

IS MEADOWLARK HABITAT SEGREGATION WITHIN SYMPATRY
BEHAVIORALLY MEDIATED?

BY

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THESIS

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ABSTRACT

The Eastern Meadowlark (*Sturnella magna*) and Western Meadowlark (*Sturnella neglecta*) are morphologically and ecologically similar species that co-occur within a recently expanded zone of secondary contact. Although spatial patterns of sympatric meadowlark populations have been previously compared, these comparisons have been qualitative in nature and lack the quantitative evidence necessary to provide a rigorous understanding of meadowlark habitat use within sympatry. At the patch scale, area-sensitivity, vegetation structure, and vegetation composition have been identified as important factors influencing habitat selection. It is also widely recognized that community assemblage is influenced by mechanisms beyond simple habitat relationships, such as interspecific competition. Within sympatry, Eastern and Western Meadowlarks establish and maintain mutually exclusive, multi-use territories. However, the influence this aggressive behavior may have on ecological relationships between these species is not well understood. In the following investigation, I examined environmental factors and behavioral mechanisms influencing Eastern Meadowlark and Western Meadowlark habitat use and distribution patterns at a large remnant sand prairie in northwestern Illinois. In the first study, I examined habitat use of both species occurring in the same area at the same time. Complementary to the habitat study, I examined the response of Eastern and Western Meadowlarks to conspecific and congeneric playback. Fieldwork was conducted during the 2007, 2008, and 2009 breeding seasons at the Lost Mound Unit of the Upper Mississippi National Wildlife and Fish Refuge in Carroll and Jo Daviess counties, IL. Meadowlarks responded to habitat features in different ways. Eastern Meadowlark density was best predicted by increasing cover of standing dead vegetation and decreasing exposure of bare ground, while Western Meadowlark density was best predicted by increasing cover of crown vetch (*Securigera*

varia). Meadowlarks were also segregated across the study area. The relative composition of meadowlarks among study plots differentiated along vegetation gradients such that plots were likely to be dominated by Eastern Meadowlarks as percent graminoid cover increased and crown vetch cover decreased. In addition to segregating ecologically, male meadowlarks were capable of discriminating congeners from conspecifics. Although both species responded to both conspecific and congeneric playback, males responded more to conspecific than congeneric playback. However, I found that Eastern Meadowlarks responded stronger to congeneric playback than did Western Meadowlarks. The results of the experimental playback study suggest that Eastern Meadowlarks are socially dominant to Western Meadowlarks, and may play an important role in shaping the patch-scale spatial patterns I observed between these species at Lost Mound.

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CHAPTER 1 – GENERAL INTRODUCTION: GRASSLAND BIRD HABITAT SELECTION, CONSERVATION AND MANAGEMENT

Grassland Bird Management and Conservation

The decline of North American grassland bird populations is well documented (Peterjohn and Sauer, 1999; Vickery and Herkert, 2001; Brennan and Kuvlesky, 2005). Evidence of these declines can be seen from the annual North American Breeding Bird Survey data, gathered since 1966 (Sauer et al., 2008). The scale of grassland bird decline has also been consistently greater than for any other avifaunal group (Knopf, 1994; Sauer et al., 2008).

Loss of breeding habitat resulting from an increased intensity in industrial agricultural practices as well as urban sprawl are widely recognized as primary causes of grassland bird decline (Rodenhouse and Best, 1983; Frawley and Best, 1991; Herkert, 1995, 1997; Vickery and Herkert, 2001; Murphy, 2003; Ribic et al., 2009). In response to this “unfolding conservation crisis” (Brennan and Kuvlesky, 2005), restorations and farmland set-aside programs such as the Conservation Reserve Program, have been used to expand grassland habitat in order to ameliorate some of the deleterious effects associated with habitat reduction (Herkert, 1994a, 2009; Johnson and Igl, 1995; Patterson and Best, 1996; Helzer and Jelinski, 1999; Vickery et al., 1999; Fletcher and Koford, 2002, 2003; Kennedy et al., 2008; Bakker and Higgins, 2009; Ribic et al., 2009). Underlying these types of initiatives is the premise that bird distributions are closely linked with habitat (reviewed in Heglund, 2002), and resources (i.e. Ideal Free Distribution model, Fretwell and Lucas, 1969). A general assumption has been that increasing the supply of grassland habitat ultimately leads to overall population increases of target species (Palmer et al., 1997; Ahlering and Faaborg, 2006). Yet, many environmental factors are likely involved in the actual habitat selection processes of a bird (Hildén, 1965; Cody, 1985), and for

most species these processes are poorly understood (reviewed in Ahlering et al., 2006, 2009). How grassland birds perceive and select habitat is still a major question in avian ecology, confounded by a lack of information on the appropriate scale needed to study habitat selection (Ribic et al, 2009).

Given the conservation and management implications and the assumption that grassland birds will locate and settle in the highest-quality habitat, studies designed to identify the environmental cues that attract grassland birds to a location have increased in recent decades (Jones, 2001). Some studies provide evidence that habitat selection in grassland birds occurs at multiple scales (Wiens et al., 1987; Thogmartin et al., 2006). As a result, multi-scale analyses have commonly been employed to compare the importance between habitat patches and landscapes (reviewed in Ribic et al., 2009). While regional conservation plans may be best informed by a multi-scale perspective, conservation efforts are often constrained to the management of specific parcels of land (Sample and Mossman, 1997; Fletcher and Koford, 2002; Rouget, 2003; Nocera et al., 2008; Ribic et al., 2009).

At the patch scale, three factors are particularly important including area sensitivity (i.e. patch size), habitat structure (i.e. plant height) and vegetation composition (i.e. species richness). Site occupancy for many species is strongly influenced by area sensitivity, which has been shown to affect breeding behavior and reproductive success (reviewed in Ribic et al., 2009). Vegetation height and density are important as they relate to concealment from predators and brood parasites, food accessibility and foraging behavior options among species (Cody, 1968; Herkert, 1993; Butler and Gillings, 2004; Devereaux et al., 2004, 2004, 2006; Davis, 2005; Willson et al., 2005; Churchwell et. al., 2008; Romanowski and Zmihorski, 2008; Douglas et al., 2009). Vegetation composition also has an effect on grassland bird community structure

(Rotenberry and Wiens, 1980; Rotenberry, 1985; Fletcher and Koford, 2002), especially in relation to the link between acquisition of food resources and vegetation composition (Quinn et al., 1991; Kemp et al., 1990, 2002; Jonas et al., 2002; Schaffers et al., 2008). Still, information on what habitat quality means for grassland birds is imperfect, as evidenced by the inconsistencies and the range of variables used to examine grassland bird habitat use and selection (Fisher and Davis, 2010).

Grassland Bird Habitat Selection

Grasslands are disturbance-dependent ecosystems characterized by a high degree of variation in annual precipitation, which in turn causes resources to vary erratically among locations and years (Anderson, 2006). Consequently, the same level of site fidelity exhibited by species occupying more stable habitats (e.g. cliff nesting Larid species), is inhibited from developing in grassland birds (McNicholl, 1975; Cody, 1985). The appearance of grassland habitat can also change dramatically during a breeding season (Bowles, 1993), and the factors affecting the success of breeding (such as the emergence of food resources) are often not observable until long after birds have already established territories (Svårdson, 1949; Hildén, 1965). This requires grassland birds to have some ability to track environmental cues associated with the factors that determine breeding success, when making settlement decisions (Hildén, 1965; Cody, 1985; Orians and Wittenberger, 1991). Therefore, the ability to identify, and to some degree predict suitable breeding conditions based on early spring environmental cues should be advantageous (Ahlering, 2009). In this way, natural selection has favored a behaviorally flexible habitat selection process that allows individuals to make independent decisions each year based on whether resources are sufficient for breeding at a given location

(Cody, 1985). The ability to track resources helps explain large annual fluctuations observed in certain population demographics (Igl and Johnson, 1997), the difficulty in demonstrating consistent spatial patterns at multiple scales (Winter et al., 2005; Winter et al., 2006), and the lack of desired effects in response to management efforts, despite finely-tuned treatments (Van Dyke et al., 2004).

Interspecific Interactions

The development of wildlife habitat quality indexes in general, is hindered by the fact that natural communities are the product of ecological processes that extend beyond those of simple habitat relationships (Rosenzweig, 1991; Wootton, 1994; Ward and Scholssberg, 2004; Ward, 2005; Ahlering and Faaborg, 2006; Fletcher, 2007; Campomizzi et al., 2008). Ecologists have shown in numerous studies that interspecific competition, in particular, can regulate habitat occupancy patterns as well as the resources exploited by ecologically similar species (Svärdson, 1949; MacArthur, 1958; Terborgh and Weske, 1975; reviewed in Schoener, 1983; reviewed in Tilman, 1987; Sherry and Holmes, 1988; Taniguchi and Nakano, 2000; Twomey et al., 2008). In many of these instances, interspecific aggression plays a large role, and is highly directed by a socially dominant species at one or two species with overlapping ecologies (Gochfeld, 1979; Lawton and Hassell, 1981; reviewed in Schoener, 1983; Leisler 1988; Robinson and Terborgh, 1995; Martin and Martin, 2001a and 2001b). Since this behavior demands much time and energy, natural selection should favor a reduction of aggressive behavior through ecological divergence (Orians and Willson, 1964). However, in structurally simple environments like grasslands, the options of divergent modes of resource exploitation are limited (Orians and Willson, 1964). Interspecific aggression can be maintained and sometimes even promoted by

convergence on common characters where sympatry has been recently established between ecologically and morphologically similar species (Cody, 1969; Rohwer, 1973).

Because of their high degree of mobility, birds have labile distribution edges and are able to move into the range of another species and colonize patches within it (reviewed in Bull, 1991). The resulting competitive interactions that take place at distribution edges are commonly condition-specific, where species are likely to exhibit expanded tolerances of their typical habitat associations, and where environmental factors can alter the competitive superiority between an interacting species pair (Dunson and Travis, 1991; Twomey et al., 2008; Taniguchi and Nakano, 2000). This can potentially play a significant role in patch-scale habitat use patterns, because within a variable environment, individuals of the species most closely adapted to the current local conditions would be able to monopolize the highest quality habitat (Thomas and Holloway, 2005; Carothers 1986; Sherry & Holmes 1988). However, conditions may not persist long enough for the dominant species to exclude competitors, thereby promoting an unstable coexistence (Hutchinson 1961; Connell, 1978).

Wiens (1985) raised two questions, among others, to guide investigations concerning habitat selection of birds in variable environments that remain relevant to grassland bird habitat selection and, therefore, grassland bird conservation. Can patterns of habitat use and distribution of co-occurring species be mediated through interspecific interactions? Do species respond individually to environmental factors, largely independent of interspecific interactions? The aim of this thesis is to examine the degree to which interspecific competition interacts with environmental factors in a variable environment to influence habitat use and distribution patterns of Eastern Meadowlark (*Sturnella magna*) and Western Meadowlark (*Sturnella neglecta*).

Eastern and Western Meadowlark Ecology

The recent establishment of a secondary contact zone between Eastern and Western Meadowlarks presents an ideal set of circumstances in which to examine the previously outlined questions. Since Audubon's 1844 discovery of meadowlarks west of the Mississippi, the relationship between the two species has long intrigued avian ecologists (reviewed in Lanyon, 1957). As a result, a rich foundation of scientific literature exists on which to base subsequent investigations of these species.

Molecular techniques established that the two species diverged over 2.6 million years ago (Klicka and Zink, 1997). Historically, these obligate grassland species were widely distributed across the prairie biome, existing largely in allopatry except for a narrow zone of sympatry extending from Oklahoma north to Ontario, east of which, Eastern Meadowlark was a common breeder and west of which, Western Meadowlark could be found breeding throughout (Lanyon, 1956). Meadowlarks have since experienced range expansions similar to other grassland birds over the past 100 years (reviewed in Askins, 1999), most notably for the Western Meadowlark, which expanded east into the Upper Midwest region during the first half of the 20th century (reviewed in Lanyon, 1956). It is largely speculative when the two species came into secondary contact, and the earliest records date to the late 1800s (Allen, 1880; McGee, 1880). Lanyon (1957) proposed that the two species likely remained isolated until as recently as, "... the arrival of white men in North America."

These species are so similar in their ecologies, that they have even been treated as ecological equivalents by avian ecologists (Wiens and Rotenberry, 1979). Yet, differences do exist. Johnson et al. (2004) gives the most recent and comprehensive review on meadowlark habitat associations. As noted above, meadowlarks have wide-ranging distributions and studies

have fittingly shown that Eastern and Western Meadowlarks utilize a variety of grassland habitat (reviewed in Johnson et al., 2004). Because of this range in habitat tolerance exhibited by both species, it is difficult to frame habitat associations for these birds concisely. Furthermore, effect sizes and measures of variance are rarely reported in grassland bird habitat-association studies (Fisher and Davis, 2010), and although a habitat suitability index has been developed for the Eastern Meadowlark (Schroeder and Sousa, 1982), it is largely theoretical and untested. No habitat suitability index has been developed for Western Meadowlark at this point.

Outside of sympatry, both Eastern and Western Meadowlarks utilize a variety of grassland types, generally preferring sites with high percent cover of native forbs and grasses, with little to no woody plant coverage (reviewed in Johnson et al., 2004). Furthermore, they have similar area requirements (Helzer and Jelinski, 1999) and are highly insectivorous, foraging preferentially on similar prey items (Kaspari and Joern, 1993; Kobal et al., 1998). However, Eastern Meadowlarks are typically found in moderately tall grasslands with moderately dense vegetation and abundant litter cover, whereas Western Meadowlarks are characteristic of short grasslands with sparse vegetation and shallow litter cover (reviewed in Johnson et al., 2004). Although general qualitative comparisons of habitat use and spatial patterns of sympatric meadowlark populations have been reported (Lanyon, 1956a, 1962; Szijj, 1966), this has not previously been studied empirically.

Within the expanding zone of sympatry, both species exhibit interspecific territorial behavior that results in the complete segregation of their multi-use territories (Lanyon, 1956, 1957). Although infrequent cases of mixed pairings and interbreeding-s have been reported (reviewed in Rowher, 1979) the species remain reproductively isolated, exhibiting an extremely high degree of hybrid sterility (Lanyon, 1979), and maintain distinctive songs (Ordal, 1976). In

some cases, both species defended their territories against congeners with equal vigor and frequency (Lanyon, 1956, 1957), suggesting that excluding another species from a territory has more to do with securing an adequate amount of resources, namely food, than securing mates. Murray (1971, 1981) contended that this behavior could only be adaptive for the dominant member of the interacting species pair, and though increased fighting within sympatry has been observed (Rohwer, 1973), a consensus regarding the participation of each species in aggressive interactions has not been reached and an ecological basis for this behavior remains in question.

Study Objectives

Interspecific competition between bird species has typically been examined in two ways; (1) by characterizing differences in habitat use of ecologically similar species that have been observed to hold exclusive territories (Morse, 1971; Terborgh and Weske, 1975; Sherry and Holmes, 1988; Martin and Martin, 2001a) and (2) by using playback experiments when aggressive behaviors have been observed (Catchpole, 1978; Catchpole and Leisler, 1986; Robinson and Terborgh, 1995; Martin et al., 1996; Martin and Martin, 2001b). In the following investigation, presented as two studies (Chapters 2 and 3), I examined environmental and behavioral mechanisms influencing habitat use and distribution patterns of Eastern Meadowlarks and Western Meadowlarks at a large remnant sand prairie in northwestern Illinois during the 2007, 2008, and 2009 breeding seasons.

