). The model containing randomly available groundcover density was also supported ( $\Delta AIC = 0.670$ ,  $\omega_i = 0.222$ ); Field Sparrow daily survival rates tended to increase as groundcover density increased, but the relationship was relatively weak ( $\beta = 0.034$ ;  $SE = 0.018$ ; 95% CI: -0.001, 0.068). Song Sparrow DSR was also best explained by snake activity ( $\omega_i = 0.544$ , Table 3.5), but survival rates decreased as snake activity increased. No other models were supported.

#### *Daily survival rates – site scale*

The most important variable predicting daily survival rates of Field Sparrow at the site scale was groundcover density (Table 3.5), and no other models were competitive. Field Sparrow DSR increased an estimated 17.40% across the range of groundcover density observed at all sites. Structural complexity best explained Song Sparrow DSR, with nest survival increasing 13.56% from the lowest observed structural complexity to the highest. There was support for a negative relationship between activity between mesopredators and Song Sparrow DSR, and, interestingly, a positive relationship with activity of cowbirds.

### *Nest site selection*

Field Sparrows selected for significantly less dense groundcover ( $t = -2.130$ ,  $df = 36.624$ ,  $p = 0.040$ ) and greater structural complexity ( $t = -2.917$ ,  $df = 36.716$ ,  $p = 0.006$ ) than Song Sparrows.

Both species showed some evidence of adjusting nest-site selection, particularly relative to groundcover, based on activity of potential predators within a plot. As mesopredator activity increased, Field Sparrow selected for nest sites that were more dense than available (Table 3.6, Figure 3.2). As cowbird activity increased, Song Sparrow selected nest sites that were less dense than available (Table 3.6, Figure 3.3). No other models were included in the top model set.

I found little evidence that Field Sparrows adjusted selection of structural complexity in response to predator activity (Table 3.7). While models containing activity of avian predators and small mammals were equally plausible as the intercept-only model, confidence intervals of both predator covariates overlapped zero. Likewise, the null model containing only the effect of year best explained the variation between structural complexity at random and Song Sparrow nest sites.

### **Discussion**

Activity of predators, particularly snakes and cowbirds, was linked to nest survival and nest site selection of both Field and Song Sparrows in urban parks, though some relationships were counterintuitive and not supportive of my original hypothesis. Whereas survival of Song Sparrow nests declined with increasing snake activity, nest

survival of Field Sparrow rose. At the site scale, nest survival rates of Field Sparrow improved on plots with denser groundcover, while nest survival rates of Song Sparrow increased with increasing structural complexity. There was little evidence that species selected for structural complexity at nest sites based on predator activity. Composition of groundcover at nest sites in relation to random sites, however, was weakly linked to activity of both mesopredators and cowbirds.

Consistent with other studies, my results suggest that snakes can depress nest survival for Song Sparrows. Snakes are often the most frequently observed predators of grassland and shrubland bird nests (Morrison and Bolger 2002, Thompson and Burhans 2003), and are known to reduce nesting success in openland systems (Zimmerman 1984, Sperry *et al.* 2008, Klug *et al.* 2010). In particular, garter snakes (*Thamnophis radix*, *T. sirtalis*), which represent 90% of the snakes encountered in my study, likely take large numbers of Song Sparrow eggs and nestlings (Nice 1937). The apparent nest-site preferences of Song Sparrows (i.e., dense groundcover) may have increased their vulnerability to predation by snakes, which were encountered most often in dense vegetation.

The observed positive association between nest survival of Field Sparrows and activity of snakes was unexpected, as snakes have been reported as a dominant predator of Field Sparrow nests (Best 1978, Thompson and Burhans 2003). However, the species of snakes most commonly reported to prey on Field Sparrow nests (blue racer [*Coluber constrictor*], kingsnake [*Lampropeltis sp.*], black rat snake [*Elaphe obsoleta*]; Best 1978, Thompson and Burhans 2003) were absent from this system.

While it is unlikely that snakes directly improved nest success, high snake abundance could indirectly benefit nest survival where snakes suppress activity of other predators, such as small mammals (Ritchie and Johnson 2009). A post-hoc analysis accounting for habitat heterogeneity showed a moderately significant ( $\beta = -0.013$ ,  $p = 0.08$ ) decline in small mammal activity as snake activity increased, and notably, capture rates of small mammals showed a weak negative association with nest survival of Field Sparrows. Although garter snakes only occasionally consume small mammals (Gregory *et al.* 1980), small mammals might avoid areas with high levels of snake activity (Fulk 1972, Wolff *et al.* 1999, Jacob and Brown 2000). On the other hand, the absence of a positive relationship between snakes and nest survival of Song Sparrows suggests that latent habitat or landscape attributes may have contributed to the patterns detected for Field Sparrow.

At the site scale, habitat structure seemed to contribute strongly to nest survival. Increasing density of groundcover improved daily nest survival rates of the Field Sparrow, and high structural complexity was associated with higher Song Sparrow nest survival. These results are consistent with other studies linking groundcover density to improved nest success in grassland birds (Best and Stauffer 1980, Camp and Best 1994, Kershner and Bollinger 1996). Dense vegetation and high structural complexity may result in increased food availability (Klute 1994) or lower predator abundance (Klug *et al.* 2009), either of which can improve reproductive success (Zanette *et al.* 2006). Structurally complex habitats also may increase the number of potential nest sites a predator must search for prey, resulting in reduced

predator foraging efficiency and lower predation rates (potential-prey-site hypothesis; Martin 1993*b*, Chalfoun and Martin 2009). Additionally, dense groundcover provides greater concealment, which can reduce predation in some habitats (Martin 1992, Wilson and Cooper 1998, Aguilar *et al.* 2008), but not all (Colwell 1992, Rivers *et al.* 2003).

The observed shift in groundcover density at nest sites in relation to predator activity has the potential to improve nest survival of both Field and Song Sparrow. Field Sparrows selected for greater groundcover density than random as mesopredator activity increased, which could benefit nest success, as their daily survival rates were positively associated with density of groundcover at the plot scale. Given that mesopredators incidentally prey on grassland nests (Vickery *et al.* 1992, Newbury and Nelson 2007), they may be less likely to encounter a nest where vegetation is dense and impedes or discourages foraging. Indeed, Bowman and Harris (1980) provide experimental evidence that increased heterogeneity of groundcover reduces raccoons' ability to locate nests. Notably, however, the density of groundcover at Field Sparrow nests remained similar across the range of mesopredator activity (Figure 3.2), whereas random groundcover density decreased with increasing mesopredator activity. Therefore, Field Sparrows may demonstrate a preference for a specific density of groundcover, regardless of mesopredator activity.

Low density of groundcover on plots was positively associated with nest survival of Song Sparrow; therefore, responding to cowbird activity by selecting nest sites with low groundcover density may be adaptive in Song Sparrows. Cowbird

activity, which has been negatively linked to nest survival of Song Sparrows (Arcese *et al.* 1996, Smith *et al.* 2003), was lower in areas of low groundcover density, though the response was not strong. Alternatively, low density (i.e. low concealment), could increase the risk of parasitism (Larison *et al.* 1998), and some studies have shown that parasitized nests are more likely than non-parasitized nests to survive until incubation (Arcese *et al.* 1996, Hauber 2000) or fledging (Kerns *et al.* 2010), though this is not always the case (e.g. Braden *et al.* 1997, Davis and Sealy 1998, Hannon *et al.* 2009). Interestingly, both Field and Song Sparrow nest survival responded positively to cowbird activity at large scales in this study.

Neither Field nor Song Sparrow modified their selection of structural complexity at nest sites in relation to predator activity. Notably, activity of snakes, small mammals, mesopredators, and avian predators was not linked to structural complexity, suggesting that there would be little advantage to adjusting selection of complexity at nest sites. Cowbird activity, however, increased with increasing structural complexity. Though cowbird activity has been shown to reduce survival rates in some studies (Arcese *et al.* 1996, Smith *et al.* 2003), it did not influence nest survival at the plot scale in this system, and in fact, was positively linked to survival at the site scale. In sum, the reproductive advantages of selecting structural complexity of nest sites based on predator activity may be minimal, thus the lack of support for an influence of predators on structural complexity of nest sites.

This study illustrates that both predator activity and habitat heterogeneity may influence reproductive success of openland birds at different scales. At the large scale,

managing for dense groundcover comprised largely of forbs may promote nest survival. Predator activity, on the other hand, was also associated with nest survival at local scales, and therefore should be considered when making decisions regarding target/priority areas. There was some support that Field and Song Sparrow avoid predator activity via shifts in nest site selection; however, other studies provide evidence that avoidance may occur during territory selection (Norrdahl and Korpimäki 1998, Fontaine and Martin 2006, Chapter 2). Ultimately, both habitat heterogeneity and predator activity need to play role in management decisions, especially where openland birds are faced with novel nest predators.



Model	k	AIC	AIC <sub>C</sub>	ΔAIC <sub>C</sub>	ω <sub>i</sub>
<i>Spatio-temporal variation - Plot level</i>					
Site	4	-51.19	-49.94	0.00	0.571
Site + Year	5	-49.63	-47.70	2.25	0.186
Intercept-only	1	-46.86	-46.75	3.19	0.116
Site * Year	8	-51.12	-45.97	3.97	0.078
Year	2	-45.39	-45.04	4.90	0.049
<i>Temporal variation - Site level</i>					
Intercept-only	1	-35.47	-34.80	0.00	0.861
Year	2	-33.56	-31.16	3.64	0.139

Table 3.1. Creation of the base model for ranking daily survival rates at the plot and site level: Candidate models including spatio-temporal factors at the plot scale and temporal factors at the site scale, as ranked using Akaike Information Criterion.

	Groundcover density	Structural complexity (original)	Structural complexity (transformed)
<b><i>Eigenvalue</i></b>	3.000	2.184	2.184
<b><i>Proportion of variance</i></b>	0.300	0.218	0.218
Distance.Shrub	-0.311	0.291	-0.291
Distance.Tree	-0.253	0.351	-0.351
Stem.Density	0.217	-0.407	0.407
Grass	-0.377	-0.146	0.146
Forb	0.374	0.194	-0.194
Shrub	0.344	-0.298	0.298
Marsh	0.116	0.415	-0.415
Tree.Count	0.208	-0.321	0.321
Veg.Height	0.397	0.305	-0.305
Veg.Density	0.422	0.333	-0.333

Table 3.2. Eigenvalues, proportion of variance, and loadings for the first two principal components on nest site and random vegetation at the plot level. Loadings of PC2 (structural complexity) were transformed (i.e. multiplied by -1) for analysis, in order to maintain the gradient from low structural complexity to high.

Model	k	AIC	AIC <sub>C</sub>	ΔAIC <sub>C</sub>	ω <sub>i</sub>
<b><i>Field Sparrow</i></b>					
<i>Groundcover</i>					
Intercept-only	1	62.03	62.14	0.00	0.753
Year	2	64.03	64.37	2.23	0.247
<i>Structural complexity</i>					
Intercept-only	1	62.03	62.12	0.00	0.748
Year	2	64.03	64.29	2.17	0.252
<b><i>Song Sparrow</i></b>					
<i>Groundcover</i>					
Year	2	43.60	43.94	0.00	0.678
Intercept-only	1	45.32	45.43	1.49	0.322
<i>Structural complexity</i>					
Year	2	43.60	43.86	0.00	0.684
Intercept-only	1	45.32	45.40	1.55	0.316

Table 3.3. Creation of the base model for ranking the difference between random and nest groundcover density for Field Sparrow and Song Sparrow. Candidate models include only temporal factors for explaining the difference between random and nest groundcover density, as ranked using Akaike Information Criterion.

Site	Dist (m)	Plot ID	FISP				SOSP				EAME				SAVS				
			2009		2010		2009		2010		2009		2010		2009		2010		
			n	DSR	n	DSR	n	DSR	n	DSR	n	DSR	n	DSR	n	DSR	n	DSR	
CT	100	1100			4	1.000			2	0.940									
		2100			2	0.951			2	0.960									
	300	1300			7	0.903	2	1.000											
		2300			2	1.000	2	1.000	6	0.984									
	500	1500	3	1.000	2	1.000													
		2500			5	0.981	3	0.966											
1000	1K	5	0.937	4	0.915	2	1.000												
NW	100	1100	7	0.942	6	0.965			2	0.962									
		2100	5	0.838	8	0.980			3	0.981									
	300	1300			5	0.951													
		2300	3	0.949	7	0.968													
	500	1500							2	1.000									
		2500																	
1000	1K			3	0.964			4	0.920										
PC	100	1100									2	1.000							
		2100					2	0.904	4	0.896	2	0.939							
	300	1300											2	0.894	5	0.978			
		2300							3	0.926									
	500	1500			2	0.887	2	1.000	2	0.976			2	1.000	2	0.882			
		2500	2	0.841	3	0.876			5	0.940									
1000	1K																		
PV	100	1100			2	0.887													
		2100																	
	300	1300			2	0.760													
		2300			2	0.955			2	0.949									
	500	1500	3	0.881	7	0.894	3	0.962											
		2500	3	1.000	3	0.908													
1000	1K					4	0.937	2	0.832										

Table 3.4. Summary of the number of nests found on each plot during 2009 and 2010, including daily survival rates (DSR) for plots with at least two nests. All standard errors are <0.0001.

Model	k	AIC	AIC <sub>c</sub>	ΔAIC <sub>c</sub>	ω <sub>i</sub>	β	β SE	95% CI		
<i>Plot scale</i>										
<i>Field sparrow</i>										
Snakes	5	-29.82	-26.49	0.00	0.311	0.032	0.016	<b>0.001</b>	-	<b>0.064</b>
Groundcover density	5	-29.15	-25.82	0.67	0.222	0.034	0.018	0.001	-	0.068
Null	4	-27.04	-24.93	1.55	0.143	-	-	-	-	-
<i>Song sparrow</i>										
Snakes	5	-70.42	-64.96	0.00	0.544	-0.008	0.003	<b>-0.014</b>	-	<b>-0.002</b>
<i>Site Scale</i>										
<i>Field sparrow</i>										
Groundcover density	2	-33.656	-31.256	0.000	0.772	0.0474	0.0113	<b>0.0253</b>	-	<b>0.0695</b>
<i>Song sparrow</i>										
Structural complexity	2	-32.631	-29.631	0.000	0.378	0.0319	0.0114	<b>0.0095</b>	-	<b>0.0543</b>
Mesopredators	2	-31.330	-28.330	1.302	0.197	-0.6030	0.2548	<b>-1.1024</b>	-	<b>-0.1036</b>
Cowbirds	2	-30.665	-27.665	1.966	0.141	0.0586	0.0272	<b>0.0053</b>	-	<b>0.1119</b>

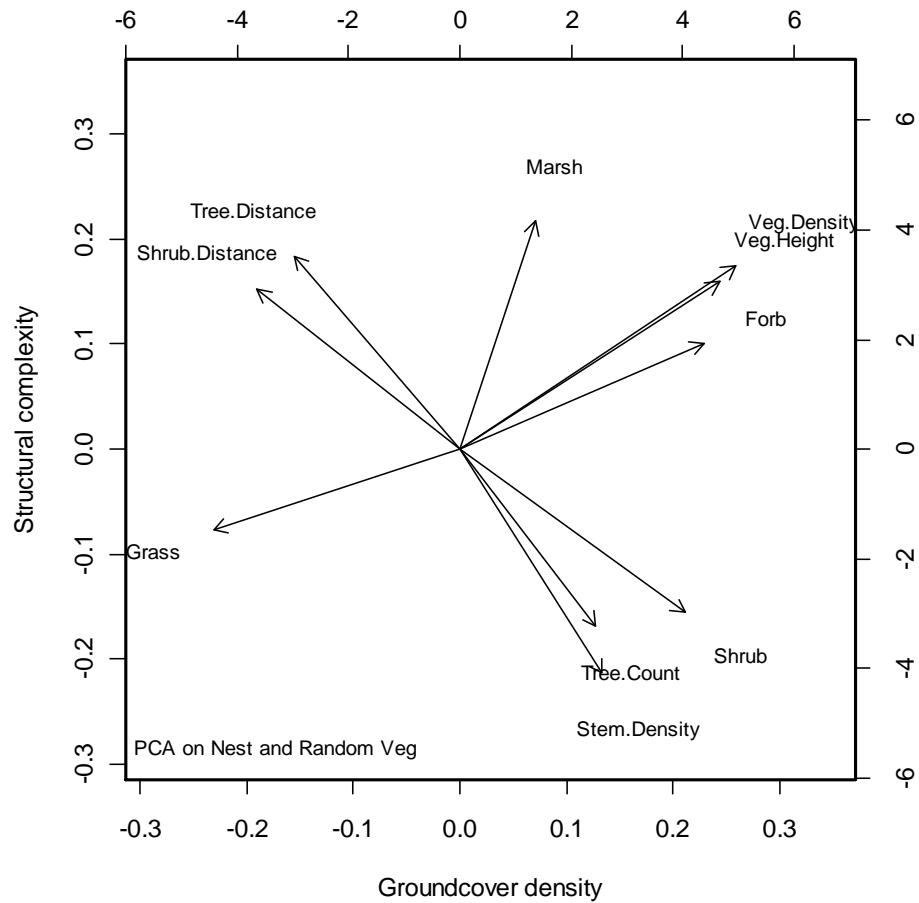
Table 3.5. Daily survival rate (DSR) models for DSR of Field Sparrow and Song Sparrow at both the plot and site scales. At the plot level, the modified null model accounts for site-level variation. Table includes, ω<sub>i</sub>, parameter estimates, standard errors of parameter estimates, and confidence intervals of parameter estimates. **Boldface** denotes confidence intervals that do not overlap zero. Only competitively ranked models (ΔAIC<sub>c</sub> < 2) are shown.

