GRASSHOPPER SPARROWS ON THE MOVE: PATTERNS AND CAUSES OF WITHIN-SEASON BREEDING DISPERSAL IN A DECLINING GRASSLAND SONGBIRD

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# Abstract

Dispersal is a behavior common to virtually all taxa with important consequences for gene flow, demography, and conservation. Mobile animals such as birds frequently engage in breeding dispersal, but the factors shaping this behavior are not well understood. In mid-continental grasslands, preliminary evidence suggested that Grasshopper Sparrows (*Ammodramus savannarum*) engaged in breeding dispersal within a single breeding season. This intriguing pattern shaped my research questions: (1) what are the patterns of within-season breeding dispersal in Grasshopper Sparrows? (2) why do some individual sparrows disperse, and others do not? and (3) what shapes settlement decisions following dispersal? I tested hypotheses based on spatial and temporal variation in nest predation, nest parasitism, and food availability. I studied Grasshopper Sparrows at 18 experimentally-managed watersheds with different fire and grazing regimes at Konza Prairie Biological Station during 2013–2015. To describe patterns, I combined re-sighting of 779 marked individuals, territory mapping, and radio-telemetry to quantify territory densities, turnover, and dispersal distances. To determine if nest predation or nest parasitism affected dispersal, I monitored the fate of 223 nests. I estimated food intake rates using plasma metabolites, and prey availability using sweep sampling. Densities of territorial Grasshopper Sparrows varied seasonally in management-specific ways. Turnover was remarkably high, with over half of territorial males being replaced each month. Over a third of males changed territories within-season, dispersing 0.1–9 km between breeding attempts. Dispersal decisions were related to past nest predation, but not nest parasitism. Dispersal likely yields fitness benefits, as sparrows that dispersed increased their chances of nest survival by 23% relative to site-faithful individuals. However, food availability did not affect settlement decisions. My study provides the first evidence of within-season breeding dispersal in

Grasshopper Sparrows, and represents one of few tests of alternative hypotheses explaining dispersal decisions of songbirds. My results are consistent with a growing literature on the role of predation shaping dispersal, but suggest, somewhat surprisingly, that food is not important in post-dispersal habitat selection. High dispersal capacity coupled with adaptability to temporal and spatial change may be typical of grassland songbirds, implying that demographic studies and management decisions must consider their mobility for conservation.

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# Chapter 1 - Not all who wander are lost: within-season breeding dispersal in a declining grassland songbird

## Introduction

Dispersal, or the permanent movements an individual makes between sites over time, plays a critical role in the social, genetic, and spatial structure of animal populations (Hanski 1999). Dispersal shapes species distributions, and is the demographic mechanism underlying population connectivity. Dispersal is fundamental to gene flow and demographic rescue, and has important implications for individual fitness (Ronce 2007). Dispersal rates and movements differ between age classes, where natal dispersal is the movement of a juvenile from a natal site to the site of first reproduction, and breeding dispersal is the movement of adults between consecutive breeding attempts (Greenwood and Harvey 1982). Most of our knowledge is on natal dispersal, as juveniles are more likely to disperse and move longer distances (Clobert et al. 2012). Conversely, breeding dispersal is less ubiquitous and the factors shaping variation in dispersal behavior are not well understood.

In especially mobile organisms such as birds, many species engage in breeding dispersal between years (Winkler et al. 2004, Howlett and Stutchbury 2007, Botsch et al. 2012, Chacon et al. 2013, Cline et al. 2013, Ganey et al. 2014, Pearson and Colwell 2014). Breeding dispersal has been hypothesized to be influenced by multiple exogenous and endogenous factors, such as population density, habitat quality, food, predation risk, and age, sex, individual condition, and experience (Greenwood and Harvey 1982, Haas 1998, Powell and Frasch 2000, Klemp 2003, Pakanen et al. 2011, Fernández-Chacón et al. 2013, Gow and Stutchbury 2013). Few studies have examined causes of within-season breeding dispersal, where an individual disperses between breeding attempts within a single season. Most of what we know about within-season

breeding dispersal comes from tree-nesting songbirds that breed in habitats that are relatively stable in space and time (Haas 1998, Gregoire and Cherry 2007, Betts et al. 2008, Gow and Stutchbury 2012, Cline et al. 2013). Within-season breeding dispersal is relatively uncommon and dispersal distances are small; only 2–15% of individuals disperse within-season, and most distances represent movements of <1 territory away (Drilling and Thompson 1991, Howlett and Stutchbury 1997, Haas 1998, Betts et al. 2008, Chalfoun and Martin 2010). Dispersal theory predicts that we should see greater prevalence of within-season dispersal in spatially and temporally variable habitats, where predictability of habitat quality is low (Roff 1975, McPeek and Holt 1992, Switzer 1993). Species dependent upon variable habitats may adopt a more mobile strategy, where dispersal and habitat selection decisions are plastic in response to changing local environmental conditions. In grassland ecosystems, disturbances of fire, grazing, and plant succession create a dynamic landscape within- and between seasons. Coupled with these structural and compositional changes, high intra- and inter-annual variability in growing season rainfall and temperature distinguish grasslands as dynamic environments that are highly variable within and among years (Knapp et al. 1998). Within-season breeding dispersal behavior therefore may be particularly common in grassland species.

Currently, information regarding within-season movement in grassland birds is scant and largely anecdotal. Some grassland-obligate migratory birds, including the Henslow's Sparrow (*Ammodramus henslowii*), and Baird's Sparrow (*A. bairdii*), are characterized as shifting in and out of territories (Herkert et al. 2001) and defending new areas later in the season (Vickery 1996). Species accounts for both Henslow's Sparrows and Baird's Sparrows detail disappearances of singing males with establishment of new males in the same territory areas (Herkert et al. 2002). In other grassland species such as the Sedge Wren (*Cistothorus platensis*),

nearly all individuals disperse within-season, having multiple, completely discrete breeding areas (Bedell 1996, Robbins 2015). Preliminary evidence from a population of Grasshopper Sparrows (*A. savannarum*) in the Flint Hills of eastern Kansas revealed some Grasshopper Sparrows remain faithful to a single territory the entire summer, whereas others engage in movements more than 10 territories away from previous territories. Present anecdotal evidence suggests that within-season breeding dispersal may be a common strategy among grassland songbirds. Currently, evidence for within-season movement in grassland birds is circumstantial; however, knowledge of the patterns and ecological explanations of dispersal is unknown. A better description of within-season breeding dispersal would enable investigation of the ecological and evolutionary basis for within-season breeding dispersal. Quantifying rates of within-season dispersal could also improve estimates of adult survival (Sandercock 2006), understanding of habitat selection decisions, and survey design. Moreover, grassland birds have suffered the largest declines of any other avian guild (Sauer et al. 2014), so identifying the patterns of within-season breeding dispersal decisions of these migratory species is essential to effective management and prevention of ongoing declines.

My objective was to provide the first comprehensive description of the spatial and temporal patterns of within-season breeding dispersal in a grassland songbird, the Grasshopper Sparrow. My second objective was to provide a framework for future tests of alternative hypotheses explaining the ecological and potential adaptive consequences of within-season breeding dispersal behavior in birds. I studied a population of Grasshopper Sparrows breeding in tallgrass prairie of the Flint Hills region of eastern Kansas during the 2013–2015 breeding seasons, and used three types of data to describe the spatial and temporal patterns of within-season breeding dispersal. I monitored changes in density, turnover, and the movements of

individuals, through territory surveys, re-sighting of individuals in new areas, and radio-telemetry.  I explored temporal and spatial patterns of density and turnover in relation to time of season, year, density of conspecifics, and rangeland management effects based on grazing and prescribed burning.

## Methods

### Study species and study site

Grasshopper Sparrows are songbirds in the family Emberizidae that rely on native grasslands year-round (Vickery 1996). The Grasshopper Sparrow is distributed from southern Canada to throughout much of the USA, Mexico, Caribbean, and parts of Central and South America (Vickery 1996). The western subspecies, *A. savannarum perspallidus,* is migratory and breeds across the western half of North America. In tallgrass prairie, *A. s. perspallidus* are most abundant in areas managed on a fire interval of every 2–3 years with low-intensity cattle grazing (Powell 2008). Arthropods make up 70% of Grasshopper Sparrow diet during breeding and largely consist of grasshoppers, arachnids, beetles, and caterpillars (Joern 1988). Quantity and community composition of arthropod prey for Grasshopper Sparrows is strongly affected by fire and grazing on herbaceous vegetation (Jonas and Joern 2007). Burning every 2–3 years allows intermediate amounts of dead grass to accumulate for sparrows to use as nesting cover and material, and grazing produces barer patches they use for foraging (Powell 2008).

Grasshopper Sparrows arrive in Kansas during mid-March with an earliest arrival date of 21 March (Zimmerman 1993). Males usually arrive ~5 days before females and establish territories soon after arrival. Pairs form in late April/early May, and clutch initiation begins soon afterward (Vickery 1996). Grasshopper Sparrows build domed nests on the ground that are made of soft grasses and roots, placed at the base of overhanging grass or forbs. Clutches contain 4-5

eggs, with onset of female incubation after laying of the penultimate egg. Each breeding attempt takes approximately 24 to 43 days from incubation to post-fledging. Males typically defend territories and sing from conspicuous perches until early August.

I studied Grasshopper Sparrows between April–August 2013–2015 in the Flint Hills of eastern Kansas, ~5 km north of the city of Manhattan. I studied sparrows at Konza Prairie Biological Station (Fig. 1.1), a 3,487-ha tract of tallgrass prairie co-owned by Kansas State University and The Nature Conservancy. Konza has been part of the Long-Term Ecological Research network since 1981 and is divided into replicated watershed units that are experimentally managed with fire and grazing (Knapp 1998). Core treatments include year-long bison grazing or no grazing, and prescribed fires on an annual to every two, four, or 20-year interval. Six additional watersheds at Konza are patch-burn grazed in two replicate sets. Patch-burn grazing involves a three-year rotational burn regime in combination with warm-season cattle (cow/calf pairs) grazing (Fuhlendorf and Engle 2001). I also studied sparrows at the Rannell's Flint Hills Prairie Preserve, a 1,175-ha tract of tallgrass prairie owned by Kansas State University, located adjacent to Konza (Fig. 1.1). The Rannell's Preserve includes pastures managed under an "intensive early stocking" regime consisting of late April burning and double-stocking of steers from April to July (Owensby et al. 2008). I included pastures at the Rannell's Preserve to study sparrow responses to intensive early stocking, as this rangeland management scheme is not part of the experimental design of Konza; intensive early stocking is also the predominant rangeland management within the Flint Hills. I consider my study site to be the Konza Prairie Biological Station and the adjacent Rannell's Preserve collectively, and hereafter, refer to it as "Konza."

Climatic conditions at Konza are characteristic of eastern tallgrass prairie, receiving 835 mm mean annual precipitation with high inter-annual variability in rainfall (CV=25%) and plant productivity (Knapp 1998, Knapp and Smith 2001). Over 75% of annual precipitation falls during the April-September growing season, and determines aboveground biomass and flowering of dominant grasses and forbs (Nippert et al. 2006, Raynor et al. 2015).

Grasshopper Sparrows are abundant in grasslands that are grazed and burned on a 1–3 year burn interval in varying densities, with up to 10 territories per 10-ha plot (Powell 2006, 2008, Rahmig et al. 2009). Accordingly, I selected a variety of watershed units that encompass burn-grazing dynamics that may affect patterns of Grasshopper Sparrow densities, movement, and habitat selection decisions throughout the breeding season. I selected 18 watershed units in replicated combinations of (a) bison grazing ($N = 4$) or no grazing ($N = 6$), burned either annually or every two-years. Additionally, I selected (b) intensive early stocking ($N = 2$), and (c) patch-burn grazing units ($N = 6$). I randomly located a 10-ha plot (~316 m$^2$) within each unit located $\geq$ 20 m from any road or fence line (see Fig. 1.1 to see 10-ha plots and unit names).

### Individual capture, re-sighting, territory surveys, and radio-telemetry

I captured males in mist-nets from late April until mid-August. I placed nets near primary song perches within territories, and attracted males to nets by using song playbacks. I placed a numbered USGS band and a unique combination of three colored leg bands on each individual. I sexed birds by the presence of cloacal protuberances (males) or brood patches (females) and took standard morphometric measurements. Because female Grasshopper Sparrows do not sing, spend most of their time on the ground (Vickery 1996), and usually are only detected by flushing them from nests, I did not include females in my estimates of density, turnover, and individual movements.

During breeding, males sing and use flight and wing displays to defend territories. Males sing from prominent perches at high rates, often performing territorial songs at ~45 times/hr (Lohr et al. 2013, Williams and Boyle, pers. obs.). I considered males to be territorial if they sang primary "buzz" songs, performed perched wing displays or flutter-flights, or initiated aggressive chases with other males (Vickery 1996). I considered males to be mated when they sang the "warble" song associated with pair-bond formation (Vickery 1996), or when I observed males acting non-aggressively with another non-singing bird that I presumed to be female (Vickery 1996).

To ensure males were making dispersal movements between breeding attempts, I determined whether males were engaged in breeding. I characterized male reproductive status based on a 5-point rank scale for reproductive index (Rivers et al. 2003). I classified a male as 1 if he sang only the "buzz" song; 1.5 if he sang the warble song; 2 if I sighted two birds together acting non-aggressively; 3 if I observed an individual giving alarm calls or carrying nesting material; 4 if I observed evidence of nestlings, such as food provisioning behavior; and 5 if I observed fledglings (Vickery et al. 1992, Rivers et al. 2003). Reproductive indices do not allow for estimation of nest survival, but are an effective method for collecting reproductive data on species with cryptic behavior (Vickery et al. 1992).

To monitor movements and dispersal distances, I re-sighted color-banded males on 10-ha plots every week (mean = 8.4 days, SD = 3.1, range = 6–17 days) and opportunistically within entire watersheds, recording the location of territorial males with hand-held GPS units (GPSmap 60CSx, Garmin, Olathe, KS). I used radio-telemetry in combination with re-sighting to monitor dispersal. I fit males with radio-transmitters using the figure-eight style leg harness (Rappole and Tipton 1991). In 2014, I fit males with 0.5 g BD-2 VHF radio-transmitters (Holohil Systems

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Ltd., Carp, ON, Canada) and in 2015, I used 0.56 g PicoPip Ag376 VHF radio-transmitters (Lotek Wireless, Newmarket, ON, Canada) that transmitted a signal over longer distances (0.8 km in 2014 vs. 1.6 km in 2015). Both transmitter types and harnesses together (0.7 g) weighed an average of 4% body mass (mean = 17.40 g, SE = 0.16 of male Grasshopper Sparrows fit with transmitters). I was confident that transmitters would not induce considerable stress to Grasshopper Sparrows, as there were no measurable negative effects of transmitters for similarly-sized songbirds (Rae et al. 2009, Streby et al. 2013).

My objective with radio-telemetry was to establish when and where individuals dispersed rather than to collect detailed movement data. Thus, I located each focal individual every other day between 06:00 to 18:00. I located birds using a 3-element folding Yagi and portable handheld radio receivers (R-1000, Communications Specialists; Biotracker Receiver, Lotek Wireless) and recorded locations using GPS. When I could not relocate birds, I searched ~ 42 hours per bird over a two–week period (~6 hrs/day every two days) on foot and using a car-mounted omni directional antenna (Lotek Wireless, Newmarket, ON, Canada). I systematically searched a ≥ 5 km radius from the last location the individual was seen previously, and also searched opportunistically during territory surveys. I assumed radio-tagged birds dispersed beyond my study site if I could not relocate them following these search methods. Although I was unable to rule out the possibility that some of these birds died, I refound 7 of 10 lost birds, suggesting that the 3 birds that disappeared did indeed disperse beyond my search radius. The maximum dispersal distance I could have detected within my study site was 11.1 km, which represents the longest straight–line distance between the two farthest watersheds (Fig. 1.1, watersheds 2A to COA).

To determine seasonal variation in densities of territorial males and turnover of territory

holders, a field crew of 4–6 observers mapped territories of all singing males every week (mean

= 8.4 days, SD = 3.1, range = 6-17 days) within each 10-ha plot. I mapped territory locations

using aerial imagery and marked 1–8 territory locations with GPS. I performed surveys between

06:00 and 11:00, typically surveying two plots each morning, with 1.5 − 3 hours for each plot.

To avoid observer effects, I avoided plots being surveyed by the same observer twice in a row,

and alternated observers between early (first survey) and later (second survey) time periods. My

survey protocol required that observers traverse plots in different ways each time, ensuring

complete coverage of the entire 10-ha area and within 75 m earshot of singing males at any point

within the plot.

## Data analyses

I present three lines of evidence for within-season breeding dispersal: (1) changes in

density of territorial males within plots over time; (2) turnover of territorial males within plots;

and (3) direct observations of individuals occupying new territories ≥ 100 m from their initial

territories.

Grasshopper Sparrow territories range in size from 40–90 m$^2$ across their breeding range

(Delany et al. 1995, Vickery 1996, Jones et al. 2007) and are ~40 m$^2$ at Konza (mean ± SD; 43 ±

26 m; Williams and Boyle, unpubl. data). Thus, a 100 m cutoff represents movements of more

than two territories away from a previous territory. I therefore considered Grasshopper Sparrows

to have dispersed if they: (a) displayed territorial behavior ≥100 m away from the centroid of

their original territory or nest location, or (b) were not re-sighted at their initial territory ≥ 1 week

after the nest failed/fledged. Conversely, I considered sparrows as site-faithful if they: (a)

continued to display territorial behavior within 100 m away from their original territory or nest, or (b) were re-sighted again >1 week after the nest failed/fledged on their initial territory.

*Seasonal changes in density*: To measure spatial and temporal variation in density, I divided each season into early, mid, and late time periods. Early, mid, and late time periods correspond to early, mid, and late breeding, with each representing potential multiple consecutive breeding attempts (e.g., first, second, and third nesting attempts). Within each time period I conducted three to five surveys. Dates of each time period varied slightly among years due to differences in the timing of field efforts, but fell between 3 May –1 June for early season, 2 June and 5 July for mid-season, and 6 July to 3 August for late season (Fig. 1.2). I calculated density in each time period as the mean number of unique territorial males detected during territory surveys within each 10-ha plot. I calculated change in density between periods by subtracting the density of one period from the previous time period. I related plot-level changes in density to temporal and spatial patterns of landscape-level management regimes such as grazing or burning separately, and general management type (i.e., ungrazed, bison, intensive early stocking, and patch-burn grazing). I also related plot-level seasonal changes in density to densities of Grasshopper Sparrows. Results from a playback experiment on a population of Grasshopper Sparrows in Illinois found that densities of sparrows increased later in the season at sites where playbacks were used (Andrews et al. 2015). Since I wanted to explore the role of social information on habitat selection decisions, I also related plot-level changes in density (i.e., early to mid-season, and mid- to late season) to the density of conspecifics during early and mid-season.

In many plots, I either never detected territorial sparrows, or detected only a single territorial individual during a single time period. Thus, 5–6 plots had an average density of <1

which caused the data to be positively skewed. Since the distribution of densities was not normally distributed, I added 0.1 to each density value and ln-transformed all values to normalize data. Although I attempted to locate every territorial male within 10-ha plots on every survey, some birds were likely not detected due to weather (e.g., cold temperatures, high wind, fog), affecting bird behavior and/or the ability of observers to detect birds. Despite these potential issues, the majority of territorial males can be heard singing from any point within the 316 m$^2$ plot. Observers spent 1.5–3 hours surveying each plot, which meant that a territorial male had to cease singing during that period to not be detected. Since song rates can be $\geq$ 45 times/hr (Lohr et al. 2013), it would be highly unlikely for a male to go undetected during a survey. However, to account for potential differences in detection, I explored whether different approaches to calculating density altered results. I tested two other metrics of density: (1) the maximum number of birds sighted on any survey, and (2) the mean of the two surveys on which the highest number of birds were recorded. Each metric gave the same result as my first estimate of density (e.g., the mean number of birds of all surveys for a given time period), so my results appear relatively robust despite imperfect detection.

*Turnover of territorial males within plots*: Even on plots where density remained fairly constant over the season, the identity of individuals holding territories changed. Thus, the turnover of individuals provides a second metric useful for quantifying dispersal rates. I calculated turnover using a modification of an equation from Brown and Brown (1977):

Turnover rate = (N individuals present only in first period + N individuals present only in second period) / (total N individuals in first period + total N individuals in second period)*100.

I calculated turnover as the replacement of territory holders from early to mid-season, and mid-to late season. To assess turnover, I examined aerial maps of 10-ha plots that included specific territory locations of unmarked and banded territorial males. Since each time period covers three to five surveys, if a territorial male was present in one survey and absent during any other surveys, the male was still counted for that time period. If a male dispersed >100 m but remained within the plot, I still counted him as present for that time period. For unmarked individuals, if an unbanded male detected in one survey was detected again in a subsequent survey in the same general location, I assumed the unmarked male was the same individual. However, if an unbanded male was detected in a previously unoccupied area, I considered the new location occupied by a new male. Similarly, if an unbanded individual was replaced by a banded male or vice versa, I considered it to be territory replacement as well. My criteria for turnover serves as a conservative way to estimate dispersal tendency, as I consider males that dispersed within plots as still present for a given time period.

I related plot-level turnover rates to temporal and spatial patterns of density and landscape-level management regimes such as grazing, burning, and management type (i.e., ungrazed, bison, intensive early stocking, and patch-burn grazing). Because I was interested in assessing spatial and temporal variation in turnover rates, I restricted analyses to plots in which I detected ≥ 2 territorial males at some point during the season. Since turnover is bounded between 0 and 1, with 0 being no turnover and 1 being 100% turnover, I arcsine-transformed turnover rates to normalize data.

*Dispersal distances of marked birds*: For birds that defended two or more territories during a season, I measured the dispersal distance as the Euclidean distance between the centroids of territory locations.