The first study (Chapter 2) examined habitat use patterns of both species within sympatry. Based on their morphological and ecological similarities, I expected that features associated with optimal habitat should be similarly important between species within sympatry. Theory predicts that one species should monopolize the most productive habitat (Fretwell and

Lucas, 1969). Therefore, if interspecific territorialism between Eastern and Western Meadowlarks has an ecological basis, differences in habitat associations should be apparent, such that one species is exclusively associated with features characteristic of quality habitat while the other species is associated primarily with sub-optimal habitat features. Conversely, if habitat use is largely independent of interspecific interactions, habitat associations between these species should converge rather than differentiate.

Complementary to the first study, I examined the response of Eastern and Western Meadowlarks to conspecific and congeneric playback (Chapter 3). Data from these experiments were used to address whether (1) Eastern and Western Meadowlarks respond to conspecifics differently than to heterospecifics, (2) dissimilarities in heterospecific response indicated consistent asymmetric aggressive behavior of one species towards the other, and (3) behavioral interactions between species reflected ecological interactions I observed in the first study. The results of this study allowed me to make inferences about the social hierarchy between these species and whether interspecific aggressive behavior might be an important mechanism in shaping habitat use in this species pair when they occur in sympatry.

The information gained from this investigation is valuable for grassland bird research and conservation planning, because it emphasizes mechanisms influencing habitat-use and distribution patterns operating at the patch-scale that broad-scale management models will not capture (Orians and Wittenberger, 1991). Additionally, ecological changes to the landscape resulting from human influences and climate change can alter breeding and non-breeding ranges of many bird species, whereby previously allopatric species can become sympatric (Askins, 1999; Martin, 2001; Wiens et al., 2009), thereby warranting a closer examination of the ecologies of interacting species that have recently established sympatric or parapatric

distributions (reviewed in Bull, 1991). Further, while behavioral interactions have been the focus of several studies of habitat use and distribution in other ecosystems (Terborgh and Weske, 1975; Catchpole and Leisler, 1986; Robinson and Terborgh, 1993; Poling and Hayslette, 2006; Singleton et. al., 2010), behaviorally mediated habitat use patterns in grassland bird species have been far less commonly examined (though see Rowher, 1973; Gochfeld, 1979; Ahlering and Faaborg, 2006; Nocera et al., 2009). Additional demonstration of the importance of interspecific behavior in grassland settings may generate increased research interest and better inform grassland bird conservation efforts. Finally, management within a highly fragmented landscape is often limited to publicly owned lands, comprising less than 1% of the landscape in places like the Upper Midwest (Thomgartin et al., 2006). In this context, patch oriented research is a fitting scale to inform and enhance grassland bird conservation and management.

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CHAPTER 2 –VEGETATION FEATURES PREDICT HABITAT SEGREGATION IN SYMPATRIC MEADOWLARKS

ABSTRACT

The Eastern and Western Meadowlark are morphologically and ecologically similar species that co-occur within a recently expanded zone of secondary contact. Where they co-occur, Eastern and Western Meadowlarks establish and maintain mutually exclusive, multi-use territories. In this study I examined how well food resources and habitat associations could predict Eastern and Western Meadowlark densities as well as the relative composition of Eastern to Western Meadowlarks across a large remnant grassland, using an information theoretic approach. I found that Eastern and Western Meadowlarks responded to habitat features in different ways. Eastern Meadowlark density was best predicted by increasing cover of standing dead vegetation and decreasing exposure of bare ground, while Western Meadowlark density was best predicted by increasing cover of crown vetch. Meadowlarks were also segregated across the study area. The relative composition of meadowlarks among study plots differentiated along vegetation gradients such that plots were likely to be dominated by Eastern Meadowlarks as percent graminoid cover increased and crown vetch cover decreased. These results indicate differential habitat use between sympatric meadowlarks, which likely reflect differences in behavioral interactions between these species detailed in Chapter 3.

KEYWORDS

Meadowlark, asymmetric habitat use, sympatry, grassland bird

INTRODUCTION

The extent to which grassland birds have declined over the past several decades has generated great alarm among conservationists, and much research has concentrated on grassland bird habitat selection and use. Studies have addressed grassland bird habitat use by focusing primarily on identifying relationships with patch size and shape, as well as habitat structure and composition (reviewed in Ribic et al., 2009; and Fisher and Davis, 2010). Comparatively few studies have investigated how interspecific interactions may affect habitat use within grassland bird communities (though see Gochfeld, 1979; and Ahlering and Faaborg, 2006), yet it is generally accepted that these interactions influence the selection process of birds (Hildén, 1965; Cody, 1985). Interspecific competition, in particular, is widely thought to regulate resource acquisition and habitat occupancy between ecologically similar species (Svärdson, 1949; MacArthur, 1958; Terborgh and Weske, 1975; Schoener, 1983; Tilman, 1987; Sherry and Holmes, 1988; Peiman and Robinson, 2010).

The Eastern Meadowlark (*Sturnella magna*) and Western Meadowlark (*Sturnella neglecta*) are short-distance migrants, and are remarkably similar in their appearance and ecologies. Both species prefer areas with little woody vegetation that are dominated by native warm-season graminoids (reviewed in Johnson et al., 2004), and are only mildly area-sensitive (Herkert, 1994; Helzer and Jelinski, 1999). They are also both ground-nesting birds and seem to differ only marginally in terms of the structural nature of their breeding habitat (Herkert et al., 1993; Bowles, 1995; Lanyon, 1995; Davis and Lanyon, 2008). Eastern Meadowlarks are typically found in moderately tall grasslands with moderately dense vegetation and abundant litter cover, whereas Western Meadowlarks are characteristic of short grasslands with sparse vegetation and shallow litter cover (reviewed in Johnson et al., 2004). Additionally, Eastern and

Western Meadowlarks are primarily insectivorous, with Orthoptera contributing greatly to the diet of both species, and have similar foraging habits (Kaspari and Joern, 1993; Kobl et al., 1998). These species also share similar nest predators and parasites (Lanyon, 1995; Davis and Lanyon, 2008). In essence, these species occupy nearly the exact same niche.

The distributions of Eastern and Western Meadowlarks have been expanding as a result of recent ecological changes at the periphery of their ranges (Lanyon, 1956a), presenting a case where interspecific interactions are likely involved in shaping distribution patterns within areas where they co-occur. Within sympatry Eastern and Western Meadowlarks establish non-overlapping, multi-use territories (Lanyon, 1957; Lanyon, 1962; Szijj, 1966; Rohwer, 1973). Although spatial patterns of sympatric meadowlark populations have been previously compared (Lanyon, 1956a, 1962; Szijj, 1966; Rohwer, citation), those comparisons were qualitative in nature and lack the quantitative evidence necessary to provide a rigorous understanding of meadowlark habitat use within sympatry.

The aim of this study was to quantify used and unused Eastern and Western Meadowlark habitat, and to determine which features were important predictors of density within a species as well as the relative composition between species across an area of sympatry. Additionally, the results of this study would establish a basis on which to evaluate the extent behavioral interactions between these species might be involved in mediating spatial patterns. Because of the morphological and ecological similarities between Eastern and Western Meadowlarks, I assumed that features associated with optimal habitat such as an abundance of food and adequate cover for concealment against predators, would be important predictors of density for both species. However, theory predicts that one species should monopolize the most productive habitat (Fretwell and Lucas, 1969). Therefore, differences in Eastern and Western Meadowlark

habitat associations might be apparent, and the relative composition between species across the study area would be best predicted by features characteristic of quality habitat as well as those associated with sub-optimal conditions.

METHODS

Study Area

I examined Eastern and Western Meadowlark patch-scale habitat use and distribution patterns at the Lost Mound Unit of the Upper Mississippi River National Wildlife and Fish Refuge in northwest Illinois, USA (42°15' N, 90°20' W). This site was formerly the Savanna Army Depot, and contains a large (approximately 2,500 ha) remnant sand prairie (Wenny et al., 2006). The sand originated from Wisconsinan glacial outwash (Bowles, 1993), and soils at the site have been classified as Sparta loamy sands and have low organic material content (Symstad, 2004). The site experienced a long period of intense cattle grazing (1950-1999), approximately 100 years of fire suppression beginning as late as 1917, and extensive road and building development (1940's). Although the sand prairie remains largely intact and is dominated by native warm season grasses such as Little blue-stem (*Schizachyrium scoparium*), Indian grass (*Sorghastrum nutans*) and Sand dropseed (*Sporobolus cryptandrus*) (Wenny and Symstad, 2002; Symstad, 2004), invasion of woody plants such as Red cedar (*Juniperus virginiana*) and Honey locust (*Gleditsia triacanthos*) and exotic plants such as Crown vetch (*Securigera varia*), Yellow sweetclover (*Melilotus officinalis*) and Spotted knapweed (*Centaurea stoebe*) have degraded large areas of the prairie.

I established study sites at twenty-four grassland areas, 40 ha in size that were loosely stratified across the site. Areas were selected to include as little woody vegetation cover as

possible in order to minimize the influence of woody vegetation on preferences in microhabitat conditions by the birds (Martin, 1998). Within these twenty-four grassland areas, I established one 100-m radius study plot at the center of each grassland area were set up, in which meadowlarks, vegetation, and food resources were surveyed.

Meadowlark Population Survey

At each study plot, meadowlark abundance was observed by conducting 100 m fixed-radius point counts (Hutto et al., 1986). Point counts began at sunrise and continued for approximately four hours afterward. All meadowlarks seen or heard at a study plot were counted within a five-minute period, and distance from the center point to each bird was measured using a laser range finder. Point counts were conducted in late May (Appendix A). Surveys were not conducted during periods of rain or excessive wind (exceeding 24km/hr). I used program DISTANCE to model the detection probability of Eastern and Western Meadowlarks (Thomas et al., 2006). Results indicated that my detection probability was uniformly high within 100 m, so I calculated Eastern and Western Meadowlark densities and the Easternness of study plots as the number of birds within a 100-m plot divided by the area of that plot, and the proportion of Eastern to Western Meadowlarks within plots, respectively.

Vegetation Sampling

I measured vegetation characteristics (Table 7) beginning in early June in 2007 and beginning in late May in 2008 and 2009. Within each study plot, I randomly established two 80-m long transects. Percent cover of each plant species was measured within 0.5m x 1 m quadrats that alternated every 20m on either side of each transect, for a total of 10 quadrats per study plot. Bare ground exposure and standing dead vegetation cover were also measured such that the total cover of each quadrat was equal to at least 100%. Percent cover for each plant species was

grouped by functional type (i.e. graminoid or flowering plant, Table 7) resulting in one value per functional type per study plot.

Vegetation structure was measured at four randomly selected points within each study plot, and vegetation height and density were measured following Robel et al. (1970). Litter depth (cm) readings were also taken at each of the four cardinal directions from the Robel pole. I also measured the density of trees (woody species > 2 m in height) for each study plot. Vegetation structure sampling periods overlapped vegetation composition sampling periods.

Orthoptera Sampling

Orthopterans constitute a large percentage of both Eastern and Western Meadowlark diets (with preferences for those greater than 15 mm in size), and increase in importance as the breeding season progresses (Kaspari and Joern, 1993; Kobal et al., 1998). I surveyed orthopterans twice each year. The first survey overlapped vegetation sampling periods in each year (early June), and the second survey occurred in mid July of each year. Orthopterans were collected by taking 100 sweeps through the vegetation along both vegetation transects at each study plot using sweep nets following Evans et al. (1983). Orthopterans captured in each sample were then removed from the sweep net, separated from vegetation that was also captured, and stored in 70% ethanol for subsequent identification. Using Capinera et al. (2004) and Kirk and Bomar (2005), orthopterans were identified to the subfamily level and placed into three size classes based on body length (0-14.9 mm, 15-29.9 mm, and 30+ mm). Kaspari and Joern (1993) found that meadowlarks avoided prey smaller than 15 mm in size and had increasing preference for prey between 15 mm and 35 mm in size. Abundance per subfamily was used to calculate a relative Shannon diversity index for each study plot, while abundance per size class was totaled to give an estimate of relative food abundance for each study plot (Table 2).

Candidate Model Development

I constructed two sets of candidate models a priori to determine the effects of habitat, food and competitor influences on meadowlark density and proportion within study plots (Appendix B). I used the same model set to examine how density was influenced for both species, because species with similar morphologies and ecologies are expected to select habitat in similar ways (Price, 1991). A difference candidate model set was constructed to examine how the proportion of Eastern Meadowlarks to Western Meadowlarks (Easternness) was influenced based on food and habitat associations (Appendix B). Covariates included maximum height and vertical density of vegetation (live or dead), litter depth, tree density, and percent bare ground in my models to represent the vertical and horizontal structure of study plots. These variables also reflect overall patch health and potential trade-offs between concealment, the need for vigilance, and foraging efficiency (Lusk et al., 2003; Fisher and Davis, 2010). Percent cover of graminoids, flowering plants, and standing dead vegetation were included to represent the composition of study plots. Because of poor moisture-holding capacity of the sandy soils at Lost Mound, the general appearance of vegetation can be very different between years with different precipitation levels (Bowles, 1993). Additionally, these composition variables also reflect the abundance of suitable nesting substrate, and factors related to prey abundance and diversity (Siemann, 1998; Schaffers et al., 2008; Fisher and Davis, 2010). I also included early- and late-season abundance and diversity of prey items (small, medium and large orthopterans) to represent the importance of food resources as the breeding season progresses (Kaspari and Joern, 1993). Grassland birds are also likely to use cues early in the breeding season, such as vegetation characteristics, to predict the availability of late-season resources, such as food, which ultimately affect breeding success (Hildén, 1965, Cody, 1985). Finally, I included congener

presence and density as variables to detect signs of territorial avoidance between species, because it has been suggested that meadowlarks may form colonies at sites within sympatry in order to reduce the frequency of interspecific interactions (Rohwer, 1973). Variables that were highly correlated ($|r| > 0.50$) were not used in the same model (Tables 3 and 4). A total of 13 models were constructed to examine density and 11 models to examine Easternness (Appendix B).

Statistical Analysis

I used generalized linear mixed models in program SAS 9.2 (SAS Institute, 2008) and an Information Theoretic Approach to evaluate support for my competing models. I used a normal distribution to model the probability of the response variables as linear functions of my covariates, Eastern Meadowlark density and Western Meadowlark density, and a binary distribution to model Easternness, as a binary function of my covariates (SAS 9.2, SAS Institute 2008). For the response variables, Eastern and Western Meadowlark density, all models included an intercept term and up to six predictor variables. For the response variable, Easternness, all models included an intercept term and up to two predictor variables. The number of estimable parameters for each model allowed me to optimize the model likelihood without sacrificing the precision of the individual covariate estimates by over-parameterizing the data (Anderson, 2008). I used 60 discrete observations of Eastern and Western Meadowlark densities, and 23 observations of the proportion of Eastern to Western Meadowlarks, over a three-year period of from 2007 to 2009. To account for repeated sampling of points across years, I treated plot as a random effect. Models were ranked using Akaike's Information Criterion corrected (AIC_c) for small sample sizes (Burnham and Anderson, 2002). I considered models with $\Delta-AIC_c$ of ≤ 2 to have substantial support (Burnham and Anderson, 2002). To account for model-selection uncertainty, I used model-averaging to estimate coefficients and unconditional

95% confidence intervals for parameters contained within models that summed to 90% of the Akaike weight (Anderson, 2008). Parameters whose confidence intervals excluded zero were considered influential predictors.