Model	k	AIC	AIC <sub>C</sub>	ΔAIC <sub>C</sub>	ω <sub>i</sub>	β	β SE	95% CI		
<i>Field sparrow</i>										
Mesopredators	2	61.46	62.21	0.00	0.606	<b>-11.893</b>	<b>5.218</b>	<b>-22.120</b>	-	<b>-1.666</b>
Null	1	64.52	64.76	2.55	0.169	-	-	-	-	-
Small mammals	2	66.21	66.96	4.76	0.056	1.090	2.057	-2.942	-	5.122
Avian predators	2	66.22	66.97	4.77	0.056	-1.117	2.154	-5.338	-	3.104
Snakes	2	66.23	66.98	4.78	0.056	0.096	0.187	-0.271	-	0.463
Cowbird	2	66.37	67.12	4.92	0.052	-0.158	0.434	-1.008	-	0.691
Snakes + Cowbirds + Avian predators + Small mammals + Mesopredators	6	64.51	71.51	9.31	0.006	Snakes 0.046 Cowbirds -0.514 Avian -1.143 Small mammal 4.064 Mesopredator -15.266	0.178 0.439 2.087 2.155 5.793	-0.303 -1.375 -5.234 -0.159 -26.621	-	0.394 0.347 2.948 8.287 -3.912
<i>Song sparrow</i>										
Cowbird	3	49.28	51.68	0.00	0.589	<b>1.286</b>	<b>0.566</b>	<b>0.177</b>	-	<b>2.396</b>
Null	2	52.67	53.76	2.08	0.208	-	-	-	-	-
Snakes	3	53.83	56.23	4.55	0.061	0.190	0.230	-0.261	-	0.641
Mesopredators	3	54.03	56.43	4.75	0.055	-9.258	12.917	-34.575	-	16.059
Small mammal	3	54.38	56.78	5.10	0.046	1.525	3.184	-4.715	-	7.765
Avian predators	3	54.61	57.01	5.32	0.041	-1.068	4.749	-10.375	-	8.239
Snakes + Cowbirds + Avian predators + Small mammals + Mesopredators	7	54.60	73.26	21.58	0.000	Snakes 0.092 Cowbirds 1.323 Avian -3.727 Small mammal 0.761 Mesopredator -11.428	0.281 0.672 5.011 3.761 13.180	-0.459 0.006 -13.549 -6.610 -37.260	-	0.643 2.641 6.095 8.133 14.405

Table 3.6. Nest site selection models for predicting the difference between density of available groundcover and groundcover at nest sites. For Song sparrow, modified null model contains year effect. Table includes, ω<sub>i</sub>, parameter estimates, standard errors of parameter estimates, and confidence intervals of parameter estimates. **Boldface** denotes confidence intervals that do not overlap zero. A positive β indicates that as predators increased, birds exhibited stronger selection for nest sites with less dense groundcover than available. A negative β shows they selected denser groundcover with increasing predators.

Model	k	AIC	AIC <sub>C</sub>	ΔAIC <sub>C</sub>	ω <sub>i</sub>		β	β SE	95% CI	
<i>Field sparrow</i>										
Null	1	62.03	62.27	0.00	0.314		-	-	-	-
Avian predators	2	62.05	62.80	0.53	0.240		2.639	1.930	-1.143	- 6.420
Small mammals	2	63.07	63.82	1.55	0.144		-1.780	1.894	-5.492	- 1.932
Cowbird	2	63.68	64.43	2.16	0.107		-0.230	0.404	-1.021	- 0.562
Snakes	2	63.78	64.53	2.26	0.101		-0.084	0.175	-0.428	- 0.260
Mesopredators	2	63.94	64.69	2.42	0.093		-1.623	5.570	-12.541	- 9.294
Snakes + Cowbirds + Avian + Small mammals + Mesopredators	6	67.94	74.94	12.67	0.001	{	Snake	-0.124	0.195	-0.505 - 0.258
							Cowbirds	0.067	0.481	-0.876 - 1.009
							Avian	2.907	2.284	-1.570 - 7.384
							Small mammal	-2.355	2.358	-6.977 - 2.266
							Mesopredator	-1.693	6.339	-14.119 - 10.732
<i>Song sparrow</i>										
Null	2	43.60	44.69	0.00	0.356		-	-	-	-
Mesopredators	3	43.13	45.53	0.84	0.234		-12.753	8.752	-29.907	- 4.402
Avian predators	3	43.84	46.24	1.54	0.165		3.930	3.233	-2.406	- 10.266
Small mammals	3	44.89	47.29	2.60	0.097		1.719	2.268	-2.727	- 6.165
Cowbirds	3	45.29	47.69	3.00	0.080		-0.244	0.491	-1.206	- 0.719
Snakes	3	45.60	48.00	3.31	0.068		-0.002	0.171	-0.337	- 0.334
Snakes + Cowbirds + Avian + Small mammals + Mesopredators	7	46.65	65.32	20.63	0.000	{	Snakes	-0.029	0.212	-0.444 - 0.385
							Cowbirds	-0.458	0.506	-1.449 - 0.534
							Avian	3.249	3.773	-4.147 - 10.645
							Small mammal	2.840	2.832	-2.711 - 8.391
							Mesopredator	-13.411	9.925	-32.864 - 6.041

Table 3.7. Nest site selection models for predicting the difference between structural complexity at random locations and complexity at nest sites. For Song sparrow, modified null model contains year effect. Table includes, ω<sub>i</sub>, parameter estimates, standard errors of parameter estimates, and confidence intervals of parameter estimates. **Boldface** denotes confidence intervals that do not overlap zero. A positive β indicates that as predators increased, birds more strongly selected nest site with lower structural complexity. A negative β shows they selected for greater complexity with increasing predators.



PC1: Increasing groundcover density



- Low density

+ High density

PC2: Increasing structural complexity (*after transformation*)



(b) - Low complexity

+ High complexity

Figure 3.1. Interpreting principal components at the site scale: (a) biplot of first two principal components, and (b) illustration of the habitat gradient represented by the first two components, after transforming (i.e. reversing) PC2 (structural complexity) loadings.



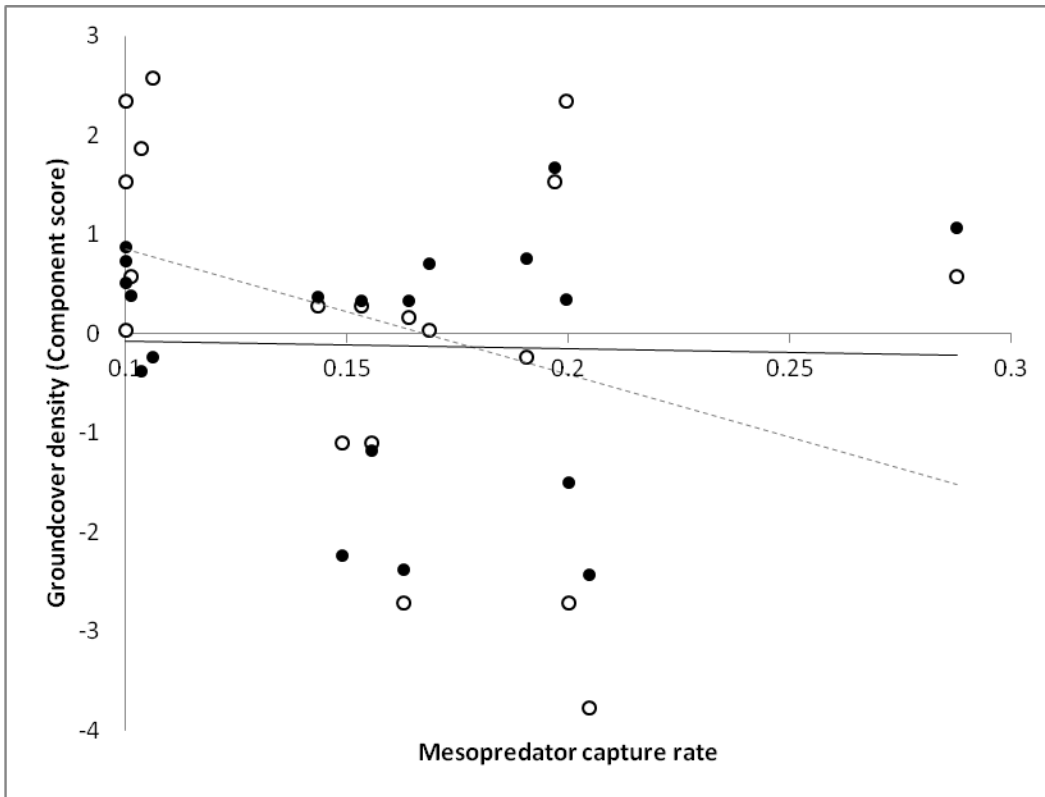


Figure 3.2. Graph shows how random groundcover density (open circles; dashed line:  $\beta = -12.66$ ,  $SE = 8.175$ , 95% CI:  $-29.907, 4.587$ ) and groundcover density at Field Sparrow nest sites (black circles; solid line:  $\beta = -0.767$ ,  $SE = 6$ , 95% CI:  $-13.433, 11.900$ ) change with increasing mesopredator capture rates.

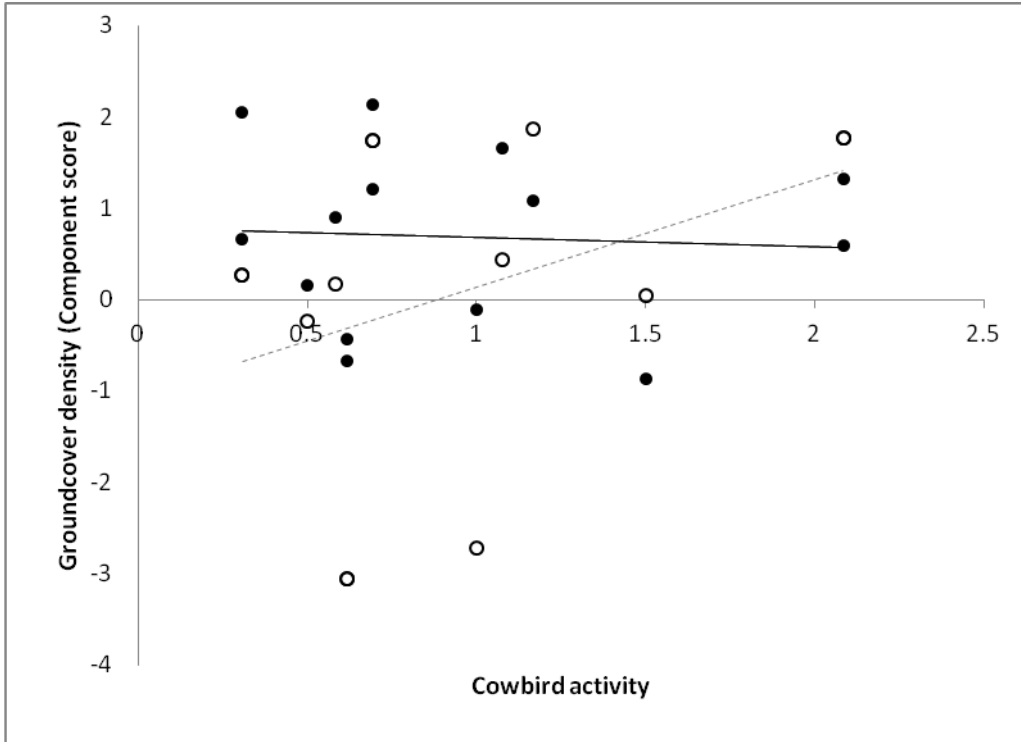


Figure 3.3. Graph shows how random structural complexity (open circles; dashed line:  $\beta = 1.171$ ,  $SE = 0.822$ , 95% CI: -0.621, 2.963) and structural complexity at Song Sparrow nest sites (black circles; solid line:  $\beta = -0.104$ ,  $SE = 0.478$ , 95% CI: -1.145, 0.936) change with increasing cowbird encounter rates, i.e. activity.

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## APPENDIX A

Layout of each study site, including location of mesopredator feeding station and boundaries of 2-ha plots. Mesopredator feeding stations were established between October 2009 and March 2010 as part of a larger study of population dynamics of mesocarnivores. A shelter including a continuous supply of dry cat food and fresh water was made available to resident mesocarnivores, including eight feral cats (*Felus catus*) that were radio-collared and released at each site upon establishment. Photo and video surveillance cameras recorded activity at each feeding station. Cats that dispersed from the site continued to be tracked, and, when available, replacements were released on site.