*Statistical Analysis:* I related plot-level metrics of density and turnover to watershed management, including burning, grazing, and management type (ungrazed, bison, intensive early stocking, and patch-burn grazing), time period, and year. I assessed these relationships by multiple linear regression (for continuous explanatory variables) and analysis of variance (ANOVA; for categorical explanatory variables) using JMP statistical software (SAS Institute, Inc., 2009). To assess differences in temporal patterns among management regimes, I included interactions between time period and burning, grazing, and management type (ungrazed, bison, intensive early stocking, and patch-burn grazing) using generalized linear models. I presented means ± SE for all results.

## Results

### Seasonal changes in density

I captured and color-banded 198 to 236 adult male Grasshopper Sparrows per year (total: 779; Table 1.2). In 2013, densities of Grasshopper Sparrows ranged from 0 to 3.4 territories/10 ha (1.09 ± 0.24 territories/10 ha). In 2014, densities of Grasshopper Sparrows ranged from 0 to 7.2 territories/10 ha (2.72 ± 0.66 territories/10 ha). In 2015, densities of Grasshopper Sparrows ranged from 0 to 9.7 territories/10 ha (2.55 ± 0.69 territories/10 ha). Densities of Grasshopper Sparrows did not change over the season ($F_{2, 161} = 1.9$, $P = 0.161$), but tended to be highest early in the breeding season and declined later in the season (early: 2.50 ± 0.38 territories/10 ha; mid: 2.00 ± 0.36 territories/10 ha; late: 1.85 ± 0.34 territories/10 ha). Densities did not differ among years ($F_{2, 161} = 1.3$, $P = 0.265$).

Grasshopper Sparrow densities were consistently highest in cattle-grazed watersheds ($F_{2, 161} = 36.2$, $P < 0.001$), and lowest in ungrazed watersheds (Fig. 1.3, panels A-C). Grasshopper Sparrow densities were highest in watersheds two years since burn ($F_{2, 161} = 49.7$, $P = 0.005$; Fig.

1.3, panels A-C). The relationship between density and fire regime tended to depend on grazing treatment ($F_{2, 2} = 2.7$, $P = 0.070$), with unburned, cattle-grazed watersheds having the highest densities ($2.59 \pm 0.42$ territories/10 ha; Fig. 1.3, panels A-C). Densities differed among management regimes ($F_{3, 53} = 17.5$, $P < 0.001$) and were highest in intensive early stocked watersheds (intensive early stocking: $6.37 \pm 0.75$ territories/10 ha; patch-burn grazing: $2.89 \pm 0.34$ territories/10 ha; bison: $1.16 \pm 0.22$ territories/10 ha; ungrazed: $0.57 \pm 0.14$ territories/10 ha; Fig. 1.3, panels A-C). The relationship between densities of Grasshopper Sparrows and management type did not depend on time of season ($F_{6, 161} = 0.4$, $P = 0.870$). However, at the watershed level, idiosyncratic changes in density over the season were evident among management types (Fig. 1.3, panels A-C). Densities tended to decline over time, but densities within intensive early stocked watersheds remained relatively constant (early: $5.75 \pm 0.94$ territories/10 ha; mid: $6.46 \pm 0.77$ territories/10 ha; late: $6.90 \pm 0.70$ territories/10 ha; Fig. 1.3, panels A-C).

Plot-level changes in density from early to mid-season and mid- to late season were not positively associated with the density of conspecifics during early and mid-season. Instead, densities of Grasshopper Sparrows during early and mid-season declined with seasonal increases in density from early to mid-season, and mid- to late season ($F_{1, 107} = 6.7$, $P = 0.011$; Fig. 1.4). The negative relationship between early season density and early to mid-season changes in density ($F_{1, 53} = 3.9$, $P = 0.052$) was stronger than the negative relationship between mid-season density and change in density later in the season ($F_{3, 53} = 17.5$, $P = 0.137$). Seasonal changes in densities of Grasshopper Sparrows did not differ among years ($F_{2, 107} = 1.3$, $P = 0.276$).

**Turnover of territorial males within plots**

Overall raw mean turnover of territorial males among all years and watersheds was 0.52 $\pm$ 0.04, indicating that the identity of over half of territory holders changed each month. Turnover rates ranged from 0.25 to 0.78 territorial males/month (Table 1.1). Turnover rates did not vary consistently among management regimes or time periods (management: $F_{3, 72} = 0.9$, $P = 0.449$, time period: $F_{1, 72} = 0.4$, $P = 0.510$). Turnover rates did not differ among years ($F_{2, 72} = 2.4$, $P = 0.101$), but tended to be highest for 2015 (0.96 $\pm$ 0.07 territorial males/month) and lowest in 2014 (0.82 $\pm$ 0.08 territorial males/month). Turnover rates did not differ between burned or unburned watersheds ($F_{1, 72} = 0.7$, $P = 0.397$) or grazing treatments ($F_{2, 72} = 0.5$, $P = 0.630$). However, I found suggestive evidence that the relationship between turnover and fire regime depended on grazing treatment ($F_{2, 2} = 2.7$, $P = 0.064$), with burned, ungrazed watersheds having the highest turnover rates (0.96 $\pm$ 0.14 territorial males/month). Patterns of turnover rates and management regimes did not depend on time of season ($F_{3, 3} = 0.05$, $P = 0.984$). To test whether watersheds that contained high densities of Grasshopper Sparrows experienced high turnover, I explored the relationship between turnover between early to mid-season and mid- to late season with densities of Grasshopper Sparrows during early and mid-season. I found no association between turnover and seasonal changes in density ($F_{1, 72} = 0.03$, $P = 0.853$; Fig. 1.5).

**Known movements of marked birds**

I deployed radio-transmitters on 19 males in 2014 and 2015. Nine of 19 males dispersed and established new territories 120–1229 m from initial territories (491 $\pm$ 17.6 m; median = 334 m). An additional seven remained on initial territories throughout the breeding season. I presume that the remaining three males were killed or left the study site, as they were not detected again, despite intensive search efforts.

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Of 647 marked territorial males, 33% ($N = 213$) dispersed within breeding seasons. I also noted dispersal for five females that traveled 144 m to 1321 m between nests. Dispersal tendency among territorial males was similar among years (24.2% in 2013; 35.7% in 2014; 37.7% in 2015). Dispersal distances ranged widely from a minimum of 101 m to 8940 m (mean = 695 ± 54 m; median = 197 m; Fig. 1.6). Over half of dispersal distances were less than 400 m, and 4% dispersed >5 km between territories (Fig. 1.6). Mean and median dispersal distances estimated using re-sighting and radio-telemetry were similar (mean: 695 ± 54 m vs. 491 ± 17.6 m; median: 197 m vs 334 m, respectively) suggesting my search methods were effective.

## Discussion

My study is the one of the first comprehensive descriptions of the patterns of within-season breeding dispersal in a grassland songbird. I documented spatial and temporal changes in density, turnover, and direct dispersal distances to provide concrete, multiple lines of evidence for the prevalence of within-season breeding dispersal behavior in Grasshopper Sparrows. Densities of Grasshopper Sparrows changed within-season in management–specific ways (Fig. 1.3, panels A-C). Turnover of territorial males was remarkably high, with over half of territory holders being replaced each month. High rates of turnover indicate that over 50% of territorial Grasshopper Sparrows disperse within-season. Finally, over a third of all marked males were detected defending new territories >100 m from previous territories, with some dispersal distances ≥ 9 km between territories. Despite intensive re-sighting and radio-telemetry efforts within an 11 km study site, I undoubtedly missed individuals that dispersed within or beyond the boundaries of my study area. Thus, my estimates of dispersal distance represent minima for this species and site. However, my data provide strong evidence that within-season breeding dispersal is a very common behavioral strategy in Grasshopper Sparrows.

As an experimental landscape with replicated units manipulated by prescribed fire and grazing by large herbivores, Konza investigates fundamental sources of disturbance that shape grassland ecosystems (Knapp 1998). Coupled with climatic variability, the combined effects of climate, fire, and grazing create a spatially and temporally variable landscape that can effect habitat selection decisions within-season. My data revealed that densities are dramatically different among plots that differ in fire and grazing regime, which is consistent with studies relating grassland bird abundance to fire and grazing (Powell 2006, 2008, Hovick et al. 2014). Surprisingly, the highest densities of Grasshopper Sparrows were found on intensively early stocked watersheds burned each spring. Elsewhere in the Flint Hills, abundances of grassland birds were highest on patch-burn grazed areas rather than intensive early stocking (Hovick et al. 2012, 2014). Densities of grassland birds may differ between rangeland management regimes because of differences in habitat quality across study regions. Variation in climate affects growing season productivity and overall aboveground biomass, which can affect habitat selection decisions of songbirds. A growing literature demonstrates that densities of grassland birds are higher within patch-burn grazing management compared to intensive early stocking, but not all such benefits apply to different regions, years, or bird communities (Fuhlendorf 2006, Coppedge et al. 2008, Hovick et al. 2015).

Despite differences in density of Grasshopper Sparrows among different land management, idiosyncratic changes in density within individual watersheds over the season remained consistent in all three seasons. Both patch-burn grazed and intensive early-stocked watersheds consistently had the highest densities both within and among years, suggesting that birds reliably perceive these areas as high quality habitat. Thus, the structural and compositional characteristics of a territory that make up habitat selection choices appear to remain fairly

constant. So while the landscape itself changes according to local disturbance regimes, birds tend to select similar habitat where it is available. Thus, while birds can modify where they choose to settle, the actual habitat characteristics (e.g., grazing by cattle, unburned in current year) they use to assess high quality habitat remain the same.

Some birds base habitat settlement decisions from social information gleaned from conspecifics, as this information can be a reliable estimate of habitat quality (Doligez 2002, 2003). Social information can provide clues about quality of breeding sites and conspecific reproductive performance (Andrews et al. 2015, Rushing et al. 2015). If social information plays a role in habitat selection, this hypothesis would predict a seasonal increase in density within habitats that contain high densities of conspecifics. However, I found that density was a poor predictor of seasonal change in density. Rather, the opposite was true: I found a negative relationship between seasonal increases in density and densities of Grasshopper Sparrows, suggesting that birds may be distributing themselves more evenly across the landscape as the season progresses. Higher densities of sparrows may confer information about the relative amount of resources within that particular habitat, and sparrows thus may be distributing themselves in relation to the amount of resources available (Fretwell and Lucas 1969).

Turnover of territory holders was high in all three breeding seasons, providing evidence that within-season breeding dispersal is extraordinarily common. My analysis of the potential relationships between turnover and habitat variables suggests that turnover is not predictable based on the metrics I tested. The combination of management and seasonal effects only explained about a quarter of the variation in turnover rate. Ecological processes such as food abundance and predation risk that have direct consequences for fitness may predict variation in turnover more strongly than management effects alone. Alternatively, spatial and temporal

variability in vegetative characteristics may influence individuals to make multiple habitat selection decisions in response to changing spatial heterogeneity.

Interestingly, although densities of Grasshopper Sparrows in many plots remained fairly constant over the season, high turnover indicates that the identity of individuals was changing. The intriguing pattern of high turnover with no change in density suggests that at the same time some birds leave an area, others settle within it. Clearly, some birds are perceiving habitat as no longer suitable, whereas others are perceiving the same area as a good place to settle. Differences in simultaneous emigration and immigration rates may be due to experience of nest predation in an unpredictable environment (Fontaine and Martin 2006, Chalfoun and Schmidt 2012). In landscapes with diverse predator communities such as grasslands (Chalfoun and Schmidt 2012), predictability of predation risk may be low (Lyons et al. 2015). Consequently, individuals may settle in an area without *a priori* knowledge of predation risk, while at the same time, others disperse from an area following nest predation (Powell and Frasch 2000, Hoover 2003). Differences in co-occurring dispersal and settlement patterns may also be due to other fitness components of habitat quality, such as food availability (Klemp 2003, Gow and Stutchbury 2013). Further, there was no association between turnover and density, suggesting that the presence of other conspecifics within a particular area does not influence whether a bird chooses to leave or settle in a certain patch (Doligez 2003). With low predictability and high variation in turnover rates, my data indicate that dispersal is likely not a product of a simple decision rule (i.e., settle if good habitat, leave if not) and that more than simple habitat characteristics comes into play when making settlement and emigration decisions.

Grasshopper Sparrows may typify grassland-dependent birds of North America and elsewhere in the world. Currently, only two studies on within-season breeding dispersal of North

American grassland-obligate birds are available: one on Burrowing Owls (*Athene cunicularia*; Catlin and Rosenberg 2008) and one on Sedge Wrens (*Cistothorus platensis*; Hobson and Robbins 2009). Beyond North America, birds living in the savanna of sub-saharan Africa show patterns of within-season dispersal (Jaeger et al. 1985). Additionally, several species that exhibit within-season breeding dispersal that now occupy arable land in Europe likely were grassland specialists at one time. Skylarks (*Alauda arvensis*), Ortolan Buntings (*Emberiza hortulana*), Cirl Buntings (*Emberiza cirlus*), Corn Buntings (*Emberiza calandra*), and Woodlarks (*Lullula arborea*) all occupy habitats in farmland, cornfields, and agricultural land, as no native grassland habitat remains in this region (Dale et al. 2006, Brambilla et al. 2012). Although the causes of their movements is unknown, evidence from North American and Old World birds corroborate with results from this study that within-season breeding dispersal may be a common behavioral strategy of grassland songbirds. Consistent with theory, species adapted to these spatially and temporally heterogeneous environments adopt a more mobile strategy to track a constantly moving target of habitat quality over the course of the breeding season.

In conclusion, my study reveals several important insights applicable to the study of dispersal in a broader range of birds. First, within-season breeding dispersal may be a common strategy employed by birds to cope with changing local environmental conditions. Breeding habitat selection may remain constant throughout the breeding season, but birds make within-season shifts in response to a changing landscape (McPeek and Holt 1992, Switzer 1993). The relative importance of conspecific attraction to settlement decisions may be context-specific and responses may vary in different regions, years, or bird communities. Prevalence of within-season breeding dispersal may go unrecognized without regular, intensive re-sighting efforts that span the entire breeding season. Thorough re-sighting and territory mapping to track territorial

behavior and movements of marked individuals is necessary to identify dynamic territory shifts in areas that appear to have consistent abundance over time. Densities of breeding birds may appear to stay constant within a specific management regime, but can vary 2–3 fold across areas that differ in land use. Moreover, my study emphasizes the utility of incorporating large spatial scales into study design, as incidence of within-season breeding dispersal may go unnoticed if dispersal movements are longer than the width of the study area. Consequently, managers should consider birds' mobility not only for survey design, but also for determining the spatial scales at which habitat should be managed for conservation.

My comprehensive description of the incidence and patterns of within-dispersal sets the stage for future empirical tests of the ecological and evolutionary causes of within-season breeding dispersal. Future work should test predictions of alternative hypotheses relating to ecological processes such as predation risk, food availability, and nest microhabitat that explain dispersal and subsequent settlement decisions at a mechanistic level. Increasing understanding of the factors that explain dispersal in birds and the role of spatial and temporal variability in shaping dispersal and settlement decisions is critical for both advancing dispersal theory and improving conservation of declining species.

**Figures and Tables**

**Figure 1.1:  Map showing the Konza Prairie to the west of Kansas Highway 177 and the Rannell's Preserve to the east. Internal boundary lines represent management units labeled by name, with specific management regime detailed in the map legend. Locations of 10-ha plots are marked by yellow-squares. The inset map displays the location of the study site (yellow star) within the Flint Hills ecoregion (green shading) in eastern Kansas.**

**Figure 1.2: Diagram displaying the early, mid, and late time within single breeding seasons. I calculated change in density as the difference in average density (N territorial males/10 ha) between early and mid-season, and mid and late season. I calculated turnover as the proportion of the total number of unique individuals to total individuals from early to mid-season, and mid to late season.**



# Time of season

| 3 May | 2 Jun | 6 Jul | 3 Aug |
|:---:|:---:|:---:|:---:|
| **Early** | **Mid** | **Late** | |