RESULTS

Meadowlark Data

In three field seasons, I counted 56 meadowlarks in 72 point-count surveys conducted on 24 study plots (Appendix A). Overall, more Eastern (32) than Western (24) Meadowlarks were recorded in May from 2007 to 2009, and Eastern Meadowlarks were more abundant during each sampling period. From 2007 to 2009, Eastern Meadowlarks were counted in 12 of the 24 study plots while Western Meadowlarks were observed in 9 of the 24 study plots. In only 4 of the 72 point-counts, both species were recorded together within the same study plot.

Interspecific Habitat Use

I compared 13 candidate models (Appendix B) to evaluate how well the density of each meadowlark species was predicted by the presence of congeners, habitat features, and orthopteran abundance and diversity, among study plots. I also compared 11 candidate models (Appendix B) to assess how habitat features and orthopteran abundance and diversity influenced Easternness within study plots. In general, Eastern and Western Meadowlark densities across Lost Mound were most influenced by habitat features that were qualitatively different, and the presence of heterospecifics and food availability seemed to have little effect. Easternness within a plot was most influenced by two habitat gradients, percent cover of graminoids and flowering plants.

Over half of the models in the candidate set did better at predicting Eastern Meadowlark density, than the constant model (Appendix B). A model including maximum vegetation height, percent cover of flowering plants, and percent cover of dead plant material best predicted Eastern Meadowlark density (Table 5). All three parameters were relatively important compared to the other parameters in the model set (Table 6). Additionally, there were no other competing models (i.e., no other models with $\Delta AIC_c \leq 2$), the top ranked model had 70% of the Akaike weight, and fit these data > 500 times better than the constant model based on the evidence ratio (Table 5). However, the confidence limits of model-averaged coefficients for maximum vegetation height and percent cover of flowering plants overlapped zero, indicating that these parameters were not reliable predictors of Eastern Meadowlark density (Table 6). Conversely, bare ground exposure did not appear in the top ranked models, its contribution to overall model support was also relatively low compared to other parameters in the model set, yet based on the confidence limits of its model-averaged coefficient, it was a reliable predictor of Eastern Meadowlark density (Table 6). Eastern Meadowlark density increased as cover of standing dead vegetation increased (Figure 1), and decreased as bare ground exposure increased (Figure 2). The maximum density of Eastern Meadowlarks observed (1.27/ha), corresponded with 35% cover of dead plant material and zero bare ground exposure.

Only four of the models in the candidate set did better at predicting Western Meadowlark density, than the constant model (Table 5). All four models contained percent cover of flowering plants, which was highly important relative to the other parameters in the model set (Table 6). The top ranked model only had 32% of the Akaike weight, but fit these data 93 times better than the constant model, according to the evidence ratio (Table 5). Furthermore, when Akaike weights of all four models were summed they had 98% of the Akaike weight (Table 5). The top

four models also contained the following parameters; orthopteran diversity early and late in the breeding season, maximum vegetation height, percent cover of graminoids, dead plant material, litter depth, and presence of Eastern Meadowlarks (Table 5). However, these parameters contributed relatively little to overall model support, compared to percent cover of flowering plants. In addition, the model-averaged coefficients associated confidence limits of each of those parameters indicated that they were poor predictors of Western Meadowlark density. Only percent cover of flowering plants reliably predicted Western Meadowlark density, where density increased as percent cover of flowering plants increased (Figure 3). The maximum density of Western Meadowlarks observed (0.95/ha), corresponded with 50% cover of flowering plants.

Over half of the models in the candidate set did a better job of predicting Easternness, than the constant model (Appendix B). Percent cover of flowering plants together with diversity of late-season orthopterans best predicted Easternness among study plots, though graminoid cover together with late-season orthopteran abundance was a competing model (Table 5). The top ranked model fit these data 94 times better than the constant model according to the evidence ratio, but had 53% of the total Akaike weight, which was only somewhat higher than the weight (37%) associated with the competing model (Table 5). None of the parameters within the top ranked models contributed noticeably more to overall model support more than the others. However, the coefficients and confidence limits associated with the model-averaged parameters indicated that percent cover of flowering plants and graminoids reliably predicted Easternness within study plots, while late-season orthopteran abundance and diversity did not (Table 6). Easternness increased as graminoid cover increased (Figure 4), and decreased as percent cover of flowering plants increased (Figure 5). The proportion of Eastern to Western Meadowlarks was equivalent at approximately 20% graminoid cover and 40% flowering plant cover (Figures 4 and

5). Sites were likely to be exclusively occupied by Eastern Meadowlarks when $\geq 40\%$ graminoid cover, and $\leq 30\%$ cover of flowering plants (Figures 4 and 5).

DISCUSSION

Meadowlarks utilized 16 of 24 study plots at some point in time during this study. Although Eastern and Western Meadowlark populations occurred in relatively large numbers at Lost Mound (Kleen, 2007, 2008, 2009), I rarely observed both species together. These data further confirm that Eastern and Western Meadowlarks segregate across sites where they co-occur (Lanyon, 1957; Rohwer, 1973).

Rohwer (1973) suggested that meadowlarks might form conspecific clusters within sympatry in order to mitigate increased interspecific fighting that results when these species co-occur. However, in this study, congener presence and density were not reliable predictors of either Eastern or Western Meadowlark densities. Orthoptera abundance and diversity were similarly unreliable at predicting meadowlark densities or Easternness. Therefore, clustering of species was also not primarily related to local superabundance of food or differences in foraging niches between species. Instead, meadowlark densities and the Easternness of study plots were best predicted by vegetation variables, suggesting that once birds arrived at Lost Mound, local-scale habitat characteristics had the biggest impact on settlement decisions of breeding meadowlarks. Studies have provided evidence that habitat selection in grassland birds occurs at multiple scales (Wiens et al., 1987; Thogmartin et al., 2006), and both vegetation structure and composition have been well established in shaping grassland bird communities (reviewed in Fisher and Davis, 2010).

Several models composed of a variety of variables were better than the constant model at predicting Eastern Meadowlark density, though variables related to the amount of vegetation cover were the best. Density was positively related to increasing cover of standing dead vegetation and decreasing bare ground exposure. These results closely parallel those found in several studies that have examined relationships between Eastern Meadowlark density and habitat features (reviewed in Hull, 2000), and in a broader context are consistent predictors of habitat use for many grassland bird species (reviewed in Fisher and Davis, 2010). Standing dead vegetation is a dominant cover type early in the breeding season and can provide a suitable nesting substrate for grassland birds (Davis, 2005). Additionally, standing dead vegetation may serve as an early, inclusive indicator of overall patch quality for birds when searching for suitable breeding habitat within a highly variable landscape (Ahlering et al., 2009; Fisher and Davis, 2010). Reduced bare ground exposure also increases nest concealment from brood-parasites and predators and has been linked to increased nest survival in similar grassland species (Davis, 2005; Churchwell et. al., 2008). Although other factors associated with reducing parasitism and predation risk such as vegetation height and density (Johnson and Temple, 1990; Winter, 1999; Whittingham and Evans, 2004; Davis, 2005; Churchwell et al., 2008), were not reliable predictors of Eastern Meadowlark density, vegetation height did contribute some support relative to the rest of the parameters in the model set. In general, Eastern Meadowlark density responded to a variety of habitat features thought to influence grassland bird habitat use, and in particular to vegetation parameters, in ways that were consistent with previous studies.

Conversely, only a limited set of models were better than the constant model at predicting Western Meadowlark density at Lost Mound. Among those models it was clearly evident that percent cover of flowering plants contributed the greatest support to each of those models.

Previous studies have shown negative relationships between Western Meadowlark density and increasing forb cover (reviewed in Dechant et al., 1999). Yet in this study, I observed an apparent reverse of this trend. At Lost Mound, Western Meadowlark density was likely to increase as percent cover of flowering plants increased. This may be explained by deconstructing the components incorporated within the flowering plant cover parameter. Flowering plant cover included both forb and legume cover, and while legume and flowering plant cover were strongly correlated ($r = 0.875$), forb and flowering plant cover were not correlated ($r = 0.098$). Furthermore, crown vetch cover is at least 20 times that of other legumes at Lost Mound, which comprise only about 0.1% of the total plant cover (Wenny and Symstad, 2002). Percent flowering cover should be thought of more precisely as the percent cover of crown vetch within study plots. A more accurate interpretation then would be that Western Meadowlark density was likely to increase with increasing cover of crown vetch.

Crown vetch is an exotic, invasive legume that overtops native plants, and facilitates invasion of other exotic species (Symstad, 2004; Losure et al., 2009). This plant quickly develops into dense, monotypic stands (Molano-Flores, personal communication) that reduce native plant richness and horizontal cover (Symstad, 2004). Large, dense patches of crown vetch may also hinder prey detectability and accessibility while increasing time spent watching for predators (Butler and Gillings, 2004; Devereux et al., 2004; Butler et al., 2005; Devereux et al., 2006). In addition, crown vetch produces beta-nitropropionic acid, a secondary compound toxic to non-ruminant animals (Shenk et al., 1976) and a natural insect deterrent (Byers et al., 1986). However, crown vetch is considered suitable forage for grasshoppers (Hewitt et al., 1982), which are able to consume large quantities of the legume (Wheeler, 1974). Even though little is known on how grasshoppers metabolize beta-nitropropionic acid, Orthoptera are a preferred food item

by meadowlarks (Kaspari and Joern, 1993; Kobal et al., 1998), creating a potential pathway between nitropropionic acid contained within crown vetch plant tissue and meadowlarks. Ultimately, crown vetch may act in multiple ways that negatively impact food acquisition and meadowlark breeding habitat in general, though there is currently little direct evidence to support this idea.

Although density tends to be a good indicator of habitat quality in many situations (Bock and Jones, 2004), it may fail to predict habitat quality when dominant individuals of one species are able to force large numbers of subordinate individuals of other species into less productive habitat (Van Horne, 1983). I anticipated that this might be the case for sympatric meadowlarks, and so I also assessed how the relative proportion of Eastern to Western Meadowlarks among study sites was predicted by habitat structure and composition as well as food availability and abundance. Among study plots occupied by meadowlarks, Eastern Meadowlarks were likely to become more abundant as graminoid cover increased, and as flowering (i.e., crown vetch) cover decreased. Graminoids are important for grassland birds and provide many benefits such as nesting substrate, cover from predators and abundant prey (Best et al., 1997; Davis, 2005; Flanders et al., 2006). Not surprisingly, previous work on meadowlarks outside sympatry has shown that both species prefer sites that have high cover of native graminoids (reviewed in Johnson et al., 2004). Relatively few studies have shown that grass cover is an important predictor of grassland bird community composition, because of a bias born into studies comparing grassland bird communities among sites with grassy habitat (Fisher and Davis, 2010). Therefore, differentiation along a graminoid gradient is noteworthy for such an ecologically similar species pair, especially at a location where graminoid coverage varied relatively little (Table 7). In essence, Eastern and Western Meadowlarks differentiated along the variable that

most embodies grasslands, graminoid cover (Anderson, 2006), and arguably one of the variables that best represents decaying grassland conditions at Lost Mound, crown vetch cover (Symstad, 2004).

CONCLUSIONS

Spatial patterns of sympatric meadowlark populations have been previously compared, but have lacked the quantitative evidence necessary to provide a rigorous understanding of patch-scale habitat use within sympatry. At Lost Mound Eastern Meadowlark density responded to many habitat features thought to be important in predicting grassland bird habitat use, and particularly to parameters characteristic of late-successional vegetative communities in ways similar to Eastern Meadowlarks outside of sympatry. Conversely, Western Meadowlark density was uncharacteristically tied to one vegetation feature, which is likely not very useful for breeding. Furthermore, the relative composition of Eastern and Western Meadowlarks among study plots differentiated along gradients of graminoid and crown vetch cover. Similar patterns of habitat use between co-occurring, ecologically similar species seem to be common in situations where a socially dominant member of a species pair is able to monopolize the best quality habitat (Terborgh and Weske, 1975; Morse, 1971; Gochfeld, 1979; Sherry and Holmes, 1988; Robinson, 1992; Robinson and Terborgh, 1995; Peiman and Robinson, 2010). Although I did not present direct evidence that Western Meadowlarks occupy suboptimal habitat, or that Eastern Meadowlarks restrict Western Meadowlarks from habitat patches, removal experiments could be conducted to address whether or not this is the case.

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2.1 TABLES AND FIGURES

Table 1. Summary statistics for vegetation structure and composition variables measured in study plots at Lost Mound during 2007, 2008, and 2009.

Variable ^a	Mean	SE	Min	Max	CV ^b
MAXHEIGHT					
2007 (<i>n</i> =15)	7.614	0.516	4.500	12.750	0.318
2008 (<i>n</i> =24)	6.833	0.482	0.750	10.500	0.346
2009 (<i>n</i> =24)	8.771	0.650	4.500	14.500	0.363
ROBEL					
2007 (<i>n</i> =15)	1.902	0.204	0.190	4.060	0.504
2008 (<i>n</i> =24)	1.259	0.150	0.000	2.310	0.584
2009 (<i>n</i> =24)	1.424	0.159	0.250	3.400	0.546
LITTER					
2007 (<i>n</i> =15)	2.338	0.280	0.750	5.130	0.562
2008 (<i>n</i> =24)	2.118	0.405	0.000	6.250	0.936
2009 (<i>n</i> =24)	1.678	0.315	0.000	5.500	0.918
TREES					
2007 (<i>n</i> =15)	16.182	3.741	0.000	66.000	1.084
2008 (<i>n</i> =24)	37.500	6.694	0.000	118.000	0.874
2009 (<i>n</i> =24)	36.042	5.262	0.000	89.000	0.715
BAREGROUND					
2007 (<i>n</i> =15)	7.953	2.216	0.000	28.000	1.079
2008 (<i>n</i> =24)	7.792	1.704	0.000	26.000	1.071
2009 (<i>n</i> =24)	21.521	3.535	0.200	64.900	0.805
DEADPLANT					
2007 (<i>n</i> =15)	15.420	2.564	6.000	45.000	0.644
2008 (<i>n</i> =24)	19.583	2.286	5.000	42.000	0.572
2009 (<i>n</i> =24)	18.892	2.085	4.000	40.500	0.541
GRAMINOID					
2007 (<i>n</i> =15)	48.533	3.126	37.000	78.000	0.249
2008 (<i>n</i> =24)	41.417	2.662	16.000	67.000	0.315
2009 (<i>n</i> =24)	26.708	2.167	13.000	44.000	0.398
FLOWERING					
2007 (<i>n</i> =15)	22.395	2.479	8.000	39.000	0.429
2008 (<i>n</i> =24)	24.667	2.877	0.000	71.000	0.571
2009 (<i>n</i> =24)	21.875	3.089	8.000	58.000	0.692

^a Variable Definitions: *MAXHEIGHT*, averaged maximum height of non-woody vegetation; *ROBEL*, averaged vertical density of non-woody vegetation; *LITTER*, averaged depth of litter layer; *TREES*, density of woody vegetation greater than 2m in height; *BAREGROUND*, percent exposure of bare ground; *DEADPLANT*, percent cover of standing dead plant material; *GRAMINOID*, percent cover of grass and sedge vegetation; *FLOWERING*, percent cover of forb and legume vegetation. ^b CV stands for coefficient of variation.

Table 2. Summary statistics for Orthoptera and Meadowlark variables measured among study plots at Lost Mound during 2007, 2008 and 2009.