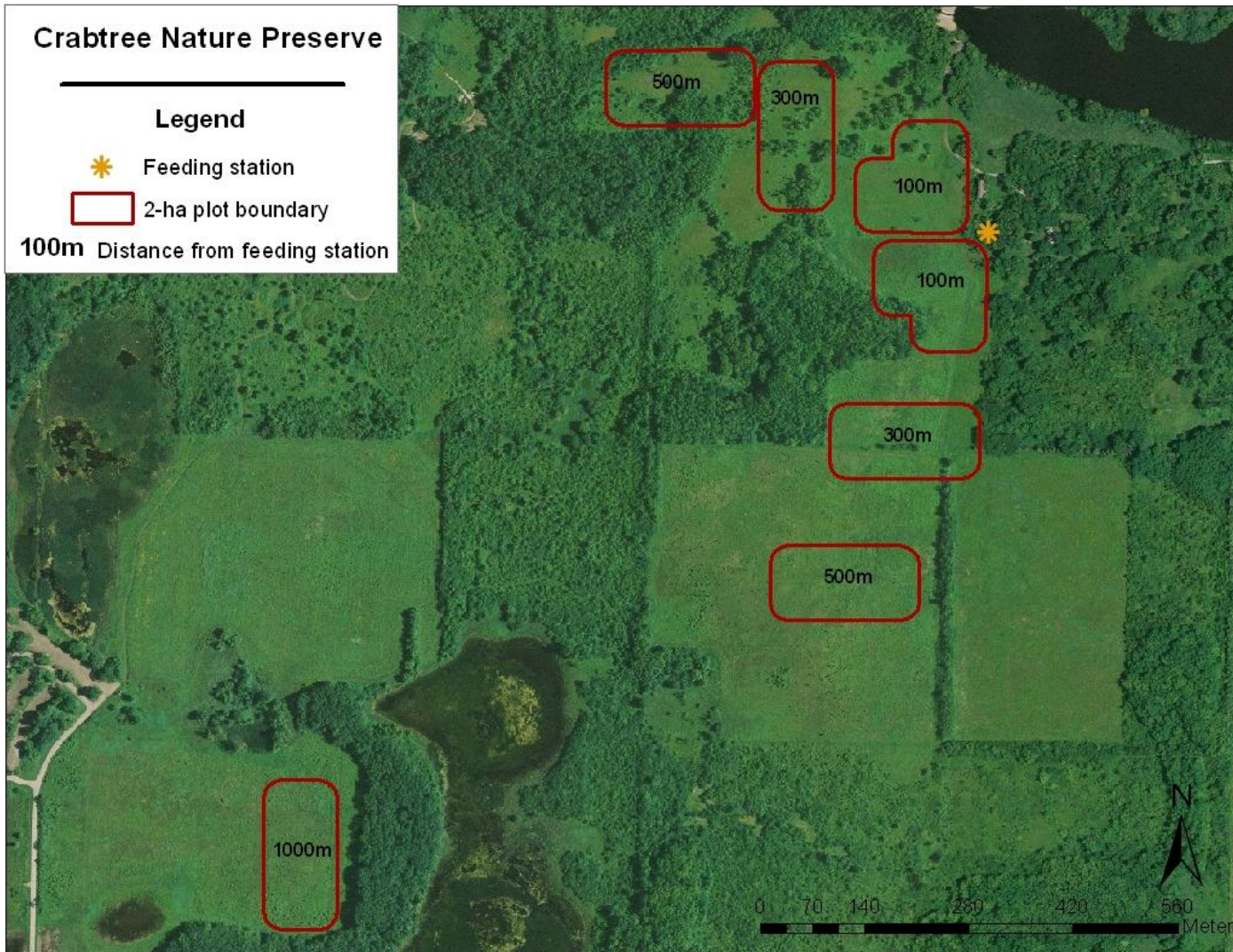
# Crabtree Nature Preserve

## Legend

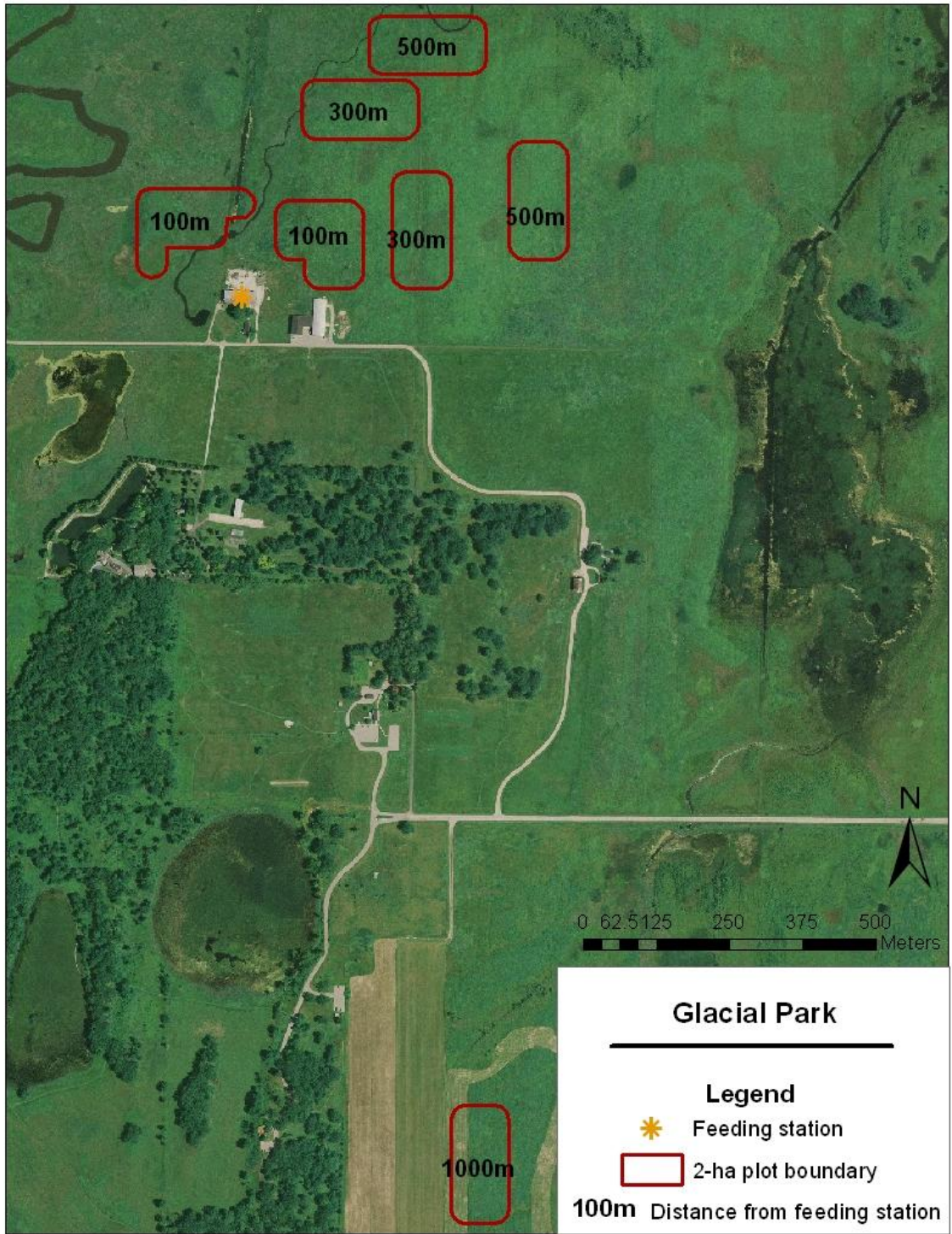
 Feeding station

 2-ha plot boundary

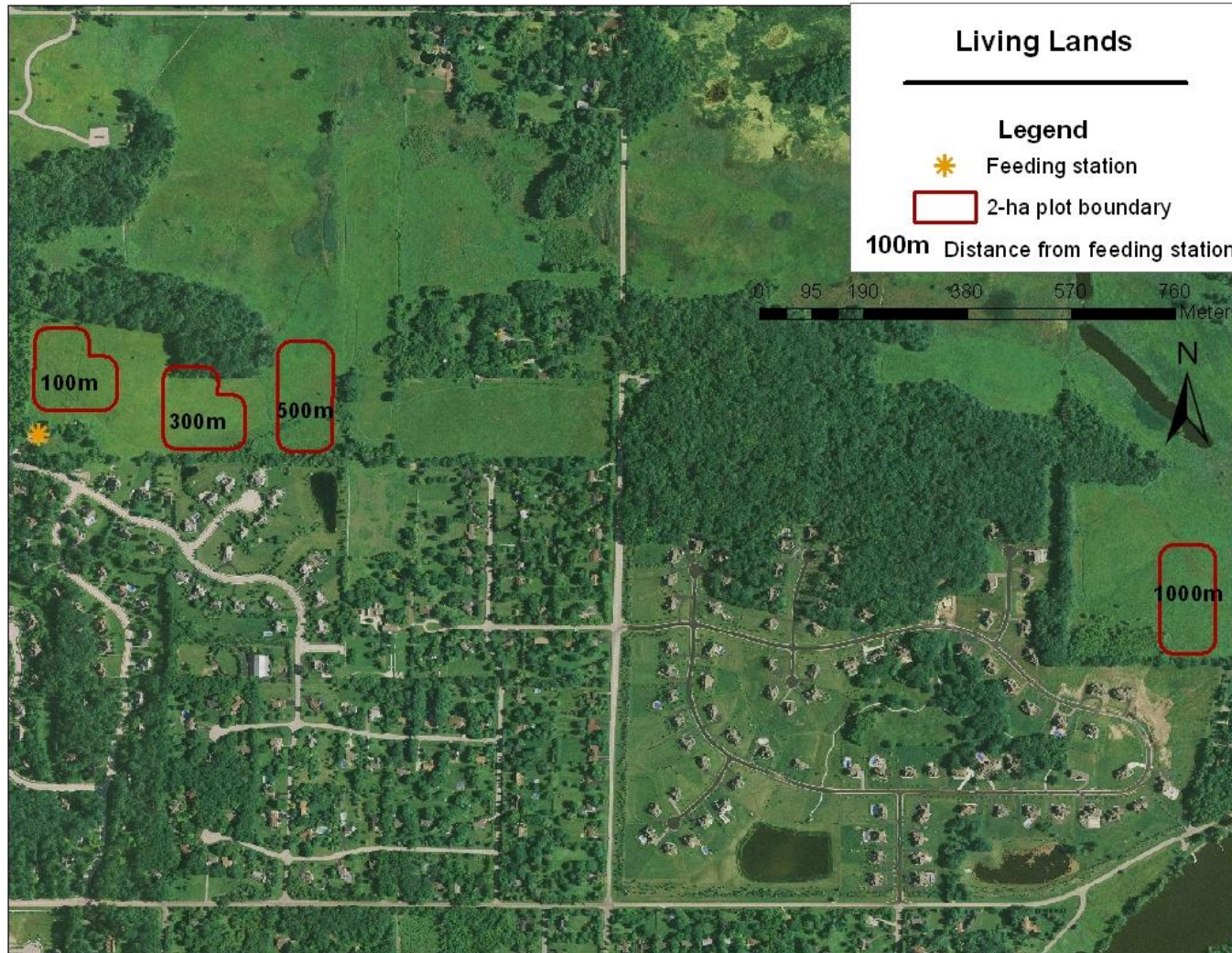
**100m** Distance from feeding station



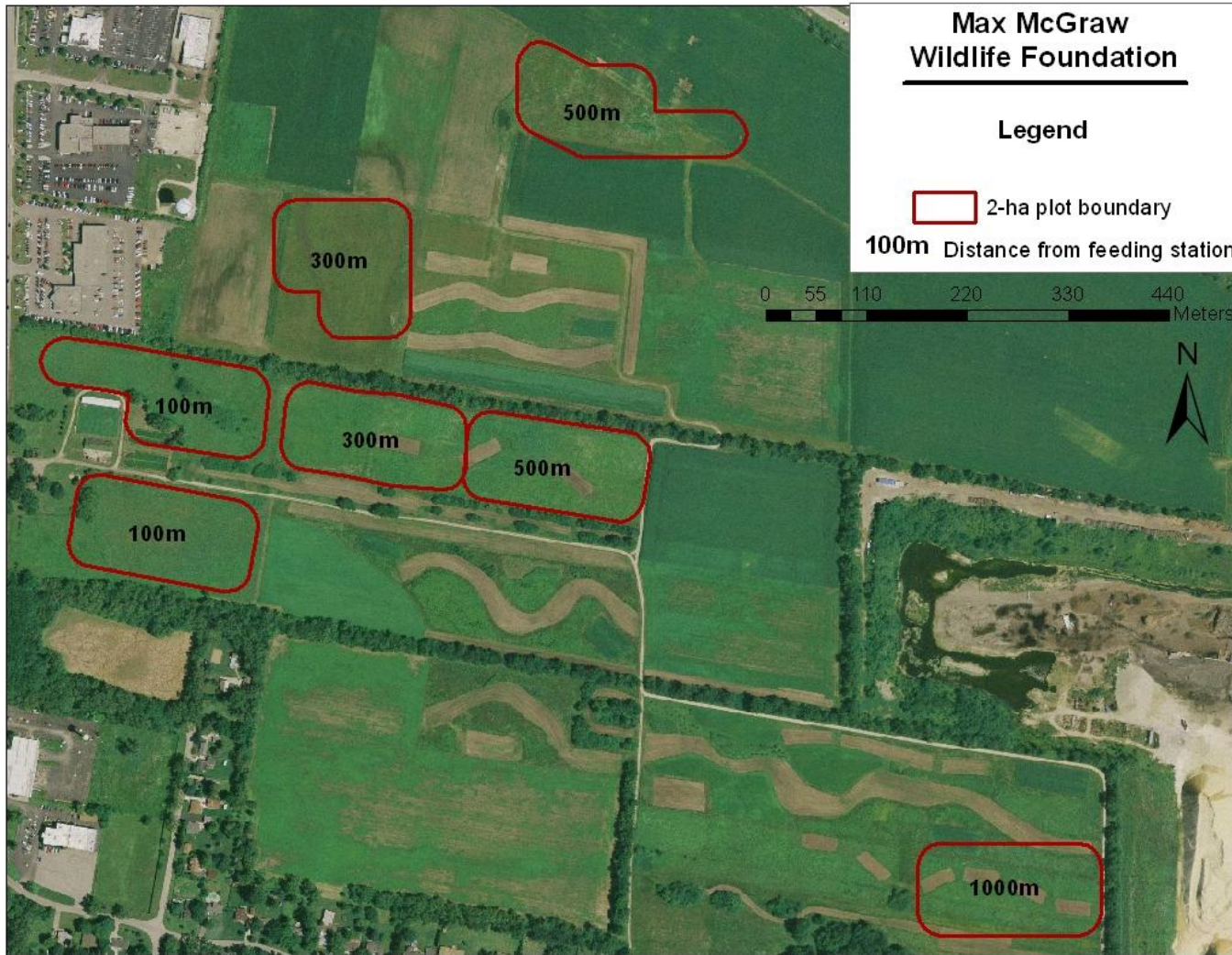




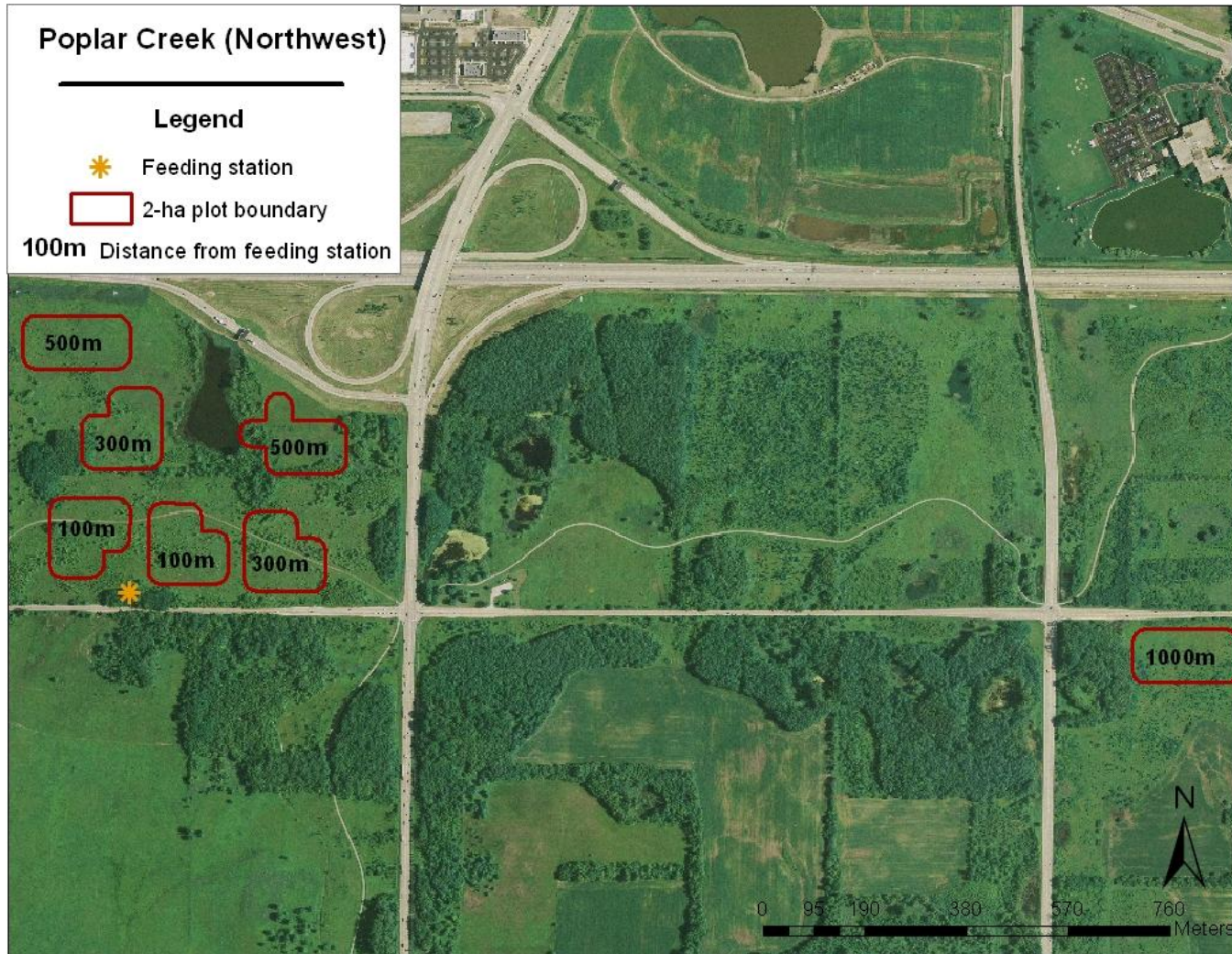




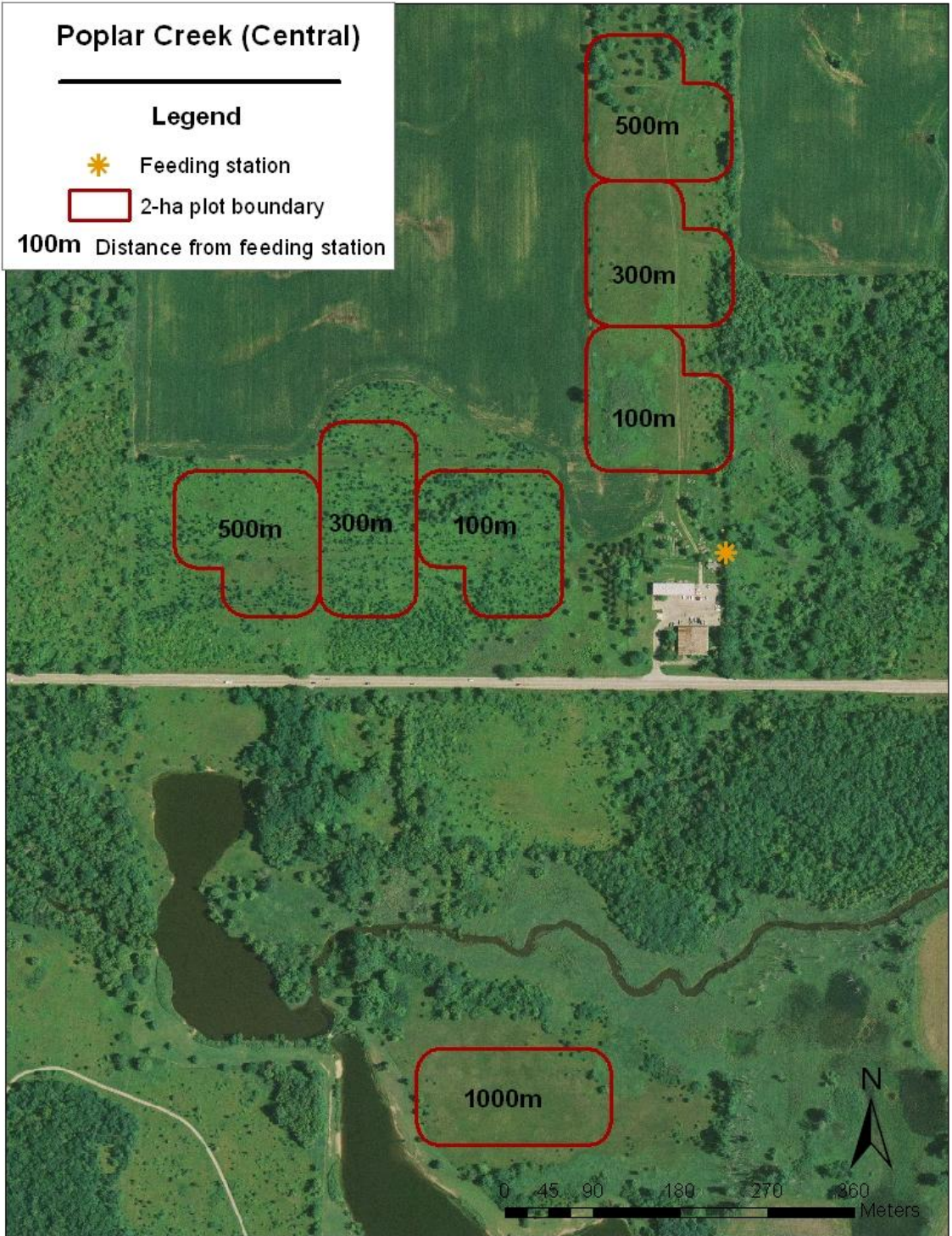
















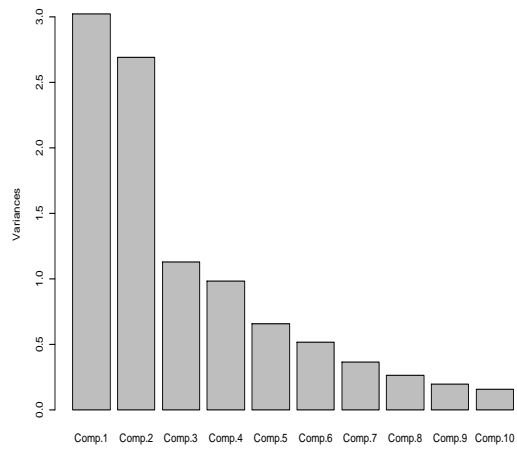
## APPENDIX B:

Summary of results from principal components analyses (PCA) on vegetation measurements taken at random locations within each plot. Results include (a) eigenvalues of each component and weights of associated variables, (b) screeplot of eigenvalues, and (c) biplot graph of loadings.

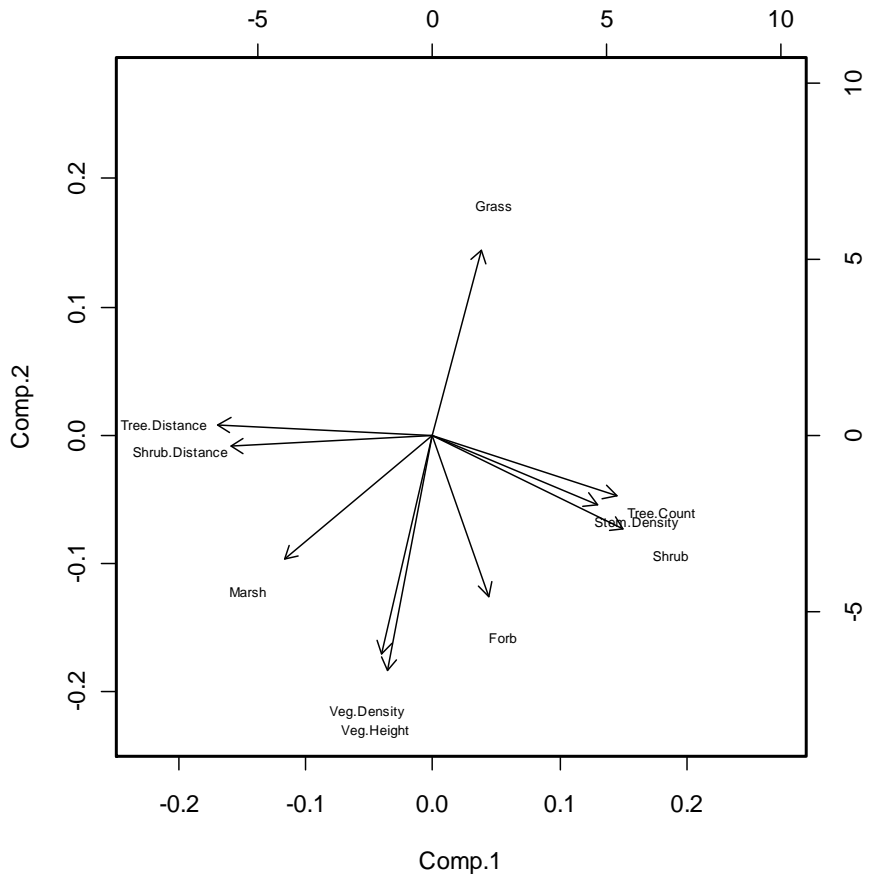
(a)

	Comp. 1	Comp. 2	Comp. 3	Comp. 4	Comp. 5	Comp. 6	Comp. 7	Comp. 8	Comp. 9	Comp. 10
<b><i>Eigenvalue</i></b>	3.023	2.695	1.129	0.982	0.660	0.518	0.367	0.266	0.200	0.160
<b><i>Proportion of variance</i></b>	0.302	0.269	0.113	0.098	0.066	0.052	0.037	0.027	0.020	0.016
Shrub.Distance	-0.435	-0.027	-0.336	-0.185	-0.325	-0.436	0.239	0.485	-0.168	0.215
Tree.Distance	-0.462	0.023	0.047	-0.417	0.247	-0.145	0.101	-0.635	0.150	0.304
Stem Density	0.353	-0.157	-0.358	-0.417	0.328	-0.329	-0.533	0.032	-0.215	-0.043
Grass	0.104	0.417	-0.089	-0.518	-0.369	0.411	0.105	-0.134	-0.414	-0.183
Forb	0.120	-0.363	0.652	-0.083	-0.033	-0.272	0.181	-0.046	-0.557	0.011
Shrub	0.409	-0.213	-0.128	-0.296	0.321	0.201	0.641	0.209	0.199	0.213
Marsh	-0.320	-0.278	-0.397	0.308	0.363	0.327	0.135	-0.111	-0.529	-0.136
Tree.Count	0.395	-0.138	-0.364	0.304	-0.442	-0.196	0.137	-0.496	-0.082	0.309
Veg.Height	-0.099	-0.531	-0.105	-0.210	-0.284	-0.044	0.101	-0.149	0.303	-0.668
Veg.Density	-0.110	-0.494	0.073	-0.158	-0.277	0.500	-0.383	0.126	0.054	0.471

(b)



(c)



## APPENDIX C:

Summary of vegetation characteristics at (1) randomly located and (2) nest  
site vegetation plots

Site	Plot	Nearest shrub	Nearest tree	Tree count plot <sup>-1</sup>	Stem count m <sup>-1</sup>	% Grass	% Forb	% Shrub	% Marsh	Groundcover height	Groundcover density
CT	1100	10.19 (2)	65.25 (8.01)	0 (0)	0.4 (0.27)	73.75 (9.44)	70 (6.12)	5.5 (4.86)	0 (0)	0.76 (0.06)	0.58 (0.04)
CT	1300	2.28 (0.66)	22.63 (6.7)	10.25 (6.16)	3.61 (1.96)	81.5 (7.84)	36.5 (13.53)	25 (14.58)	0 (0)	1.24 (0.07)	0.67 (0.06)
CT	1500	1.75 (0.57)	15.34 (4.04)	6.5 (3.33)	21.1 (9)	68.75 (5.54)	46.25 (11.06)	21.25 (5.91)	0 (0)	1.14 (0.05)	0.56 (0.05)
CT	1K	1.82 (0.38)	75.69 (7.31)	0 (0)	0.76 (0.12)	83.75 (1.25)	67.5 (9.24)	26.25 (3.15)	4.5 (0.5)	1.01 (0.05)	0.69 (0.04)
CT	2100	5.17 (1.1)	50.41 (8.42)	4.5 (4.5)	0.12 (0.03)	18.75 (14.2)	51.25 (19.62)	5.75 (4.77)	4.75 (3.47)	0.69 (0.05)	0.56 (0.05)