**Early → Mid**
- Change in density
- Turnover

**Mid → Late**
- Change in density
- Turnover
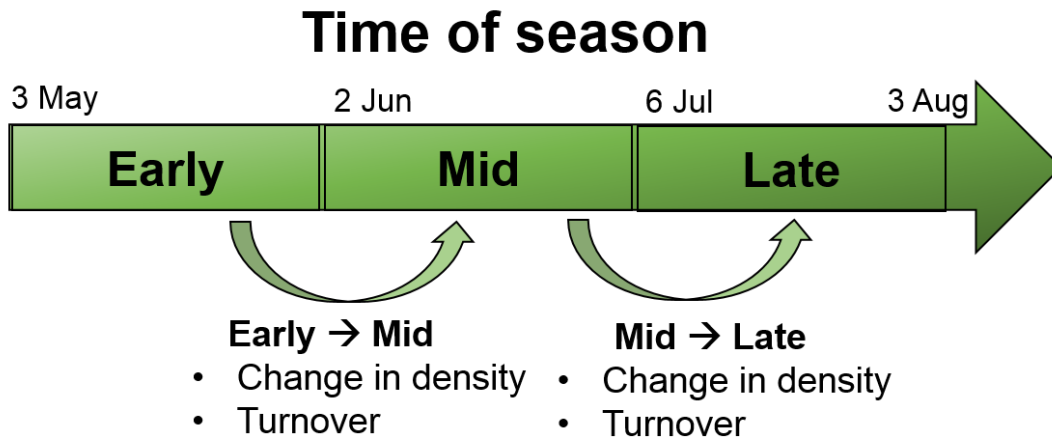
**Figure 1.3: Temporal variation in densities of territorial male Grasshopper Sparrows (mean territories/per 10 ha plot) in the 2013–2015 breeding seasons. Values for each time period for each watershed have been connected by lines. Each graph represents a single breeding season from 2013–2015, with the year in the lower right hand corner of each graph. Each symbol represents a different replicate watershed within the specified management type. Light green symbols represent a watershed burned in the current year, whereas dark green symbols represent a watershed burned 1 –2 years previously. Standard error bars have been removed for clarity.**
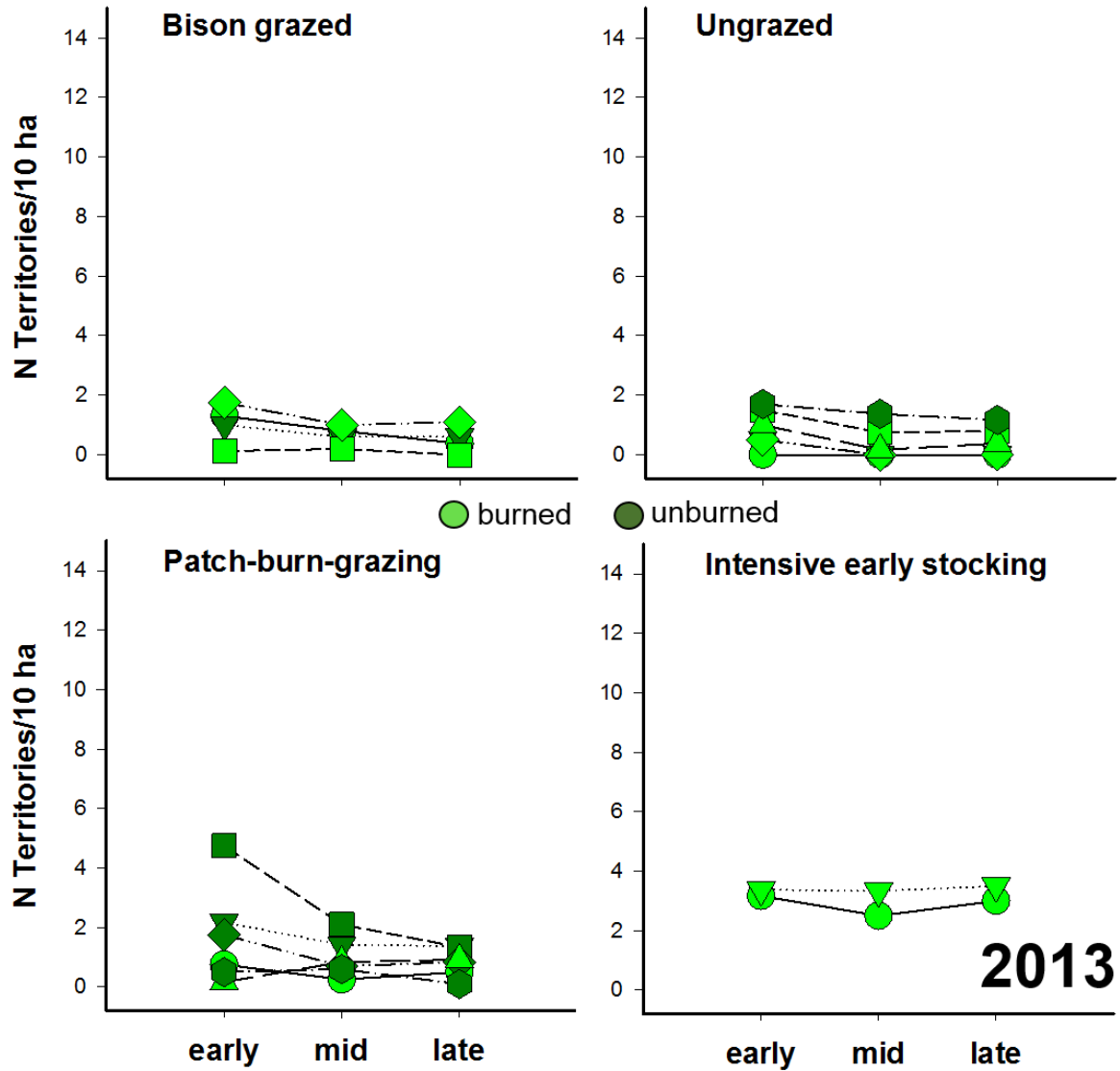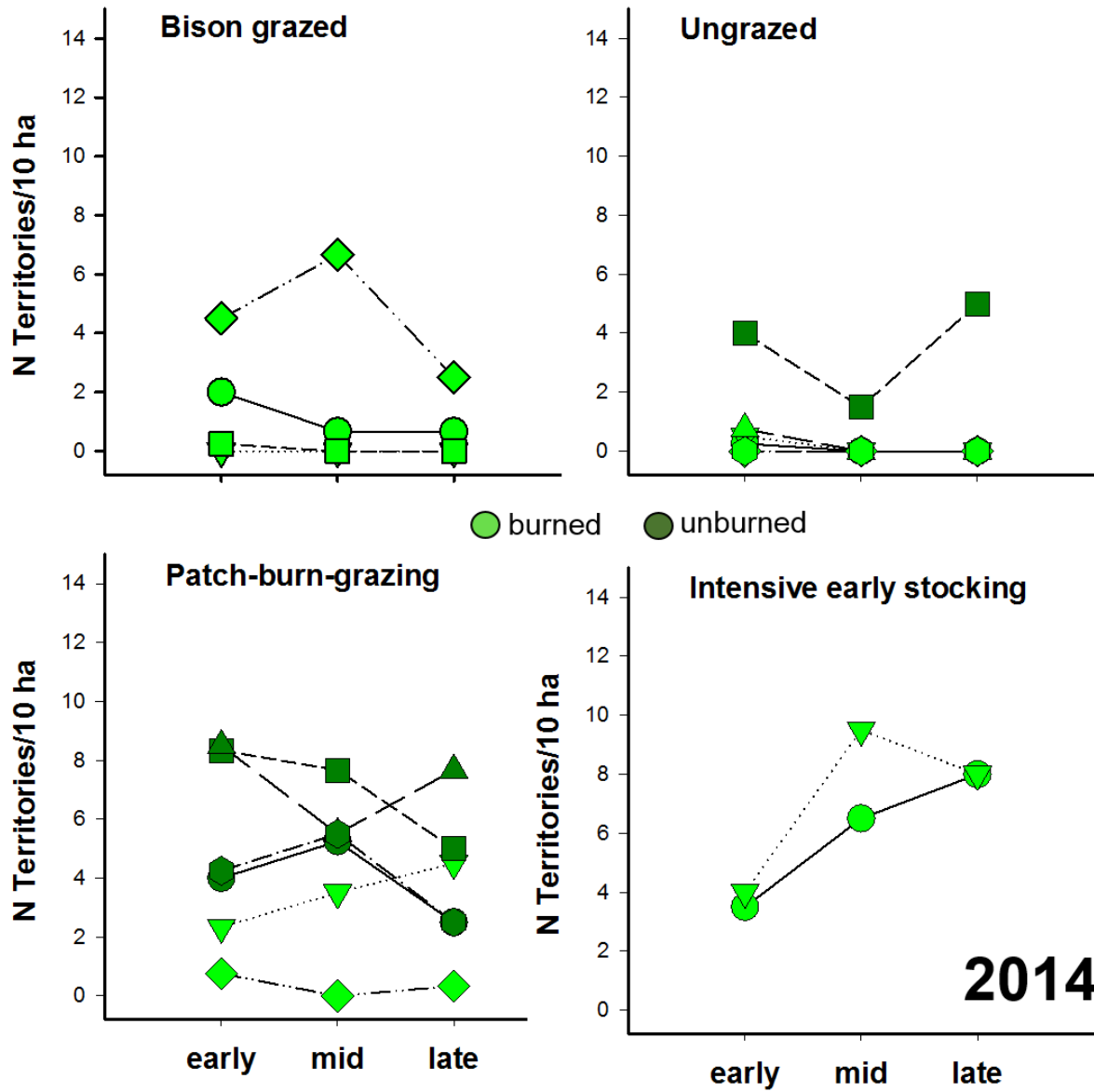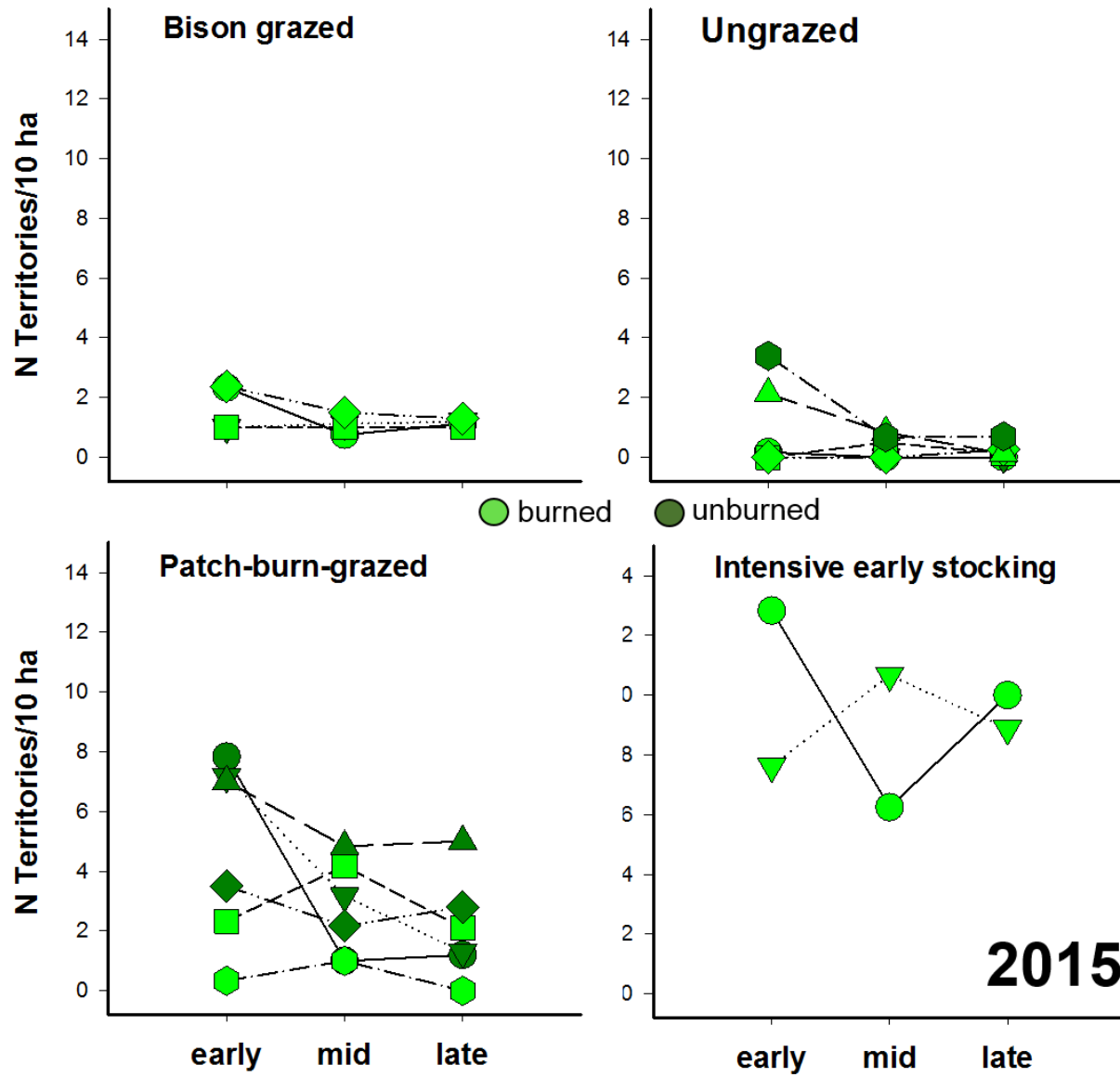
**Figure 1.4: Seasonal changes in density in relation to densities of Grasshopper Sparrows among the 2013-2015 breeding seasons ($F_{1,107}$ = 6.6, $P$ = 0.011). Values above the dotted line indicate increases in densities between time periods, and values below the dotted line indicate decreases in density. Seasonal change includes the difference in Grasshopper Sparrow densities between early and mid-season, and mid- to late season. Densities represent raw, untransformed values. Diamond shapes represent burned watersheds, and circles represent watersheds burned 1–2 years previously. Each point on the graph represents a watershed/time period/year. Standard error bars have been removed for clarity.**
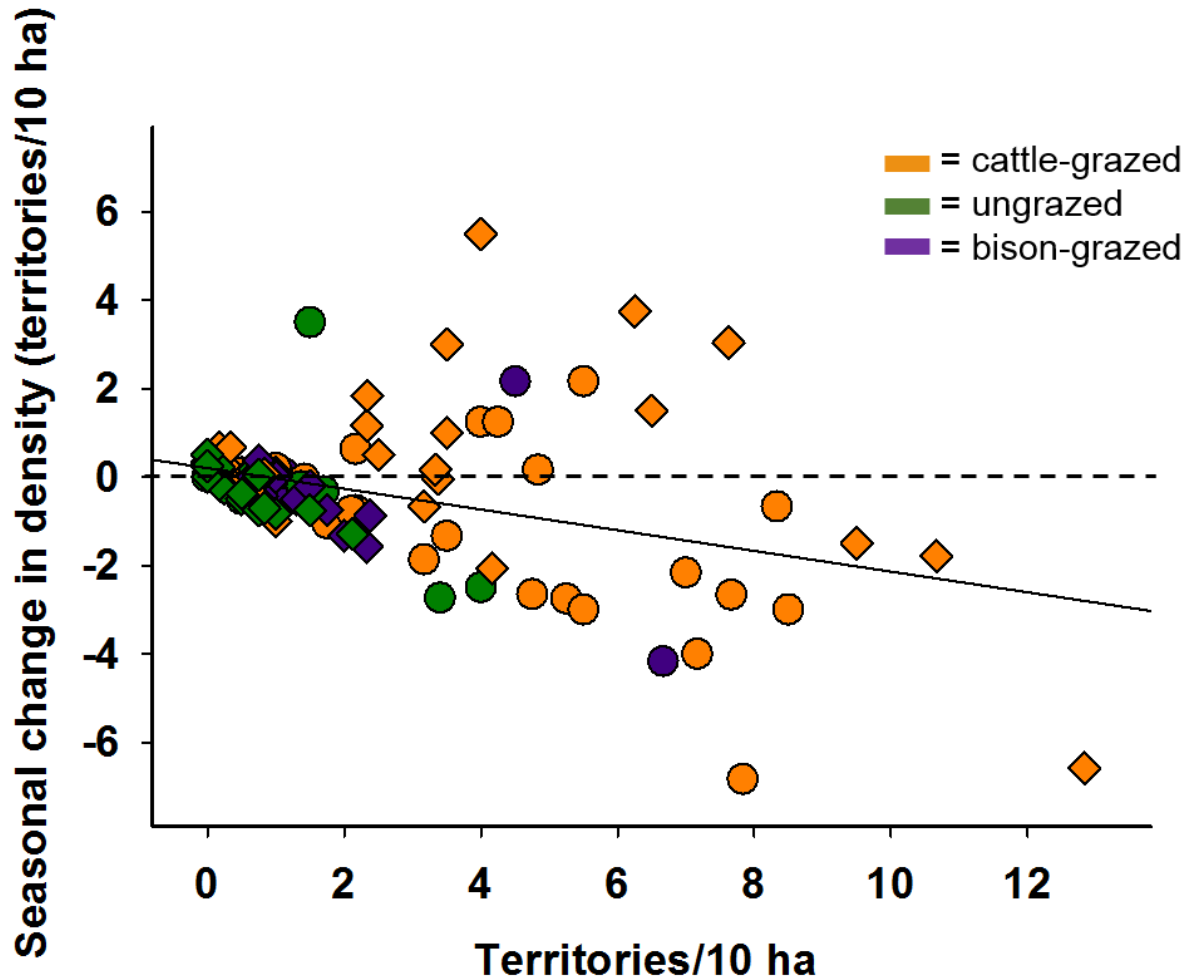
**Figure 1.5: Turnover of territorial males in relation to densities of Grasshopper Sparrows in the 2013–2015 breeding seasons. Turnover was unrelated to density in all years and time periods. Turnover represents the proportion of territorial males that were replaced between early to mid-season, and mid- to late season. Turnover values of 1 indicate complete territory replacement, whereas turnover values of 0 indicate no change. Turnover values include plots that had ≥ 2 territorial sparrows. Diamond shapes represent burned watersheds, and circles represent watersheds burned 1–2 years previously. Densities represent the mean territories/10 ha plot. Turnover and density include untransformed values. Each point on the graph represents a watershed. Standard error bars have been removed for clarity.**
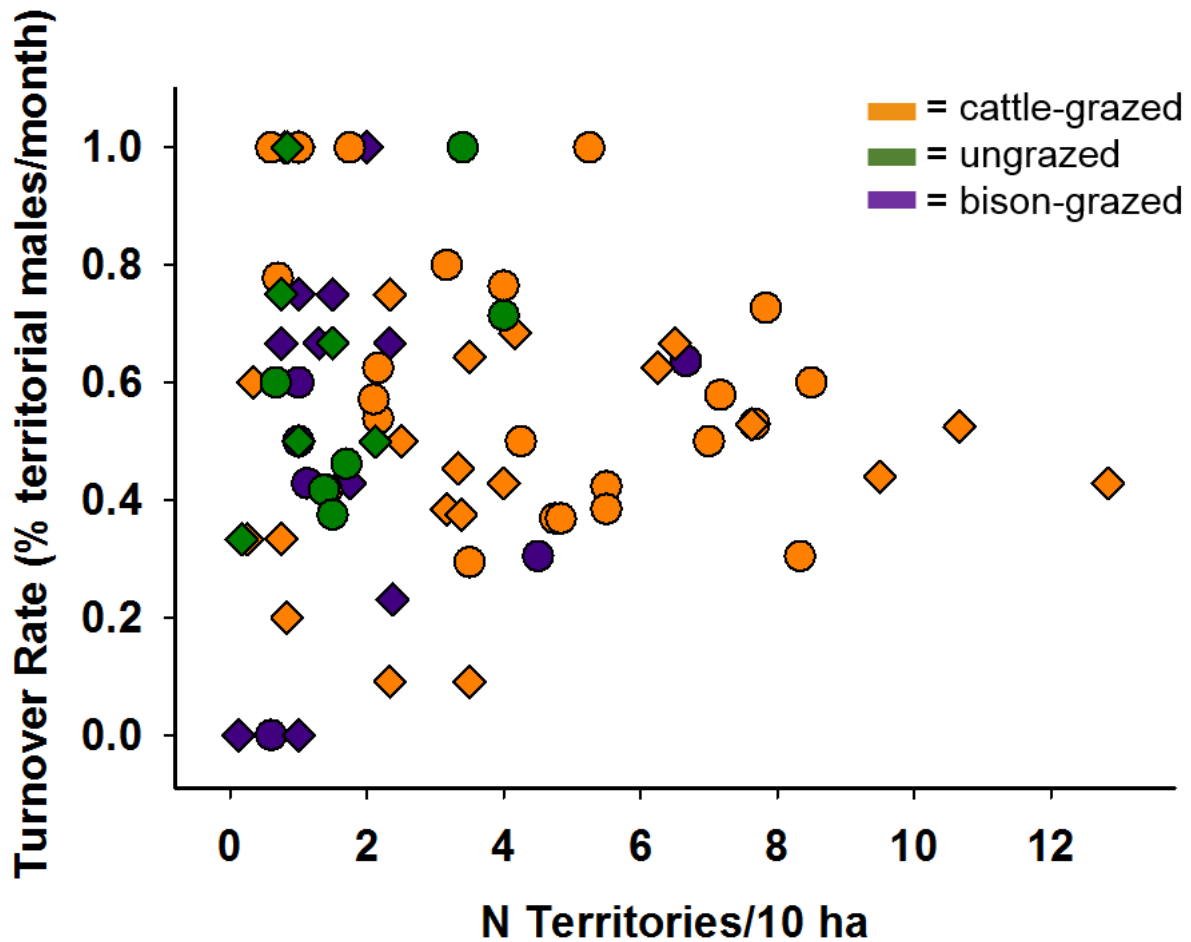
**Figure 1.6: Histogram of within-season breeding dispersal distances made by Grasshopper Sparrows in 2013-2015. The break on the x-axis represents a change from bins of 100 m intervals to 500 m intervals. The break on the y-axis is shown to display variation in larger dispersal distances > 1000 m.**
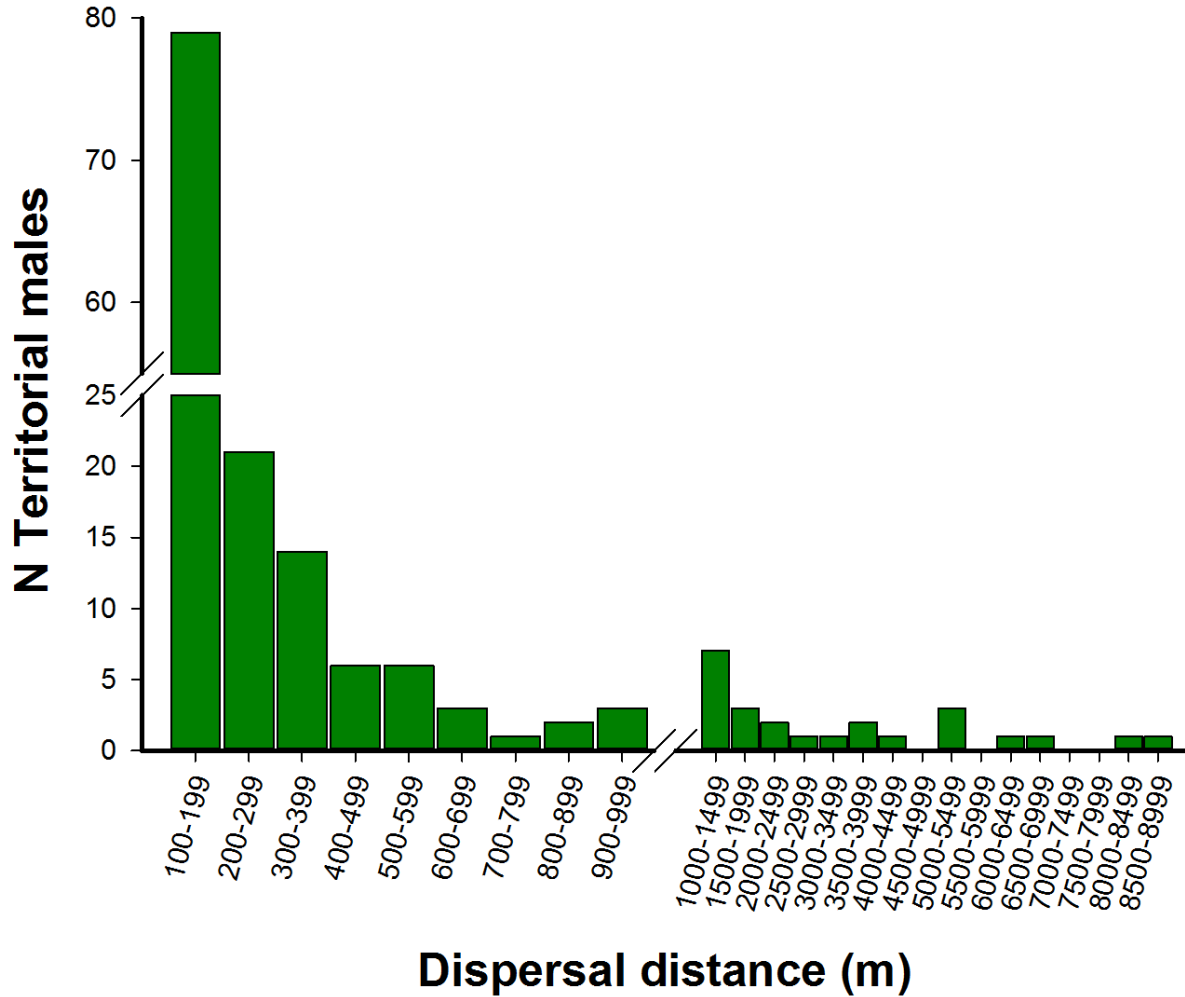
**Table 1.1: Table displaying watershed names, watershed-level treatments, densities of Grasshopper Sparrows (mean territories/10 ha plot) per year, turnover of territorial males (per 10 ha plot) per year, and total number of color-banded birds marked per watershed for all years (2013–2015) combined. Values of density and turnover represent means ± SE. Burn interval is the number of years between fires. Management types include ungrazed, patch-burn grazing (i.e., PBG), intensive early stocking (i.e., IES) and bison-grazed. PBG and IES are both grazed by cattle.**

| Watershed | Burn Interval | Mgmt Type | N birds marked | Turnover 2013 | Density 2013 | Turnover 2014 | Density 2014 | Turnover 2015 | Density 2015 |
|---|---|---|---|---|---|---|---|---|---|
| 1B | 1 | ungrazed | 0 | 0.00 ± 0.00 | 0.00 ± 0.00 | 0.50 ± 0.50 | 0.08 ± 0.08 | 0.50 ± 0.50 | 0.06 ± 0.06 |
| 2A | 2 | ungrazed | 11 | 0.50 ± 0.50 | 0.17 ± 0.17 | 0.50 ± 0.50 | 0.17 ± 0.17 | 0.00 ± 0.00 | 0.00 ± 0.00 |
| 2D | 2 | ungrazed | 17 | 0.71 ± 0.04 | 1.02 ± 0.24 | 0.54 ± 0.17 | 3.50 ± 1.04 | 1.00 ± 0.00 | 0.21 ± 0.15 |
| C3A | 3 | PBG | 84 | 0.33 ± 0.00 | 0.50 ± 0.14 | 0.88 ± 0.12 | 3.92 ± 0.79 | 0.86 ± 0.14 | 3.34 ± 2.25 |
| C3B | 3 | PBG | 89 | 0.48 ± 0.06 | 1.65 ± 0.26 | 0.37 ± 0.28 | 3.44 ± 0.63 | 0.69 ± 0.11 | 3.88 ± 1.73 |
| C3C | 3 | PBG | 95 | 0.47 ± 0.10 | 2.73 ± 1.04 | 0.42 ± 0.11 | 7.00 ± 1.02 | 0.72 ± 0.03 | 2.87 ± 0.65 |
| C3SA | 3 | PBG | 56 | 0.89 ± 0.11 | 1.09 ± 0.33 | 1.00 ± 0.00 | 0.36 ± 0.38 | 0.46 ± 0.17 | 2.82 ± 0.39 |
| C3SB | 3 | PBG | 117 | 0.60 ± 0.40 | 0.64 ± 0.24 | 0.51 ± 0.09 | 7.22 ± 0.89 | 0.43 ± 0.07 | 5.61 ± 0.70 |
| C3SC | 3 | PBG | 19 | 1.00 ± 0.00 | 0.40 ± 0.15 | 0.44 ± 0.06 | 4.08 ± 0.87 | 0.8 ± 0.20 | 0.44 ± 0.29 |
| COA | 1 | IES | 79 | 0.44 ± 0.06 | 2.89 ± 0.20 | 0.38 ± 0.29 | 6.00 ± 1.32 | 0.53 ± 0.10 | 9.69 ± 1.91 |
| COB | 1 | IES | 67 | 0.41 ± 0.04 | 3.40 ± 0.05 | 0.43 ± 0.01 | 7.17 ± 1.64 | 0.53 ± 0.01 | 9.06 ± 0.88 |
| K1A | 1 | ungrazed | 0 | 0.50 ± 0.50 | 0.17 ± 0.17 | 0.00 ± 0.00 | 0.00 ± 0.00 | 0.50 ± 0.50 | 0.08 ± 0.08 |
| K1B | 1 | ungrazed | 7 | 0.41 ± 0.08 | 0.51 ± 0.25 | 0.50 ± 0.50 | 0.25 ± 0.25 | 0.75 ± 0.25 | 1.03 ± 0.59 |
| K2A | 2 | ungrazed | 19 | 0.44 ± 0.02 | 1.41 ± 0.16 | 0.00 ± 0.00 | 0.00 ± 0.00 | 0.80 ± 0.20 | 1.59 ± 0.91 |
| N1A | 1 | bison | 9 | 0.83 ± 0.17 | 0.83 ± 0.27 | 0.50 ± 0.50 | 1.11 ± 0.44 | 0.67 ± 0.00 | 1.40 ± 0.48 |
| N1B | 1 | bison | 19 | 0.50 ± 0.50 | 0.11 ± 0.06 | 0.50 ± 0.50 | 0.08 ± 0.08 | 0.88 ± 0.13 | 1.00 ± 0.00 |
| N2A | 2 | bison | 3 | 0.25 ± 0.25 | 0.73 ± 0.13 | 0.00 ± 0.00 | 0.00 ± 0.00 | 0.51 ± 0.09 | 1.11 ± 0.06 |
| N2B | 2 | bison | 46 | 0.21 ± 0.21 | 1.28 ± 0.24 | 0.47 ± 0.17 | 4.56 ± 1.20 | 0.49 ± 0.26 | 1.73 ± 0.33 |