Variable ^a	Mean	SE	Min	Max	CV ^b
EARLYSMALLORTHOP					
2007 (n=22)	168.727	23.064	16	439	0.641
2008 (n=24)	65.750	13.204	3	264	0.984
2009 (n=24)	54.208	8.576	6	180	0.775
EARLYMEDORTHOP					
2007 (n=22)	8.636	1.749	0	24	0.950
2008 (n=24)	0.042	0.042	0	1	4.899
2009 (n=24)	0.208	0.085	0	1	1.991
EARLYORTHOPDIVERSITY					
2007 (n=22)	3.036	0.112	2.192	4.423	0.173
2008 (n=24)	0.783	0.056	0.279	1.374	0.353
2009 (n=24)	3.287	0.213	1.652	5.744	0.318
LATESMALLORTHOP					
2007 (n=20)	142.750	27.251	27	596	0.854
2008 (n=24)	69.583	8.251	4	201	0.581
2009 (n=24)	71.292	6.518	25	144	0.448
LATEMEDORTHOP					
2007 (n=20)	33.600	4.621	9	76	0.615
2008 (n=24)	33.708	4.761	4	92	0.692
2009 (n=24)	17.000	2.770	0	58	0.798
LATEORTHOPDIVERSITY					
2007 (n=20)	3.000	0.109	2.172	3.811	0.163
2008 (n=24)	0.831	0.051	0.377	1.339	0.302
2009 (n=24)	1.171	0.055	0.683	1.536	0.229
EAMEDENSITY					
2007 (n=23)	0.181	0.053	0.000	0.640	1.394
2008 (n=24)	0.120	0.294	0.000	1.270	2.458
2009 (n=24)	0.133	0.047	0.000	0.640	1.721
WEMEDENSITY					
2007 (n=23)	0.292	0.095	0.000	1.000	1.275
2008 (n=24)	0.458	0.509	0.000	1.000	1.110
2009 (n=24)	0.208	0.415	0.000	1.000	1.991

^a Variable Definitions: *EARLYSMALLORTHOP*, abundance of orthopterans less than 15mm in size during the 1st sampling period of each year; *EARLYMEDORTHOP*, abundance of orthopterans 15mm to 29mm in size during the 1st sampling period of each year; *LATESMALLORTHOP*, abundance of orthopterans less than 15mm in size during the last sampling period of each year (round 2 was used for 2007, round 3 was used for 2008 and 2009); *LATEMEDORTHOP*, abundance of orthopterans 15mm to 29mm in size during the last sampling period of each year (round 2 was used for 2007, round 3 was used for 2008 and 2009); *EARLYORTHOPDIVERSITY*, Shannon diversity index for orthopterans during the 1st sampling period of each year based on subfamilies; *LATEORTHOPDIVERSITY*, Shannon diversity index for orthopterans during the last sampling period of each year based on subfamilies; *EAMEDENSITY*, density of Eastern Meadowlarks per hectare; *WEMEDENSITY*, density of Western Meadowlarks per hectare. ^b CV stands for coefficient of variation.

Table 3. Correlation matrix of vegetation structure and composition. Years pooled, $n = 62$.

VARIABLE	maxheight	robel	litter	trees	bareground	deadplant	graminoid	flowering
maxheight	1.000							
robel	0.650	1.000						
litter	0.383	0.585	1.000					
trees	0.162	0.078	0.118	1.000				
bareground	-0.178	-0.280	-0.487	0.052	1.000			
deadplant	0.332	0.170	0.531	0.236	-0.486	1.000		
graminoid	0.230	0.512	0.310	0.126	-0.480	0.091	1.000	
flowering	-0.109	-0.047	0.109	-0.304	-0.304	-0.113	-0.300	1.000

Table 4. Correlation matrix of Orthoptera diversity and abundance, early and late in the breeding season. Years pooled, $n = 67$.

VARIABLE	earlysmallorthop	earlymedorthop	earlyorthopdiversity	latesmallorthop	latemedorthop	lateorthopdiversity
earlysmallorthop	1.000					
earlymedorthop	0.598	1.000				
earlyorthopdiversity	0.074	0.181	1.000			
latesmallorthop	0.424	0.090	0.140	1.000		
latemedorthop	0.417	0.284	-0.251	0.249	1.000	
lateorthopdiversity	0.501	0.590	0.444	0.347	0.043	1.000

Table 5. Competing models ($\leq \Delta AIC_C$) quantifying relationships between Eastern and Western Meadowlark densities with vegetation structure and composition, diversity and abundance of food resources, and heterospecific presence and density (Table 3a and b); and between Easternness and vegetation structure and composition and diversity and abundance of food resources. Competing models are presented in the order of their importance, and constant models are also included for comparison. See Table 1 for variable definitions.

Hypothesis	K	AIC _C	ΔAIC_C	w_i	Evd. Ratio
Eastern Meadowlark Density					
flowering + avgmheight + deadplant	4	-0.11	0.00	0.699	1.000
constant	1	12.34	12.45	0.001	505.223
Western Meadowlark Density					
flowering + earlyorthodiversity + lateorthodiversity	4	-15.77	0	0.320	1.000
avgrobel + graminoid + flowering	4	-15.28	0.49	0.250	1.278
flowering + avgmheight + deadplant	4	-15.26	0.51	0.248	1.290
eameoccupancy + flowering + avglitter	4	-14.48	1.29	0.168	1.906
constant	1	-6.71	9.06	0.003	92.759
Easternness					
flowering + lateorthodiversity	4	26.29	0	0.528	1.000
graminoid + latemedorthop	3	27.01	0.72	0.369	1.433
constant	2	35.37	9.08	0.006	93.691

Table 6. Relative contribution (Σw_i) of variables within restricted model set, as well as model-averaged coefficients (β), and unconditional lower (LCL) and upper (UCL) confidence limits.

Variable	Relative Contribution	β	LCL	UCL
Eastern Meadowlark Density				
MAXHEIGHT	0.974	0.027	-0.072	0.126
FLOWERING	0.708	0.002	-0.002	0.006
DEADPLANT*	0.699	0.008	0.002	0.014
GRAMINOID	0.175	0.001	-0.003	0.005
LITTER	0.122	0.036	-0.001	0.074
BAREGROUND*	0.115	-0.004	-0.008	0.000
TREES	0.101	0.000	-0.001	0.003
Western Meadowlark Density				
FLOWERING*	0.985	0.007	0.003	0.011
EARLYORTHOPDIVERSITY	0.322	0.024	-0.015	0.064
LATEORTHOPDIVERSITY	0.320	-0.012	-0.070	0.045
MAXHEIGHT	0.255	0.002	-0.016	0.020
GRAMINOID	0.255	-0.002	-0.006	0.002
ROBEL	0.250	0.019	-0.058	0.096
DEADPLANT	0.248	0.002	-0.003	0.007
LITTER	0.169	-0.004	-0.035	0.027
EAMEOCCUPANCY	0.169	0.022	-0.094	0.137
Easternness				
FLOWERING*	0.556	-0.120	-0.228	-0.013
LATEORTHOPDIVERSITY	0.530	0.383	-0.795	1.561
GRAMINOID*	0.393	0.117	0.016	0.218
LATEMEDORTHOP	0.379	-0.033	-0.079	0.014

Note: * indicates influential predictors.

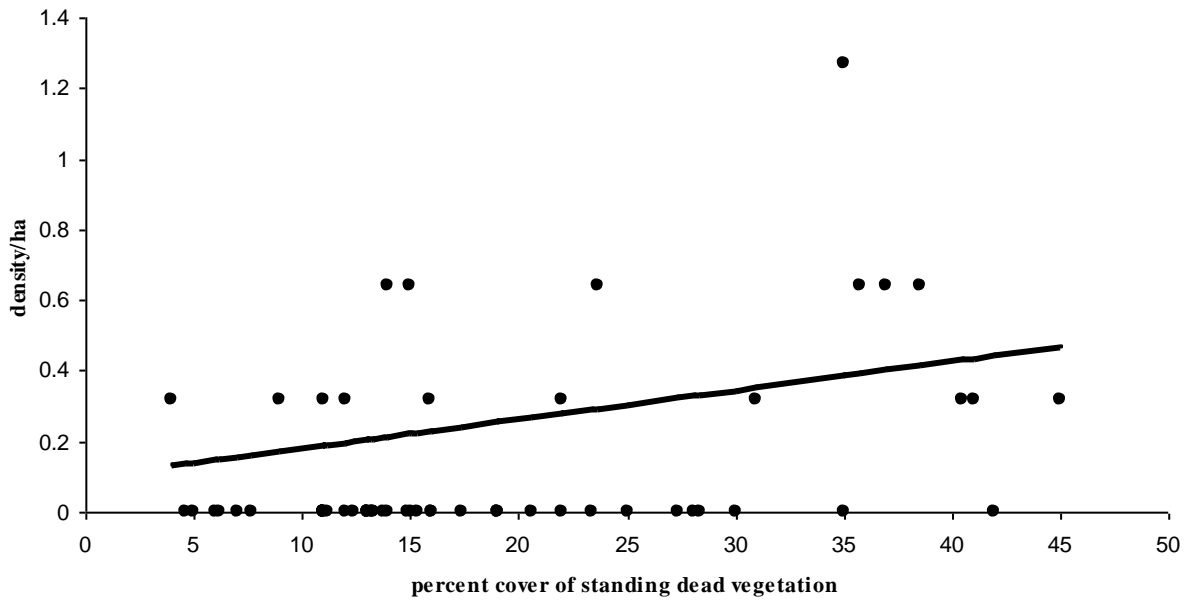


Figure 1. Relationship between Eastern Meadowlark density and standing dead vegetation cover. Solid line represents the predicted probability of density at a particular patch, and dots represent observed densities among patches.

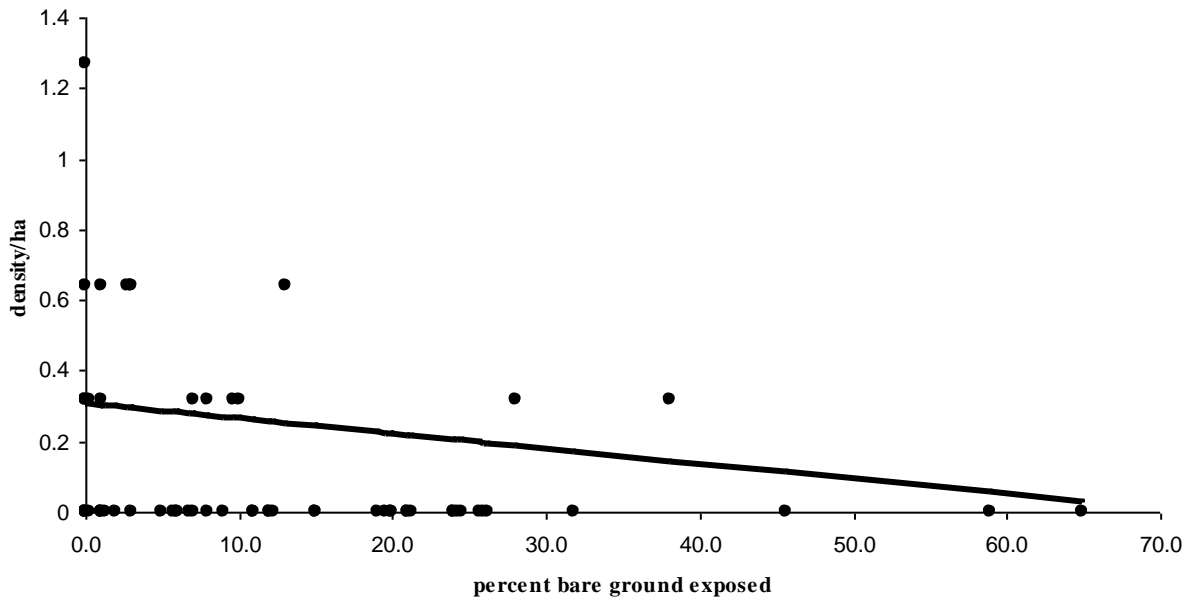


Figure 2. Relationship between Eastern Meadowlark density and bare ground exposure. Solid line represents the predicted probability of density at a particular patch, and dots represent observed densities among patches.

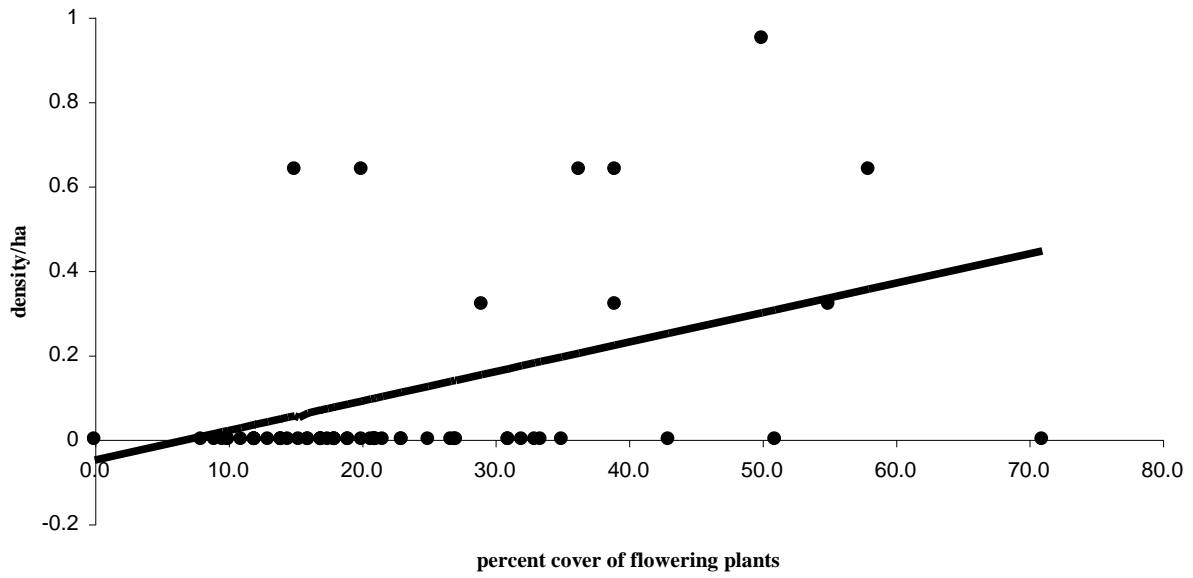


Figure 3. Relationship between Western Meadowlark density and flowering plant cover (i.e. crown vetch). Solid line represents the predicted probability of density at a particular patch, and dots represent observed densities among patches.

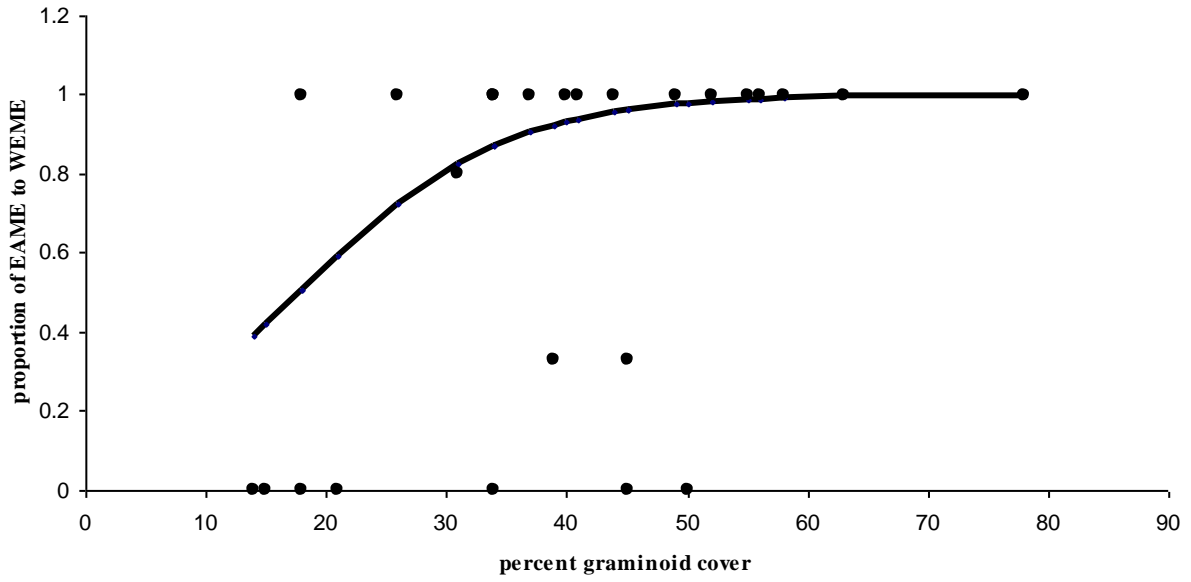


Figure 4. Relationship between composition of meadowlarks at a patch and graminoid cover. Solid line represents the predicted proportion at a particular patch, and dots represent observed proportion among patches.