CT	2300	6.63 (1.25)	57.25 (7.44)	0 (0)	0.14 (0.04)	41.25 (24.86)	87.5 (4.33)	5.75 (3.2)	5.5 (4.86)	1.13 (0.03)	0.98 (0.05)
CT	2500	2.43 (0.38)	97.06 (2.03)	0 (0)	0.32 (0.1)	63.75 (9.44)	72.5 (3.23)	17.5 (5.95)	25.5 (10.01)	0.82 (0.04)	0.46 (0.03)
GP	1100	24.7 (6.88)	87.44 (7)	0 (0)	0.01 (0.01)	23.75 (11.06)	42.5 (16.14)	0.75 (0.75)	45 (21.02)	1.01 (0.05)	0.85 (0.03)
GP	1300	70.03 (8.1)	100 (0)	0 (0)	0.01 (0.01)	55 (19.36)	55 (18.48)	0.25 (0.25)	38.75 (21.35)	1.39 (0.05)	1.12 (0.05)
GP	1500	51.62 (9.53)	100 (0)	0 (0)	2.39 (2.39)	28.75 (7.18)	84.75 (5.92)	8.25 (8.25)	2.5 (2.5)	1.39 (0.06)	1.15 (0.06)
GP	1K	1.73 (0.45)	100 (0)	0 (0)	4.69 (2.35)	33 (11.5)	48.75 (13.29)	13.5 (5.68)	10.75 (9.78)	0.84 (0.03)	0.76 (0.03)
GP	2100	95.56 (3.56)	98.94 (1.06)	0 (0)	0 (0)	25 (21.79)	13.75 (4.27)	0 (0)	70 (23.36)	0.83 (0.05)	0.5 (0.03)
GP	2300	52.14 (9.7)	100 (0)	0 (0)	0.01 (0.01)	5 (2.89)	15 (10.07)	0.67 (0.67)	84 (12.06)	1.14 (0.05)	0.9 (0.04)
GP	2500	48.31 (12.25)	100 (0)	0 (0)	0.09 (0.09)	11 (5.57)	58 (17.72)	1.2 (0.97)	46 (14.78)	1.05 (0.05)	0.87 (0.04)
LL	1100	41.11 (8.83)	83.63 (5.78)	0 (0)	0.02 (0.02)	98.25 (0.25)	2.5 (0.5)	0.25 (0.25)	0 (0)	0.57 (0.02)	0.36 (0.01)
LL	1300	38.39 (9.6)	68.31 (8.96)	0.25 (0.25)	0.18 (0.18)	93.5 (3.07)	3.75 (1.38)	1.25 (1.25)	0.75 (0.75)	0.71 (0.04)	0.43 (0.02)
LL	1500	0.86 (0.27)	53.83 (7.01)	0 (0)	10.1 (2.29)	36.25 (13.75)	45 (20.62)	30.5 (18.1)	0.25 (0.25)	0.85 (0.03)	0.71 (0.03)
LL	1K	51.03 (9.39)	84.63 (6.56)	0 (0)	0.01 (0.01)	82.5 (11.81)	11.5 (4.05)	0 (0)	15 (15)	0.77 (0.04)	0.59 (0.03)
MM	1100	11.17 (3.96)	62.69 (6.99)	0 (0)	0.14 (0.07)	60.5 (23.07)	39 (23.16)	1.25 (0.25)	0 (0)	1.15 (0.06)	1.09 (0.07)
MM	1300	5.74 (2.71)	61.38 (8.2)	0 (0)	0.66 (0.17)	18.25 (5.45)	79.25 (5.22)	1.75 (0.63)	0 (0)	0.88 (0.04)	0.73 (0.03)
MM	1500	9.77 (3.19)	54.31 (5.39)	0 (0)	0.14 (0.03)	53.75 (8.51)	47.5 (8.29)	1.5 (0.65)	0 (0)	0.95 (0.05)	0.89 (0.05)
MM	1K	6.33 (1.9)	83.19 (6.31)	0 (0)	0.21 (0.03)	36.5 (13.12)	41.75 (18.39)	1.25 (0.48)	0 (0)	0.66 (0.08)	0.27 (0.05)
MM	2100	1.84 (0.39)	30.24 (4.43)	0.5 (0.29)	1.33 (0.58)	65 (9.57)	47.5 (13.62)	9.5 (3.8)	0.5 (0.29)	0.7 (0.02)	0.62 (0.02)
MM	2300	11.08 (1.65)	93.94 (3.72)	0 (0)	0.02 (0.01)	92 (2.86)	6.75 (2.84)	1 (0.71)	0 (0)	0.59 (0.03)	0.35 (0.01)
MM	2500	66.04 (11.38)	100 (0)	0 (0)	0.03 (0.03)	15 (11.68)	51.75 (23.62)	1.25 (0.48)	0 (0)	1.52 (0.17)	0.52 (0.09)

Continued

Mean and (standard error) of vegetation measurements at random locations within Crabtree Nature Preserve (CT), Glacial Park (GP), Living Lands (LL), Max McGraw Wildlife Foundation (MMWF), Northwest Poplar Creek (NW), Poplar Creek (PC), and Prairieview (PV). Where unit is not specified, data is in meters.