**Table 1.2: Color-banded Grasshopper Sparrows over the 2013-2015 field seasons captured and present at Konza. The re-sights column includes birds encountered in addition to newly-captured birds that year.**

| Year | N newly color-banded individuals | | N re-sights |
|------|-------|---------|-------------|
|      | Males | Females |             |
| 2013 | 198   | 5       | 203         |
| 2014 | 213   | 62      | 349         |
| 2015 | 236   | 65      | 390         |
| **Total** | 647 | 132 |             |

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# Chapter 2 - To stay or go: factors shaping within-season breeding dispersal decisions

## Introduction

Dispersal, or the one-way directional movement from a natal site or site of breeding, is fundamental to nearly all living organisms. Natal dispersal is the movement away from the natal site to the site of first breeding, and breeding dispersal is the movements between successive sites of reproduction (Greenwood and Harvey 1982, Clobert et al. 2012). As the key process resulting in gene flow, dispersal has important consequences for biogeography, meta-population dynamics, community ecology, and life history (Jønsson et al. 2016). Dispersal plays a vital role in maintaining connectivity of spatially-structured populations, and allows individuals to track favorable environmental conditions in an increasingly fragmented world (Ronce 2007). From an applied standpoint, understanding dispersal can inform demographic models, because dispersal confounds our ability to estimate true survival and project future population trajectories (Sandercock 2006)

Although a large literature seeks to explain the patterns and processes of dispersal, we still lack a concrete understanding of the causes of individual variation in dispersal behavior. This lack is largely due to the methodological constraints of studying dispersal, made especially difficult in highly vagile organisms. Consequently, the long-standing question of why some, but not other individuals disperse remains (Ronce 2007). Given the importance of dispersal to community and meta-population ecology, understanding the ecological and evolutionary causes and consequences of variation in dispersal is therefore critical to improve the management and conservation of natural populations.

There are three ultimate hypotheses explaining dispersal: (1) inbreeding avoidance, to reduce potential adverse genetic consequences; (2) kin selection, such that parents or young can disperse away from a previous brood to reduce competition with kin; and (3) avoidance of unfavorable conditions, relating to spatial and temporal variability in habitat quality (Clobert et al. 2012). While the inbreeding avoidance hypothesis has largely been applied to explaining natal dispersal, and the kin selection and habitat variability hypotheses applied to breeding dispersal, all three hypotheses are applicable to both natal and breeding dispersal.

Much of what we know about the evolutionary ecology of dispersal comes from studies on natal dispersal, as natal dispersal is more prevalent and occurs in virtually all organisms (Greenwood and Harvey 1982, Clobert et al. 2012). Conversely, breeding dispersal is less common and the ecological causes that shape individual variation in this behavior are not well understood (Clobert et al. 2012). This information gap exists largely because the decision to disperse or not often involves a complex, decision-making process.  An individual must assess the current state of habitat quality, based on food availability, predation risk, nest parasitism risk, and availability and quality of mates or nest-sites, and determine whether dispersing will confer greater fitness benefits than staying.

If habitat variability explains the decision to disperse, individuals would likely disperse to areas of perceived higher habitat quality (Forero et al. 1999, Serrano et al. 2001, Betts et al. 2008).  Accordingly, if individuals disperse in response to avoidance of nest predation or nest parasitism, dispersal should follow an unsuccessful breeding attempt (Dow and Fredga 1983, Thompson and Hale 1989, Daniels and Walters 2000, Fisher and Wiebe 2006, Roshier et al. 2008, Pearson and Colwell 2014, Kolecek et al. 2015).  Additionally, with *a priori* knowledge of the risks of nest predation or nest parasitism, individuals would likely select sites where the

perceived risks are lower (Greig-Smith 1982, Powell and Frasch 2000, Fisher and Wiebe 2006, Pakanen et al. 2011).

Birds are among the most mobile of animals. Many bird species engage in annual migrations that span continents. Both migrants and residents also sometimes engage in breeding dispersal, both between years and within breeding seasons. Breeding dispersal between years has been well-documented in many avian lineages, from raptors to shorebirds to passerines (Forero et al. 1999, Serrano et al. 2001, Betts et al. 2008, Friedrich et al. 2015, Kolecek et al. 2015). In general, females disperse more often and longer distances than males (Beletsky and Orians 1991, Stenzel et al. 1994, Bötsch et al. 2012), but in waterfowl and some shorebirds, the sexes display the opposite pattern (Rohwer and Anderson 1988, Anderson et al. 1992). Younger and less experienced individuals are more likely to disperse than older individuals (Greenwood and Harvey 1982). Older individuals tend to secure higher quality territories and are thus more likely to return the following year (Greenwood and Harvey 1982, Betts et al. 2008).

Within-season breeding dispersal – defined as the movement between consecutive breeding attempts within a single breeding season – is less common than between-year breeding dispersal  (Greenwood and Harvey 1982). Most of what we know about within-season breeding dispersal comes from birds that breed in forest (Drilling and Thompson 1991, Hughes and Hyman 2011, Bötsch et al. 2012, Gow and Stutchbury 2013), marshland/coastal (Monnett and Rotterman 1980, Beletsky and Orians 1991, Stenzel et al. 1994), and urban areas (Shields 1984, Beheler et al. 2003, Gilroy et al. 2010), where predictability of relative habitat quality is high. However, within-season breeding dispersal is expected to be common in temporally and spatially variable environments, where predictability of habitat quality is low (Roff 1975, McPeek and Holt 1992). Theory predicts that birds living in the most variable environments should be most

likely to engage in facultative dispersal movements, where movement decisions depend upon habitat quality, density of conspecifics, breeding success, and other predictors of local fitness (Roff 1975).

Some of the most dynamic habitats in North America are grasslands, which are shaped by fire, grazing by large herbivores, succession, and unpredictable rainfall (Knapp and Smith 2001). Many land management techniques common to grasslands can mimic these natural sources of disturbance by manipulating the timing and extent of prescribed fire and grazing (Fuhlendorf et al. 2009). Thus, both historically and contemporarily, grasslands can change dramatically over short time scales, so predictability of habitat quality is low (Wiens 1974, Knapp and Smith 2001). Spatial and temporal variation in habitat quality mediated by local disturbance regimes can affect birds via several ecological processes, such as predation or nest parasitism risk, and prey availability. Moreover, rates of nest predation and Brown-headed Cowbird nest parasitism are high in grasslands and lead to low overall nest survival (Jensen and Cully 2005, Rahmig et al. 2009, Hovick et al. 2012). Predation or nest parasitism consequently may play a major role in dispersal decisions, especially if birds adopt a "win-stay, lose-switch" strategy (Chalfoun and Martin 2010). It is thus important to understand the ecological factors that lead to within-season dispersal to more fully integrate our current theoretical understanding of dispersal in variable environments with field-based, empirical tests of hypotheses. Moreover, as one of the most threatened ecosystems in the world, grasslands now cover only 4% of their former extent and grassland songbirds have suffered the largest declines out of any other avian taxa (Sauer et al. 2014). An understanding of dispersal behavior is thus critical to identify the causes of ongoing declines and make effective management and conservation decisions in grassland landscapes.

An ideal species in which to investigate the role of habitat variability in shaping dispersal decisions is the Grasshopper Sparrow (*Ammodramus savannarum*; Emberizidae), a small, migratory songbird that depends on grasslands year-round (Vickery 1996). Recent evidence from a population of Grasshopper Sparrows breeding in the Flint Hills of eastern Kansas revealed that individuals vary in within-season dispersal behavior; some individuals defend the same territory the entire breeding season, whereas others disperse several kilometers to new territories within a single summer (Chapter 1). Within-season breeding dispersal of Grasshopper Sparrows is common, with 30–50% of birds dispersing to new territories mid-season, sometimes over distances greater than 8 km (Chapter 1). This intriguing pattern of movement thus makes the Grasshopper Sparrow an interesting species in which to examine the underlying ecological reasons of why some birds disperse, and others do not.

The goal of my study was to test key predictions of the habitat variability hypothesis in explaining within-season breeding dispersal in Grasshopper Sparrows. Specifically, I tested whether nest predation or avoidance of nest parasitism was more important than management effects alone in driving the decision to disperse. I studied a population of Grasshopper Sparrows nesting in the Flint Hills region of eastern KS during the summers of 2014–2015. I used a two-tiered modeling approach to test the effects of dispersal status, time, and management (e.g., grazing, burning) on nest survival. For the first tier, I explored patterns of nest survival in response to management and seasonal trends on all nests. For the second tier, I tested multiple predictions at both the population and individual levels on a subset of nests for which I had dispersal information. If predation avoidance explains within-season dispersal, I predicted that (1) birds that suffer nest failure due to predation would be more likely to disperse. If nest parasitism avoidance explains within-season dispersal, I predicted that (2) birds that suffer

greater parasitism incidence and number of cowbird eggs would be more likely to disperse. If early predation confers information about how risky an environment is, I predicted that (3) birds that suffer nest predation early in the nesting cycle would be more likely to disperse. As I was interested in explaining whether nest predation or parasitism avoidance played a role in settlement following dispersal, I predicted that (4) nest success would be greater and parasitism incidence and the number of cowbird eggs would be lower following dispersal than before dispersal, at both the population and individual level.

## Methods

### Study species and study site

Grasshopper Sparrows are small-bodied (~17 g) passerines that rely on native grasslands for both breeding and non-breeding (Vickery 1996). Grasshopper Sparrows are distributed from southern Canada to throughout much of the USA, Mexico, Caribbean, and parts of Central and South America (Vickery 1996). In tallgrass prairie, Grasshopper Sparrows are migratory and breed in areas managed on a fire interval of every 2–3 years with low–intensity cattle grazing (Powell 2008). Burning every 2–3 years allows intermediate levels of dead vegetation to accumulate that sparrows to use as nesting cover and material, and grazing produces bare patches of ground that sparrows use for foraging (Powell 2008). The quantity and community composition of arthropod prey for Grasshopper Sparrows is strongly affected by the effects of fire and grazing on forbs and graminoids (Jonas and Joern 2007). Grasshopper Sparrows mainly consume arthropods during the breeding season, preferring grasshoppers, arachnids, beetles, and caterpillars (Joern 1988).

Grasshopper Sparrows arrive in northeast Kansas during mid-March with an earliest arrival date of 21 March (Zimmerman 1993). Males arrive ~5 days before females and establish

territories soon after arrival. Pairs form in late April or early May, and clutch initiation begins soon afterward. Grasshopper Sparrows build domed nests made of grasses and roots placed on the ground, at the base of overhanging grass or forbs. Females incubate clutches of 4–6 eggs following laying of penultimate egg (Vickery 1996). Nest parasitism by Brown-headed Cowbirds (*Molothrus ater*) are high in Kansas, with 50% of nests containing 1–3 eggs (Rivers et al. 2010). Incubation lasts 10-12 days, and young fledge after 8–9 days (Vickery 1996). Each breeding attempt takes approximately 24 to 43 days from incubation to post-fledging (Vickery 1996). Two to four weeks post-fledging, young disperse away from natal territories (Vickery 1996). Males typically defend territories and sing from fixed perches until late August.

I studied Grasshopper Sparrows between April–August 2014–2015 in the Flint Hills of eastern Kansas, located ~5 km north of the city of Manhattan. I studied sparrows within the Konza Prairie Biological Station (Fig. 2.1), a 3,487-ha tract of tallgrass prairie co-owned by Kansas State University and The Nature Conservancy. Konza has been part of the Long-Term Ecological Research network since 1981 and is divided into replicated watershed units that are experimentally managed with fire and grazing (Knapp 1998). Core treatments include year-long bison grazing or no grazing, and prescribed fires occur on an annual to every two, four, or 20-year interval. Six additional watersheds within Konza are patch-burn grazed in two replicate sets, managed with a three-year rotational burn regime in combination with warm-season cattle (cow/calf pairs) grazing (Fuhlendorf and Engle 2001). I also studied sparrows at the Rannell's Flint Hills Prairie Preserve, a 1,175-ha tract of tallgrass prairie owned by Kansas State University, located adjacent to Konza (Fig. 2.1). The Rannell's Preserve includes pastures managed under an "intensive early stocking" regime consisting of late April burning and double-stocking of steers from April to July (Owensby et al. 2008). I included pastures at the Rannell's

Preserve to study Grasshopper Sparrow responses to intensive early stocking, as this rangeland management scheme is not implemented at the Konza Prairie, and is the predominant rangeland management in the Flint Hills region. I consider my study site to be the Konza Prairie Biological Station and the Rannell's Preserve collectively, and hereafter, refer to it as "Konza." I selected 18 watershed units in replicated combinations of (a) bison grazing or no grazing (i.e., bison, ungrazed), and (b) annual spring burns or two-year burns, or (c) intensive early stocking and (d) patch-burn grazing. Climatic conditions at Konza are characteristic of eastern tallgrass prairie, with 835 mm mean annual precipitation and high inter-annual variability in rainfall (CV=25%) and plant productivity (Knapp 1998, Knapp and Smith 2001). Over 75% of annual precipitation falls during the April-September growing season, and determines relative biomass and timing of flowering of dominant grasses and forbs (Nippert et al. 2006, Raynor et al. 2015).

### Individual capture, re-sighting surveys, and radio-telemetry

I captured males using song playbacks at mist-nets deployed adjacent to primary song perches and within known territories. I captured females by flushing them off nests into mist-nets placed ~ 2 m from nest entrances. I placed a numbered USGS band and unique combinations of three colored leg bands to identify each individual. I sexed birds by the presence of cloacal protuberances (males) or brood patches (females), and took standard morphometric measurements.

To monitor seasonal and temporal variation in within-season dispersal, I conducted re-sighting surveys for all unmarked and banded individuals every week (mean = 8.4 days, SD = 3.1, range = 6–17 days) within each watershed. I recorded territory locations using aerial imagery and marked 1–8 territory locations with a handheld GPS unit (Garmin, Olathe, KS). I considered males to be territorial if they engaged in territorial behavior such as singing,

performing perched wing displays or sustained flutter-flights, or initiated aggressive interactions (e.g., chases, actual fighting) with other males. I considered males to be mated when they sang the "warble" song associated with pair-bond formation, or when I observed males interacting non-aggressively with another bird (presumed female; Vickery 1996).

I used radio-telemetry in combination with re-sighting to detect breeding dispersal. I captured males presumed to be the fathers at active nests based on repeated nest observations. I fit males with radio-transmitters using the figure-eight style leg harness (Rappole and Tipton 1991). In 2014, I fit males with 0.5g BD-2 VHF radio-transmitters (Holohil Systems Ltd., Carp, ON, Canada) and in 2015, I used 0.56g PicoPip Ag376 VHF radio-transmitters (Lotek Wireless, Newmarket, ON, Canada) that transmitted over longer distances (0.8 km in 2014 vs. 1.6 km in 2015). Both transmitter types and harnesses together (0.7 g) weighed an average of 4% of body mass (mean =17.40 g, SE = 0.16 of male Grasshopper Sparrows fit with transmitters). I was confident that transmitters would not induce considerable stress to Grasshopper Sparrows, as there were no measurable negative effects of transmitters for similarly-sized species (Rae et al. 2009, Streby et al. 2013).

My objective with radio-telemetry was to establish when and where individuals dispersed rather than to collect detailed movement data. Thus, I located each focal individual every other day between 06:00 to 18:00. I followed movements using a 3-element folding Yagi and portable handheld radio receivers (R-1000, Communications Specialists; Biotracker Receiver, Lotek Wireless) and recorded bird locations using GPS. When I could not relocate birds, I searched ~ 42 hours per bird over a two–week period (~6 hrs/day every two days) on foot and using a car-mounted omni directional antenna. I systematically searched a ≥ 5 km radius from the last location the individual was seen previously, and also searched opportunistically during territory

surveys. I assumed radio-tagged birds dispersed if I could not relocate them following these search methods. I was unable to rule out the possibility that some of these birds died, but I later refound most of the lost birds ($n = 7/10$), suggesting that most birds that disappeared did indeed disperse beyond my search radius.

## Nest searching and monitoring

I searched for nests using behavioral observations of carrying food or insistent chipping, haphazardly flushing females from nests, and rope dragging (Higgins et al. 1969). I recorded nest locations using handheld GPS units and placed two spray-painted rocks and pin flags 5 m from the nest. If birds attending the nest were unbanded, I captured and banded them. I candled eggs to estimate age (Lokemoen and Koford 1996), counted the number of eggs or nestlings of both Grasshopper Sparrows and Brown-headed Cowbirds, and monitored nests every two days to determine nest fates. For nests first located post-hatching, I aged the nestlings based on feather development growth characteristics, body size, and whether the eyes were opened (Vickery 1996). I distinguished Brown-headed Cowbird eggs from host eggs by size and pigmentation, and identified cowbird nestlings based on body size and rictal flange (gape) color.

To estimate exact fail and fledge times, I embedded iButton temperature loggers (Maxim Integrated Products, Inc.) at the base of the nest cup and at paired (ambient) locations from the nest. iButtons logged temperature at 10-minute intervals until they were reset following nest failure/fledging. iButtons provide data on patterns of incubation behavior, where stable temperatures occur throughout most of the day when the female is on the nest, and peaks or lows in temperature occur during off-bout periods. I determined fail or fledge times based on the time in which temperature of the nest iButton matched that of the ambient iButtons, and no longer showed reliable patterns of incubation. I considered a nest to be successful if at least one host or

cowbird chick fledged, confirmed by sightings of the fledgling(s), agitated parents chipping, or carrying food nearby. If I could not confirm sighting of a fledgling, I assumed a nest fledged if contents disappeared at fledging age (8-9 days) and saw fecal droppings at or near the nest site. I assumed nests failed due to predation when all contents disappeared from nests prior to the expected fledging date and I did not see or hear any adult activity nearby. I considered nests as failed if signs at the nest site indicated the nest failed due to trampling or female abandonment. For nests that had iButtons, I paired Konza weather station data with off-bout periods to determine whether failures were associated with severe storm events. I classified the upper quartile of rainfall events as severe, based on a cutoff of 11.65 mm of rainfall per hour.

To test the population-level prediction that nests following dispersal were more successful that previous nests, I categorized nests found throughout the breeding season as either "early" or "late" nests based on specific criteria. As the typical nesting period lasts 24 days for Grasshopper Sparrows (Vickery 1996), I calculated the earliest date a nest could successfully fledge (based on a five–egg clutch) based on the earliest first egg lay date from 2014 (April 30) and 2015 (May 11). I estimated a minimum of one week to select a territory and build a nest, and another week to engage in dispersal movements, which resulted in June 8 (2014) and June 18 (2015). To be as conservative as possible, I added another week to the later date of June 18 to come up with June 25 as the latest date a nest could be initiated. I thus divided the season into two halves, with all nests with initial egg lay dates before June 25th as early nests, and all nests after this date as late nests (for range of nest initiation dates, see Fig. 2.9). For 19 individuals (11 in 2014; 8 in 2015) I found more than one nest; for these nests, I classified each nest as the first, second, or third nest based on the order in which I found them. I categorized these nests as first, second, or third without the above criteria applied.