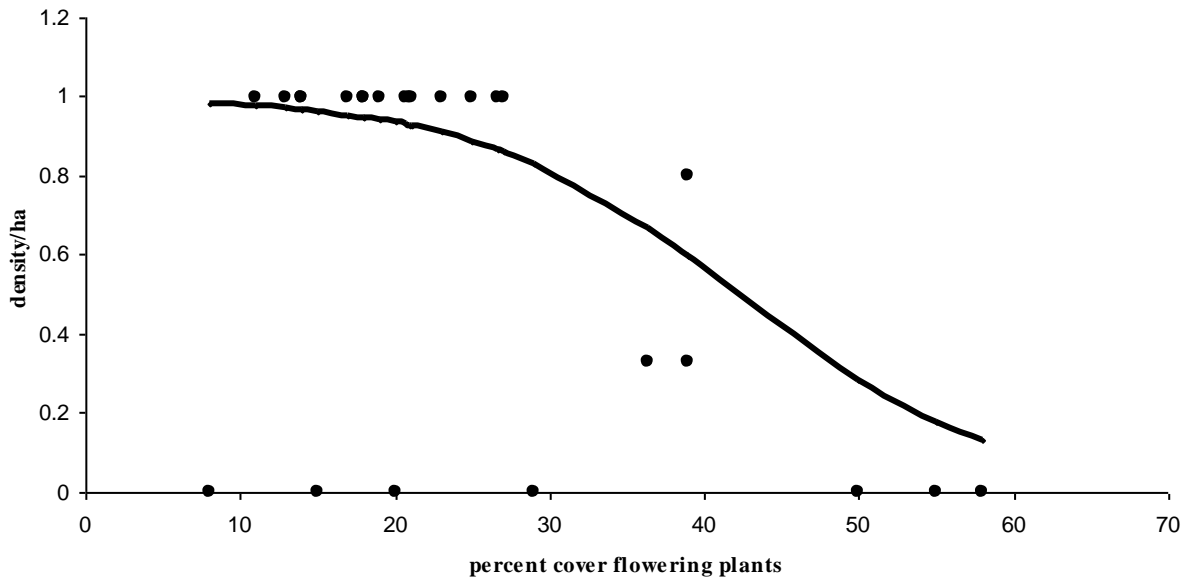


Figure 5. Relationship between composition of meadowlarks at a patch and flowering plant cover (i.e. crown vetch). Solid line represents the predicted probability of density at a particular patch, and dots represent observed proportion among patches.

CHAPTER 3 – DO SYMPATRIC MEADOWLARKS DISCRIMINATE AND RESPOND DIFFERENTLY BETWEEN CONSPECIFIC AND CONGENERIC PLAYBACK?

ABSTRACT

Interspecific aggression is an important spacing mechanism that has been observed between many ecologically similar species pairs. Although sympatric Eastern and Western Meadowlarks exhibit aggression towards each other, a consensus regarding the participation of each species in these interactions has not been reached and an ecological basis for this behavior remains in question. In this study, I examined behavioral responses of Eastern and Western Meadowlarks to experimental song playback at a location where these species co-occur in large numbers. I found that (1) males of both species were able to discriminate between conspecific and congeneric playback, (2) both species responded to conspecific songs significantly more than they did to congeneric playback, although (3) Eastern Meadowlark response to congeneric playback was stronger than Western Meadowlark response. These results provide additional information about the behavioral relationship between Eastern and Western Meadowlarks, and may also aid in explaining the patch-scale distribution patterns described in Chapter 2.

KEYWORDS

Interspecific aggression, sympatry, meadowlark, experimental song playback

INTRODUCTION

Aggressive interactions between ecologically similar species are widespread (Peimann and Robinson, 2010) and typically occur within variable habitats where distributions overlap (Murray, 1971, 1981; Terborgh and Weske, 1975; Bull, 1991; Taniguchi and Nakano, 2000; Twomey et al., 2008). Theory suggests that aggression will commonly be directed towards species that overlap in their use of resources, in order to maintain an exclusive territory and thus the resources within that territory (Orians and Willson, 1964; Fretwell and Lucas, 1969; Cody 1969; Morse, 1974; Robinson and Terborgh, 1995; Martin and Martin, 2001). Alternatively, some authors propose that interspecific territoriality does not always reflect ecological interactions between closely related species, or that it is always adaptive, but that it results from mis-directed intraspecific aggression (Murray 1971, 1981; Mikami and Kawata, 2004) or that other factors such as relative body size, prior residency, and hunger state may influence an individual's willingness to behave aggressively towards heterospecifics (Peiman and Robinson, 2010). While interspecific aggression has been observed in a number of situations mediating patch-scale spatial patterns among birds (Sherry and Holmes, 1988; Robinson, 1992; Robinson and Terborgh, 1995; Martin et al., 1996; Martin and Martin, 2001; Peiman and Robinson, 2010), few examples can be cited where this occurs among grassland birds (Gochfeld, 1979).

Ever since Audubon's 1844 discovery of a second meadowlark species west of the Mississippi River, the relationship between Eastern Meadowlark (*Sturnella magna*) and Western Meadowlark (*Sturnella neglecta*) has captured the interest of avian ecologists (reviewed in Lanyon, 1957). These species are strikingly similar in appearance, as well as ecology (Lanyon 1995; Davis and Lanyon, 2008). Despite regular and continuous contact within sympatry during the breeding season (Lanyon, 1956a; Szijj, 1966; Rowher, 1972), Eastern and Western

Meadowlarks remain reproductively isolated (Lanyon, 1979; Rowher, 1979). However, interspecific, multi-use territories are established and maintained on breeding grounds that result in the complete segregation of these species' territories (Lanyon, 1956b; Lanyon, 1962; Rowher, 1973).

Investigations of interspecific interactions between Eastern and Western Meadowlarks have reported various, sometimes contradicting, conclusions regarding the ability of male meadowlarks to discriminate between these species (Lanyon, 1956b; Falls and Szijj, 1959; Szijj, 1966; Rowher, 1973). Lanyon (1956b) observed that Eastern and Western Meadowlarks exhibit identical territorial defense behaviors with equal frequency and intensity as intraspecific territorial defense, and concluded that males do not practice species discrimination. Szijj (1966) also concluded that males of both species were unable to discriminate between conspecifics and congenics based on experiments testing male response to visual stimuli (i.e. stuffed decoys). However, congeneric recognition and subsequent aggressive interactions between meadowlarks may be rooted more on songs than morphologic differences (Lanyon, 1957). Falls and Szijj (1959) presented some evidence in support of this hypothesis, showing that some sympatric male Eastern and Western Meadowlarks do respond differently to conspecific and congeneric song. Rowher (1973) also documented that sympatric meadowlarks respond more aggressively to congeneric playback than non-sympatric meadowlarks, and additionally found that the amount of fighting increases at locations where Eastern and Western Meadowlark co-occur.

In this study, I examined behavioral responses of Eastern and Western Meadowlarks using experimental song playback at a location where these species co-occur in large numbers. Data from these experiments were used to address (1) whether Eastern and Western Meadowlarks respond to conspecifics differently than to congenics, and (2) if there was a

difference congeneric response between species. The results will provide important information about the behavioral relationship between Eastern and Western meadowlarks, and whether interspecific behavior might be an important mechanism in shaping the patch-scale spatial patterns.

METHODS

Playback Setup

Playback experiments are a common method used to examine the extent that interspecific behavioral interactions are involved in shaping distribution patterns among co-occurring bird species (Catchpole, 1978; Robinson and Terborgh, 1995; Martin and Martin, 2001). In this study, the experimental design closely followed that of Martin et al. (1996). Experimental trials were conducted on eight unmarked territorial male Eastern Meadowlarks and seven unmarked territorial male Western Meadowlarks from June – July 2009. Playback trials were conducted between 0600 – 1200 hours, on mornings with generally clear skies and calm wind.

I selected singing male Eastern and Western Meadowlarks that defended territories located at least 400 m apart from each other and permitted continuous observation, on which to conduct playback trials. Within each focal male's territory, I placed a digital speaker system (FOXPRO FX6 game caller, FOXPRO Inc.), 0-2 m above the ground, and set flagging on four sides of the playback speaker at distances of 5 m and 10 m to assist in distance estimation. Each playback trial lasted 11 minutes, during which time three song stimuli were broadcast at fixed volumes (Table 7). I continuously observed focal males from a minimum distance of 100m during these 11 minutes. I cataloged behaviors of target males (Table 8), while another observer recorded these data onto paper. Three playback trials were conducted on each target bird, for a

total of 45 trials ($n = 24$ and 21 for Eastern and Western Meadowlarks, respectively). If no response occurred during the first playback trial, the experiment was stopped, data were dismissed, and it was repeated at another time. Additionally, if neighboring birds appeared, and I could not distinguish whether the target male was responding to playback or the presence of another individual, the playback trial was stopped and these data were not used in the analysis.

Song Stimuli

The three song stimuli consisted Eastern Meadowlark, Western Meadowlark, and Northern Cardinal songs (Table 7). Northern Cardinal song was used as a control in the playback experiment to compare response of Eastern and Western Meadowlarks to playback of another passerine present in the general area. Due to differences in ecology, song morphology and a general lack of interactions between Northern Cardinals and meadowlarks, Northern Cardinal was considered an ideal control species for use in this song playback experiment. I obtained several digital files containing songs of individuals recorded for each species, mainly within the Midwest region, from the Cornell Lab of Ornithology's Macaulay Library. Appropriate representations of each species' songs (Falls et al., 1988) were then selected from these recordings (high quality recordings), periods between songs were digitized in 16 bits/44 khz and edited using Soundtrack Pro (Apple Inc.). Edited songs from one of the three different individuals recorded from each species were then selected at random and created into a 1 minute long .mp3 file following the prescription of song order for Eastern and Western Meadowlarks (Table 7). Playback tracks reflected natural song rates for each species. Three trials were conducted on each target male separated by a period of at least 20 minutes, consisting of different recordings selected at random, in order to avoid playback habituation of target males (Falls and D'Agincourt, 1981).

Statistical Analysis

Behavioral data (Table 8) were gathered and analyzed for seven 1-minute intervals during the playback trial (Table 7). I used SAS 9.2 (SAS Institute, 2008) for all statistical analyses. I analyzed behavioral differences using general and generalized linear mixed models (SAS PROC MIXED and GLIMMIX) treating location and trial within location as random effects, and examined differences in behavior between species, among playback intervals, and for the interactions between species and playback interval. Two behaviors, overlapping songs and number of flights, were relatively rare and were analyzed based on presence or absence of the response rather than the number of times of these behaviors occurred within a playback period. For these analyses, I used generalized linear mixed models with a binary distribution and logit link function. Overlapping song and latency to flight could only be assessed during playback intervals, and the control interval could not be included in the analysis of minimum distance to the playback speaker because focal birds did not approach the playback speaker within 10 m. Finally, non-stimulus intervals were lumped into the analysis of minimum distance approached to the playback speaker, due to scarcity of data during non-stimulus intervals. I tested for pairwise differences between species and playback intervals of interest using Tukey's post hoc test.

RESULTS

I tested eight Eastern Meadowlarks and seven Western Meadowlarks for a total of 45 experimental trials. Males did not change their vocal activity when presented with conspecific and congeneric songs (Figure 6, Table 9). Additionally, the interaction between species and stimulus did not affect the vocal activity during trials ($p = 0.1916$).

The percent of trials in which overlapping song occurred did not differ between species ($p = 0.5193$), but was significantly different among playback intervals ($p < 0.0001$; Table 9). Overlapping song was more frequent during control playback interval than either conspecific playback ($p = 0.0002$) or the congeneric playback, for both species ($p = 0.0009$; Figure 7). However, the frequency of overlapping song did not differ between congeneric and conspecific playback ($p = 0.5459$; Figure 7). The interaction between species and stimulus did not significantly affect the frequency overlapping song occurred among trials ($p = 0.8294$; Table 9).

The percent of trials in which I observed flight towards the playback speaker did not differ between species ($p = 0.6321$), but was significantly different among playback intervals ($p < 0.0001$; Table 9). Flight towards the playback speaker was observed most during the conspecific playback followed by the congeneric playback and least during the control playback, for both species (Figure 8). The interaction between species and stimulus did not significantly affect the frequency that flight towards the playback speaker was observed among trials ($p = 0.6256$; Table 9).

The speed at which focal males initiated flight in response to conspecific playback was not different between species ($p = 0.7803$; Figure 9). Eastern males similarly did not differ in their response time between conspecific and congeneric playback ($p = 0.5030$), and Western males were only marginally slower at responding to congeneric than conspecific playback ($p = 0.0754$; Figure 9). However, Eastern Meadowlarks took flight significantly sooner (by more than two song cycles) during congeneric playback than Western Meadowlarks ($p = 0.0183$). Differences in latency to flight between control and congeneric as well as conspecific playback were not significant (Figure 9). The interaction between species and stimulus marginally affected latency to flight of focal males ($p = 0.0795$; Table 9).

The distance that focal males approached the playback was significantly affected by an interaction between species and stimulus ($p = 0.0090$, Table 9). During conspecific and congeneric playback intervals, Eastern males tended to approach closer to the playback speaker than Western males did. Additionally, Eastern males moved away from the playback speaker following playback intervals, while Western males did not (Figure 10).

DISCUSSION

Meadowlarks differentiated between conspecific, congeneric and control playback in ways that indicate males identify congeners and conspecifics differently than other species. There was no difference in the vocal activity of Eastern and Western males among the different playback intervals, which may simply reaffirm that song is used for a variety of purposes other than territorial defense, such as mate attraction. Yet, individuals from both species overlapped the control playback in nearly half of all experimental trials, while they rarely overlapped either the conspecific or congeneric playback. These data suggest that males adjusted the timing of their songs in order to avoid overlap with conspecific and congeneric playback. Birds may sing asynchronously with their neighbors to avoid acoustical interference (Ficken et al., 1974). However, this is not likely the case with meadowlarks, given the differences in song frequency between species (Lanyon, 1957; Rowher, 1973; Ordal, 1976). Previous work with Eastern Meadowlarks (Knapton, 1987), demonstrated that males pay little to no attention to the songs of other coexisting, heterospecific species. In contrast, meadowlarks have long been known to respond to congeneric song (McGee, 1880; Falls and Szijj, 1952). Szijj (1966) presented evidence that female meadowlarks recognize and respond differently to songs of male congeners than to songs of male conspecifics. Asynchronous singing in response to congeneric

playback therefore suggests that males of both species recognize the song of their congener, and that some level of information transfer is facilitated by the behavior.