Continued

Site	Plot	Nearest shrub	Nearest tree	Tree count plot <sup>-1</sup>	Stem count m <sup>-1</sup>	% Grass	% Forb	% Shrub	% Marsh	Groundcover height	Groundcover density
NW	1100	1.77 (0.67)	17.85 (3.61)	2 (0.91)	7.33 (3.87)	46.25 (11.43)	48.75 (10.87)	34 (9.84)	0.75 (0.48)	0.82 (0.04)	0.59 (0.04)
NW	1300	7.19 (2.77)	36.75 (8.19)	4.75 (3.54)	5.68 (4.63)	31.25 (11.61)	19.5 (9.19)	27 (10.87)	31.25 (22.96)	1.18 (0.07)	0.97 (0.08)
NW	1500	8.61 (1.47)	76.44 (7.13)	0 (0)	0.27 (0.26)	7.5 (4.33)	29 (13.27)	1.5 (1.19)	87.5 (7.5)	1.09 (0.06)	0.76 (0.05)
NW	1K	17.73 (8.2)	17.81 (3.49)	5.5 (3.2)	0.24 (0.19)	37.5 (20.16)	40.5 (14.61)	2 (1.08)	11.75 (6.3)	0.81 (0.05)	0.72 (0.05)
NW	2100	0.8 (0.14)	13.09 (1.95)	3.75 (1.65)	0.43 (0.05)	38.75 (12.48)	42.5 (4.79)	10 (2.89)	4.5 (3.52)	0.69 (0.05)	0.44 (0.02)
NW	2300	0.82 (0.14)	16.75 (3.68)	2.75 (1.89)	3.59 (1.5)	56.25 (8.98)	50 (4.08)	23.5 (12.61)	2.5 (0.96)	0.68 (0.04)	0.53 (0.06)
NW	2500	24.58 (8.96)	30.69 (5.62)	1.5 (1.5)	2.09 (1.41)	67.5 (16.52)	47.5 (10.1)	30 (17.8)	13.75 (12.14)	1.16 (0.09)	0.75 (0.06)
PC	1100	7.41 (3.88)	63 (6.99)	0 (0)	0.41 (0.22)	28.75 (10.08)	27 (8.26)	7 (4.45)	0.75 (0.48)	0.75 (0.04)	0.25 (0.01)
PC	1300	3.14 (0.54)	73.42 (9.13)	0 (0)	0.97 (0.82)	62.5 (10.31)	31.25 (14.2)	7.25 (3.22)	0.25 (0.25)	0.7 (0.04)	0.33 (0.02)
PC	1500	28 (7.35)	41.75 (9.52)	0.75 (0.75)	0.15 (0.08)	90 (3.54)	16 (9.06)	0.5 (0.29)	1.5 (1.19)	0.57 (0.04)	0.49 (0.04)
PC	1K	25.31 (4.4)	73.88 (7.56)	0 (0)	0.01 (0)	100 (0)	3.75 (3.75)	0.5 (0.5)	0 (0)	0.43 (0.02)	0.35 (0.01)
PC	2100	1.25 (0.21)	5.08 (0.99)	6.25 (2.02)	1.56 (0.29)	22.5 (7.5)	68.75 (4.27)	16.25 (3.75)	1.25 (1.25)	0.9 (0.03)	0.51 (0.03)
PC	2300	16.13 (8.25)	23.11 (7.62)	1.75 (0.85)	0.64 (0.23)	8.75 (3.15)	51.25 (18.3)	10 (4.56)	7.25 (5.95)	0.98 (0.04)	0.54 (0.05)
PC	2500	4.12 (0.89)	12.41 (2.24)	4 (1.47)	0.39 (0.17)	35 (20.72)	60 (19.47)	3 (1.15)	0.25 (0.25)	0.73 (0.03)	0.52 (0.02)
PV	1100	2.38 (0.62)	16.09 (2.57)	0 (0)	0.3 (0.28)	61.25 (20.85)	63.75 (19.83)	9.5 (8.51)	29.75 (23.62)	0.77 (0.06)	0.76 (0.23)
PV	1300	17.44 (4.28)	68.06 (8.75)	0 (0)	0.04 (0.04)	97.25 (2.43)	4.25 (2.14)	0.25 (0.25)	6.5 (4.63)	0.51 (0.03)	0.31 (0.01)
PV	1500	28.77 (10.01)	35.53 (6.42)	1 (0.71)	0.4 (0.25)	71.25 (18.3)	20 (13.69)	1 (0.58)	2.5 (2.5)	0.73 (0.05)	0.32 (0.04)
PV	1K	5.76 (1.48)	19.78 (2.09)	0 (0)	0.27 (0.02)	45 (10.21)	55 (13.07)	2 (0)	9.75 (3.45)	0.81 (0.03)	0.54 (0.03)
PV	2100	2.29 (0.4)	43.08 (7.82)	0.5 (0.29)	0.6 (0.22)	65 (16.83)	57.5 (7.77)	8.25 (2.32)	7.75 (2.78)	1.03 (0.04)	0.81 (0.04)
PV	2300	16.34 (6.18)	39 (9.29)	2.25 (1.93)	0.32 (0.2)	6.25 (4.73)	25 (20)	11.25 (9.66)	88.75 (7.18)	1.25 (0.06)	0.94 (0.94)
PV	2500	34.52 (9.51)	89.63 (4.88)	0 (0)	0.3 (0.28)	61.25 (20.85)	63.75 (19.83)	9.5 (8.51)	29.75 (23.62)	1.01 (0.06)	0.53 (0.03)



Site	Plot	n	Nearest shrub	Nearest tree	Tree count		% Grass	% Forb	% Shrub	% Marsh	Groundcover height	Groundcover density
					plot <sup>-1</sup>	Stem count m <sup>-1</sup>						
CT	1100	2	1.73 (1.28)	33.5 (26.5)	2 (2)	0.17 (0.06)	85 (5)	30 (0)	5.5 (4.5)	0 (0)	0.99 (0.26)	0.5 (0.15)
CT	1300	7	1.35 (0.46)	17.64 (6.59)	1.86 (0.96)	0.72 (0.43)	62.14 (5.1)	50.71 (4.68)	9.57 (6.77)	0 (0)	0.69 (0.07)	0.42 (0.05)
CT	1500	4	0.66 (0.45)	6.1 (2.58)	10.5 (4.92)	1.22 (0.15)	90.75 (2.69)	33.25 (14.54)	16.25 (4.27)	0 (0)	0.92 (0.16)	0.53 (0.02)
CT	1K	5	0.61 (0.13)	31.9 (17.82)	3 (1.38)	5.46 (3.06)	49 (12.29)	56 (8.86)	27 (6.44)	16 (9.67)	1.23 (0.15)	0.72 (0.09)
CT	2100	2	0.28 (0.23)	30 (19)	0 (0)	0.52 (0.24)	32.5 (12.5)	62.5 (2.5)	7.5 (2.5)	2 (2)	0.84 (0.12)	0.66 (0.13)
CT	2300	1	1.75	78 (-)	0 (-)	0.56 (-)	40 (-)	60 (-)	3 (-)	0 (-)	0.66 (-)	0.33 (-)
CT	2500	5	0.87 (0.32)	94.4 (5.6)	0 (0)	0.94 (0.37)	15.4 (6.57)	68 (7.35)	25.8 (13.85)	9 (6.6)	0.84 (0.04)	0.41 (0.06)
NW	1100	11	0.61 (0.16)	13.14 (2.21)	1.55 (0.61)	15.57 (9.82)	34 (6.13)	40.18 (6.59)	29.45 (7.17)	0 (0)	0.71 (0.03)	0.39 (0.04)
NW	1300	4	0.44 (0.2)	19.5 (2.96)	0 (0)	5.97 (4.5)	55 (13.23)	41.25 (9.66)	17.75 (7.64)	0.75 (0.75)	0.62 (0.03)	0.46 (0.01)
NW	1500	0	-	-	-	-	-	-	-	-	-	-
NW	1K	3	0.58 (0.22)	8.67 (3.35)	0.67 (0.67)	3.75 (2.91)	55 (24.66)	27.33 (11.85)	28 (21.01)	1 (1)	0.75 (0.04)	0.46 (0.15)
NW	2100	9	0.31 (0.09)	11.18 (2.93)	2.22 (1.28)	8.47 (2.64)	53.56 (6.62)	33.78 (8.59)	31.22 (6.82)	0.44 (0.34)	0.84 (0.17)	0.4 (0.04)
NW	2300	11	0.35 (0.08)	11.64 (2.1)	2.36 (1.15)	8.64 (2.35)	36.82 (6.85)	41.45 (6.98)	22.36 (4.53)	0.64 (0.45)	0.64 (0.05)	0.42 (0.05)
NW	2500	0	-	-	-	-	-	-	-	-	-	-
PC	1100	1	0.05 (-)	5.75 (-)	1 (-)	1.06 (-)	60 (-)	30 (-)	15 (-)	0 (-)	0.75 (-)	0.41 (-)
PC	1300	1	2.5 (-)	51 (-)	0 (-)	0.28 (-)	70 (-)	75 (-)	5 (-)	0 (-)	0.66 (-)	0.39 (-)
PC	1500	2	1.25 (0.75)	8.65 (1.65)	1 (1)	0.94 (0.88)	64.5 (33.5)	33.5 (31.5)	4.5 (4.5)	0 (0)	0.78 (0.25)	0.45 (0.19)
PC	1K	0	-	-	-	-	-	-	-	-	-	-
PC	2100	1	0.7 (-)	13 (-)	0 (-)	2.09 (-)	40 (-)	45 (-)	30 (-)	0 (-)	0.54 (-)	0.39 (-)
PC	2300	0	-	-	-	-	-	-	-	-	-	-
PC	2500	5	1.41 (0.53)	6.7 (0.8)	4.2 (1.24)	0.78 (0.27)	57.6 (6.41)	48.8 (12.81)	13.2 (2.6)	0.4 (0.24)	0.83 (0.09)	0.49 (0.05)
PV	1100	1	1 (-)	7.5 (-)	2 (-)	5.41 (-)	30 (-)	60 (-)	15 (-)	0 (-)	0.67 (-)	0.55 (-)
PV	1300	3	5.17 (3.43)	20.67 (2.96)	0 (0)	0.12 (0.08)	77 (10.44)	25.67 (9.94)	4 (1)	3.33 (3.33)	0.84 (0.2)	0.6 (0.21)
PV	1500	8	14.29 (12.27)	12.31 (1.92)	0.5 (0.27)	1.23 (0.66)	73.12 (8.76)	13.88 (3.28)	14.12 (5.59)	1.5 (1)	0.76 (0.07)	0.44 (0.12)
PV	1K	0	-	-	-	-	-	-	-	-	-	-
PV	2100	0	-	-	-	-	-	-	-	-	-	-
PV	2300	1	7.5 (-)	34 (-)	0 (-)	0 (-)	60 (-)	40 (-)	0 (-)	0 (-)	- (-)	- (-)
PV	2500	6	4.79 (1.46)	56.83 (14.64)	0 (0)	0.13 (0.05)	67.5 (6.29)	31.33 (7.24)	3.5 (2.43)	2.67 (2.47)	0.9 (0.1)	0.52 (0.05)

Mean and (standard error) of vegetation measurements at Field Sparrow nest sites located within Crabtree Nature Preserve

(CT), Northwest Poplar Creek (NW), Poplar Creek (PC), and Prairieview (PV). Where unit is not specified, data is in meters.

Site	Plot	n	Nearest shrub	Nearest tree	Tree count		% Grass	% Forb	% Shrub	% Marsh	Groundcover height	Groundcover density
					plot <sup>-1</sup>	Stem count m <sup>-1</sup>						
CT	1100	1	0.75 (-)	7 (-)	3 (-)	1.24 (-)	65 (-)	50 (-)	35 (-)	0 (-)	0.92 (-)	0.83 (-)
CT	1300	2	2.25 (0.75)	11.5 (7.5)	1.5 (1.5)	0.32 (0.17)	90 (0)	82.5 (2.5)	5 (0)	0 (0)	1.17 (0.02)	0.82 (0.01)
CT	1500	0	-	-	-	-	-	-	-	-	-	-
CT	1K	2	0.75 (0.25)	0.85 (15)	0 (0)	0.96 (0.29)	20 (10)	82.5 (2.5)	32.5 (7.5)	0 (0)	1.11 (0.04)	0.88 (0.16)
CT	2100	2	0.95 (0.05)	24.5 (10.5)	0 (0)	0.83 (0.04)	70 (20)	90 (0)	7.5 (7.5)	0 (0)	0.96 (0.03)	0.76 (0.03)
CT	2300	8	1.66 (0.63)	34.12 (7.05)	0 (0)	0.48 (0.14)	26.62 (8.09)	75.88 (9.77)	6.88 (2.08)	0 (0)	0.89 (0.1)	0.73 (0.12)
CT	2500	3	1.1 (0.49)	100 (0)	0 (0)	0.45 (0.2)	7.33 (0.67)	69.33 (9.26)	9 (2.08)	10.67 (5.17)	0.91 (0.07)	0.4 (0.1)
NW	1100	1	0.2 (-)	2.25 (-)	2 (-)	3.18 (-)	80 (-)	40 (-)	18 (-)	0 (-)	0.65 (-)	0.56 (-)
NW	1300	1	0.05 (-)	11.3 (-)	0 (-)	8.28 (-)	50 (-)	60 (-)	33 (-)	4 (-)	0.86 (-)	1.07 (-)
NW	1500	1	0.65 (-)	26 (-)	0 (-)	1.2 (-)	3 (-)	80 (-)	15 (-)	10 (-)	0.75 (-)	0.64 (-)
NW	1K	2	0.4 (0.15)	11 (0)	1 (0)	0.71 (0.59)	37.5 (22.5)	67.5 (22.5)	14 (6)	0 (0)	1.02 (0.05)	0.95 (0.12)
NW	2100	2	0.28 (0.03)	12.5 (10.5)	1 (1)	4.37 (2.63)	55 (5)	30 (15)	12.5 (2.5)	0 (0)	0.55 (0.11)	0.37 (0.01)
NW	2300	0	-	-	-	-	-	-	-	-	-	-
NW	2500	0	-	-	-	-	-	-	-	-	-	-
PC	1100	0	-	-	-	-	-	-	-	-	-	-
PC	1300	2	1.1 (0.9)	47 (3)	0 (0)	0.6 (0.54)	43 (28)	64.5 (25.5)	5.5 (4.5)	0.5 (0.5)	0.88 (0.27)	0.69 (0.4)
PC	1500	4	1.63 (1.13)	5.98 (0.98)	1.75 (0.48)	1.14 (0.32)	68.75 (14.74)	36.25 (6.25)	12.5 (9.19)	0.25 (0.25)	0.76 (0.14)	0.46 (0.13)
PC	1K	0	-	-	0 (0)	-	-	-	-	-	-	-
PC	2100	4	0.66 (0.45)	5.15 (1.88)	6.25 (2.1)	3.22 (2.54)	28 (4.6)	80 (3.67)	9.25 (3.64)	0.5 (0.5)	0.85 (0.12)	0.56 (0.13)
PC	2300	3	0.63 (0.32)	5.04 (0.62)	3.67 (0.33)	3.69 (1.95)	40 (15)	53.33 (13.02)	24.33 (13.74)	0 (0)	0.89 (0.25)	0.66 (0.12)
PC	2500	6	0.53 (0.18)	8.73 (1.6)	2.33 (1.36)	2.14 (0.88)	45.33 (11.39)	60 (3.99)	16.83 (8.73)	0.33 (0.21)	0.92 (0.07)	0.68 (0.14)
PV	1100	0	-	-	-	-	-	-	-	-	-	-
PV	1300	0	-	-	-	-	-	-	-	-	-	-
PV	1500	3	1.67 (0.33)	15.33 (2.6)	0.33 (0.33)	0.54 (0.24)	56.67 (20.28)	34.33 (25.57)	4 (1)	13.33 (13.33)	1.2 (0.2)	0.48 (0.14)
PV	1K	6	2.85 (0.77)	14.25 (2.76)	0.17 (0.17)	2.94 (2.79)	49.17 (4.55)	72.5 (7.61)	8.33 (6.37)	1.33 (0.71)	0.88 (0.05)	0.65 (0.05)
PV	2100	0	-	-	-	-	-	-	-	-	-	-
PV	2300	2	0.58 (0.43)	31 (21)	0.5 (0.5)	8.42 (7.17)	30 (10)	72.5 (7.5)	17.5 (17.5)	2.5 (2.5)	0.93 (0.1)	0.72 (0.08)
PV	2500	1	0.1 (-)	100 (-)	0 (-)	37.88 (-)	85 (-)	25 (-)	20 (-)	1 (-)	0.84 (-)	0.53 (-)

Mean and (standard error) of vegetation measurements at Song Sparrow nest sites located within Crabtree Nature Preserve

(CT), Northwest Poplar Creek (NW), Poplar Creek (PC), and Prairieview (PV). Where unit is not specified, data is in meters.

APPENDIX D:

Summary of number of avian species observed on surveys at each site in 2009 and 2010.