Grasshopper Sparrow territories range in size from 40–90 $m^2$ across their breeding range (Delany et al. 1995, Vickery 1996, Jones et al. 2007) and are ~40 $m^2$ at Konza (mean ± SD; 43.27 ± 26.05 m; E. Williams and A. Boyle, unpubl. data). Thus, a 100 m cutoff represents movements of more than two territories away from a previous territory. I therefore considered Grasshopper Sparrows to have dispersed if they (a) displayed territorial behavior >100 m away from the centroid of their original territory or nest location, or (b) were not re-sighted at their initial territory ≥ 1 week after nest completion. For Grasshopper Sparrows in which I found their nests prior to any dispersal movements, I considered their nests as "pre-dispersal" nests. For Grasshopper Sparrows in which I had nest information following dispersal movements, I considered their nests as "post-dispersal" nests. New appearances of unbanded birds in watersheds frequently occurred throughout the season, and since I regularly surveyed these areas with extensive mist-netting and re-sighting efforts, it is highly likely these birds are showing up from dispersing elsewhere. Thus, for birds that were initially banded at nests after June 25, I considered their nests as "post-dispersal" nests (Fig. 2.9). Conversely, I considered Grasshopper Sparrows as site-faithful if they (a) displayed territorial behavior <100 m away from their original territory or nest, or (b) were re-sighted again >1 − week after nest completion on their initial territory.

## Data analyses

I conducted a two-tiered modeling approach to test my population- and individual-level set of predictions. For the first tier, I explored patterns of nest survival in response to management and seasonal effects on all nests found in the 2014 and 2015 seasons. I examined additive and interactive effects of time (linear or quadratic trend), management effects (grazing treatment, years since burn, burned in current year), management type (intensive early stocking,

patch-burn grazed, ungrazed, bison), and year effects (2014, 2015). For the second tier, I included the supported variables from the first tier. I tested multiple predictions at both the population and individual levels for a subset of nests for which I could classify parents as dispersed or site-faithful individuals. I excluded nests for which I had unbanded or unconfirmed parents, nests that failed due to abandonment/human disturbance, or nests that were still active at the end of the monitoring period. For the second tier, I tested for additive and interactive effects on nest survival of dispersal status (e.g., site-faithful, pre-dispersal, post-dispersal), year, and grazing.

I conducted nest survival analyses using an information-theoretic approach in the nest survival procedure of program MARK (ver. 6.2; White and Burnham 1999). Program MARK uses a maximum-likelihood approach and the logit-link function to estimate daily survival probabilities (White and Burnham 1999, Dinsmore et al. 2002). I ranked models according to Akaike's Information Criterion, adjusted for small sample sizes (AIC$_c$) and considered models with $\Delta$AIC$_c$ $\leq 2$ to be equally parsimonious (Burnham and Anderson 2003). I used R (R Development Core Team, 2015) and the package RMark (Laake and Rexstad 2008) to construct nest survival models for program MARK. I extrapolated daily nest survival estimates to the 24-day exposure period (incubation to fledging) and estimated variances using the Delta method (Powell 2007).

To test the population-level prediction of whether daily nest survival is greater following dispersal, I compared daily nest survival estimates of post-dispersal nests with nest survival of pre-dispersal nests. I then tested the individual-level prediction by estimating daily nest survival for a subset of nests ($N = 38$) for which I had first and second nests of the same individual pre- and post-dispersal, and first and second nests of site-faithful individuals. I then compared the

individual nest survival estimates of first and second nests for each individual, and then calculated the change in survival as the difference between nest survival estimates of the two nests. I tested whether the difference in nest survival differed between dispersed and site-faithful individuals using analysis of variance in JMP (Ver. 11; SAS Institute). A positive mean difference in survival between first and second nests would indicate that nest survival is greater in nests following dispersal. Although there is little statistical power and large uncertainty in individual estimates of nest survival, I wanted to explore whether subsequent nests followed a general positive or negative shift in survival from previous nests.

To test whether dispersal was associated with nest parasitism, I compared frequencies of parasitized to unparasitized nests between site-faithful, pre-dispersal, and post-dispersal nests using Pearson's contingency table analysis in JMP (Ver. 11; SAS Institute). I then tested whether the mean number of cowbird eggs differed between site-faithful, pre-dispersal, and post-dispersal nests using analysis of variance. To determine whether parasitism plays a role in nest-site selection and settlement following dispersal, I assessed whether the mean number of cowbird eggs declined in second nests compared to first nests of the same individuals using analysis of variance. To ensure that potential decline in parasitism incidence or number of cowbird eggs in subsequent nests was not a function of seasonal effects in parasitism risk, I tested for an association between parasitism incidence (parasitized vs. unparasitized) or mean number of cowbird eggs and nest initiation date over the season using multiple regression. Finally, to test whether nest predation early in the nesting cycle influences dispersal behavior, I tested whether the likelihood of dispersal was dependent upon nest age at failure using logistic regression.

# Results

During the 2014 and 2015 breeding seasons, I found and monitored 223 nests of Grasshopper Sparrows ($N = 116$ in 2014, $N = 107$ in 2015). Raw nest success for all nests was 34% (76 of 223; 37% in 2014, 33% in 2015) and 39% of nests contained $\geq 1$ cowbird eggs (86 of 223). Nests received $1.87 \pm 0.09$ cowbird eggs on average (2014: $1.93 \pm 0.12$; 2015: $1.82 \pm 0.14$). Nests failed as a result of predation (76%; $N = 111$), cowbird parasitism (e.g.; kicking out all eggs, poking holes in all eggs, killing nestlings; $N = 6$), human interference ($N = 17$), abandonment for unknown reasons ($N = 5$), inclement weather ($N = 5$), and cow trampling ($N = 2$).

## Nest survival

*Temporal and spatial patterns of nest survival.* To explore time and management effects on nest survival, I included 223 nests with known fates. Daily nest survival across the entire breeding season for both years was $0.8931 \pm 0.0084$ SE. The top model explaining variation in overall nest survival was an additive model of year and grazing treatment (Table 2.1), with daily nest survival being higher in 2014 ($0.9136 \pm 0.0098$) than in 2015 ($0.8618 \pm 0.0149$). Daily nest survival was highest in ungrazed watersheds in both years, followed by bison-grazed watersheds (Fig. 2.2). Year and management treatment effects were consistently included in the most competitive models (Table 2.1). Confidence intervals broadly overlap for each management type, but ungrazed watersheds tended to have the highest daily nest survival for both 2014 and 2015 (Fig. 2.3). Nest survival on patch-burn watersheds was no different than on intensive-early-stocked watersheds ($0.8905 \pm 0.0109$ vs. $0.8873 \pm 0.0157$; Fig. 2.3).

*Nest survival of dispersers and site-faithful birds.* To examine the influence of nest survival on dispersal behavior, I included 152 nests with known fates (site-faithful: $N = 55$; pre-

dispersal: $N = 56$, post-dispersal: $N = 41$). My top model included an additive model of dispersal

status and year effects, which had nearly five times the support of the next competing model

(Table 2.2). I found no support for an interaction between year and dispersal status (Table 2.2;

Fig. 2.4). Site-faithful birds had the highest nest survival in both years ($0.9692 \pm 0.0087$ in 2014;

$0.9492 \pm 0.0129$ in 2015; Fig. 2.4). Of the dispersers, pre-dispersal nests had lower daily nest

survival than post-dispersal nests (Fig. 2.4). Daily nest survival of site-faithful nests was higher

than pre-dispersal nests in both years, with non-overlapping confidence intervals (Fig. 2.4). Nest

survival extrapolated over the entire nesting period for sparrows that subsequently dispersed was

~13.6 times lower than nest survival for site-faithful sparrows. Overall, the probability of a nest

surviving the 24-days from incubation to fledge was $0.3673 \pm 0.0085$ for site-faithful individuals,

$0.0274 \pm 0.0002$ for pre-dispersal individuals, and $0.1327 \pm 0.0030$ for post-dispersal individuals.

*Individual consequences of dispersal on nest success.* To examine the consequences of

dispersal for nest success, I compared the daily nest survival estimates of first and second nests

of birds that remained on-territory ($N = 11$ individuals, 22 nests) and first and second nests of

dispersed individuals (i.e., pre- and post-dispersal, $N = 8$ individuals, 16 nests). I included 38

nests with known fates and modeled dispersal status (e.g., site-faithful vs. disperser) with nest

order (e.g., first, second; Table 2.3). The top model only included dispersal status, with ~2.7

times the support of the next competing model of dispersal status and nest order (Table 2.3).

Daily nest survival of second nests of dispersers was higher than first nests ($0.8761 \pm 0.0440$ vs.

$0.8652 \pm 0.0426$). In contrast, nest survival of site-faithful individuals remained constant from

first to second nests ($0.9454 \pm 0.0193$ vs. $0.9401 \pm 0.0238$; Fig. 2.5). The change in nest survival

between first and second nests of dispersed differed from site-faithful individuals ($F_{1,18} = 30.8$; $P$

$< 0.0001$), with dispersers experiencing positive change in nest survival in second nests ($0.10 \pm$

0.02 change in daily nest survival from second to first nests; Fig. 2.5, 2.6). In contrast to dispersers, nest survival of site-faithful individuals declined in second nests (-0.04 ± 0.02 change in nest survival from second to first nests; Fig. 2.5, 2.6).

## Cowbird parasitism

I tested whether the frequency of parasitized nests differed between site-faithful ($N = 55$) and pre-dispersal nests ($N = 56$) to determine whether nest parasitism avoidance was associated with dispersal. The nests of birds that subsequently dispersed were parasitized at similar frequencies as nests of birds that remained on territory ($X^2 = 0.01$, $P = 0.921$; Fig. 2.7). However, nests following dispersal (post-dispersal nests; $N = 8$ of 41) were parasitized less than nests prior to dispersal ($X^2 = 10.54$, $P = 0.005$; Fig. 2.7). The mean number of cowbird eggs differed as a function of dispersal status ($F_{2, 151} = 3.6$; $P = 0.030$; Fig. 2.8), with post-dispersal nests receiving fewer cowbird eggs. The mean number of cowbird eggs in site-faithful and pre-dispersal nests was not different (mean ± SE, site-faithful: 0.87 ± 0.14; pre-dispersal: 0.98 ± 0.16). However, the mean number of cowbird eggs in post-dispersal nests was two times lower than either site-faithful or pre-dispersal nests (0.42 ± 0.15; Fig. 2.8).

To examine whether parasitism avoidance plays a role in settlement following dispersal, I tested whether the mean number of cowbird eggs declined in nests after dispersal. The mean number of cowbird eggs between first and second nests of site-faithful and dispersed sparrows did not differ ($F_{1, 18} = 0.86$; $P = 0.367$). Second nests of dispersers tended to have fewer cowbird eggs (-0.63 ± 0.51 cowbird eggs) than second nests of site-faithful individuals (no change; 0.0 ± 0.44 cowbird eggs). I found no evidence for a seasonal decline in parasitism incidence that might explain lower parasitism in post-dispersal nests ($F_{1, 10} = 1.3$; $P = 0.278$), nor any association between mean number of cowbird eggs in nests and nest initiation date ($F_{1, 222} = 0.03$; $P = $

0.858). Birds were more likely to disperse if nests failed earlier in the nesting cycle; with each one-day increase in the nesting cycle at which nests failed, the odds of dispersing increased 1.216-fold (log likelihood ratio $X^2 = 10.5$, $P < 0.001$).

## Discussion

My data provides strong support that predation avoidance, and not nest parasitism avoidance, was associated with the decision to disperse between nesting attempts in Grasshopper Sparrows. Birds that subsequently dispersed suffered nearly 10 times lower nest survival than did individuals that remained on territory. Dispersal following breeding failure due to predation is consistent with several studies reporting similar results of breeding dispersal after nest failure, both within-season (Greig-Smith 1982, Powell and Frasch 2000, Catlin and Rosenberg 2008, Bötsch et al. 2012) and between seasons (Blakesley et al. 2006, Pearson and Colwell 2014, Palestis and Hines 2015, Shitikov et al. 2015). My results also suggest that dispersal may function to increase reproductive success at the individual level; second nests following dispersal were more successful than first nests, whereas second nests of site-faithful birds were less successful. Moreover, daily nest survival succeeding dispersal (i.e., all post-dispersal nests) was higher than survival of nests that occurred prior to dispersal (i.e., all pre-dispersal nests). Nests that failed early in incubation increased the likelihood of dispersing, suggesting that birds perceive environments especially risky when experiencing predation early in the nesting cycle (Powell and Frasch 2000). Furthermore, my results suggest that birds are able to somewhat accurately assess predation and nest parasitism risk during post-dispersal habitat selection, as nests following dispersal had greater success and suffered lower parasitism.

My results suggest that birds make within-season dispersal decisions based on past experience of nest predation. Dispersal following nest predation is consistent with the "decision

rules hypothesis," where birds adopt a "stay if successful, go if unsuccessful" strategy (Bollinger and Gavin 1989, Hoover 2003). The decision rules hypothesis has been tested in several species exhibiting between-year breeding dispersal, but rarely for birds displaying within-season breeding dispersal behavior (Catlin and Rosenberg 2008). My findings suggest that the role of predation and previous reproductive success in driving differences in site fidelity between years is also largely applicable to explaining differences in territory fidelity within-season. Moreover, the fact that the likelihood of dispersal is dependent upon nest age upon failure is further evidence that birds are indeed making experienced-based choices rather than dispersing simply as a result of differential mortality (Hoover 2003). My findings corroborate with other studies reporting dispersal after early nesting cycle losses (Jackson et al. 1989). Powell and Frasch (2000) found that Wood Thrushes gain a greater fitness advantage by dispersing when nests were depredated early in the nesting cycle, rather than later. Nests that are depredated early in incubation provide strong cues about the relative riskiness of a particular nesting site, and birds seem to adjust their behavior according to nest predation risk (Pakanen et al. 2014).

Contrary to prediction, nest parasitism was not important in shaping dispersal decisions. I found that parasitism incidence was not different between site-faithful sparrows and sparrows that subsequently dispersed, suggesting that whether a nest is parasitized or not is inconsequential to leaving a territory. Despite the impacts of reduction in overall reproductive output (i.e., reduced clutch sizes and number of young fledged; Hovick and Miller 2013), nest parasitism does not seem to play a role in the decision to disperse. Likewise, parasitism does not affect daily nest survival, as Hovick and Miller (2013) found that survival rates were similar between non-parasitized and parasitized nests. Since parasitism has minor effects on nest survival when compared to direct predation (Hovick and Miller 2013), it may be that

Grasshopper Sparrows perceive nest parasitism as less of a threat. Furthermore, incidence of cowbird parasitism on grassland songbirds has been highest in the Great Plains region (Jensen and Cully 2005), so Grasshopper Sparrows may have ultimately adjusted their behavior to adapt to parasitism pressure of cowbirds over evolutionary time scales (Rothstein et al. 2002, Peer et al. 2013).

Despite the apparent unimportance of parasitism to dispersal decisions, nest parasitism does seem to play a role in post-dispersal habitat selection. I found that parasitism incidence and the mean number of cowbird eggs in nests were lower in nests following dispersal movements, compared to nests prior to dispersal. I found no evidence for a seasonal decline in parasitism risk or the number of cowbird eggs to explain the reduction in parasitism incidence and number of cowbird eggs present in post-dispersal nests. Nest parasitism risk to Grasshopper Sparrows does not decrease as the summer progresses, unlike patterns for Bell's Vireo (*Vireo bellii*) and Dickcissels (*Spiza americana*) at the same site (Sandercock et al. 2008). The absence of a seasonal trend in parasitism suggests that birds are indeed locating areas where risk of nest parasitism is lower. Whether spatial predictability in parasitism risk exists, and whether birds can accurately assess this risk is unknown. However, parasitism often increases with proximity to grassland edges and woody vegetation (Strausberger and Ashley 1997, Robinson 2000, Patten et al. 2006). Recent grazing and burning also tended to increase parasitism rates (Johnson and Temple 1990, Patten et al. 2006). Although the mechanisms underlying nest parasitism avoidance behavior are unknown, my data are suggestive that sparrows may consider parasitism risk in habitat selection decisions following dispersal, and mitigate this risk by selecting areas where parasitism risk is lower.

Consistent with prediction, my results suggest that dispersal may be an adaptive response to breeding failure due to predation, as nests following dispersal had higher daily nest survival than nests prior to dispersal. My data suggest that Grasshopper Sparrows modify post-dispersal habitat selection decisions to areas with a greater probability of nest survival. Greater success in nests following dispersal may be a result of behavioral changes in response to perceived predation risk (Chalfoun and Martin 2007, Gow and Stutchbury 2013). If *a priori* knowledge of the predator community exists, birds may disperse outside a predator's home range (Powell and Frasch 2000). In landscapes with complex and diverse nest-predator assemblages such as tallgrass prairie, however, accurately predicting where to go and how far to go may be difficult (Chalfoun and Schmidt 2012). When birds do not have *a priori* knowledge of the predator community, birds may select alternative nesting substrate (e.g., areas with greater concealment, shrub density, etc.) to decrease probability of predation (Kearns and Rodewald 2013), or disperse to a new area that is perceived as less risky. Incongruence between distance dispersed or riskiness of sites and ensuing nest success may result if predictability of predation risk is low, or birds inaccurately assess the relative "safe-ness" of a site (Chalfoun and Schmidt 2012). Forthcoming studies relating nest-habitat characteristics to predation rates may reveal the mechanisms behind reduced predation at post-dispersal nests (Williams and Boyle, unpubl. data). The results from this study, however, suggest that Grasshopper Sparrows at least are able to mitigate predation risk by selecting sites where probability of nest predation is lower, and nest success greater.

Nest survival tended to be highest in ungrazed and bison-grazed areas burned every two years. Although Grasshopper Sparrow abundances are consistently highest in cattle-grazed areas with a burning frequency of 1-3 years (Chapter 1; Hovick et al. 2014), they have greater

reproductive success in ungrazed and bison grazed areas.  When encountering a mosaic of habitats made up of different land management regimes, sparrows appear to preferentially choose cattle-grazed areas. An apparent mismatch between habitat choice and fitness results, as sparrows more often than not choose habitat where ultimately, nest survival is lower.

Surprisingly, Grasshopper Sparrow nest survival was no different between patch-burn-grazed units and intensive-early-stocking units (Fig. 2.3), in contrast to recent results from Oklahoma where nest survival was slightly higher in patch-burn grazed units than in intensively-early stocked pastures (Davis et al. 2016). My study is based on an analysis of roughly twice the number of nests as in the Oklahoma study ($N = 223$ vs. $N = 98$), it is unlikely that my failure to detect higher nest survival in patch-burn grazed habitat was due to insufficient statistical power. Thus, although a growing literature demonstrates that density, diversity, and stability of grassland bird assemblages are improved with patch-burn grazing management, not all such benefits apply to different regions, years, or bird communities (Fuhlendorf et al. 2006, Coppedge et al. 2008, Fuhlendorf et al. 2009, Pillsbury et al. 2011, Hovick et al. 2014, Hovick et al. 2015). Direct estimates of the ecological processes affected by different land management regimes is needed to determine how management may influence the ecology of local nest predators, which in turn affect grassland bird nest survival (Lyons et al. 2015). While my study reveals the importance of intensive-early stocking and patch-burn grazing rangeland management practices to habitat selection, management alone remains a poor predictor of nest success and reproductive output (Hovick et al. 2012, this study). Rather, identifying the direct ecological effects of predation risk, nest parasitism risk, food availability, and vegetative characteristics, mediated by different management regimes, is more important in predicting nest success and dispersal behavior.

The factors shaping within-season dispersal reflect broad patterns of between-year breeding dispersal in a suite of avian taxa (Serrano et al. 2001, Kim et al. 2007, Catlin and Rosenberg 2008, Ponchon et al. 2015, Shitikov et al. 2015). Dispersal is a strategy employed by birds to cope with unpredictable spatial and temporal change, often characteristic in grasslands. My results support the habitat variability hypothesis in shaping dispersal decisions and reveal the mechanistic basis for why some birds disperse, while others do not (Clobert et al. 2012). My findings suggest that birds engage in adaptive, facultative within-season breeding dispersal to avoid nest predation. In landscapes where only a few predator species are responsible for the majority of nest losses, the association between environmental factors and nest failure can be highly predictable (Lyons et al. 2015). However, in landscapes with diverse predator communities such as in grasslands, patterns between nest loss and the environment are less tractable. In such instances, birds can disperse following predation, and make subsequent settlement decisions based on the best information available locally.

Current estimates of reproductive success may not be adequate to sustain local or regional populations of many grassland species long-term (Lyons et al. 2015). However, current estimates of reproductive success may underestimate multiple within-season breeding attempts by birds, especially if dispersal occurs outside the study area. Within-season breeding dispersal may be a more common strategy of birds breeding in variable environments (Roff 1975, McPeek and Holt 1992). Thus, high dispersal propensity coupled with adaptability to temporal and spatial change may allow grassland birds to increase reproductive success and capitalize on multiple resources within a single season. Managers should thus consider the dispersal capacity of grassland birds when estimating adult survival, and in reserving grassland habitat for multiple species. A high propensity for dispersal may suggest that grassland birds can quickly colonize

new habitats, which may be especially important for newly restored grasslands. Increasing understanding of the incidence of dispersal in grassland birds and the role of habitat variability in shaping dispersal and settlement decisions is critical for both advancing dispersal theory and improving conservation of these declining species.