However, both species discriminated the use of flight in response to conspecific, congeneric, and control playback. Males took flight most frequently during conspecific playback, significantly less during congeneric playback, rarely during control playback, and so infrequently during the non-stimulus intervals that I was not able to include these data in my analyses. Additionally, Western males responded significantly quicker to conspecific than to congeneric playback, though Eastern males responded as quickly to congeneric as they did to conspecific playback.

There was also some evidence that suggests Eastern Meadowlarks respond more strongly to congeneric song than Western Meadowlarks. Eastern males took significantly less time to fly towards the playback speaker than Western males, during congeneric playback. When they flew, Eastern males also tended to approach closer to the playback speaker than Western males. Furthermore, Eastern males moved away from the playback speaker following song playback, though Western males did not. In general, the response of Eastern males to congeneric playback was more immediate and direct than the response of Western males.

Although aggressive behavior between species is often thought to reflect the intensity of the ecological interactions between them, it may not always be the case. Data from this study indicates that aggressive response to congeneric playback does not result misdirected intraspecific aggression, in meadowlarks. However, the stronger reaction of Eastern males to congeneric playback may be related to adaptations evolved in response to intraspecific competition (reviewed in Falls and D'Agincourt, 1981). Specifically, Eastern Meadowlarks have evolved song repertoires with 10 times as many song types as Western Meadowlarks (Lanyon,

1957). Repertoire size is an indicator of male quality, and is positively correlated with territory size and fledgling success in Western Meadowlarks (Horn et al., 1993; Aweida, 1995).

However, repertoire size is also related to decreased neighbor-stranger recognition, which is thought to lessen territorial strife (Weeden and Falls, 1959). Compared to Western Meadowlarks, Eastern Meadowlarks have a reduced ability to discriminate between neighbor and stranger signals (Falls and D'Agincourt, 1981). So, a reduction of this ability may inherently lead Eastern Meadowlarks to engage in aggressive territorial interactions more often than Western Meadowlarks, and ultimately be responsible for the behavior patterns I observed at Lost Mound.

CONCLUSIONS

In this study, two different types of behavior commonly used in territorial disputes between meadowlarks, song and flight, were used to examine the response of Eastern and Western Meadowlark males to both conspecific and congeneric playback. Comparisons between responses provided some information about the behavioral relationship between Eastern and Western Meadowlarks within sympatry. First, males of both species discriminated responses between conspecific and congeneric playback at Lost Mound, though Western males did so in more ways than Eastern males. Secondly, when males of both species differed in their response to conspecific and congeneric playback, the response to conspecific playback was stronger than the response to congeneric playback. Finally, when species differed in response to congeneric playback by species, Eastern males responded to congeneric playback more aggressively than Western Meadowlarks.

Interspecific aggression is widespread in animals, appearing in an estimated 78% of studies involving a focal species (Peiman and Robinson, 2010), and is often directed asymmetrically by a dominant species towards ecologically similar, but subordinate species (Robinson and Terborgh, 1995). Interspecific aggression can mediate spatial patterns between species, and typically results in dominant members of a species pair gaining priority access to habitat patches of the best quality, while subordinate members are restricted to suboptimal patches (Morse, 1974; Terborgh and Weske, 1975; Sherry and Holmes, 1988; Robinson, 1992; Robinson and Terborgh, 1995; Martin and Martin, 2001). In Chapter 2, I presented data that showed Eastern and Western Meadowlarks were segregated by habitat features at Lost Mound. I further demonstrated that Eastern Meadowlarks at Lost Mound were associated with habitat features similar to those reported outside sympatry, while Western Meadowlarks were associated with habitat features that were atypical of those reported outside sympatry.

Given the ecological similarities that have been reported between these species outside sympatry, as well as the increased strife that occurs within sympatry, the data that I have presented adds further weight to the idea that interspecific aggression is involved in structuring habitat use between meadowlarks within sympatry. Although I have not presented direct evidence that Western Meadowlarks occupy suboptimal habitat at Lost Mound, or that Eastern Meadowlarks restrict Western Meadowlarks from habitat patches, these data could be gathered by conducting removal experiments.

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3.1 TABLES AND FIGURES

Table 7. Experimental design of song playbacks (following Martin et al., 1996; and Martin and Martin, 2001) presented to territorial male Eastern and Western Meadowlarks.

STIMULUS	DURATION (MIN)	BEHAVIORAL OBSERVATIONS COLLECTED
Pre-stimulus (no stimulus)	1	YES
Heterospecific song	1	YES
Post stimulus 1 (no stimulus)	1	YES
Silent Break	2	NO
Control song	1	YES
Post stimulus 2 (no stimulus)	1	YES
Silent Break	2	NO
Conspecific song	1	YES
Post stimulus 3 (no stimulus)	1	YES

Note: A 3-min period of silence before the second and third song playbacks controlled for carryover in response from the previous song playback (Martin and Martin, 2001).

Table 8. Variables used to measure behavioral responses of territorial male Eastern and Western Meadowlarks to song playback, which were modeled after those commonly observed in territory defense of meadowlarks (Lanyon, 1957; Falls and D'Agincourt, 1981; Knapton, 1987) as well as in other ecologically similar species pair (Martin et al., 1996; Martin and Martin, 2001).

Variable	Description
Number of songs	Total number of times focal bird sang during an interval.
Number of overlapping songs	Total number of times a focal bird sang during an interval.
Number of flights	Total number of flights > 1 m made by the focal bird during each interval.
Latency to flight (s)	Time until the focal bird flew toward the playback speaker.
Minimum distance approached to playback speaker (m)	Minimum distance focal bird approached playback speaker during an interval.

Table 9. Results of general and generalized linear mixed models comparing behavioral data gathered from playback experiments involving territorial male Eastern and Western Meadowlarks ($n = 8$ and 7 for Eastern and Western Meadowlarks, respectively).

Dependent Variable and Effect	df	<i>F</i> Value	<i>P</i> > <i>F</i>
Songs			
playback interval	6	0.52	0.7911
species	1	1.35	0.2669
species*playback interval	6	1.46	0.1916
Frequency of Overlapping Song			
playback interval	2	10.6	< 0.0001
species	1	0.44	0.5193
species*playback interval	2	0.19	0.8294
Frequency of Flight			
playback interval	6	7.03	< 0.0001
species	1	0.24	0.6321
species*playback interval	6	0.73	0.6256
Latency to Flight			
playback interval	2	0.71	0.4970
species	1	4.14	0.0636
species*playback interval	1	3.22	0.0795
Minimum Distance to Speaker			
playback interval	2	1.56	0.2249
species	1	0.09	0.7688
species*playback interval	2	5.48	0.0090

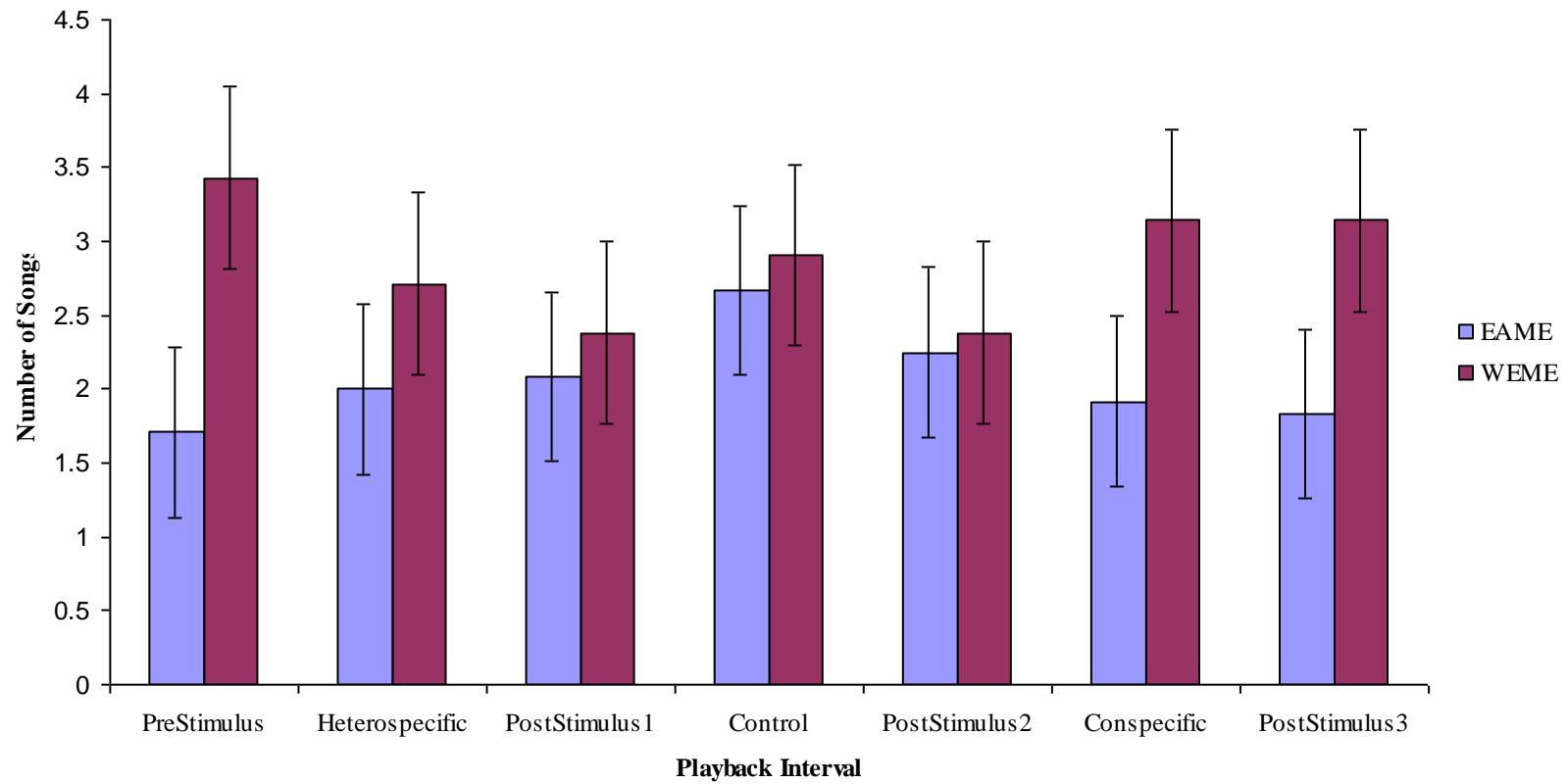


Figure 6. Least squares means (\pm SE) comparing differences in vocal activity between species and among playback intervals.

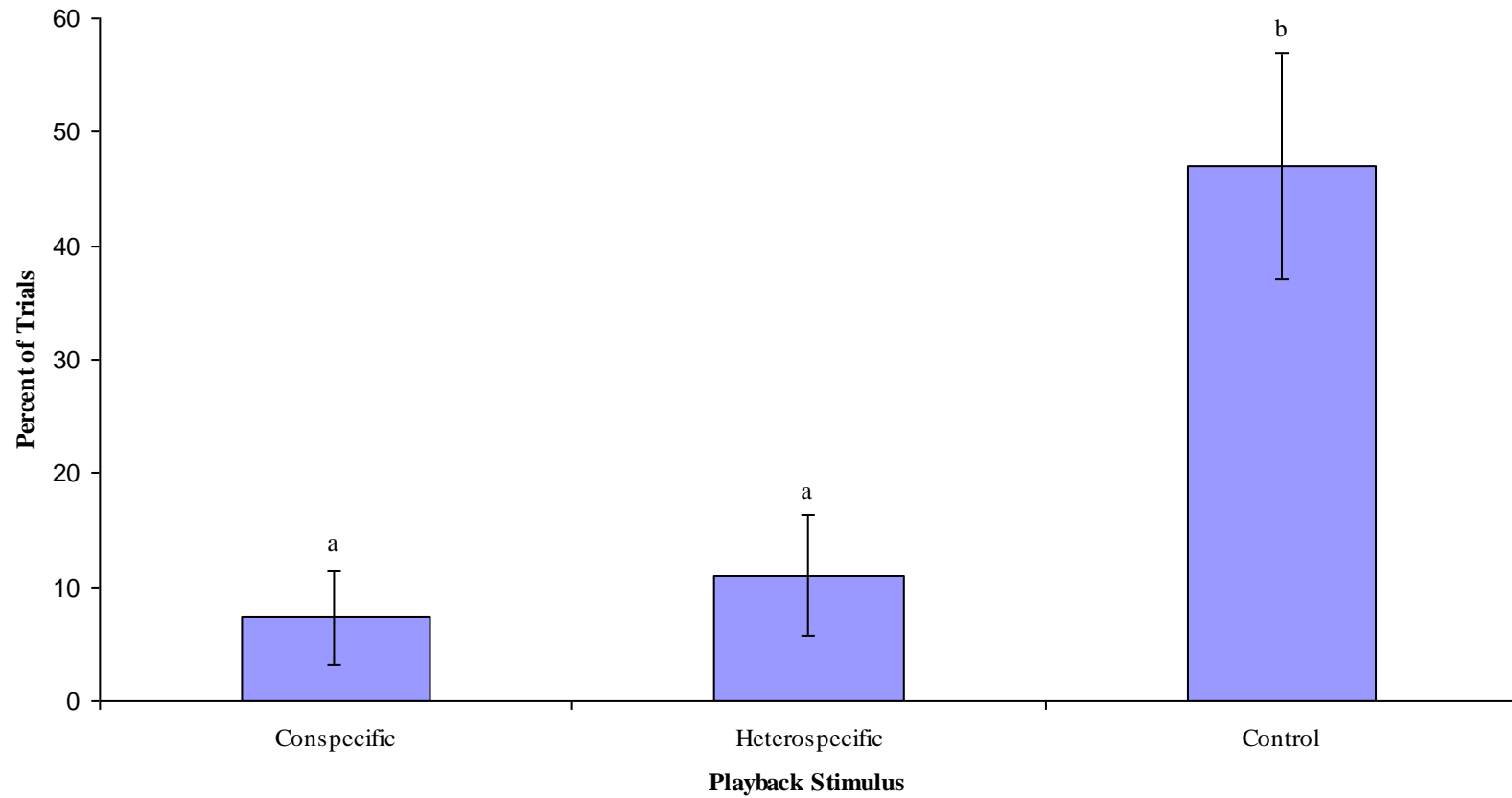


Figure 7. Least squares means (\pm SE) comparing differences in the frequency of overlapping song among playback. Bars with different letters above them were significantly different ($p > 0.05$) from each other.