Site	Species		Observed on % of surveys	
	Common Name	Scientific Name	2009	2010
<b><i>Crabtree Nature Preserve</i></b>				
	American Goldfinch	<i>Carduelis tristis</i>	25%	62%
	American Robin	<i>Turdus migratorius</i>	17%	62%
	Barn Swallow	<i>Hirundo rustica</i>	17%	-
	Black-capped Chickadee	<i>Poecile atricapilla</i>	17%	46%
	Blue-gray Gnatcatcher	<i>Poliotilta caerulea</i>	17%	46%
	Brown Thrasher	<i>Toxostoma rufum</i>	-	15%
	Cedar Waxwing	<i>Bombycilla cedrorum</i>	-	23%
	Clay-colored Sparrow	<i>Spizella pallida</i>	33%	23%
	Common Yellowthroat	<i>Geothlypis trichas</i>	58%	69%
	Common Yellowthroat	<i>Geothlypis trichas</i>	-	15%
	Eastern Bluebird	<i>Sialia sialis</i>	17%	38%
	Eastern Towhee	<i>Pipilo erythrophthalmus</i>	33%	54%
	Field Sparrow	<i>Spizella pusilla</i>	58%	92%
	Gray Catbird	<i>Dumetella carolinensis</i>	17%	69%
	Great Crested Flycatcher	<i>Myiarchus crinitus</i>	17%	-
	House Wren	<i>Troglodytes aedon</i>	58%	62%
	Indigo Bunting	<i>Passerina cyanea</i>	50%	54%
	Northern Cardinal	<i>Cardinalis cardinalis</i>	25%	62%
	Rose-breasted Grosbeak	<i>Pheucticus ludovicianus</i>	17%	-
	Song Sparrow	<i>Melospiza melodia</i>	58%	92%
	Tennessee Warbler	<i>Vermivora peregrina</i>	17%	-
	Tree Swallow	<i>Tachycineta bicolor</i>	17%	23%
	Willow Flycatcher	<i>Empidonax traillii</i>	-	15%
	Yellow Warbler	<i>Dendroica petechia</i>	17%	23%
	Yellow-shafted Flicker	<i>Colaptes auratus</i>	-	15%
<b><i>Glacial Park</i></b>				
	American Goldfinch	<i>Carduelis tristis</i>	44%	27%
	American Robin	<i>Turdus migratorius</i>	56%	-
	Barn Swallow	<i>Hirundo rustica</i>	78%	73%
	Bobolink	<i>Dolichonyx oryzivorus</i>	89%	55%
	Canada Goose	<i>Branta canadensis</i>	22%	-
	Common Yellowthroat	<i>Geothlypis trichas</i>	89%	73%
	Dickcissel	<i>Spiza americana</i>	33%	36%
	Eastern Meadowlark	<i>Sturnella magna</i>	89%	82%
	European Starling	<i>Sturnus vulgaris</i>	22%	-
	Field Sparrow	<i>Spizella pusilla</i>	33%	-
	Great Egret	<i>Ardea alba</i>	22%	-
	Henslow's Sparrow	<i>Ammodramus henslowii</i>	44%	18%

Continued

Continued

Site	Species		Observed on % of surveys	
	Common Name	Scientific Name	2009	2010
<b>Glacial Park</b>				
	House Sparrow	<i>Passer domesticus</i>	67%	-
	Indigo Bunting	<i>Passerina cyanea</i>	22%	27%
	Killdeer	<i>Charadrius vociferus</i>	44%	-
	Mallard	<i>Anas platyrhynchos</i>	22%	-
	Savannah Sparrow	<i>Passerculus sandwichensis</i>	67%	36%
	Sedge Wren	<i>Cistothorus platensis</i>	-	64%
	Song Sparrow	<i>Melospiza melodia</i>	89%	91%
	Swamp Sparrow	<i>Melospiza georgiana</i>	22%	-
	Tree Swallow	<i>Tachycineta bicolor</i>	56%	18%
	Yellow-shafted Flicker	<i>Colaptes auratus</i>	33%	-
<b>Living Lands</b>				
	American Goldfinch	<i>Carduelis tristis</i>	36%	54%
	American Robin	<i>Turdus migratorius</i>	45%	38%
	Barn Swallow	<i>Hirundo rustica</i>	-	23%
	Black-capped Chickadee	<i>Poecile atricapilla</i>	-	23%
	Bobolink	<i>Dolichonyx oryzivorus</i>	36%	38%
	Cedar Waxwing	<i>Bombycilla cedrorum</i>	-	15%
	Common Yellowthroat	<i>Geothlypis trichas</i>	36%	62%
	Eastern Bluebird	<i>Sialia sialis</i>	18%	46%
	Eastern Kingbird	<i>Tyrannus tyrannus</i>	-	23%
	Eastern Meadowlark	<i>Sturnella magna</i>	36%	69%
	Field Sparrow	<i>Spizella pusilla</i>	45%	62%
	Gray Catbird	<i>Dumetella carolinensis</i>	27%	15%
	Henslow's Sparrow	<i>Ammodramus henslowii</i>	27%	38%
	House Sparrow	<i>Passer domesticus</i>	27%	-
	Indigo Bunting	<i>Passerina cyanea</i>	27%	15%
	Northern Cardinal	<i>Cardinalis cardinalis</i>	18%	31%
	Savannah Sparrow	<i>Passerculus sandwichensis</i>	-	31%
	Sedge Wren	<i>Cistothorus platensis</i>	-	23%
	Song Sparrow	<i>Melospiza melodia</i>	45%	69%
	Tree Swallow	<i>Tachycineta bicolor</i>	27%	54%
	Yellow Warbler	<i>Dendroica petechia</i>	18%	31%
<b>Max McGraw Wildlife Foundation</b>				
	American Goldfinch	<i>Carduelis tristis</i>	57%	62%
	American Robin	<i>Turdus migratorius</i>	57%	54%
	Barn Swallow	<i>Hirundo rustica</i>	-	15%
	Brown Thrasher	<i>Toxostoma rufum</i>	29%	23%

Continued

Continued

Site	Species		Observed on % of surveys	
	Common Name	Scientific Name	2009	2010
<b>Max McGraw Wildlife Foundation</b>				
	Common Yellowthroat	<i>Geothlypis trichas</i>	71%	85%
	Dickcissel	<i>Spiza americana</i>	29%	38%
	Downy Woodpecker	<i>Picoides pubescens</i>	29%	-
	Gray Catbird	<i>Dumetella carolinensis</i>	43%	54%
	Indigo Bunting	<i>Passerina cyanea</i>	71%	46%
	Killdeer	<i>Charadrius vociferus</i>	29%	31%
	Northern Cardinal	<i>Cardinalis cardinalis</i>	57%	77%
	Ring-necked Pheasant	<i>Phasianus colchicus</i>	43%	15%
	Savannah Sparrow	<i>Passerculus sandwichensis</i>	71%	100%
	Song Sparrow	<i>Melospiza melodia</i>	71%	100%
	Tree Swallow	<i>Tachycineta bicolor</i>	43%	23%
	White-crowned Sparrow	<i>Zonotrichia leucophrys</i>	-	23%
	Yellow Warbler	<i>Dendroica petechia</i>	29%	15%
<b>Northwest Poplar Creek</b>				
	American Goldfinch	<i>Carduelis tristis</i>	42%	82%
	American Robin	<i>Turdus migratorius</i>	42%	94%
	Baltimore Oriole	<i>Icterus galbula</i>	17%	12%
	Black-capped Chickadee	<i>Poecile atricapilla</i>	-	24%
	Blue-gray Gnatcatcher	<i>Poliopitila caerulea</i>	33%	65%
	Brown Thrasher	<i>Toxostoma rufum</i>	17%	35%
	Cedar Waxwing	<i>Bombycilla cedrorum</i>	-	18%
	Clay-colored Sparrow	<i>Spizella pallida</i>	33%	24%
	Common Yellowthroat	<i>Geothlypis trichas</i>	50%	76%
	Downy Woodpecker	<i>Picoides pubescens</i>	-	12%
	Eastern Bluebird	<i>Sialia sialis</i>	17%	18%
	Eastern Kingbird	<i>Tyrannus tyrannus</i>	-	24%
	Eastern Meadowlark	<i>Sturnella magna</i>	-	47%
	Eastern Towhee	<i>Pipilo erythrophthalmus</i>	25%	47%
	Field Sparrow	<i>Spizella pusilla</i>	42%	94%
	Gray Catbird	<i>Dumetella carolinensis</i>	17%	35%
	House Wren	<i>Troglodytes aedon</i>	17%	59%
	Indigo Bunting	<i>Passerina cyanea</i>	25%	18%
	Orchard Oriole	<i>Icterus spurius</i>	-	12%
	Savannah Sparrow	<i>Passerculus sandwichensis</i>	25%	71%
	Song Sparrow	<i>Melospiza melodia</i>	58%	94%
	Tree Swallow	<i>Tachycineta bicolor</i>	17%	-

Continued

Continued

Site	Species		Observed on % of surveys	
	Common Name	Scientific Name	2009	2010
<b>Northwest Poplar Creek</b>				
	Warbling Vireo	<i>Vireo gilvus</i>	17%	12%
	Willow Flycatcher	<i>Empidonax traillii</i>	17%	47%
	Yellow Warbler	<i>Dendroica petechia</i>	50%	76%
	Yellow-shafted Flicker	<i>Colaptes auratus</i>	17%	12%
<b>Central Poplar Creek</b>				
	American Goldfinch	<i>Carduelis tristis</i>	44%	46%
	American Robin	<i>Turdus migratorius</i>	67%	85%
	Baltimore Oriole	<i>Icterus galbula</i>	33%	23%
	Blue-gray Gnatcatcher	<i>Poliopitila caerulea</i>	-	46%
	Bobolink	<i>Dolichonyx oryzivorus</i>	-	62%
	Brown Thrasher	<i>Toxostoma rufum</i>	-	54%
	Cedar Waxwing	<i>Bombycilla cedrorum</i>	-	46%
	Common Yellowthroat	<i>Geothlypis trichas</i>	56%	69%
	Eastern Bluebird	<i>Sialia sialis</i>	22%	38%
	Eastern Kingbird	<i>Tyrannus tyrannus</i>	44%	54%
	Eastern Meadowlark	<i>Sturnella magna</i>	67%	62%
	Eastern Towhee	<i>Pipilo erythrophthalmus</i>	-	23%
	Field Sparrow	<i>Spizella pusilla</i>	67%	85%
	Gray Catbird	<i>Dumetella carolinensis</i>	22%	15%
	Henslow's Sparrow	<i>Ammodramus henslowii</i>	-	23%
	House Wren	<i>Troglodytes aedon</i>	22%	54%
	Indigo Bunting	<i>Passerina cyanea</i>	-	23%
	Least Flycatcher	<i>Empidonax minimus</i>	22%	-
	Mourning Dove	<i>Zenaida macroura</i>	22%	-
	Northern Cardinal	<i>Cardinalis cardinalis</i>	-	23%
	Orchard Oriole	<i>Icterus spurius</i>	22%	15%
	Savannah Sparrow	<i>Passerculus sandwichensis</i>	67%	92%
	Song Sparrow	<i>Melospiza melodia</i>	67%	85%
	Tree Swallow	<i>Tachycineta bicolor</i>	44%	69%
	Warbling Vireo	<i>Vireo gilvus</i>	33%	38%
	Willow Flycatcher	<i>Empidonax traillii</i>	44%	38%
	Yellow Warbler	<i>Dendroica petechia</i>	56%	62%
	Yellow-shafted Flicker	<i>Colaptes auratus</i>	-	23%
<b>Prairieview</b>				
	American Goldfinch	<i>Carduelis tristis</i>	38%	86%
	American Robin	<i>Turdus migratorius</i>	25%	71%
	American Woodcock	<i>Scolopax minor</i>	-	14%

Continued

Continued

Site	Species		Observed on % of surveys	
	Common Name	Scientific Name	2009	2010
<i>Prairieview</i>				
	Baltimore Oriole	<i>Icterus galbula</i>	25%	29%
	Barn Swallow	<i>Hirundo rustica</i>	50%	14%
	Black-capped Chickadee	<i>Poecile atricapilla</i>	-	36%
	Blue-gray Gnatcatcher	<i>Poliophtila caerulea</i>	25%	29%
	Brown Thrasher	<i>Toxostoma rufum</i>	-	36%
	Cedar Waxwing	<i>Bombycilla cedrorum</i>	-	29%
	Common Yellowthroat	<i>Geothlypis trichas</i>	38%	71%
	Downy Woodpecker	<i>Picooides pubescens</i>	-	29%
	Eastern Bluebird	<i>Sialia sialis</i>	25%	29%
	Eastern Kingbird	<i>Tyrannus tyrannus</i>	25%	36%
	Eastern Meadowlark	<i>Sturnella magna</i>	38%	86%
	European Starling	<i>Sturnus vulgaris</i>	-	14%
	Field Sparrow	<i>Spizella pusilla</i>	38%	86%
	Gray Catbird	<i>Dumetella carolinensis</i>	-	43%
	Henslow's Sparrow	<i>Ammodramus henslowii</i>	25%	-
	House Wren	<i>Troglodytes aedon</i>	25%	57%
	Indigo Bunting	<i>Passerina cyanea</i>	38%	71%
	Northern Cardinal	<i>Cardinalis cardinalis</i>	38%	50%
	Orchard Oriole	<i>Icterus spurius</i>	38%	36%
	Red-bellied Woodpecker	<i>Melanerpes carolinus</i>	-	36%
	Rose-breasted Grosbeak	<i>Pheucticus ludovicianus</i>	-	36%
	Savannah Sparrow	<i>Passerculus sandwichensis</i>	-	21%
	Sedge Wren	<i>Cistothorus platensis</i>	-	29%
	Song Sparrow	<i>Melospiza melodia</i>	38%	93%
	Tree Swallow	<i>Tachycineta bicolor</i>	25%	93%
	Willow Flycatcher	<i>Empidonax traillii</i>	-	36%
	Yellow Warbler	<i>Dendroica petechia</i>	38%	57%
	Yellow-shafted Flicker	<i>Colaptes auratus</i>	38%	14%



## APPENDIX E:

Summary of predator activity observed at each plot during 2009 and 2010. Activity of snakes and avian predators are recorded as average “encounter rate,” i.e., the average number observed on a predator survey. Activity of small mammals and mesopredators is recorded as capture rates.

Site	Year	Plot	Avian <sup>1</sup>		Snake <sup>1</sup>		Small Mammal <sup>2</sup>		Mesopredator <sup>3</sup>
			$\mu$	SE	$\mu$	SE	including <i>Microtus sp.</i>	excluding <i>Microtus sp.</i>	
CT	2009	1100	0.286	0.184	0.727	0.304	0.256	0.000	0.100
		1300	0.286	0.184	1.000	0.426	0.272	0.160	0.100
		1500	0.714	0.286	1.364	0.453	0.256	0.232	0.199
		2100	0.143	0.143	0.182	0.122	0.264	0.024	0.102
		2300	0.429	0.202	0.727	0.557	0.168	0.096	0.168
		2500	0.429	0.202	0.364	0.279	0.048	0.016	0.165
		1K	1.571	0.297	-	-	0.200	0.128	-
	2010	1100	0.077	0.077	5.286	1.076	0.053	0.000	0.165
		1300	0.077	0.077	0.214	0.114	0.167	0.113	0.104
		1500	0.154	0.104	0.929	0.412	0.140	0.100	0.100
		2100	0.077	0.077	2.214	0.526	0.080	0.013	0.164
		2300	0.077	0.077	2.286	0.707	0.160	0.153	0.186
		2500	0.231	0.122	5.143	1.195	0.040	0.000	0.191
		1K	0.000	0.000	-	-	-	-	-
GP	2009	1100	0.000	0.000	3.364	0.834	0.243	0.133	0.145
		1300	0.125	0.125	8.091	1.719	0.145	0.113	0.100
		1500	0.000	0.000	12.636	1.586	0.087	0.062	0.100
		2100	0.000	0.000	3.800	1.590	0.185	0.124	0.265
		2300	0.000	0.000	1.182	0.423	0.229	0.058	0.100
		2500	0.125	0.125	1.000	0.357	0.160	0.025	0.100
		1K	0.000	0.000	1.300	0.684	0.229	0.025	-
	2010	1100	0.000	0.000	2.231	0.411	0.344	0.024	0.101
		1300	0.000	0.000	1.231	0.568	0.112	0.008	0.100
		1500	0.000	0.000	5.462	1.175	0.448	0.032	0.100
		2100	0.000	0.000	0.231	0.166	0.368	0.072	0.100
		2300	0.091	0.091	1.538	0.573	0.424	0.000	0.100
		2500	0.000	0.000	0.615	0.331	0.392	0.008	0.100
		1K	0.000	0.000	2.231	0.482	0.000	0.000	-

<sup>1</sup>Mean ( $\mu$ ) and standard error of individuals observed on a weekly survey for predator activity (i.e., "encounter rate"). <sup>2</sup>Capture rate of small mammals (i.e., total number of captures/number of trap nights). <sup>3</sup>Capture rate interpolated from 25 traps located at stratified random locations across the site.