# Figures and Tables

**Figure 2.1: Map showing the Konza Prairie to the west of Kansas Highway 177 and the Rannell's Preserve to the east. Internal boundary lines represent a unit labeled by name, with specific management regime detailed in the map legend. Locations of 10-ha plots are marked by yellow squares. The inset map displays the location of the study site (yellow star) within the Flint Hills ecoregion (green shading) in eastern Kansas.**

**Figure 2.2: Effects of grazing management on Grasshopper Sparrow nest survival during the 2014 and 2015 breeding seasons.**
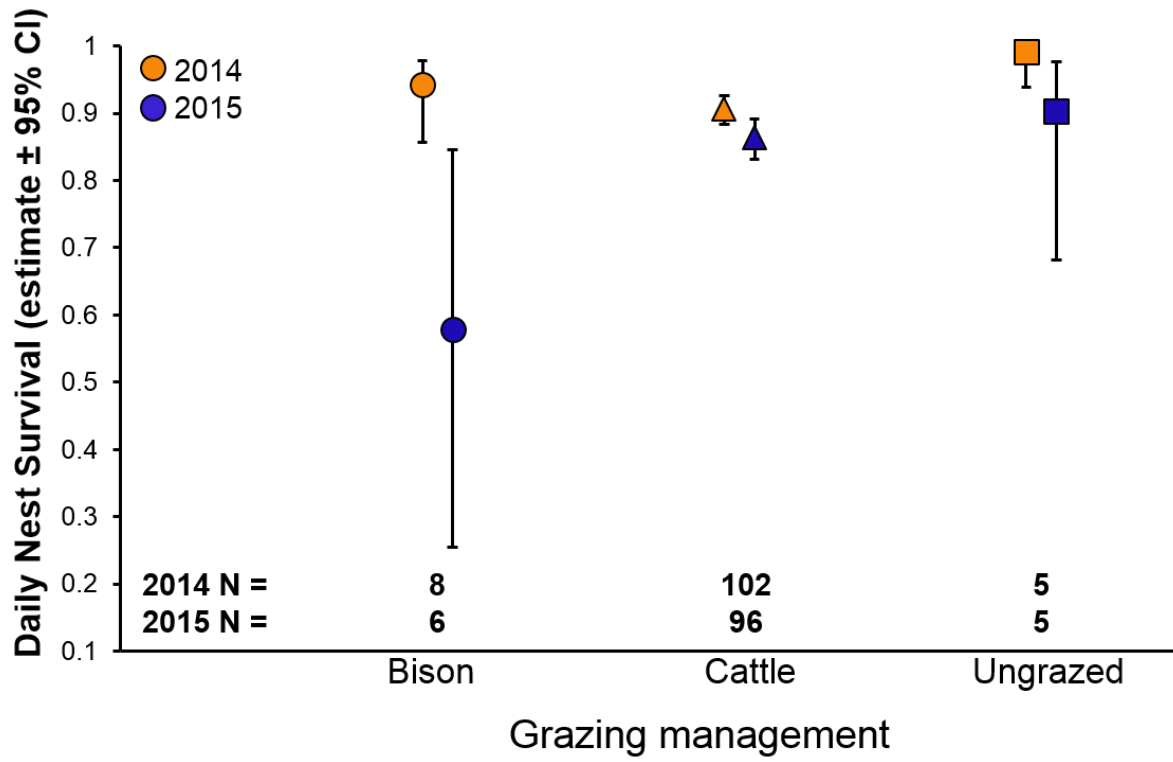
**Figure 2.3:** **Effects of rangeland management type on daily nest survival of Grasshopper Sparrows during the 2014 and 2015 breeding seasons. Bison = bison-grazed; IES = intensive early stocking; PBG = patch-burn grazing; Ungrazed = no grazing.**
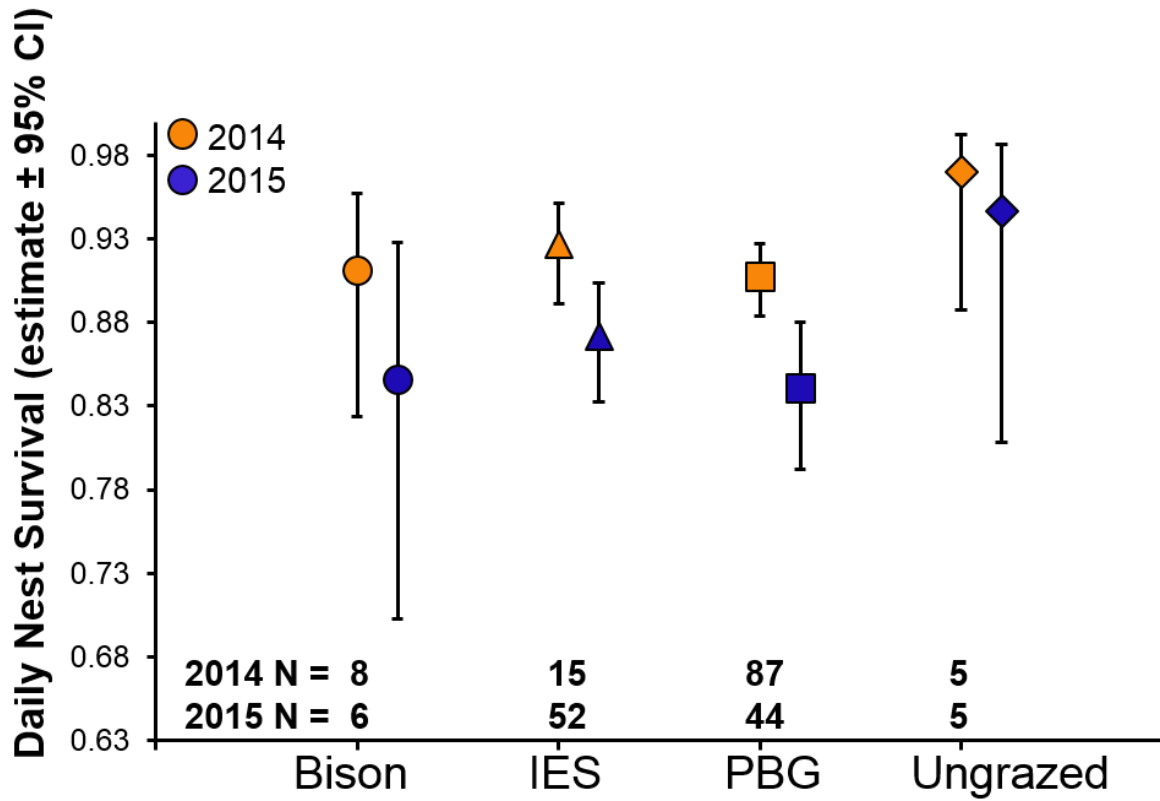
**Figure 2.4: Daily nest survival for site-faithful (*N* = 55), pre-dispersal (*N* = 56), and post-dispersal (*N* = 41) nests of Grasshopper Sparrows breeding during the 2014 and 2015 seasons.**
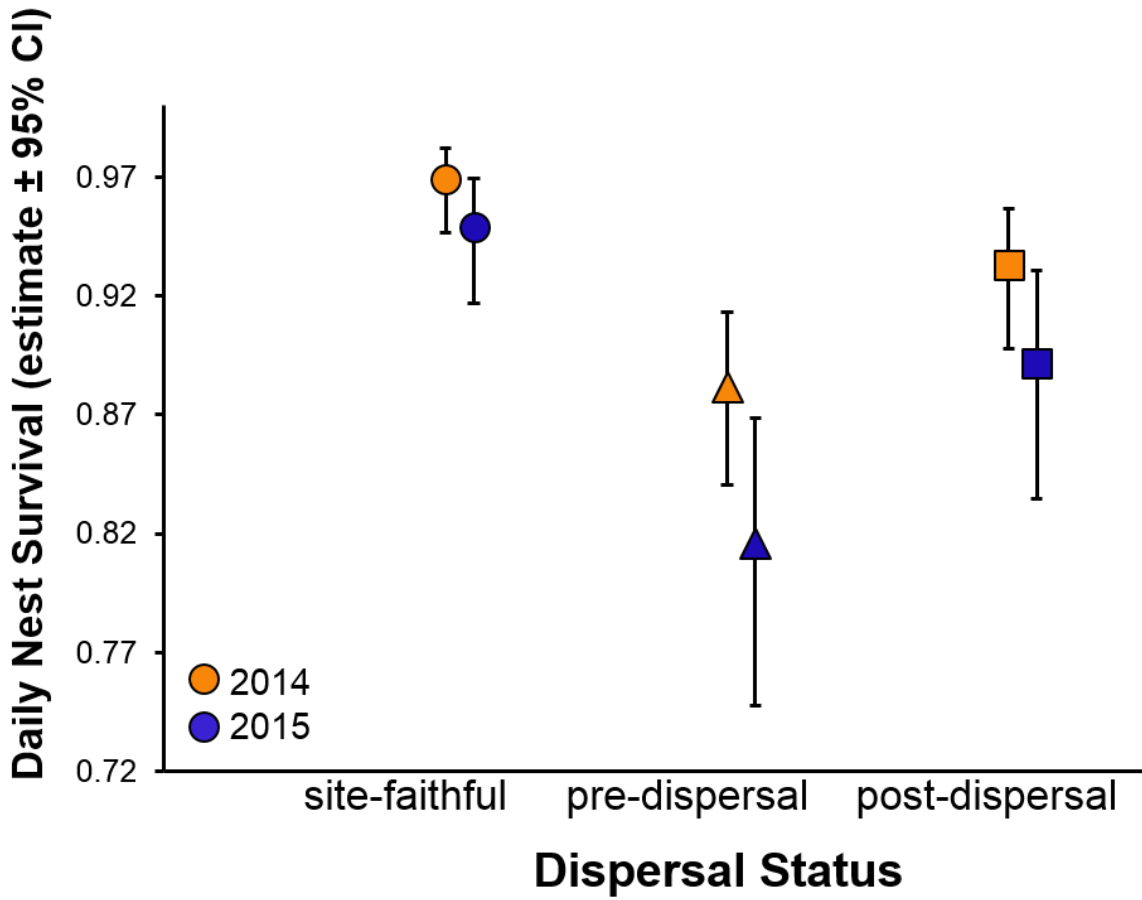
**Figure 2.5: Comparison of nest survival of first and second nests for site-faithful (*N*=11 individuals) and dispersed (pre- and post-dispersal nests; *N*=8 individuals) Grasshopper Sparrows breeding at the Konza. Four site-faithful individuals had successful first and second nests.**
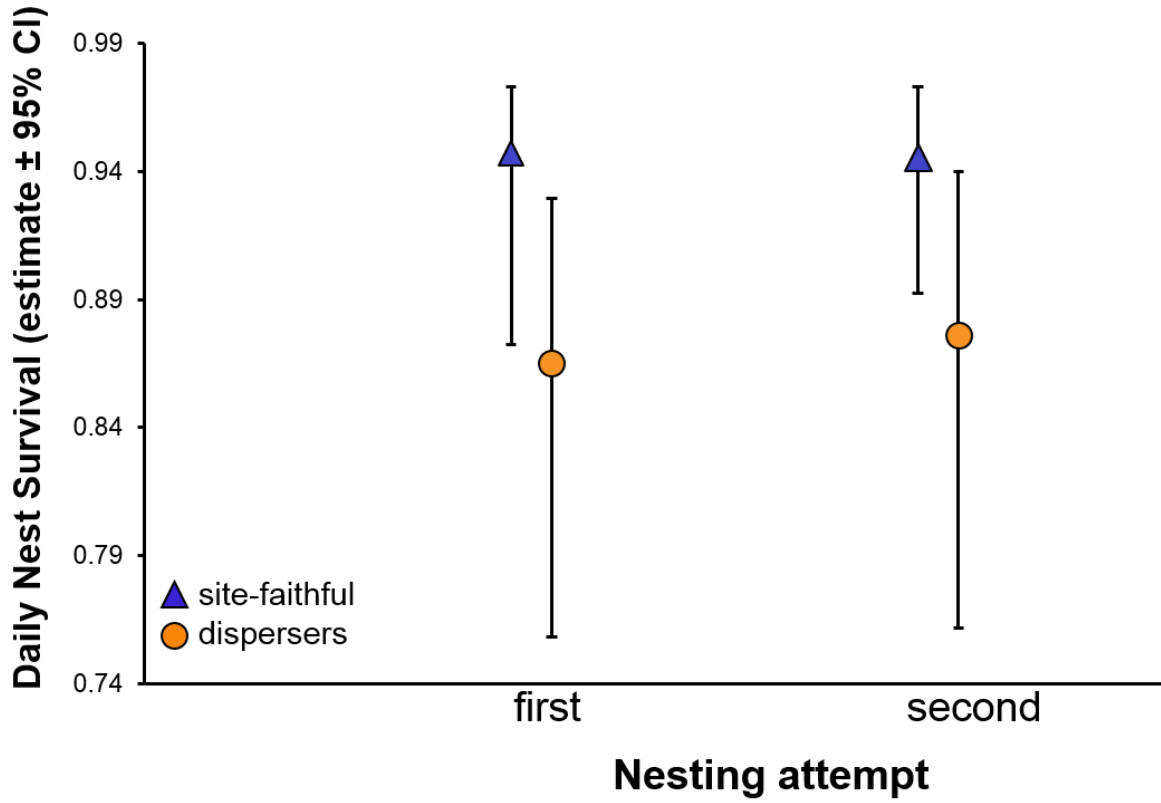
**Figure 2.6: Differences in nest survival of first and second nests for site-faithful (*N* = 11 individuals) and dispersed (pre- and post-dispersal nests; *N* = 8 individuals) Grasshopper Sparrows breeding at the Konza Prairie. Four site-faithful individuals had successful first and second nests (overlapping lines of daily nest survival = 1.0).**
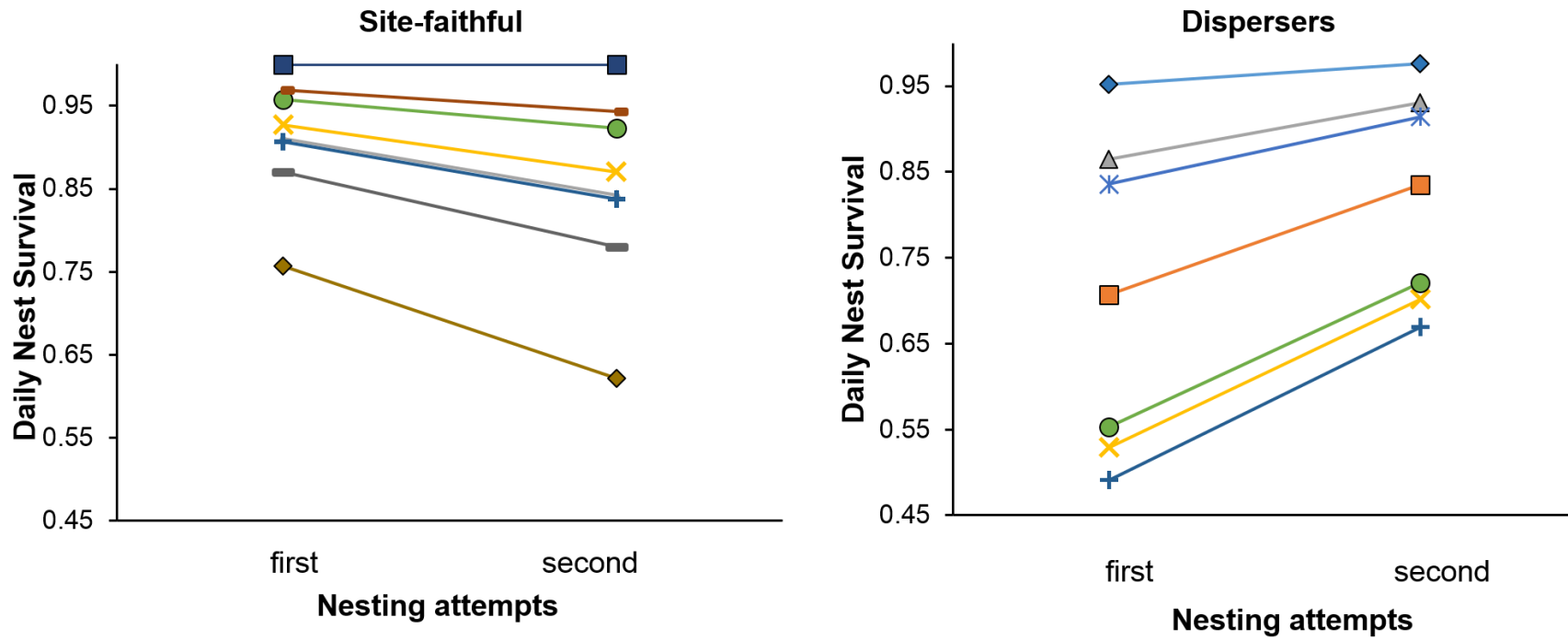
**Figure 2.7: Differences in parasitism incidence in site-faithful ($N$ = 55), pre-dispersal ($N$ = 56), and post-dispersal ($N$ = 41) nests of Grasshopper Sparrows breeding at the Konza. Sample sizes are indicated in bold within bars for each group. Parasitism incidence represents the frequency of unparasitized to parasitized nests.**
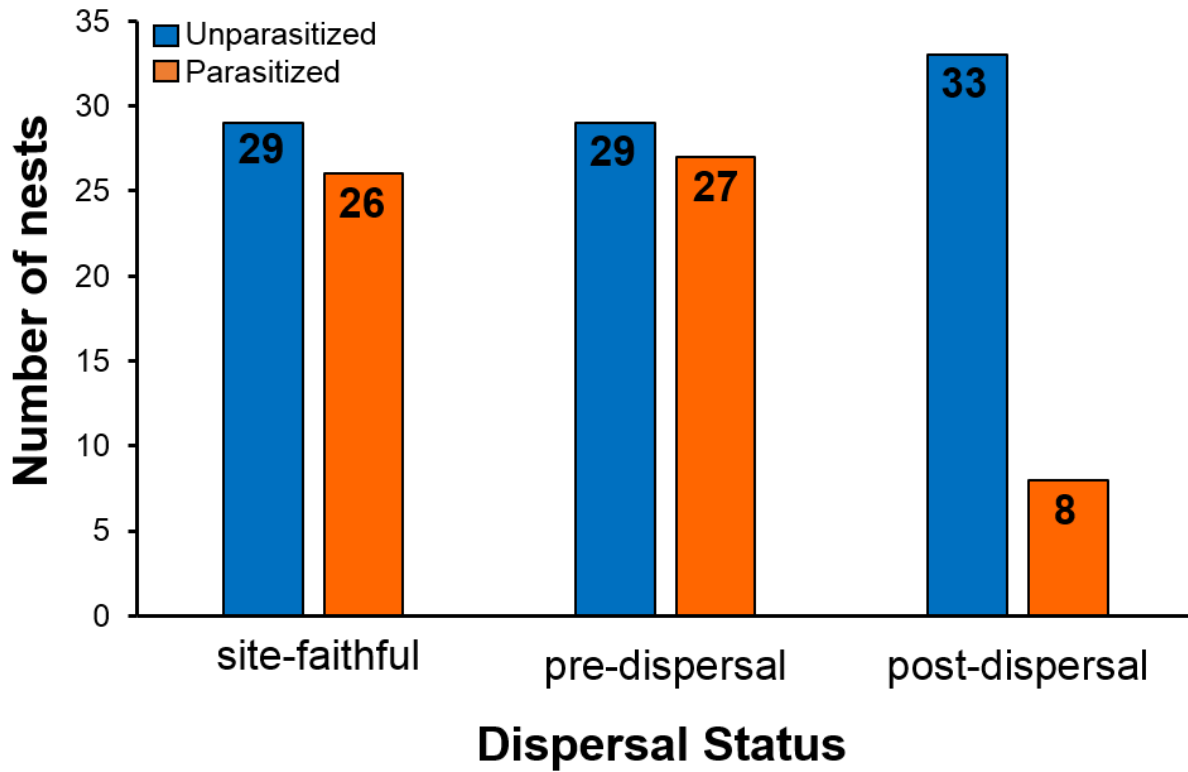
**Figure 2.8: Variation in the mean number of Brown-headed cowbird eggs in nests of site-faithful, pre-dispersal, and post-dispersal nests of Grasshopper Sparrows breeding during the 2014 and 2015 seasons.**
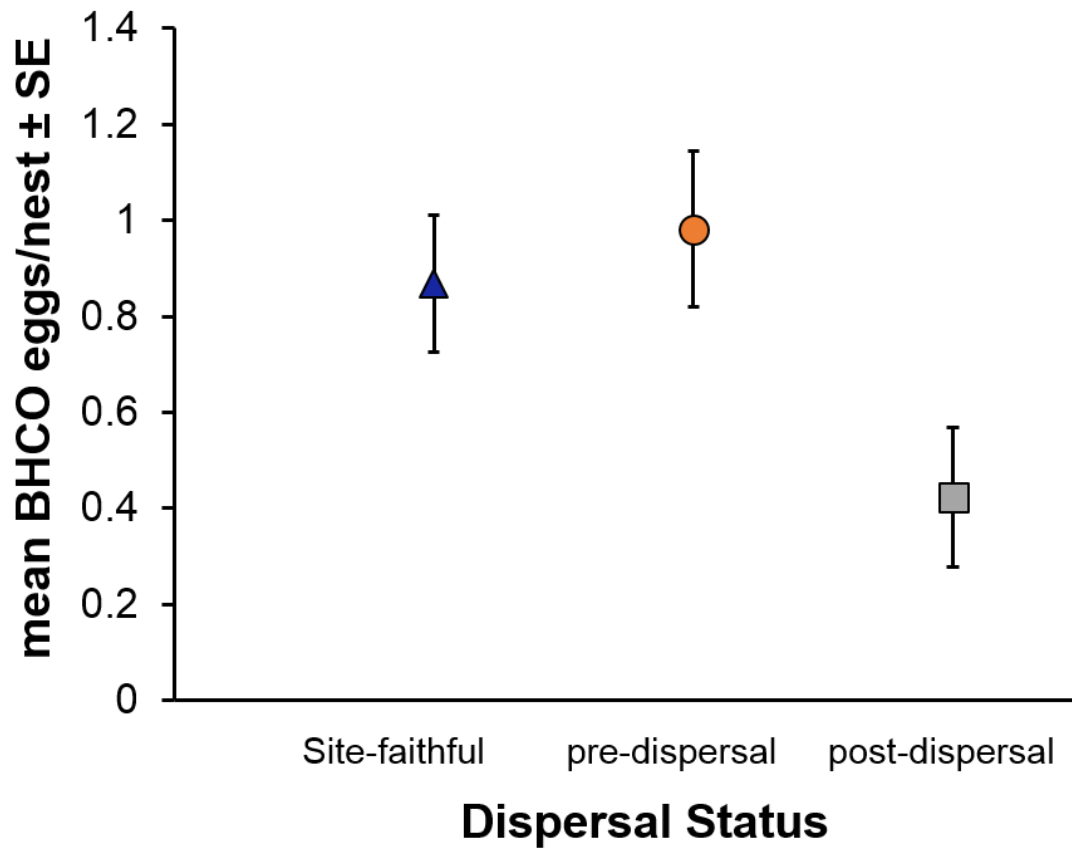
**Figure 2.9: Frequency of nests over the range of nest initiation dates (30-Apr to 30-Jul) for site-faithful, pre-dispersal, and post-dispersal nests. Most site-faithful and pre-dispersal nests occurred before my June 25 cutoff for "early" nests, whereas most post-dispersal nests occurred after June 25 corresponding with "late" nests. Pre-dispersal nests occurring after June 25 include known second nesting attempts prior to dispersal, whereas post-dispersal nests occurring before June 25 include known second nesting attempts following dispersal.**
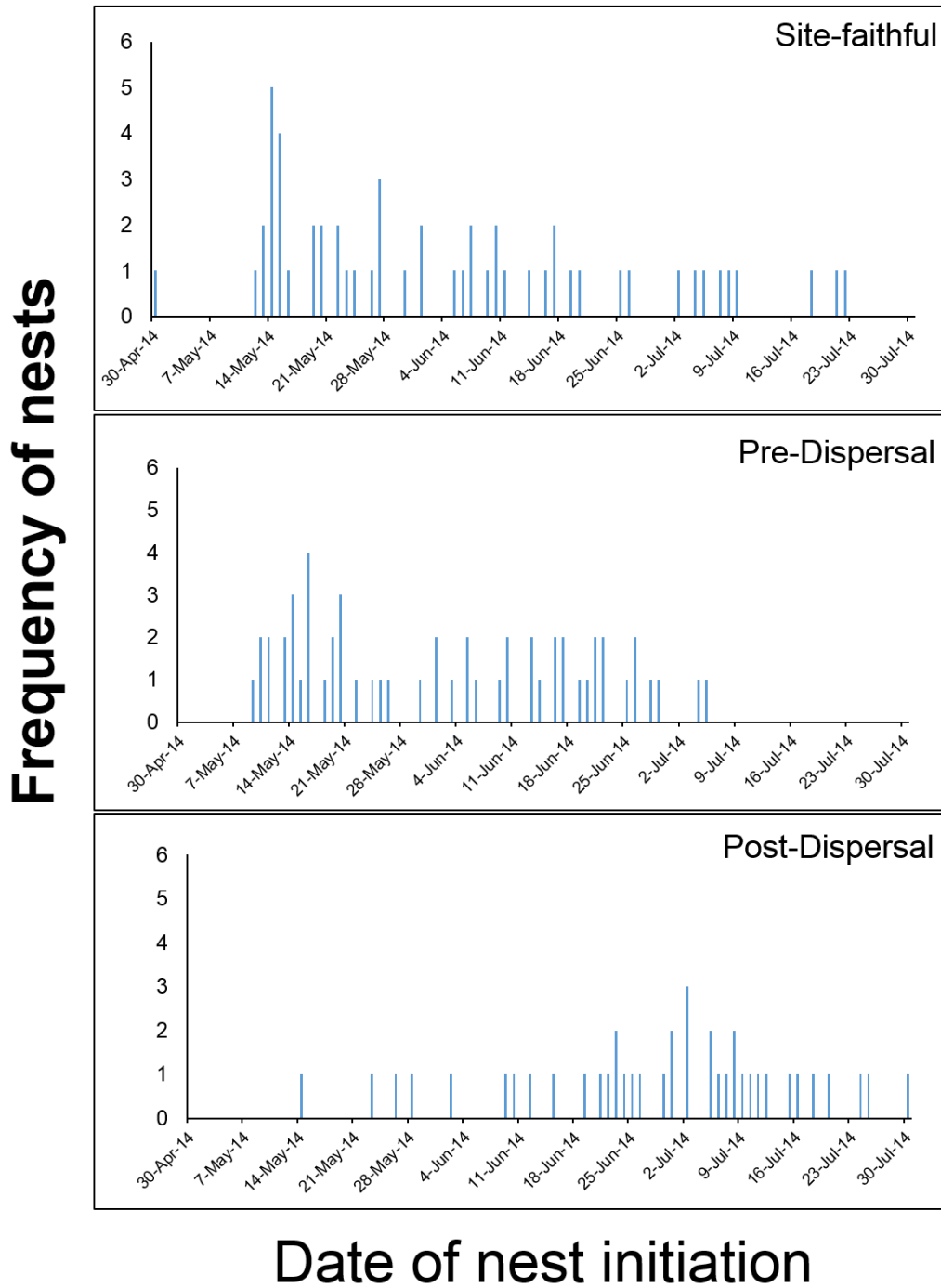
**Table 2.1: Models explaining effects of year (2014–2015); grazing treatment (cattle, bison, ungrazed); and management type (bison, ungrazed, intensive early stocking, and patch-burn grazed) on Grasshopper Sparrow nests ($N$ = 223) at Konza during May–August 2014–2015. Models with ΔAIC values >5 were not included in this table. + signs indicate additive effects; * indicate interactive effects.**