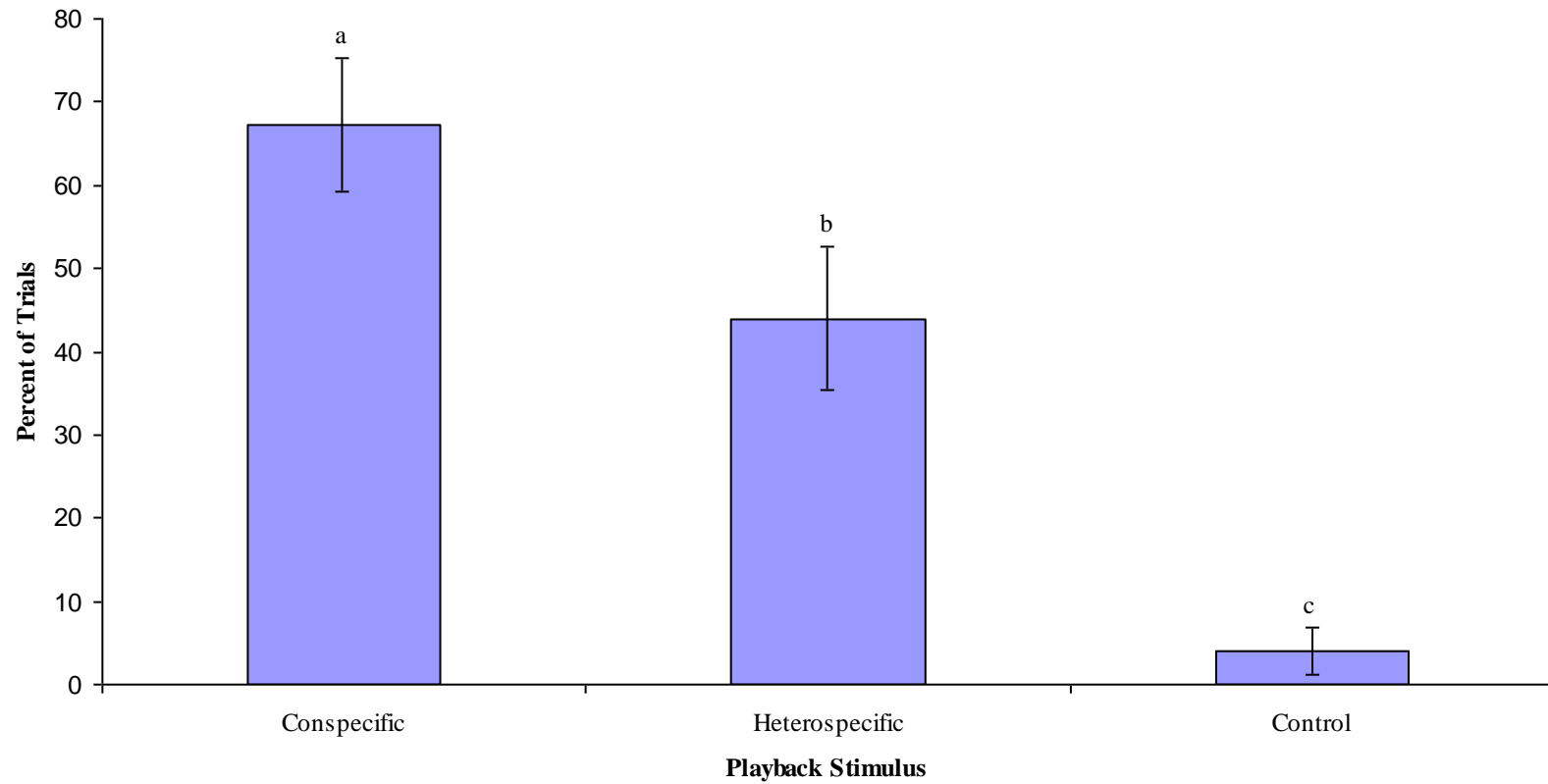


Figure 8. Least squares means (\pm SE) comparing differences in the frequency meadowlarks flew towards playback speaker among playback intervals. Bars with different letters above them were significantly different ($p > 0.05$) from each other.

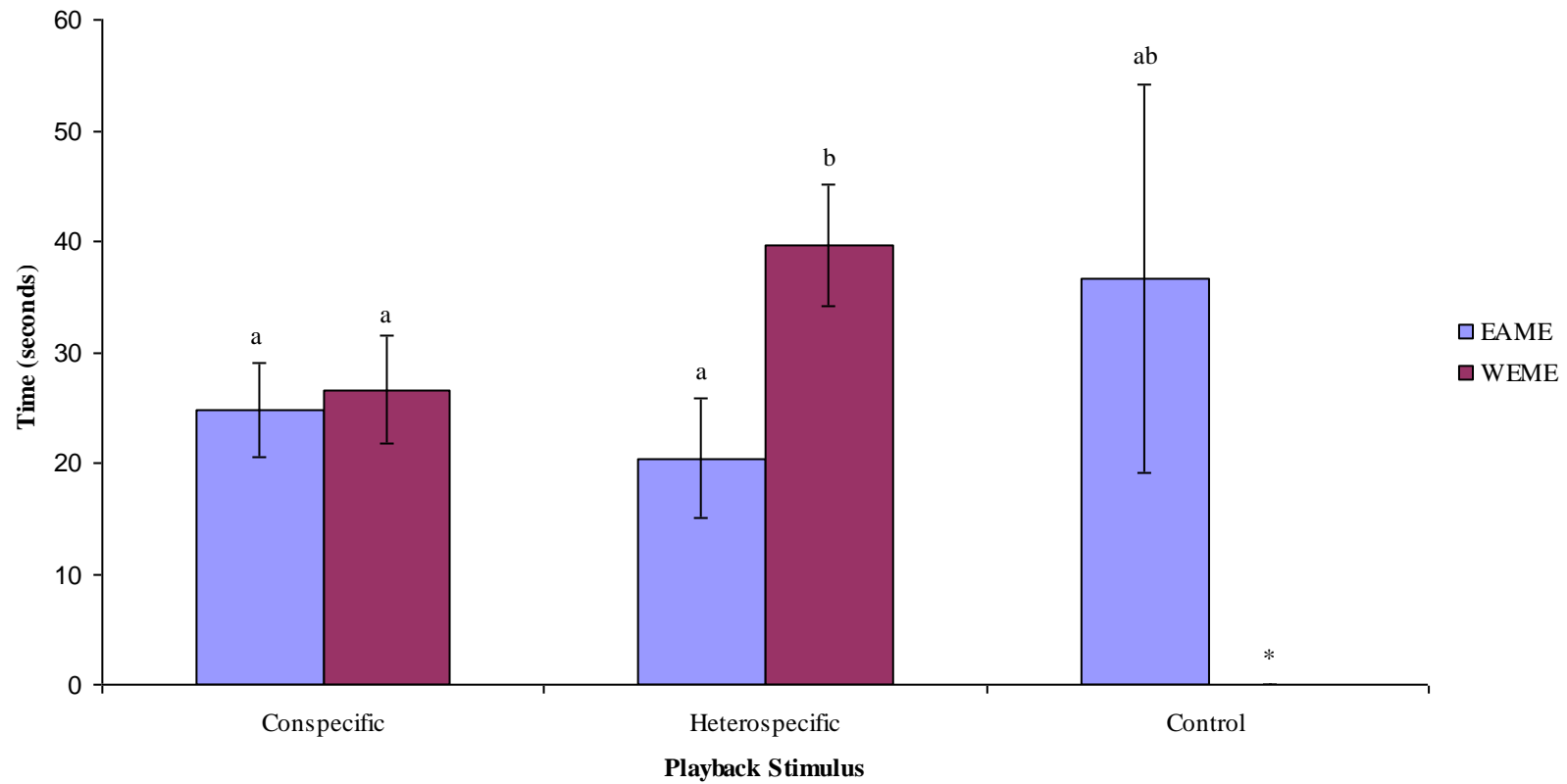


Figure 9. Least squares means (\pm SE) comparing differences in the latency to flight among playback intervals. * Western Meadowlarks did not fly during the control playback interval. Bars with different letters above them were significantly different ($p > 0.05$) from each other.

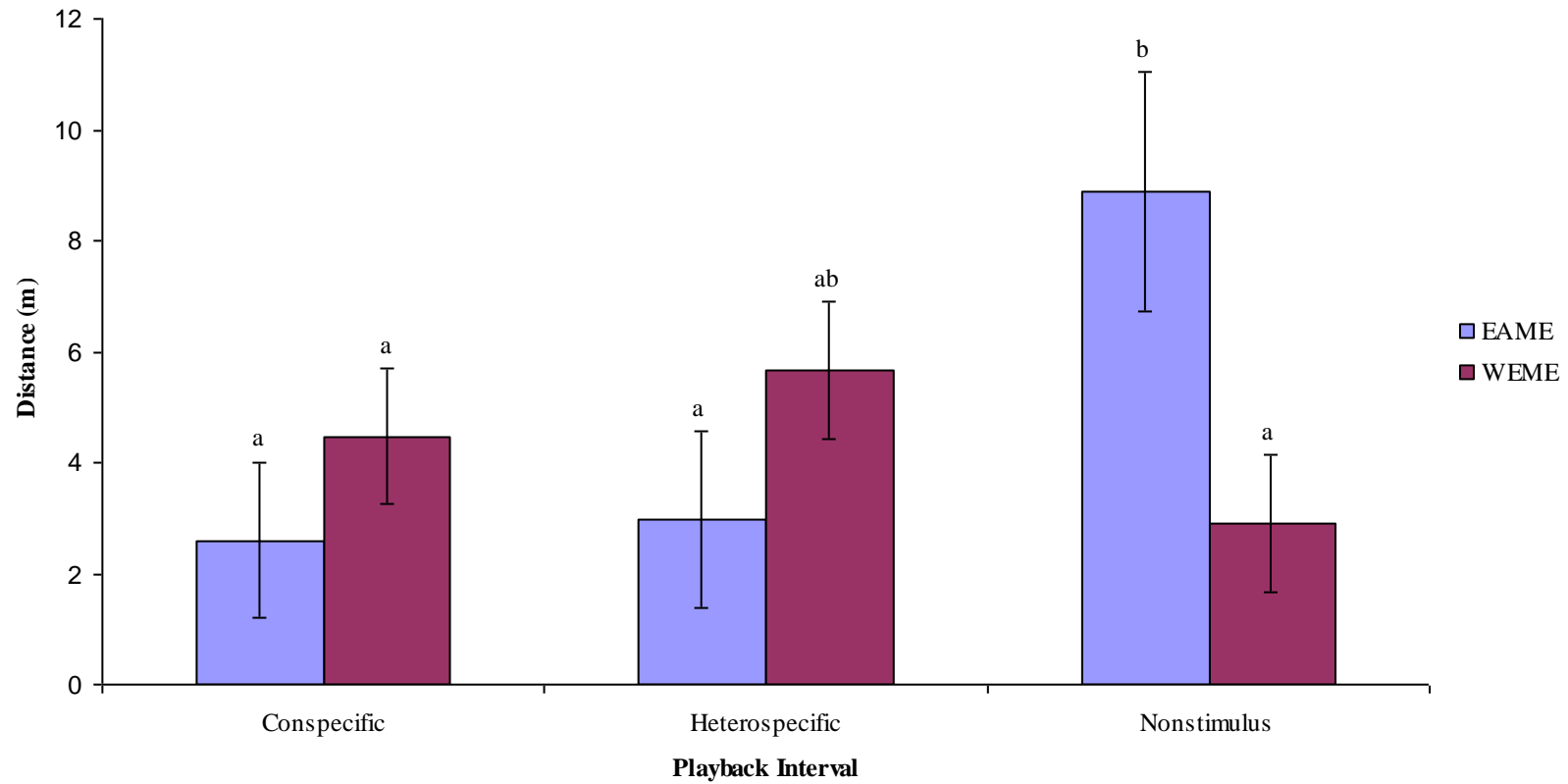


Figure 10. Least squares means (\pm SE) comparing differences in the minimum distance approached to the playback speaker among conspecific, heterospecific, and non-stimulus intervals. Bars with different letters above them were significantly different ($p > 0.05$) from each other.

CHAPTER 4 – MEADOWLARKS AT LOST MOUND: SYNTHESIS OF RESEARCH AND RECOMMENDATIONS

Introduction

Lost Mound Unit of the Upper Mississippi National Wildlife Refuge, formerly known as the Savanna Army Depot from 1917-2003, is located in Carroll and Jo Daviess counties of northwestern Illinois. This refuge contains a large remnant sand prairie (approximately 2,800 ha) and is currently home to two of the largest breeding populations of Eastern Meadowlark (*Sturnella magna*) and Western Meadowlark (*Sturnella neglecta*) in the state (personal communication, M. Ward). Although spatial patterns of sympatric meadowlark populations have been previously compared (Lanyon, 1956a, 1962; Szijj, 1966; Rohwer, 1972), those comparisons were qualitative in nature and lack the quantitative evidence necessary to provide a rigorous understanding of meadowlark habitat use within sympatry. Similarly, investigations of interspecific interactions between Eastern and Western Meadowlarks have reported various, sometimes contradicting, conclusions regarding the ability of male meadowlarks to discriminate between species (Lanyon, 1956b; Falls and Szijj, 1959; Szijj, 1966; Rowher, 1973), thereby bringing into question the nature of subsequent aggressive interactions that occur between them.

The following paper summarizes the results of the two studies I conducted in order to examine how behavioral interactions and environmental factors influence patch-scale habitat use and distribution patterns of sympatric Eastern and Western Meadowlarks. In the first study, I examined habitat use of both species occurring in the same area at the same time.

Complementary that study, I examined the response of Eastern and Western Meadowlarks to conspecific and congeneric playback. Results from those studies are then put into a historical context in order to better understand the factors that have influenced population trends between

these species at this site, and recommendations aimed at enhancing management and conservation efforts for both species at Lost Mound, are offered.

Summary of Results

At Lost Mound Eastern Meadowlark density responded to many habitat features thought to be important in predicting grassland bird habitat use, and particularly to vegetation parameters in ways similar to Eastern Meadowlarks outside of sympatry. Specifically, Eastern Meadowlark density was positively related to increasing standing dead vegetation, and negatively related to increasing bare ground exposure. Conversely, Western Meadowlark density was uncharacteristically tied to one vegetation feature, crown vetch, which is likely not very useful for breeding. Furthermore, the relative composition of Eastern and Western Meadowlarks among study plots differentiated along gradients of graminoid and crown vetch cover. These variables in particular, represent a dichotomy emblematic of conditions at Lost Mound. The sand prairies at Lost Mound remain mostly intact, but several factors, such as the spread of crown vetch, have degraded large areas of remnant conditions by reducing species richness and abundance of plants and insects. Eastern Meadowlarks dominated patches best defined by the parameter most symbolic of central grasslands in North America, graminoids (Anderson, 2006), while Western Meadowlarks were most abundant in patches distinguished by one of the best representatives of decaying conditions at Lost Mound, crown vetch (Symstad, 2004).

Meadowlarks were also able to discriminate use of two different types of behavior commonly used in territorial disputes, song and flight, in response to conspecific, congeneric and control playback. Meadowlarks sang asynchronously during conspecific and congeneric playback, but not during control playback. Additionally, males flew towards the playback speaker most frequently during conspecific playback, significantly less during congeneric

playback, and only rarely during control playback. Therefore, aggressive response to congeners does not likely result from misdirected intraspecific aggression in meadowlarks. There was also some evidence to suggest Eastern Meadowlarks respond more strongly to congeneric playback than Western Meadowlarks. However, the stronger reaction of Eastern males to congeneric playback may be related to adaptations evolved in response to intraspecific competition (reviewed in Falls and D'Agincourt, 1981).

These results are not direct evidence supporting that Western Meadowlarks occupy suboptimal habitat, or that Eastern Meadowlarks have restricted Western Meadowlarks from habitat at Lost Mound. However, they are consistent with other studies that have found that meadowlarks segregate spatially and behave aggressively towards each other within sympatry (Lanyon, 1957; Rohwer, 1973), and that Eastern Meadowlarks exhibit greater territorial aggression than Western Meadowlarks (Falls and D'Agincourt, 1981; Horn et al., 1993; Aweida, 1995). Together, this information adds further weight to the idea that interspecific aggression is involved in structuring patch-scale habitat use between meadowlarks within sympatry.