Continued

Conintued			Avian <sup>1</sup>		Snake <sup>1</sup>		Small Mammal <sup>2</sup>		Mesopredator <sup>3</sup>
Site	Year	Plot	$\mu$	SE	$\mu$	SE	including <i>Microtus sp.</i>	excluding <i>Microtus sp.</i>	
LL	2009	1100	0.143	0.143	1.250	0.653	0.007	0.007	-
		1300	0.143	0.143	1.083	0.336	0.073	0.000	-
		1500	0.143	0.143	4.333	0.700	0.167	0.020	-
		1K	0.143	0.143	1.417	0.417	0.107	0.020	-
	2010	1100	0.308	0.237	1.063	0.433	0.040	0.000	0.228
		1300	0.077	0.077	1.313	0.681	0.032	0.000	0.334
		1500	0.000	0.000	2.063	0.609	0.024	0.024	0.258
		1K	0.077	0.077	1.188	0.379	0.176	0.000	-
MM	2009	1100	0.000	0.000	-	-	0.347	0.087	-
		1300	0.286	0.286	-	-	0.427	0.253	-
		1500	0.000	0.000	-	-	0.413	0.153	-
		2100	0.286	0.184	-	-	0.560	0.267	-
		2300	0.000	0.000	-	-	0.527	0.000	-
		2500	0.000	0.000	-	-	0.473	0.147	-
		1K	0.571	0.297	-	-	0.547	0.287	-
	2010	1100	0.077	0.077	0.000	0.000	0.287	0.107	0.475
		1300	0.308	0.133	0.000	0.000	0.300	0.073	0.273
		1500	0.000	0.000	0.071	0.071	0.300	0.093	0.187
		2100	0.308	0.175	0.000	0.000	0.393	0.160	0.309
		2300	0.154	0.104	0.000	0.000	0.180	0.000	0.157
		2500	0.000	0.000	0.000	0.000	0.147	0.000	0.100
NW	2009	1100	0.000	0.000	0.385	0.241	0.407	0.180	0.197
		1300	0.143	0.143	2.692	0.499	0.480	0.287	0.109
		1500	0.000	0.000	0.923	0.473	0.380	0.260	0.112
		2100	0.143	0.143	0.769	0.378	0.427	0.233	0.168
		2300	0.000	0.000	0.154	0.104	0.353	0.127	0.288
		2500	0.000	0.000	0.692	0.286	0.193	0.107	0.179
		1K	0.000	0.000	-	-	0.093	0.080	-
	2010	1300	0.077	0.077	4.929	0.911	0.313	0.213	0.106
		1500	0.000	0.000	3.214	0.984	0.227	0.073	0.100
		2100	0.077	0.077	2.733	0.628	0.047	0.040	0.100

Continued

Continued		Avian <sup>1</sup>		Snake <sup>1</sup>		Small Mammal <sup>2</sup>		Mesopredator <sup>3</sup>	
Site	Year	Plot	$\mu$	SE	$\mu$	SE	including <i>Microtus sp.</i>	excluding <i>Microtus sp.</i>	
PC	2009	2300	0.000	0.000	0.333	0.211	0.020	0.013	0.101
		2500	0.154	0.154	0.400	0.163	0.200	0.053	0.200
		1K	0.077	0.077	-	-	-	-	-
		1100	0.143	0.143	2.000	0.519	0.553	0.077	0.153
		1300	0.143	0.143	1.692	0.720	0.070	0.003	0.181
		1500	0.143	0.143	0.000	0.000	0.120	0.040	0.203
		2100	0.000	0.000	1.000	0.226	0.413	0.243	0.200
	2010	2300	0.000	0.000	1.308	0.414	0.327	0.270	0.200
		2500	0.000	0.000	0.615	0.213	0.210	0.170	0.143
		1K	0.143	0.143	1.500	0.379	0.257	0.073	-
		1100	0.083	0.083	2.615	0.636	0.260	0.040	0.159
		1300	0.000	0.000	2.231	0.579	0.000	0.000	0.130
		1500	0.083	0.083	0.154	0.104	0.000	0.000	0.139
		2100	0.000	0.000	6.000	0.981	0.333	0.307	0.172
PV	2009	2300	0.000	0.000	7.000	1.171	0.173	0.153	0.162
		2500	0.000	0.000	1.538	0.501	0.020	0.020	0.153
		1K	0.000	0.000	3.462	1.678	0.133	0.127	-
		1100	0.167	0.167	0.462	0.183	0.267	0.227	0.205
		1300	0.333	0.211	0.167	0.112	0.147	0.053	0.202
	2010	1500	0.500	0.342	0.250	0.179	0.420	0.287	0.163
		2100	0.333	0.333	3.333	0.497	0.127	0.067	0.200
		2300	0.333	0.333	0.923	0.329	0.120	0.060	0.247
		2500	0.000	0.000	4.083	1.485	0.087	0.087	0.155
		1K	0.167	0.167	2.583	1.083	0.407	0.113	-
2010	1100	0.769	0.257	0.077	0.077	0.067	0.053	0.118	
	1300	0.308	0.237	0.154	0.104	0.033	0.007	0.205	
	1500	0.385	0.180	0.385	0.140	0.173	0.067	0.200	
	2100	0.000	0.000	2.231	0.735	0.000	0.000	0.142	
	2300	0.000	0.000	0.385	0.241	0.087	0.087	0.427	
		2500	0.077	0.077	0.231	0.122	0.173	0.173	0.149
		1K	0.308	0.175	5.167	0.895	0.020	0.013	-

## APPENDIX F:

Territory density models for plot-level densities of the five most common species in the study system. Modified null model includes site, year, structural complexity, and groundcover openness. Table includes,  $\omega_i$ , parameter estimates, standard errors of parameter estimates. All models are shown.

Model	k	AIC	AIC <sub>C</sub>	ΔAIC <sub>C</sub>	ω <sub>i</sub>		β	β SE	95% CI		
<b><i>Field Sparrow</i></b>											
Null	10	172.512	176.305	0.000	0.332		-	-	-	-	-
Small mammals	11	172.521	177.152	0.847	0.217		-1.5025	1.0721	-3.6038	-	0.5988
Snakes	11	173.378	178.010	1.704	0.141		0.0764	0.0711	-0.0629	-	0.2157
Mesopredators	11	174.423	179.054	2.749	0.084		0.6515	2.1646	-3.5911	-	4.8940
Distance	11	174.470	179.102	2.796	0.082		0.0001	0.0006	-0.0011	-	0.0014
Avian predators	11	174.483	179.114	2.809	0.081		-0.1613	0.9380	-1.9998	-	1.6772
Snakes * Small mammals	13	173.209	179.827	3.521	0.057	Snakes	-0.0075	0.1036	-0.2105	-	0.1956
						Small mammals	-2.9580	-1.4540	-0.1082	-	-5.8078
						Snakes * Small mammals	0.7309	0.5438	-0.3349	-	1.7967
Snakes + Small mammals + Mesopredators + Avian predators	14	176.788	184.566	8.260	0.005	Snakes	0.0917	0.0728	-0.0509	-	0.2344
						Small mammals	-1.7273	1.0928	-3.8692	-	0.4146
						Mesopredators	0.8151	2.2405	-3.5763	-	5.2066
						Avian predators	0.2062	0.9559	-1.6673	-	2.0797
<b><i>Song sparrow</i></b>											
Small mammals	11	236.807	243.754	0.000	0.317		1.3361	0.7033	-0.0423	-	2.7145
Null	10	238.414	244.055	0.301	0.273		-	-	-	-	-
Distance	11	238.332	245.280	1.526	0.148		-0.0007	0.0005	-0.0017	-	0.0003
Mesopredators	11	239.286	246.234	2.480	0.092		1.3148	1.2235	-1.0834	-	3.7129
Snakes	11	239.501	246.449	2.694	0.082		0.0384	0.0395	-0.0390	-	0.1159
Avian predators	11	240.125	247.072	3.318	0.060		-0.4393	0.8261	-2.0585	-	1.1798
Snakes * Small mammals	13	238.896	249.007	5.253	0.023	Snakes	1.1403	0.8457	-0.5172	-	2.7978
						Small mammals	1.9903	1.0287	-0.0259	-	4.0065
						Snakes * Small mammals	-3.3465	4.2969	-11.7684	-	5.0754
Snakes + Small mammals + Mesopredators + Avian predators	14	239.983	251.983	8.229	0.005	Snakes	0.0474	0.0418	-0.0345	-	0.1294
						Small mammals	1.4421	0.7150	0.0407	-	2.8434
						Mesopredators	1.2671	1.2437	-1.1705	-	3.7047
						Avian predators	-0.6358	0.8620	-2.3254	-	1.0538

Continued

Continued

Model	k	AIC	AIC <sub>C</sub>	ΔAIC <sub>C</sub>	ω <sub>i</sub>		β	β SE	95% CI		
<i>Common yellowthroat</i>											
Mesopredators	11	206.563	211.195	0.000	0.408		-4.7590	2.3362	-9.3380	-	-0.1800
Small mammals	11	208.135	212.766	1.572	0.186		1.4933	0.8244	-0.1226	-	3.1092
Null	10	209.434	213.227	2.032	0.148		-	-	-	-	-
Distance	11	209.379	214.011	2.816	0.100		-0.0010	0.0007	-0.0024	-	0.0004
Snakes	11	209.918	214.549	3.355	0.076		-0.0485	0.0406	-0.1281	-	0.0310
Avian predators	11	211.393	216.024	4.829	0.036		0.2063	1.0063	-1.7660	-	2.1787
Snakes + Small mammals + Mesopredators + Avian predators	14	208.447	216.225	5.030	0.033	Snakes	-0.0416	0.0436	-0.1270	-	0.0437
						Small mammals	1.2006	0.8446	-0.4548	-	2.8560
						Mesopredators	-5.0272	2.4071	-9.7451	-	-0.3093
						Avian predators	-0.1570	0.9883	-2.0941	-	1.7801
Snakes * Small mammals	13	211.569	218.187	6.993	0.012	Snakes	-0.2744	0.8963	-2.0312	-	1.4823
						Small mammals	1.4549	1.2088	-0.9144	-	3.8242
						Snakes * Small mammals	-0.7033	4.1023	-8.7438	-	7.3371
<i>Eastern meadowlark</i>											
Null	10	72.763	76.556	0.000	0.425		-	-	-	-	-
Mesopredators	11	74.392	79.024	2.468	0.124		-4.5703	8.1000	-20.4462	-	11.3057
Avian predators	11	74.410	79.042	2.485	0.123		-1.6571	2.9577	-7.4541	-	4.1399
Small mammals	11	74.612	79.243	2.687	0.111		-0.9526	2.4790	-5.8114	-	3.9062
Distance	11	74.703	79.335	2.778	0.106		0.0004	0.0019	-0.0033	-	0.0041
Snakes	11	74.753	79.385	2.829	0.103		-0.0179	0.1824	-0.3753	-	0.3396
Snakes * Small mammals	13	78.568	85.186	8.630	0.006	Snakes	-0.3454	3.7317	-7.6596	-	6.9688
						Small mammals	-0.9969	3.3139	-7.4922	-	5.4984
						Snakes * Small mammals	-0.7738	17.7404	-35.5450	-	33.9974
Snakes + Small mammals + Mesopredators + Avian predators	14	79.691	87.468	10.912	0.002	Snakes	-0.0391	0.1899	-0.4113	-	0.3331
						Small mammals	-1.0448	2.6040	-6.1487	-	4.0590
						Mesopredators	-5.7765	8.4556	-22.3495	-	10.7966
						Avian predators	-1.8394	2.8600	-7.4451	-	3.7663

Continued

183

Continued

Model	k	AIC	AIC <sub>C</sub>	ΔAIC <sub>C</sub>	ω <sub>i</sub>		β	β SE	95% CI		
<i>Savannah sparrow</i>											
Small mammals	11	78.645	83.277	0.000	0.400		-5.0089	2.4090	-9.7305	-	-0.2873
Mesopredator	11	78.990	83.622	0.345	0.337		-14.4597	8.3800	-30.8845	-	1.9651
Null	10	82.087	85.880	2.603	0.109		-	-	-	-	-
Avian predators	11	82.744	87.376	4.099	0.052		-4.2660	3.9548	-12.0174	-	3.4854
Snakes	11	83.945	88.576	5.299	0.028		-0.0744	0.1999	-0.4662	-	0.3174
Distance	11	83.994	88.626	5.349	0.028		0.0004	0.0015	-0.0025	-	0.0033
Snakes + Small mammals + Mesopredators + Avian predators	14	81.143	88.920	5.643	0.024	Snakes	0.0272	0.2112	-0.3868	-	0.4411
						Small mammals	-3.9690	2.2310	-8.3418	-	0.4038
						Mesopredators	-15.0700	10.9600	-36.5516	-	6.4116
						Avian predators	2.9940	5.6530	-8.0859	-	14.0739
Snakes * Small mammals	13	82.442	89.060	5.783	0.022	Snakes	-0.0005	0.3260	-0.6395	-	0.6384
						Small mammals	-6.0190	3.8270	-13.5199	-	1.4819
						Snakes * Small mammals	0.4962	1.7800	-2.9926	-	3.9850
<i>All species</i>											
Null	10	328.972	332.765	0.000	0.399		-	-	-	-	-
Mesopredators	11	330.062	334.694	1.929	0.152		-0.8545	0.9066	-2.6314	-	0.9224
Avian predators	11	330.346	334.977	2.213	0.132		-0.3842	0.4914	-1.3474	-	0.5789
Distance	11	330.782	335.414	2.649	0.106		-0.0001	0.0003	-0.0007	-	0.0005
Small mammals	11	330.854	335.486	2.721	0.102		0.1446	0.4221	-0.6828	-	0.9720
Snakes	11	330.916	335.548	2.783	0.099		-0.0058	0.0246	-0.0541	-	0.0425
Snakes * Small mamm	13	334.425	341.043	8.278	0.006	Snakes	-0.0250	0.0414	-0.1062	-	0.0562
						Small mammals	-0.1454	0.6139	-1.3486	-	1.0579
						Snakes * Small mammals	0.1305	0.2061	-0.2735	-	0.5345
Snakes + Small mamm	14	335.133	342.911	10.146	0.002	Snakes	-0.0064	0.0252	-0.0558	-	0.0430
						Small mammals	0.1787	0.4295	-0.6632	-	1.0206
						Mesopredators	-0.8859	0.9043	-2.6583	-	0.8865
						Avian predators	-0.4168	0.4909	-1.3789	-	0.5453

184



## APPENDIX G:

Territory density models for site-level densities of the five most common species in the study system. Modified null model includes site, year, structural complexity, and groundcover openness. Table includes,  $\omega_i$ , parameter estimates, standard errors of parameter estimates. All models are shown.