| Model | k[a] | Deviance[b] | AICc[c] | ΔAICc[d] | $w_i$[e] |
|---|---|---|---|---|---|
| Year + Grazing Trt | 5 | 849.6 | 859.7 | 0.0 | 0.484 |
| Year * Grazing Trt | 7 | 847.9 | 862.0 | 2.3 | 0.151 |
| Year * Mgmt Type | 8 | 846.8 | 862.9 | 3.2 | 0.096 |
| Year | 2 | 859.1 | 863.1 | 3.4 | 0.088 |
| Year + Mgmt Type | 5 | 854.3 | 864.3 | 4.7 | 0.047 |

[a] k: the number of parameters used in each model.

[b] Deviance: calculated as -2ln$L$, where $L$ = maximum likelihood expression.

[c] AIC$_c$: Akaike's information criterion adjusted for small sample sizes; calculated as the deviance + 2K + a correction term.

[d] ΔAIC$_c$: difference in the AIC of the next model vs. the best-fit model.

[e] $w_i$: model weight; calculated by the exp(-1/2 *ΔAIC$_c$) divided by the sum of this quantity for all models.

**Table 2.2: Models explaining effects of dispersal status group (site-faithful, pre-dispersal, and post-dispersal nests); year effects (2014–2015); grazing treatment (cattle, bison, ungrazed); management type (bison, ungrazed, intensive early stocking, and patch-burn grazed), and constant survival (Null) on Grasshopper Sparrow nests ($N = 152$) at Konza during May–August 2014–2015. + signs indicate additive effects; * indicate interactive effects.**

| Model | $k^a$ | Deviance[b] | AICc[c] | ΔAICc[d] | $w_i{}^e$ |
|---|---|---|---|---|---|
| Year + Dispersal Status | 4 | 558.9 | 567.0 | 0.0 | 0.735 |
| Dispersal Status | 3 | 564.1 | 570.2 | 3.2 | 0.149 |
| Year*Dispersal Status | 6 | 558.6 | 570.7 | 3.7 | 0.115 |
| Grazing Trt | 3 | 581.6 | 587.6 | 20.6 | 0.000 |
| Year + Grazing Trt | 4 | 580.3 | 588.3 | 21.4 | 0.000 |
| Mgmt Type | 4 | 581.6 | 589.6 | 22.6 | 0.000 |
| Year | 2 | 585.8 | 589.8 | 22.8 | 0.000 |
| Null | 1 | 587.9 | 589.9 | 22.9 | 0.000 |

[a] k: the number of parameters used in each model.
[b] Deviance: calculated as -2ln$L$, where $L$ = maximum likelihood expression.
[c] AICc: Akaike's information criterion adjusted for small sample sizes; calculated as the deviance + 2K + a correction term.
[d] ΔAICc: difference in the AIC of the next model vs. the best-fit model.
[e] $w_i$: model weight; calculated by the exp(-1/2 *ΔAICc) divided by the sum of this quantity for all models.

**Table 2.3: Models explaining effects of dispersal status group (site-faithful, dispersed); nest attempt (first, second); time (linear trend); and constant survival (Null) on Grasshopper Sparrow nests ($N$ =38) of the same individuals at Konza during May–August 2014–2015. + signs indicate additive effects; * indicate interactive effects.**

| Model | $k^a$ | Deviance[b] | AICc[c] | ΔAICc[d] | $w_i$[e] |
|---|---|---|---|---|---|
| Dispersal Status | 2 | 139.9 | 143.9 | 0.0 | 0.468 |
| Nest Order + Dispersal Status | 4 | 139.8 | 145.9 | 2.0 | 0.172 |
| Null | 1 | 144.0 | 146.0 | 2.1 | 0.166 |
| Nest Order | 2 | 143.7 | 147.7 | 3.8 | 0.070 |
| Linear Trend | 2 | 143.9 | 148.0 | 4.0 | 0.062 |
| Nest Order * Dispersal Status | 4 | 139.8 | 148.0 | 4.1 | 0.062 |

[a] k: the number of parameters used in each model.
[b] Deviance: calculated as -2ln$L$, where $L$ = maximum likelihood expression.
[c] $AIC_c$: Akaike's information criterion adjusted for small sample sizes; calculated as the deviance + 2K + a correction term.
[d] $\Delta AIC_c$: difference in the AIC of the next model vs. the best-fit model.
[e] $w_i$: model weight; calculated by the exp(-1/2 *$\Delta AIC_c$) divided by the sum of this quantity for all models.

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# Chapter 3 - Do changes in food availability explain settlement following within-season breeding dispersal?

## Introduction

A major goal of evolutionary ecology is to understand the selective pressures that shape habitat selection in animals. Habitat selection is critically important in shaping species' distributions and influencing population dynamics (Pulliam and Danielson 1991). Determining what shapes habitat selection over an animal's annual life cycle is also integral to making informed habitat conservation and management decisions, as habitat requirements can change across spatial scales and over different life stages.

Habitat selection is a complex decision-making process that inherently involves tradeoffs between costs and benefits (Pulliam and Danielson 1991, Gaillard et al. 2010, Marchand et al. 2015). Animals must select habitat containing all of the requirements that fulfill their needs and that of their young (Hall et al. 1997). Often, selection means balancing the potential fitness benefits with the energetic costs of acquisition of quality territories, mates, food, and shelter, while mitigating potential predation risk, and coping with the presence of conspecifics and other competitors (Rosenzweig 1985). Habitat selection for sessile organisms represents a single decision that must fulfill survival, growth, and reproductive demands of an entire lifetime. Mobile animals that have discrete breeding and non-breeding ranges, on the other hand, make at least two habitat selection decisions; animals must choose an area to raise young, and an area to spend the winter. For animals that also exhibit high rates of breeding dispersal, an individual can make multiple habitat selection decisions that are fine-tuned according to past experience and current information (Cody 1985).

Some of the most mobile animals are migratory birds, particularly multi-brooded species which display high rates of between-year and within-year breeding dispersal (Weatherhead and Boak 1986, Catlin and Rosenberg 2008, Gruebler et al. 2015). For these species, habitat selection is a dynamic, ongoing process, as individuals make multiple habitat choices within a single year. Much of the avian habitat selection literature focuses on breeding habitat selection (Doligez 2002, Zanettte et al. 2011, Chalfoun and Martin 2007, Chalfoun and Schmidt 2012). Tests of the factors that characterize habitat selection usually reflect measurements made at one time during the breeding cycle. For birds that display high rates of site-fidelity, habitat selection decisions may be more static, and thus, one-time measurements may be appropriate. In contrast, birds that display high rates of within-season breeding dispersal make habitat selection decisions that are extremely labile, being able to continually modify where to select habitat in response to changes on the landscape or to changes in energetic demand. Highly dispersive individuals thus present an opportunity to study changes in habitat selection that occur on short time scales. Understanding what shapes habitat selection at the time birds make within-season choices will provide better information about the factors underlying habitat choices, and will lead to improved assessments of habitat quality for the conservation of natural populations.

Hypotheses explaining habitat selection in birds relate to habitat preferences that are thought to be shaped by the direct fitness consequences of choosing particular habitats (Orians and Wittenberger 1991, Martin 1998). Habitat choices usually relate to predation and food availability, such that birds select areas with refugia from predators and access to critical food resources (Martin 1995, 1998, Rotenberry and Wiens 1998, Zanette et al. 2014). Low risk and food-rich habitats thus allow individuals to rear high quality young that are likely to survive past fledging (Clinchy et al. 2004, Zanette et al. 2011, 2013). Most habitat selection studies

investigate patch, nest-site, or territory choice by measuring vegetative characteristics (e.g., use vs. availability metrics), or assess nest predation risk via behavioral changes and manipulation of nest-site habitat variables (e.g., visual obstruction, shrub cover/density, nest height, etc.; Johnson 1980, Cody 1981, Marzluff 1988, Hoover 2003, Kearns and Rodewald 2013, Dittmar et al. 2014). For example, birds can select subsequent nest-sites with greater shrub density and visual obstruction following predation of a previous nest (Betts et al. 2008, Chalfoun and Martin 2010, Kearns and Rodewald 2013). If *a priori* knowledge of the predator exists, an individual may choose habitat at greater distances from an unsuccessful nest to disperse outside the home range of the predator (Powell and Frasch 2000).

Many habitat selection studies neglect to recognize that the combination of predation and food supply are the determinants of habitat suitability, and it is this tradeoff between predation risk and energetic demand that determines fitness (Fretwell and Lucas 1969). The role of local food availability in affecting habitat patch use and selection is not well understood (but see McCabe 2015). Studies that do consider food availability, however, often use indirect correlates of habitat quality–such as clutch size, nestling size, or parental condition–without providing direct estimates of food availability (Korpimaki 1993, Betts et al. 2008, Chalfoun and Martin 2010, Gruebler et al. 2015). Although assessing vegetative characteristics and predation risk are crucial elements of habitat selection, birds often select habitats where foraging opportunities are greater, even at heightened predation risk (Metcalfe and Furness 1984, Pomeroy et al. 2008, McCabe and Olsen 2015). Thus, food may be an even more critical factor influencing habitat selection than avoiding predation risk. Indeed, food is thought to be a major driver in why birds select habitat, and in shaping bird movements generally (Lack 1968, Levey and Stiles 1992, Johnson and Sherry 2001).

Food may be an important consideration in spatially and temporally variable environments, such as grasslands. Grasslands experience high inter-annual variability in growing season rainfall and temperature that affects plant structure and composition (Knapp and Smith 2001). Coupled with climate, grazing and fire create dynamic landscapes that cause seasonal variation in food availability. Insect abundances and community assemblages respond strongly to the interactive effects of grazing and burning (Joern 2004, 2005, Jonas and Joern 2007, Joern and Laws 2013). One way in which birds adjust their habitat selection decisions in response to shifts in food availability is to engage in within-season dispersal. Some birds disperse to exploit seasonal peaks (e.g., insect outbreaks) or disperse to areas of higher food abundance to track changes in food resources (Sinclair 1978, Bucher 1982, Newton 2000).

The grassland-obligate songbird, the Grasshopper Sparrow (*Ammodramus savannarum*), is an ideal species in which to test alternative hypotheses explaining changes in habitat selection, as they breed in grasslands where prey abundance varies in response to disturbance regimes (Kaspari and Joern 1993, Joern and Laws 2013). Grasshopper Sparrows are highly mobile, displaying extreme variation in within-season breeding dispersal (Chapter 1). In mid-continental grasslands, at least 30–50% of territorial males disperse within-season (Chapter 1). Between years, population-level return rates range from 35-80% in the East, to 0% in western Nebraska (Crossman 1989, Delany et al. 1995, Vickery 1996, Gill et al. 2006, Jones et al. 2007, Soha et al. 2009). With the spatio-temporal variability of grasslands in combination with a high capacity for dispersal, Grasshopper Sparrows present an opportunity to test predictions that explain how changes in food availability affect habitat settlement decisions following dispersal. Despite the importance of predation and available nesting substrate in shaping habitat selection, it is probable that food availability is most important in shaping settlement decisions. Grasshoppers constitute

~70% of Grasshopper Sparrow diet (Joern 1986, Kaspari and Joern 1993, Vickery 1996), and thus, are a major factor in determining food availability for sparrows. Grasshopper abundance, diversity, and community assemblages vary according to timing of burning and presence of grazers (Jonas and Joern 2007). Hence, changes in local food abundance may influence within-season habitat selection decisions for Grasshopper Sparrows.

I tested the hypothesis that food abundance explains settlement decisions following within-season breeding dispersal of a grassland songbird. I studied a population of Grasshopper Sparrows breeding in tallgrass prairie of the Flint Hills region of eastern Kansas, and monitored territory establishment and movements over three breeding seasons. To directly measure spatial and temporal variation in food availability, I collected sweep samples three times over the breeding season. I measured food intake rates of Grasshopper Sparrows using plasma lipid metabolites (Jenni-Eiermann and Jenni 1992, Gerson and Guglielmo 2013). A fundamental assumption of the food availability hypothesis is that food indeed changes across the breeding season. To verify that this was true, I predicted that food abundance would vary throughout the season and in response to burning and grazing. If food does vary, I made several predictions at the population and individual levels. If food availability determines post-dispersal habitat selection, then (1) Grasshopper Sparrow densities would be positively associated with food intake rates; (2) Grasshopper Sparrow densities would be positively associated with food availability at any given time within the season; (3) food abundances would be greater at a bird's second territory compared to its first at the time of dispersal, and (4) food intake rates would increase from first to second territories.

# Methods

## Study species and study site

The Grasshopper Sparrow is a small (~17 g) songbird distributed from southern Canada throughout much of the USA, Mexico, and Caribbean, to parts of Central and South America (Vickery 1996). In tallgrass prairie, Grasshopper Sparrows are most abundant in areas managed on a fire interval of every 2–3 years with low-intensity cattle grazing (Powell 2008). Burning every 2–3 years allows intermediate levels of dead grass to accumulate for Grasshopper Sparrows to use as nesting cover and material, and cattle grazing produces bare patches of ground that they use for foraging (Powell 2008). Grasshopper Sparrows consume mainly arthropods during the breeding season (~70% invertebrates), preferring grasshoppers (Orthoptera), Arachnids, beetles (Coleoptera), and caterpillars (Lepidoptera) (Joern 1988). Over a third of the arthropod component of their diet consists of grasshopper species in the family Acrididae (Kaspari and Joern 1993). Adult Grasshopper Sparrows also consume 30% seeds during the breeding season, but feed only arthropods to nestlings (Kaspari and Joern 1993).

Grasshopper Sparrows arrive in Kansas during mid-March with an earliest arrival date of 21 March (Zimmerman 1993). Males usually arrive ~5 days before females and establish territories soon after arrival (Vickery 1996). Pairs form in late April/early May, and clutch initiation begins soon after (Vickery 1996). Grasshopper Sparrows can produce two or more broods per year, and each breeding attempt takes approximately 24 days (Vickery 1996). Two to four weeks post-fledging, young typically disperse away from natal territories (Vickery 1996). Timing of fall migration is poorly known, but most birds in the Flint Hills have departed by late September (Williams and Boyle, pers. obs.).

I studied Grasshopper Sparrows between April–August in 2013–2015 in the Flint Hills of eastern Kansas. I studied sparrows at Konza Prairie Biological Station (Fig. 3.1), a 3,487-ha tract of tallgrass prairie co-owned by Kansas State University and The Nature Conservancy. Konza has been part of the Long-Term Ecological Research network since 1981 and is divided into replicated watershed units that are experimentally managed with fire and grazing (Knapp 1998). Core treatments include year-long bison grazing or no grazing, and prescribed fires occur on an annual to every two, four, or 20-year interval. Six additional watersheds within Konza are patch-burn grazed in two replicate sets, managed with a three-year rotational burn regime in combination with warm-season cattle (cow/calf pairs) grazing (Fuhlendorf and Engle 2001). I also studied sparrows at the Rannell's Flint Hills Prairie Preserve, a 1,175-ha tract of tallgrass prairie owned by Kansas State University, located adjacent to Konza (Fig. 3.1). The Rannell's Preserve includes pastures managed under an "intensive early stocking" regime consisting of late April burning and double-stocking of steers from April to July (Owensby et al. 2008). I studied sparrows at the Rannell's Preserve to include intensive early stocking, as this rangeland management scheme is not represented at the Konza Prairie. I studied Grasshopper Sparrows in 18 experimental units in replicated combinations of (a) annual bison grazing or no grazing (e.g., bison, ungrazed), and (b) annual spring burns or two-year burns, or (c) intensive early stocking and (d) patch-burn grazing. I randomly-located a 10-ha plot within each unit >20 m from any road or fence line (see Fig. 3.1 for plots and unit names). I consider my study site to be the Konza Prairie Biological Station and the Rannell's Preserve, collectively, and hereafter, refer to it as "Konza."

Climatic conditions at Konza are characteristic of eastern tallgrass prairie, with mean annual precipitation of 835 mm and high inter-annual variability in rainfall (CV=25%) and plant

productivity (Knapp 1998, Knapp and Smith 2001). Over 75% of annual precipitation falls during the April-September growing season, and determines relative biomass and flowering of dominant grasses and forbs within-season (Nippert et al. 2006, Raynor et al. 2015).

**Individual capture, re-sighting, territory surveys, and radio-telemetry**

I captured males in mist-nets starting in late April until mid-August. I placed nets near primary song perches within territories, and attracted males to nets by using song playbacks. I placed a numbered USGS band and unique combinations of three colored leg bands on each individual to identify them for re-sighting. I sexed birds by the presence of cloacal protuberances (males) and took standard morphometric measurements. As female Grasshopper Sparrows are cryptic, do not sing, spend most of their time on the ground (Vickery 1996), and usually only detected if I found their nests, I did not include females in my estimates of density, food intake rates, or individual movements. To monitor the movements of individuals and dispersal distances, I conducted color band re-sighting every week (mean = 8.4 days, SD = 3.1, range = 6-17 days) and opportunistically each day within watersheds, recording the location of territorial individuals with hand-held GPS units (Garmin, Olathe, KS).