Historical Context

Current populations of Eastern and Western Meadowlarks at Lost Mound are comparable (Chapter two), but these numbers represent only a snapshot of the progressive changes to meadowlark composition at Lost Mound and to a larger degree, in Illinois (Graber and Graber, 1963; Bowles, 1993; Wenny, 2001). The first Western Meadowlark collected in Illinois occurred in 1876 near Chicago, and at that time the species was already believed to be a common summer resident in the western part of the state (Allen, 1880). However, A.O. Gross and H. A. Ray conducted avian population surveys throughout the state from 1906-1909, and Western Meadowlarks were not common enough to be included in their surveys (Graber and Graber,

1963). According to Graber and Graber (1963), Western Meadowlark only began to expand its range and population size in the northern third of the state during the first half of the 1900s. During that period of time population numbers throughout the state remained relatively similar, but Western Meadowlarks were believed to have greatly expanded in number in northern Illinois, shifting the relative composition of meadowlarks there (Graber and Graber, 1963). The upland bird community at the former Savanna Army Depot was first surveyed in 1990, during which an abundance of grassland birds were found present there, precipitating further monitoring efforts at the site (Anderson et al., 1996). J. R. Herkert surveyed the upland bird community at Lost Mound from 1991 to 1992. During that survey, Western Meadowlarks were one of two dominant species listed, while Eastern Meadowlarks were described as being less common (Bowles, 1993). Approximately ten years later, Wenny (2001) surveyed the bird community at Lost Mound again, and found that Western Meadowlarks were still 6 times (2000 breeding season) and 2.5 times (2001 breeding season) as abundant as Eastern Meadowlarks. Currently, population numbers of meadowlarks are similar in number, though the relative composition appears to be at the crux of shifting in favor of Eastern Meadowlarks (Appendix A).

Changes in meadowlark population numbers correspond with major land use change throughout the region. Lanyon (1956a) cited that a shift in Upper Midwestern agriculture from grain production to livestock and dairy production in the 1880s created optimal conditions for Western Meadowlark colonization and spread eastward. Although the sandy soils at Lost Mound prevented significant agricultural development at this site, the U.S. Army used the site as a testing a proving ground beginning in 1917, and later as a munitions storage facility up until 1999. Beginning in the late 1940s, the Army managed the site using open range cattle grazing at a stocking rate of about one animal/6.4 acres, in order to minimize fire hazard related to the

build-up of heavy graminoid fuel loads (Bowles, 1993; Ebinger et al., 2006). In effect, Army land management practices mirrored broader regional practices.

H. A. Gleason (1910) surveyed and described the vegetation at Lost Mound before grazing had significantly impacted the area, and it is from these baseline data that subsequent vegetation changes have been modeled over time. Bowles (1993) found that intense cattle grazing reduced the horizontal and vertical dimensions of vegetation, resulting in about 30% sand, grass and forb cover each, with a grass canopy well below 15 cm., and concluded that since Gleason's survey, "... overgrazing has so disrupted the natural disturbance regime ... that early-successional vegetation occupies essentially 100% of the sand prairie, and grazing-adapted species are more successful than species adapted to soil disturbance processes." Grazing pressure was reduced in 1998 and eliminated in 1999 from Lost Mound (Wenny, 2001). Following the cessation of cattle grazing, little habitat management had been implemented at the site prior to the initiation of this investigation. During that time, vegetation structure had increased in every dimension, and while graminoid cover has generally increased, bare ground exposure has generally decreased (Wenny, personal communication).

Synthesis and Recommendations

Drawing comparisons between meadowlark distributions and general habitat associations from locations within and outside sympatry, Lanyon (1956a) hypothesized that the eastward expansion of Western Meadowlarks in the north-central states during the early to mid 1900s was facilitated by regional alterations of the landscape, as well as corresponding changes in the balance between inter- and intraspecific competition. He further predicted the ecological replacement of Eastern Meadowlarks in certain localities within recently expanded areas of sympatry. Lost Mound is a microcosm within this landscape, where it appears that Lanyon's

predictions were largely confirmed, at least for a period of time. Alterations to the habitat at Lost Mound, in effect, reflected land cover changes throughout the region, and apparently resulted in the dominance of Western Meadowlarks and reduction of Eastern Meadowlarks at the site. The opportunity to examine past relationships between these species and the underlying factors influencing those relationships is gone. However, because of Army occupation at the site, Lost Mound escaped the majority of irreversible land use changes characteristic of many prairie sites in Illinois (Ridgeway, 1889; Samson and Knopf, 1994). Recent shifts in the management of Lost Mound represent a reverse trajectory in ecological conditions, and have presented a new opportunity to examine ecological and behavioral interactions between sympatric meadowlarks.

For many species with overlapping distributions, the competitive interactions that take place at the distribution edges and are commonly condition-specific, such that environmental factors can alter the competitive balance between an interacting species pair (Bull, 1991; Dunson and Travis, 1991; Twomey et al., 2008; Taniguchi and Nakano, 2000). These relationships can play significant roles in patch-scale habitat use of a coexisting species pair. Along a shifting environmental gradient, individuals of the species most closely adapted to the current local conditions would be able to monopolize the highest quality habitat (Sherry & Holmes 1988; Taniguchi and Nakano, 2000; Thomas and Holloway, 2005).

I believe that changes in habitat conditions at Lost Mound caused by a cessation of grazing (i.e., increased graminoid cover, reduction of bare ground exposure) have resulted in more patches that are favorable for Eastern Meadowlarks and in turn, fewer patches are available for Western Meadowlarks. Graminoids are important for grassland birds and provide many benefits such as nesting substrate, concealment from predators and brood parasites, as well as

abundant prey (Best et al., 1997; Davis, 2005; Flanders et al., 2006). Conversely, crown vetch at Lost Mound is potentially acting in multiple ways that negatively impact food acquisition (Chapter 2). While both Eastern and Western Meadowlarks prefer similar breeding habitat, an increased readiness for territorial strife enables Eastern Meadowlarks to enforce territorial exclusivity of breeding patches. Consequently, Western Meadowlarks may have reduced access to areas where Eastern Meadowlarks settle, and may end up using patches that in the absence of Eastern Meadowlarks would have been associated with increased breeding costs.

Although I did not demonstrate any fitness effects associated with patch occupancy on either meadowlark species, Eastern and Western Meadowlarks likely suffer reproductive costs tied to interspecific territorial behavior, as is the case with other sympatric species pairs' (Martin and Martin, 2001). Because meadowlarks rarely double brood during a breeding season (Kershner et al., 2004), the survival of birds from each nest becomes more important to population recruitment. This presents important conservation implications for these species at Lost Mound, especially if they are source populations. A comparative study examining reproductive success between species within different patches could be conducted at Lost Mound, given the large numbers of birds of each species there, in order to better inform meadowlark conservation strategies at the site.

Ultimately, because of its size and remaining ecological integrity, Lost Mound provides essential habitat for meadowlarks, and there is great potential to manage the site in ways that could support populations of both meadowlark species. Overgrazing led to the elimination of the late-successional component of prairie vegetation at Lost Mound, and skewed the relative composition of meadowlarks towards Westerns. A continued lack of grazing or management at the site will certainly facilitate the spread of exotic, invasive plants and woody encroachment

that may lead to reduced numbers of Western Meadowlarks as well as Eastern Meadowlarks. Managing for both meadowlarks presents a challenge common to grassland bird conservation and will require the successful implementation of techniques that promote a range of conditions that can be utilized by a suite of grassland birds. Patch-burn-grazing is a technique that has been developed to more naturally mimic the disturbance cycles characteristic of pre-European settlement, grassland ecosystems (Fuhlendorf and Engle, 2004). In places where this technique has been implemented, the range of conditions required by a suite of grassland birds with differing habitat preferences have successfully been reproduced (Fuhlendorf et al., 2006, 2009), which has also corresponded with increased species richness and density of some species (Stroppel, 2009). This technique seems particularly appropriate for Lost Mound, given that grazing appears to modulate the relative composition of meadowlarks there, and that prescribed fire can be used to control woody encroachment and the spread of exotic plants.

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APPENDIX A

Point Count Surveys from 2007-2009

May 2007

Point	EAME	WEME	TOTAL
A5			0
B3			0
B5			0
B6			0
C1	2		2
D2	2		2
E1		3	3
E2			0
E3	1	2	3
E6		3	3
E7	1		1
E8	1	1	2
E9	2		2
E10	2		2
E11		1	1
E14	1	2	3
E15			0
E16			0
F0			0
F1			0
F6			0
F11			0
F12	1		1
J4			0
TOTAL	13	12	25

June 2007

Point	EAME	WEME	TOTAL
A5		2	2
B3			0
B5		1	1
B6			0
C1	1		1
D2	1		1
E1		4	4
E2		4	4
E3		3	3
E6		3	3
E7		2	2
E8		3	3
E9			0
E10	1		1
E11		1	1
E14	2		2
E15	1	1	2
E16			0
F0			0
F1	2		2
F6			0
F11			0
F12		3	3
J4	2		2
TOTAL	10	27	37

July 2007

Point	EAME	WEME	TOTAL
A5			0
B3			0
B5			0
B6	1		1
C1	1		1
D2			0
E1		2	2
E2			0
E3		1	1
E6	1	1	2
E7	1		1
E8			0
E9			0
E10			0
E11			0
E14			0
E15			0
E16			0
F0		1	1
F1	1		1
F6			0
F11		2	2
F12			0
J4			0
TOTAL	13	12	25

APPENDIX A continued

May 2008

Point	EAME	WEME	TOTAL
A5	2		2
B3			0
B5			0
B6			0
C1	1		1
D2			0
E1		1	1
E2			0
E3			0
E6			0
E7	4	1	5
E8		2	2
E9	1		1
E10			0
E11			0
E14			0
E15			0
E16			0
F0			0
F1			0
F6			0
F11			0
F12			0
J4	1		1
TOTAL	9	4	13

June 2008

Point	EAME	WEME	TOTAL
A5	3	1	4
B3	1	1	2
B5	2		2
B6	2	3	5
C1	5	1	6
D2			0
E1			0
E2		2	2
E3		2	2
E6			0
E7			0
E8		2	2
E9			0
E10	2		2
E11			0
E14	1		1
E15		1	1
E16			0
F0	6	3	9
F1	3		0
F6			0
F11	1		1
F12			0
J4	1		1
TOTAL	27	16	43

July 2008

Point	EAME	WEME	TOTAL
A5	1		1
B3			0
B5			0
B6			0
C1	1		1
D2			0
E1		2	2
E2		1	1
E3	3		3
E6			0
E7	4		4
E8		1	1
E9			0
E10	1		1
E11			0
E14			0
E15			0
E16			0
F0	1		1
F1	1		1
F6			0
F11	1		1
F12			0
J4			0
TOTAL	13	4	17

APPENDIX A continued

May 2009

Point	EAME	WEME	TOTAL
A5	1		1
B3	1		1
B5			0
B6			0
C1		2	2
D2			0
E1		2	2
E2		3	3
E3		1	1
E6			0
E7			0
E8	1		1
E9	2		2
E10	2		2
E11			0
E14			0
E15			0
E16			0
F0			0
F1			0
F6			0
F11			0
F12	1		1
J4	2		2
TOTAL	10	8	18

June 2009

Point	EAME	WEME	TOTAL
A5			0
B3	2		2
B5			0
B6			0
C1	1		1
D2	4		4
E1	2	4	6
E2		2	2
E3			0
E6			0
E7			0
E8			0
E9			0
E10			0
E11			0
E14			0
E15			0
E16		3	3
F0			0
F1			0
F6	1		1
F11			0
F12			0
J4			0
TOTAL	10	9	19

July 2009

Point	EAME	WEME	TOTAL
A5	3		3
B3			0
B5			0
B6			0
C1	2		2
D2			0
E1		4	4
E2		4	4
E3			0
E6			0
E7			0
E8			0
E9	1	1	2
E10			0
E11			0
E14			0
E15	2		2
E16			0
F0			0
F1			0
F6			0
F11			0
F12	1		1
J4			0
TOTAL	9	9	18

APPENDIX B

Candidate Models Predicting Eastern Meadowlark Density, Western Meadowlark Density, and Easternness

Eastern Meadowlark Density

Model	K	AIC _C	ΔAIC _C	w _i	Evd. Ratio
flowering + avgmheight + deadplant	4	-0.11	0.00	0.699	1.000
avglitter + avgmheight + graminoid	4	3.53	3.64	0.113	6.172
trees + avgmheight + bareground	4	3.85	3.96	0.096	7.243
wemeoccupancy + graminoid + avgmheight	4	5.63	5.74	0.040	17.637
wemedensity + graminoid + avgmheight	4	6.82	6.93	0.022	31.976
bareground + earlysmallorthop + earlyorthopdiversity	4	7.73	7.84	0.014	50.400
wemeoccupancy + flowering + avglitter	4	8.56	8.67	0.009	76.325
avgmheight + trees + bareground + wemeoccupancy + earlysmallorthop + earlyorthopdiversity	6	10.09	10.20	0.004	164.022
constant	1	12.34	12.45	0.001	505.223
avgrobel + earlymedorthop + earlyorthopdiversity	4	14.85	14.96	0.000	1772.241
avgrobel + graminoid + flowering	4	15.45	15.56	0.000	2392.275
graminoid + earlysmallorthop + latemedorthop	4	16.13	16.24	0.000	3361.021
wemedensity + earlysmallorthop + earlyorthopdiversity	4	16.93	17.04	0.000	5014.054
flowering + earlyorthopdiversity + lateorthopdiversity	4	16.99	17.10	0.000	5166.754

Western Meadowlark Density

Model	K	AIC _C	ΔAIC _C	w _i	Evd. Ratio
flowering + earlyorthopdiversity + lateorthopdiversity	4	-15.77	0	0.320	1.000
avgrobel + graminoid + flowering	4	-15.28	0.49	0.250	1.278
flowering + avgmheight + deadplant	4	-15.26	0.51	0.248	1.290
eameoccupancy + flowering + avglitter	4	-14.48	1.29	0.168	1.906
constant	1	-6.71	9.06	0.003	92.759
trees + avgmheight + bareground	4	-5.94	9.83	0.002	136.319
avglitter + avgmheight + graminoid	4	-5.36	10.41	0.002	182.181
eameoccupancy + bareground + avgmheight	4	-5.24	10.53	0.002	193.446
eamedensity + graminoid + avgmheight	4	-5.16	10.61	0.002	201.341
bareground + earlysmallorthop + earlyorthopdiversity	4	-5.1	10.67	0.001	207.473
graminoid + earlysmallorthop + latemedorthop	4	-4.92	10.85	0.001	227.011
eamedensity + earlysmallorthop + earlyorthopdiversity	4	-2.75	13.02	0.000	671.826
avgmheight + trees + bareground + WEMEOccupancy + earlysmallorthop + earlyorthopdiversity	6	-0.7	15.07	0.000	1872.444
avgrobel + earlymedorthop + earlyorthopdiversity	4	-0.03	15.74	0.000	2617.566

APPENDIX B continued

Easternness					
Model	K	AIC _C	ΔAIC _C	w _i	Evd Ratio
flowering + lateorthopdiversity	4	26.29	0	0.528	1.000
graminoid + latemedorthop	3	27.01	0.72	0.369	1.433
flowering + avgrobel	3	32.17	5.88	0.028	18.916
avglitter + graminoid	3	32.47	6.18	0.024	21.977
avgmheight + earlyorthopdiversity	3	33.83	7.54	0.012	43.380
avgmheight + earlysmallorthop	4	33.95	7.66	0.011	46.062
deadplant + latemedorthop	4	34.07	7.78	0.011	48.911
Constant	2	35.37	9.08	0.006	93.691
bareground + avglitter	4	35.8	9.51	0.004	116.164
trees + bareground	4	36.2	9.91	0.004	141.883
latesmallorthop + lateorthopdiversity	3	37.36	11.07	0.002	253.408
earlymedorthop + earlyorthopdiversity	3	39.79	13.5	0.001	854.059