Model	k	AIC	AIC <sub>C</sub>	ΔAIC <sub>C</sub>	ω <sub>i</sub>		β	β SE	95% CI		
<i>Field sparrow</i>											
Snakes	5	15.124	25.124	0.000	0.712		0.2739	0.0973	0.0832	-	0.4646
Null	4	22.212	27.927	2.802	0.176		0.9966	0.1198	0.7618	-	1.2314
Mesopredators	5	20.829	30.829	5.704	0.041		-6.0389	3.9993	-13.8775	-	1.7997
Avian predators	5	21.012	31.012	5.888	0.038		-2.4697	1.6886	-5.7794	-	0.8400
Small mammals	5	21.245	31.245	6.121	0.033		-2.8066	2.0031	-6.7327	-	1.1195
Snakes + Small mammals +	8	10.022	58.022	32.897	0.000	Snakes	-0.3225	0.2570	-0.8261	-	0.1812
Mesopredators + Avian						Small mammals	-8.0003	3.4495	-14.7613	-	-1.2392
predators						Mesopredators	-6.7369	3.9826	-14.5427	-	1.0690
						Avian predators	-5.7076	2.4478	-10.5052	-	-0.9100
<i>Song sparrow</i>											
Null	4	37.280	42.994	0.000	0.624		0.6466	0.2244	0.2068	-	1.0864
Small mammals	5	34.546	44.546	1.552	0.287		6.4149	3.4864	-0.4184	-	13.2482
Mesopredators	5	38.982	48.982	5.987	0.031		-3.5786	8.5206	-20.2790	-	13.1218
Snakes	5	39.128	49.128	6.134	0.029		-0.0790	0.2645	-0.5975	-	0.4394
Avian predators	5	39.162	49.162	6.168	0.029		-0.9468	3.5972	-7.9973	-	6.1037
Snakes + Small mammals +	8	22.448	70.448	27.454	0.000	Snakes	1.5341	0.4313	0.6888	-	2.3794
Mesopredators + Avian						Small mammals	26.0075	5.7893	14.6605	-	37.3545
predators						Mesopredators	11.2502	6.6839	-1.8502	-	24.3506
						Avian predators	14.3930	4.1080	6.3413	-	22.4447

Continued

Continued

Model	k	AIC	AIC <sub>C</sub>	ΔAIC <sub>C</sub>	ω <sub>i</sub>	β	β SE	95% CI	
<i>Common yellowthroat</i>									
Null	4	41.432	47.146	0.000	0.781	-	-	-	-
Mesopredator	5	40.998	50.998	3.852	0.114	-11.6268	9.2673	-29.7907	- 6.5371
Avian predator	5	43.239	53.239	6.093	0.037	1.4352	4.2632	-6.9207	- 9.7911
Snakes	5	43.385	53.385	6.239	0.034	-0.0520	0.3158	-0.6710	- 0.5669
Small mammals	5	43.415	53.415	6.269	0.034	0.4989	5.0450	-9.3893	- 10.3871
Snakes + Small mammals + Mesopredators + Avian predators	8	43.140	91.140	43.994	0.000	Snakes	-0.8393	1.0214	-2.8412 - 1.1626
						Small mammals	-8.0793	13.7106	-34.9521 - 18.7935
						Mesopredators	-24.8582	15.8294	-55.8838 - 6.1674
						Avian predators	-2.1812	9.7290	-21.2500 - 16.8876
<i>Eastern meadowlark</i>									
Mesopredators	5	-17.507	-7.507	0.000	0.565	-1.9557	0.8096	-3.5425	- -0.3689
Null	4	-12.232	-6.518	0.990	0.344	-	-	-	-
Snakes	5	-12.482	-2.482	5.025	0.046	0.0370	0.0308	-0.0233	- 0.0973
Avian predators	5	-11.211	-1.211	6.296	0.024	-0.3402	0.4410	-1.2046	- 0.5241
Small mammals	5	-10.933	-0.933	6.575	0.021	-0.3400	0.5241	-1.3673	- 0.6872
Snakes + Small mammals + Mesopredators + Avian predators	8	-22.835	25.165	32.672	0.000	Snakes	-0.1446	0.0653	-0.2725 - -0.0166
						Small mammals	-2.1912	0.8774	-3.9109 - -0.4715
						Mesopredators	-3.3633	1.0130	-5.3488 - -1.3778
						Avian predators	-1.3392	0.6226	-2.5595 - -0.1189

Continued

Continued

Model	k	AIC	AIC <sub>C</sub>	ΔAIC <sub>C</sub>	ω <sub>i</sub>	β	β SE	95% CI	
<i>Savannah sparrow</i>									
Null	4	18.504	24.218	0.000	0.512	-	-	-	-
Small mammals	5	14.851	24.851	0.633	0.373	3.1494	1.5345	0.1417	- 6.1570
Avian predators	5	18.654	28.654	4.436	0.056	-1.6533	1.5306	-4.6532	- 1.3467
Mesopredators	5	19.469	29.469	5.251	0.037	-3.0009	3.7790	-10.4076	- 4.4059
Snakes	5	20.477	30.477	6.259	0.022	0.0151	0.1216	-0.2232	- 0.2534
esopredators + Avian predators	8	3.319	51.319	27.102	0.000	Snakes	0.6416	0.1944	0.2606 - 1.0226
						Avian predators	4.8270	1.8510	1.1990 - 8.4550
						Small mammals	10.8700	2.6090	5.7564 - 15.9836
						Mesopredators	4.3000	3.0120	-1.6035 - 10.2035
<i>All species</i>									
Mesopredators	5	41.084	51.084	0.000	0.837	-28.0100	9.3010	-46.2400	- -9.7800
Null	4	49.058	54.772	3.688	0.132	0.8834	0.3665	0.1651	- 1.6017
						1.0793	0.4748	0.1487	- 2.0099
Small mammals	5	49.568	59.568	8.484	0.012	6.2709	6.5193	-6.5069	- 19.0487
Avian predators	5	49.811	59.811	8.727	0.011	-4.9074	5.6061	-15.8954	- 6.0806
Snakes	5	50.287	60.287	9.204	0.008	0.2868	0.4210	-0.5384	- 1.1120
Snakes + Small mammals + Mesopredators + Avian predators	8	40.693	88.693	37.610	0.000	Snakes	0.8803	0.9224	-0.9276 - 2.6882
						Small mammals	17.6591	12.3817	-8.2500 26.1912
						Mesopredators	-20.1018	14.2952	-48.1204 7.9168
						Avian predators	8.9706	8.7860	-6.6090 - 41.9272

## APPENDIX H:

Daily survival rates models of Field Sparrow and Song Sparrow at plot-level. Modified null model includes site. Table includes,  $\omega_i$ , parameter estimates, standard errors of parameter estimates. All models are shown.

Model	k	AIC	AIC <sub>C</sub>	ΔAIC <sub>C</sub>	ω <sub>i</sub>		β	β SE	95% CI		
<i>Field sparrows</i>											
Snakes	5	-29.819	-26.486	0.000	0.311		0.0325	0.0159	0.0014	-	0.0636
Groundcover density	5	-29.149	-25.815	0.670	0.222		0.0336	0.0178	-0.0014	-	0.0685
Null	4	-27.039	-24.934	1.552	0.143		-	-	-	-	-
Avian predators	5	-27.232	-23.899	2.586	0.085		-0.2193	0.1626	-0.5380	-	0.0995
Small mammals	5	-26.500	-23.167	3.318	0.059		-0.2218	0.2031	-0.6199	-	0.1763
Structural complexity	6	-27.783	-22.842	3.643	0.050	Structural complexity	-0.0136	0.0196	-0.0519	-	0.0247
+ Groundcover						Groundcover density	-0.0356	0.0183	-0.0714	-	0.0003
Structural complexity	5	-25.205	-21.872	4.614	0.031		-0.0075	0.0207	-0.0480	-	0.0330
Non-voles	5	-25.157	-21.823	4.662	0.030		-0.0944	0.3092	-0.7004	-	0.5116
Mesopredators	5	-25.112	-21.778	4.707	0.030		0.0927	0.3870	-0.6659	-	0.8513
Cowbirds	5	-25.088	-21.755	4.730	0.029		-0.0121	0.0613	-0.1322	-	0.1080
Snakes * Small mammals	7	-26.266	-19.266	7.220	0.008	Snakes	0.0324	0.0243	-0.0153	-	0.0800
						Small mammals	-0.0910	0.2468	-0.5747	-	0.3927
						Snakes * Small mammals	-0.0219	0.1323	-0.2812	-	0.2374
Snakes + Small mammals +	9	-24.024	-11.167	15.319	0.000	Snakes	0.0297	0.0195	-0.0085	-	0.0679
Mesopredators +						Small mammals	-0.1167	0.2176	-0.5432	-	0.3098
Avian predators +						Mesopredators	0.0666	0.4228	-0.7620	-	0.8952
Cowbirds						Avian predators	-0.1482	0.1851	-0.5110	-	0.2147
Snakes + Non-voles +	9	-23.606	-10.749	15.736	0.000	Cowbirds	0.0288	0.0639	-0.0964	-	0.1541
Mesopredators +						Snakes	0.0331	0.0196	-0.0053	-	0.0715
Avian predators +						Non-voles	0.0487	0.3147	-0.5681	-	0.6654
Cowbirds						Mesopredators	0.0263	0.4199	-0.7967	-	0.8493
						Avian predators	-0.1557	0.1862	-0.5206	-	0.2092
						Cowbirds	0.0295	0.0645	-0.0970	-	0.1560

Continued

Model	k	AIC	AIC <sub>C</sub>	ΔAIC <sub>C</sub>	ω <sub>i</sub>		β	β SE	95% CI		
<i>Song Sparrow</i>											
Snakes	5	-70.419	-64.964	0.000	0.544		-0.0079	0.0031	<b>-0.0140</b>	<b>- -0.0018</b>	
Null	4	-65.067	-61.734	3.230	0.108		-	-	-	-	
Structural complexity	5	-66.683	-61.229	3.735	0.084		-0.0085	0.0051	-0.0185	- 0.0014	
Avian predators	5	-66.316	-60.861	4.103	0.070		0.1571	0.0988	-0.0366	- 0.3507	
Non-voles	5	-66.145	-60.691	4.273	0.064		-0.1343	0.0870	-0.3048	- 0.0362	
Groundcover density	5	-65.578	-60.124	4.841	0.048		0.0088	0.0064	-0.0037	- 0.0214	
Small mammals	5	-64.456	-59.001	5.963	0.028		-0.0691	0.0684	-0.2031	- 0.0649	
Structural complexity	6	-66.540	-58.140	6.825	0.018	Structural complexity	-0.0074	0.0051	-0.0174	- 0.0026	
+ Groundcover						Groundcover openness	0.0070	0.0063	-0.0052	- 0.0193	
Mesopredators	5	-63.389	-57.935	7.030	0.016		-0.1648	0.3441	-0.8393	- 0.5097	
Cowbirds	5	-63.116	-57.661	7.303	0.014		0.0027	0.0144	-0.0256	- 0.0309	
Snakes * Small mammals	7	-68.037	-55.593	9.371	0.005	Snakes	-0.0110	0.0066	-0.0239	- 0.0019	
						Small mammals	-0.0850	0.0858	-0.2531	- 0.0832	
						Snakes * Small mammals	0.0195	0.0321	-0.0435	- 0.0824	
Site + NoVoleCapRate	9	-66.854	-41.139	23.825	0.000	Snakes	-0.0045	0.0044	-0.3091	- 0.0625	
+ AvgNumHerps +						Non-voles	-0.1233	0.0948	-0.2031	- 0.0649	
MesoCapRate +						Mesopredators	-0.1397	0.3064	-0.1320	- 0.3423	
AvianPredRate +						Avian predators	0.1052	0.1210	-0.0132	- 0.0041	
AvgNumBHCO						Cowbirds	0.0141	0.0138	-0.0130	- 0.0411	
Snakes + Small mammals +	9	-65.554	-39.839	25.125	0.000	Snakes	-0.0054	0.0044	-0.0054	- -0.0054	
Mesopredators +						Small mammals	-0.0699	0.0707	-0.0699	- -0.0699	
Avian predators +						Mesopredators	-0.1012	0.3208	-0.1012	- -0.1012	
Cowbirds						Avian predators	0.1088	0.1303	0.1088	- 0.1088	
						Cowbirds	0.0095	0.0136	0.0095	- 0.0095	

## APPENDIX I:

Daily survival rates models of the Field Sparrow and Song Sparrow at site-level.

Modified null model includes site. Table includes,  $\omega_i$ , parameter estimates, standard errors of parameter estimates. All models are shown.



Model	k	AIC	AIC <sub>C</sub>	ΔAIC <sub>C</sub>	ω <sub>i</sub>		β	β SE	95% CI		
<i>Field Sparrow</i>											
Groundcover density	2	-33.656	-31.256	0.000	0.772		0.0474	0.0113	<b>0.0253</b>	-	<b>0.0695</b>
Cowbirds	2	-29.457	-27.057	4.199	0.095		0.0979	0.0347	<b>0.0299</b>	-	<b>0.1659</b>
Structural complexity + Groundcover	3	-32.877	-26.877	4.380	0.086	Structural complexity	-0.0169	0.0186	-0.0532	-	0.0195
						Groundcover density	0.0560	0.0149	<b>0.0268</b>	-	<b>0.0852</b>
Null	1	-24.702	-24.035	7.221	0.021						
Structural complexity	2	-24.125	-21.725	9.531	0.007		0.0277	0.0256	-0.0225	-	0.0778
Mesopredators	2	-24.014	-21.614	9.642	0.006		-0.5610	0.5425	-1.6243	-	0.5023
Snakes	2	-22.870	-20.470	10.787	0.004		-0.0067	0.0188	-0.0435	-	0.0301
Avian predators	2	-22.858	-20.458	10.798	0.003		0.0619	0.1799	-0.2907	-	0.4144
Non-voles	2	-22.745	-20.345	10.911	0.003		-0.0763	0.4218	-0.9031	-	0.7504
Small mammals	2	-22.705	-20.305	10.951	0.003		-0.0095	0.1988	-0.3992	-	0.3802
Snakes + Small mammals + Mesopredators + Avian predators + Cowbirds	6	-22.401	61.599	92.855	0.000	Snakes	-0.0276	0.1074	-0.2382	-	0.1829
						Small mammals	-0.2820	0.9127	-2.0708	-	1.5068
						Avian predators	-0.1480	0.7902	-1.6969	-	1.4009
						Mesopredators	-0.1831	1.3833	-2.8943	-	2.5281
						Cowbirds	0.0889	0.0980	-0.1031	-	0.2810
Snakes + Non-voles + Mesopredators + Avian predators + Cowbirds	6	-22.391	61.609	92.865	0.000	Snakes	-0.0154	0.0710	-0.1545	-	0.1238
						Non-voles	-0.4771	1.5650	-3.5445	-	2.5903
						Avian predators	-0.1131	0.6911	-1.4676	-	1.2415
						Mesopredators	0.1024	0.9789	-1.8162	-	2.0209
						Cowbirds	0.1028	0.0813	-0.0566	-	0.2622

Continued

Continued

Model	k	AIC	AIC <sub>C</sub>	ΔAIC <sub>C</sub>	ω <sub>i</sub>		β	β SE	95% CI		
<i>Song Sparrow</i>											
Structural complexity	2	-32.631	-29.631	0.000	0.378		0.0319	0.0114	<b>0.0095</b>	-	<b>0.0543</b>
Mesopredators	2	-31.330	-28.330	1.302	0.197		-0.6030	0.2548	<b>-1.1024</b>	-	<b>-0.1036</b>
Cowbirds	2	-30.665	-27.665	1.966	0.141		0.0586	0.0272	<b>0.0053</b>	-	<b>0.1119</b>
Null	1	-28.069	-27.269	2.362	0.116		-	-	-	-	-
Groundcover density	2	-29.636	-26.636	2.995	0.085		0.0213	0.0117	-0.0016	-	0.0443
Small mammals	2	-26.865	-23.865	5.767	0.021		0.1213	0.1563	-0.1851	-	0.4277
Structural complexity	3	-31.474	-23.474	6.158	0.017	Structural complexity	0.0256	0.0150	-0.0038	-	0.0549
+ Groundcover						Groundcover density	0.0088	0.0123	-0.0154	-	0.0330
Non-voles	2	-26.217	-23.217	6.414	0.015		0.1360	0.4163	-0.6799	-	0.9518
Snakes	2	-26.081	-23.081	6.551	0.014		-0.0012	0.0126	-0.0258	-	0.0235
Avian predators	2	-26.070	-23.070	6.561	0.014		-0.0031	0.1240	-0.2462	-	0.2400
Snakes + Small	6	-35.251	Inf	Inf	0.000	Snakes	0.0482	0.0436	-0.0372	-	0.1336
mammals +						Small mammals	0.6014	0.3944	-0.1716	-	1.3744
Mesopredators +						Avian predators	0.3308	0.3053	-0.2676	-	0.9293
Avian predators +						Mesopredators	0.2955	0.6985	-1.0736	-	1.6646
Cowbirds						Cowbirds	0.0881	0.0590	-0.0276	-	0.2038
Snakes + Non-voles +	6	-51.311	Inf	Inf	0.000	Snakes	0.0386	0.0103	<b>0.0183</b>	-	<b>0.0588</b>
Mesopredators +						Non-voles	1.5621	0.2762	<b>1.0207</b>	-	<b>2.1035</b>
Avian predators +						Avian predators	0.3811	0.0930	<b>0.1988</b>	-	<b>0.5633</b>
Cowbirds						Mesopredators	-0.0434	0.1638	-0.3645	-	0.2777
						Cowbirds	0.0955	0.0183	<b>0.0596</b>	-	<b>0.1314</b>