To determine spatial and temporal variation in densities of Grasshopper Sparrows, I mapped territories of all individuals every week (mean = 8.4 days, SD = 3.1, range = 6–17 days) within each 10-ha plot. I divided the season into early, mid, and late time periods. Within each time period I conducted three to five surveys. Dates of each time period varied slightly among years due to differences in the timing of field efforts, but fell between 3 May –1 June for early season, 2 June and 5 July for mid-season, and 6 July to 3 August for late season (Fig. 1.2, Chapter 1). I calculated density in each time period as the mean number of unique territorial males within each 10-ha plot. I also searched for unmarked and banded individuals within each

watershed, mapping territory locations using aerial imagery and marking 1-8 territory locations with GPS. I considered males to be territorial if they engaged in behavior such as singing, performing perched wing displays or sustained flutter-flights, or initiated aggressive interactions (e.g., chases, actual fighting) with other males (Vickery 1996). I considered males to be mated when they sang the "warble" song associated with pair-bond formation, or when I observed males interacting non-aggressively with another non-singing bird that I presumed to be female (Vickery 1996).

To monitor dispersal movements and distances, I used radio-telemetry in combination with color band re-sighting. I fit males with radio-transmitters using the figure-eight style leg harness (Rappole and Tipton 1991). In 2014, I fit males with 0.5g BD-2 VHF radio-transmitters (Holohil Systems Ltd., Carp, ON, Canada) and in 2015, I used 0.56g PicoPip Ag376 VHF radio-transmitters (Lotek Wireless, Newmarket, ON, Canada) that transmitted over longer distances (0.8 km in 2014 vs. 1.6 km in 2015). Both transmitter types and harnesses together (0.7 g) weighed an average of 4% of body mass (mean = 17.40 g, SE = 0.16 of male Grasshopper Sparrows fit with transmitters). I was confident that transmitters would not induce considerable stress to Grasshopper Sparrows, as there were no measurable negative effects of transmitters for similarly-sized species (Rae et al. 2009, Streby et al. 2013).

My objective with radio-telemetry was to establish when and where individuals dispersed rather than to collect detailed movement data. Thus, I located each focal individual every other day between 06:00 to 18:00. I followed movements using a 3-element folding Yagi and portable handheld radio receivers (R-1000, Communications Specialists; Biotracker Receiver, Lotek Wireless) and recorded bird locations using GPS. When I could not relocate birds, I searched ~ 42 hours per bird over a two–week period (~6 hrs/day every two days) on foot and using a car-

mounted omni directional antenna. I systematically searched a $\geq$ 5 km radius from the last location the individual was seen previously, and also searched opportunistically during territory surveys. I assumed radio-tagged birds dispersed if I could not relocate them following these search methods. Although I was unable to rule out the possibility that some of these birds died, I later refound most of the lost birds ($n = 7/10$), suggesting that most birds that disappeared did indeed disperse beyond my search radius.

## Blood sampling and processing

Plasma lipid metabolites (i.e., triglyceride concentration; hereafter, TRIG) provide an intrinsic measure of foraging rates and fat deposition. High concentration of triglycerides indicate high food intake rates, and thus a large fuel supply (Jenni-Eiermann and Jenni 1992). To test predictions based on food intake rates, I blood-sampled males within five minutes of capture (Guglielmo et al. 2002). For dispersers, I attempted to recapture males to compare estimates of food intake rates between first and second territories. I collected a <100 µl blood sample from the brachial vein in heparinized capillary tubes and stored them on ice, centrifuging them within 6–8 hours. I stored plasma at –80°C prior to metabolite analysis. I followed the TRIG assay protocols of Guglielmo et al. (2002) using a colorimetric endpoint assay (Sigma reagent A (F6426) and reagent B (T2449), and glycerol standard G7793) run on an Eon microplate spectrophotometer (Biotek Instruments, Inc.). I diluted plasma 1:1 with saline and ran assays using 5 µl diluted plasma and 240 µl and 60 µl of reagents A and B warmed to 37°C with absorbance measured at 540 and 750 nm. I analyzed residual TRIG after accounting for fat score and capture time, because both affect TRIG (Hays 2008).

**Arthropod sampling and processing**

To determine the spatial and temporal patterns of food availability, I collected sweep samples in the last two weeks of each month during May–July 2014. Although sweep sampling is not a perfect method for sampling all invertebrates present, it serves as an effective method for sampling larger insect prey (>30 mm) at higher rates than other methods (Doxon et al. 2011). As I was interested in relative abundances of arthropods, and Grasshopper Sparrows preferentially seek invertebrate prey of intermediate (15-40 mm) and larger size classes (>45m; Kaspari and Joern 1993), sweep sampling was a more appropriate method for assessing prey availability. Further, my sweep samples often contained numerous (>100s) individuals <5 mm, so I was confident that my sampling technique was an effective measure of the variation in food resources meaningful for Grasshopper Sparrows.

I sampled arthropod prey along three 80 m transects from randomly-located points within suitable grassland habitat in each watershed. One transect was located within each 10 ha plot, and two were located elsewhere in the watershed. Transect area was 150 m$^2$ (80 m x 1.88 m sweep width). I located transects ≥100 m from any other transect. I used a heavy duty sweep net (Bioquip®; 46 cm diameter, 91.5 cm handle), sweeping across the top of herbaceous plants and sparsely vegetated areas, where Grasshopper Sparrows typically forage.  I conducted 200 sweeps along each 80 m transect, and emptied the contents into plastic ziplock bags. I stored samples on ice in the field, and froze at –80°C. I followed Konza LTER insect netting protocols (CGR01 Dataset, KNZ LTER; Joern 1981), sampling between 09:00–15:00 on calm days (wind ≤ 15mph) when cloud cover was ≤50%, and ambient temperature was between 25–40°C.

I carefully separated debris from arthropods, measured potential prey items to the nearest 5 mm, counted all individuals, and identified arthropods to order. I estimated arthropod

abundance based on the orders known to be important food for Grasshopper Sparrows. I calculated "edible mass" by weighing all Orthoptera, Hemiptera, Lepidoptera, Coleoptera, and Arachnids together (Joern 1988). I averaged across transects (three per watershed) for each sampling period (May, June, July) to obtain a measure of food availability for each watershed over the breeding season. I $\log_{10}$-transformed edible mass values to satisfy assumptions of normality. As results were similar using mass or $n$ arthropods, I proceeded with analyses using mass. Hereafter, I refer to "edible mass" estimates as prey abundance.

**Food variability analyses**

I first examined spatial and temporal patterns in food abundance by testing the effects of grazing treatment (cattle, bison, ungrazed), burning treatment (years since burn: 0, 1, 2), management regime (bison, ungrazed, intensive early stocking, and patch-burn grazed), and time period within the breeding season (early, mid, and late). I analyzed additive and interactive relationships between food abundance and time and treatment effects by multiple linear regression (for continuous explanatory variables) and analysis of covariance (ANCOVA; for categorical and continuous explanatory variables) using JMP statistical software (SAS Institute, Inc., 2009).

I tested predictions at the population and individual levels. At the population level, I assessed relationships between prey abundance, food intake rates (i.e., TRIG), and seasonal densities of Grasshopper Sparrows using linear regression. To determine whether birds moved to areas of higher food availability, I related watershed-level changes in density to food abundance. I also examined patterns of food intake rates in relation to year effects, and management and seasonal effects as described previously for analyses of food abundance.

At an individual level, I assessed the relationships between food intake rates and food abundance for birds that dispersed. For individuals with 2 TRIG samples, both for dispersers (between first and second territories) and site-faithful sparrows, I calculated the difference in TRIG using a paired sample $t$ test. I then compared estimates between dispersers and site-faithful individuals using a Student's $t$ test. Because TRIG increased over each season ($F_{1, 550} = 6.0$, $P = 0.014$), I controlled for capture date when comparing TRIG estimates for the same individual. To compare food abundance between first and second territories, I calculated the difference in prey abundance between first and subsequent locations an individual held a territory at the time of dispersal, using a Student's $t$ test. For example, if a Grasshopper Sparrow was initially captured in one location and subsequently dispersed to a new location, I calculated the difference in prey abundance estimates for each watershed the bird held a territory at the time of dispersal. Hence, if a Grasshopper Sparrow dispersed but remained within the same watershed, the difference between prey abundance estimates would be zero. Likewise, if a Grasshopper Sparrow dispersed to a watershed with higher food abundance than where it dispersed from, the difference between prey abundance estimates would be positive.

## Results

I captured and color-banded 779 adults (647 males, 132 females). From both re-sighting and radio-telemetry, I detected within-season dispersal movements for 220 birds (28.2%; 213 males, 7 females). Dispersal distances ranged widely (101–8940 m, 695 ± 54 m; median = 197 m). I deployed radio-transmitters on 9 males in 2014 and 10 males in 2015. Nine of the radio-tagged birds dispersed to new territories 120 to 1229 m from initial territories (mean = 491, SE = 17.6 m). I collected 162 sweep samples in 2014, and determined triglyceride concentration of 551 blood samples in 2013–2015.

Prey abundance varied spatially and temporally over the breeding season. Prey abundance increased over the season ($F_{2, 53} = 60.0$, $P < 0.001$; Fig. 3.2) and tended to be highest on watersheds burned in the current year ($F_{2, 53} = 2.9$, $P = 0.065$). The relationship between prey abundance and burning treatment depended upon time of season (years since burn*time period: $F_{4, 53} = 3.2$, $P = 0.024$; Fig. 3.4), with burned watersheds experiencing the greatest increases in prey abundance over the season (Fig. 3.4). Prey abundances did not differ by grazing regime ($F_{2, 53} = 0.2$, $P = 0.841$). The relationship between prey abundance and grazing was related to time of season (grazing treatment*time period:  $F_{4, 53} = 2.9$, $P = 0.038$; Fig. 3.4). Prey abundances among management types did not differ ($F_{3, 53} = 0.4$, $P = 0.761$; Fig. 3.3). The association between prey abundance and management regime was related to time of season (management type*time period: $F_{6, 53} = 5.5$, $P < 0.001$; Fig. 3.4). Some ungrazed watersheds had more than ~5 times greater prey abundance than patch-burn grazed watersheds during late season (Fig. 3.4).

Prey abundance was not associated with densities of Grasshopper Sparrows ($F_{1, 53} = 0.5$, $P = 0.479$; Fig. 3.5). The relationship between prey abundance and densities of Grasshopper Sparrows was not dependent upon the time of season (prey abundance*time period: $F_{2, 53} = 0.1$, $P = 0.728$). Seasonal changes in densities of Grasshopper Sparrows were not related to prey abundance between early and mid-season ($F_{1, 17} = 0.4$, $P = 0.535$), or between mid- and late season ($F_{1, 18} = 0.2$, $P = 0. 677$; Fig. 3.7). Restricting my analyses to only the plots that Grasshopper Sparrows occupied, prey abundance and densities of Grasshopper Sparrows were unrelated ($F_{1, 35} = 0.1$, $P = 0.762$; Fig. 3.6). Additionally, the relationship between prey abundance and densities of Grasshopper Sparrows did not depend upon time of season (prey abundance*time period: $F_{2, 35} = 1.2$, $P = 0.339$). Prey abundance was positively associated with TRIG ($F_{1, 184} = 4.0$, $P = 0.046$; Fig. 3.8) indicating that my metrics of food availability reflect an

association between food abundance and foraging rates; when food is more abundant on the landscape, birds respond by consuming more.

After accounting for capture time and fat score, TRIG differed among years ($F_{2, 536} = 61.4$, $P < 0.001$), with 2015 values being substantially higher than either 2013 or 2014 (Tukey's HSD, $P < 0.001$); therefore, I included year in subsequent analyses. TRIG tended to increase over the season ($F_{2, 536} = 2.8$, $P = 0.056$), but did not differ by the number of years since watersheds were burned ($F_{2, 536} = 2.2$, $P = 0.109$). The relationship between TRIG and burning treatment depended upon time of season (years since burn*time period: $F_{4, 536} = 2.4$, $P = 0.046$), with seasonal increases in TRIG in unburned watersheds (Fig. 3.9). TRIG did not differ by grazing regime ($F_{2, 536} = 1.9$, $P = 0.152$). The relationship between TRIG and grazing was not related to time of season (grazing treatment*time period: $F_{4, 536} = 1.1$, $P = 0.347$; Fig. 3.9). TRIG did not differ among management regimes ($F_{3, 536} = 2.0$, $P = 0.106$). The relationship between TRIG and management regime was related to time of season (management type*time period: $F_{5, 536} = 2.6$, $P = 0.018$; Fig. 3.9), with seasonal increases in TRIG in patch-burn grazed watersheds. TRIG tended to decline with increases in densities of Grasshopper Sparrows ($F_{1, 536} = 3.4$, $P = 0.067$). The relationship between TRIG and densities of Grasshopper Sparrows depended on time of season ($F_{2, 536} = 8.7$, $P = 0.0002$), with TRIG declining with density during early and late season, but increasing during mid-season (Fig. 3.10, panels A-C).

After controlling for seasonal increases in TRIG, food intake rates were no different at first and second territories (Paired $t$ test, $P = 0.867$, $N = 15$ dispersers). The change in TRIG from first and second estimates was no different between dispersed and site-faithful birds ($F_{1, 25} = 0.01$, $P = 0.924$; $N = 15$ dispersers, 11 non-dispersers). I then compared prey abundance estimates between successive locations at the time an individual dispersed. I found that the mean change in

prey abundance between first and second locations was positive for dispersed birds (increase of 0.50 g/150 m$^2$, $N = 40$ dispersers) indicating that individuals select areas with higher food abundance following dispersal.

## Discussion

The seasonal and spatial patterns of food abundance, food intake rates, and Grasshopper Sparrows densities suggest that food is not the most important factor in shaping settlement decisions following within-season breeding dispersal. Somewhat surprisingly, my results do not support one of the dominant hypotheses for why birds select habitat. Evidence suggests that patterns of food abundance alone appear to be insufficient in explaining within-season settlement choices in Grasshopper Sparrows. My results suggest that further study into the factors that shape dynamic habitat selection will benefit from empirical tests of alternative hypotheses based upon predation risk, nest parasitism risk, and nest microhabitat.

Contrary to prediction, Grasshopper Sparrows did not locate territories in areas with an abundance of food or where they could maintain high fueling rates. My results are not consistent with the hypothesis that food abundance explains settlement decisions following within-season breeding dispersal. Food abundance and Grasshopper Sparrow densities were unrelated to food abundance; however, mid-season increases in density in two plots occurred in plots with high relative food availability mid-season (Fig. 3.7). This corroborates the mid-season positive trend between triglyceride concentration and density (Fig. 3.10, panel B). As I was interested in explaining variation in food availability, fueling rates, and Grasshopper Sparrows densities at the plot-level, I did not control for individual-level watershed effects in my analyses. However, when I controlled for watershed effects, the mid-season positive trend between densities of Grasshopper Sparrows and food intake rates was effectively removed ($F_{1, 138} = 2.8$, $P = 0.098$),

and watershed-level effects explained most of the variation in the model ($F_{15, 138} = 37.1$, $P <$ 0.001). The positive mid-season pattern is driven by seasonal changes in densities of Grasshopper Sparrows within the intensive early stocked watersheds. Intensive early stocked areas were the only watersheds that increased in density over the breeding season (Fig. 3.4, 3.6). As intensive early stocked watersheds are burned in April, birds do not settle there early because fire burns vegetation used as nesting substrate (Chapter 1). Lower densities in spring-burned watersheds is consistent among years, regardless of management regime (Chapter 1), suggesting that birds avoid recently burned areas, probably because they are not suitable for nesting. However, as the season progressed, densities of Grasshopper Sparrow increased dramatically within intensive early stocked watersheds, as nesting substrate and food increased. Thus, the effect of fire on prey abundance and low, early season densities of Grasshopper Sparrows is what best explains the mid-season positive relationship between densities and fueling rates, rather than birds tracking shifting food availability over the season. Patch-burn grazed watersheds had high densities of Grasshopper Sparrows in all years (Chapter 1). Unlike intensive early stocked watersheds, patch-burn grazed watersheds experienced relatively little change in densities of territorial Grasshopper Sparrows (Fig. 3.7).

At the individual level, my results are somewhat consistent with the food availability hypothesis; individuals settle in areas of higher relative prey availability following dispersal. However, food intake rates did not increase following dispersal. Additionally, food intake rates between birds that dispersed and birds that remained on territory were no different. Thus, although birds may disperse to areas of higher food availability, birds do not respond by increasing their foraging rates.

Temporal and spatial variation in food resources is one of the main determinants of habitat quality, and thus, a large literature has suggested that food is a critical factor in avian movements and habitat selection (Lack 1968, Levey and Stiles 1992, Johnson and Sherry 2001). Unexpectedly, my results provided direct and indirect evidence that food does not play a major role in shaping habitat selection in a grassland songbird. Grasshopper Sparrows may typify grassland-dependent birds of North America and elsewhere in the world. Although largely anecdotal evidence for within-season movement exists for North American grassland birds (Herkert et al. 2001, Herkert et al. 2002, Hobson and Robbins 2009, Robbins 2015), farmland birds in Europe display individual variation in within-season breeding dispersal behavior (Greig-Smith 1982, Dale et al. 2006, Gilroy et al. 2010, Brambilla et al. 2012, Gruebler et al. 2015). Most studies on European farmland birds examine patch-specific structural and vegetative attributes to explain within-season shifts in habitat selection, but many suggest that birds move to areas of higher habitat quality (Gilroy et al. 2010, Brambilla et al. 2012). Direct empirical evidence for the role of food in shaping within-season settlement is lacking, however. Evidence for within-season movement in Old World birds, in combination with the results presented here, suggest that within-season breeding dispersal is a common behavioral strategy of birds living in grasslands. Alternative ecological processes such as variation in predation risk and nest microhabitat could act alone or interact with food availability to explain within-season habitat selection decisions in variable landscapes.

It is important to note that my estimates of food abundance represent the standing crop, rather than production rates of prey availability. If Grasshopper Sparrows are not depressing arthropod densities, then my estimates of relative food abundance provide a reasonable index of relative prey availability. However, if birds do significantly reduce prey populations, then my

estimates may not accurately reflect prey availability, because I am only measuring what is leftover following foraging by birds. Compounding this potential problem is the fact that the territories of other grassland songbirds such as Eastern Meadowlarks (*Sturnella magna*) and Dickcissels (*Spiza americana*), overlap those of Grasshopper Sparrows, and all three species consume similar prey (Kaspari and Joern 1993, Temple 2002). As I did not assess foraging rates for these other species, it would be difficult to test whether these birds collectively suppress arthropod abundance. Despite these potential issues, my sweep samples likely still represent relative prey availability, as spatial and temporal variation in prey abundance was clearly evident; if birds were actually depressing prey populations, we should see little pattern to my data. Furthermore, from the perspective of an individual bird making within-season movement decisions, standing crop is probably most important, especially in areas occupied by other conspecifics. Additionally, my estimates of arthropod abundance are consistent with patterns of arthropod abundance found at Konza (Joern 2004, 2005, Jonas and Joern 2007). Although my estimates of prey availability only represent one year of data, the patterns I found are consistent with arthropod patterns in response to fire and grazing over longer time scales (CGR02 Dataset, KNZ LTER; April 1982 – Present).

Collectively, the results of this study provide strong evidence that food abundance does not shape within-season habitat selection decisions. Food may not be an important consideration for Grasshopper Sparrows as variation in food resources may not be a limiting factor in grasslands. Food may be limiting during periods of high energetic demand (e.g., nestling period, molt prior to fall departure, etc.) at relatively small local scales, but may not be limiting overall throughout the breeding cycle. Grasshopper Sparrows can depress prey populations by up to 25% (Joern 1986, Kaspari and Joern 1993), but reductions occurred during the post-fledging

period, when juvenile birds need to maximize fat deposition and overall mass quickly (Phillips and Hamer 1999). Wiens's (1974) hypothesis that prey availability is "superabundant" in grassland ecosystems may indeed be true, such that abundance of prey items could exceed consumer demands (Bourliere and Hadley 1970, Wiens 1974).

Similar to seasonal variability in food resources, another factor shaping habitat selection is the relative proximity of foraging substrate to nesting substrate. Birds could be cuing into microhabitat-scale vegetative characteristics that satisfy both nesting and foraging needs. Microhabitat-scale vegetative characteristics that include tall dead grass for nesting materials and cover would satisfy nesting needs, while having bare patches of ground to seek arthropod prey would satisfy foraging needs. So while it is not the food itself that is important, it is vegetative structural characteristics that make it easier to find food while nesting nearby, that may be more important in selecting breeding habitat. Under this hypothesis, I would expect greater densities of Grasshopper Sparrows in patch-burn grazed watersheds, which fulfill both foraging and nesting needs (Powell 2008). My results are consistent with this prediction, as both densities of sparrows and foraging rates (i.e., TRIG) are high in these areas (Fig. 3.9).

Several factors other than food, such as nest predation risk, nest parasitism risk, or social information, have been proposed to explain habitat selection in birds. Nest predation or nest parasitism avoidance may be shaping settlement decisions (Chapter 2). Tradeoffs between energetic demand and vigilance likely underlie most habitat selection decisions (Metcalfe and Furness 1984, Houston et al. 1993, Martin 1995). Breeding dispersal following nest failure, or changes in nest-site characteristics in response to nest predation or parasitism risk is common (Lima and Dill 1990, Lima 2009, Kearns and Rodewald 2013, Chalfoun and Martin 2010). Indeed, Grasshopper Sparrows were much more likely to disperse following predation than if

they were successful (Chapter 2). Alternatively, nest parasitism avoidance could influence post-dispersal habitat selection. I found an overall reduction in brood parasitism incidence and intensity in the re-nests of Grasshopper Sparrows following dispersal (Chapter 2). Birds may also produce smaller clutch sizes or fledge fewer young, which may reflect a conflict between foraging and provisioning and predator vigilance (Lima 2009). Birds often take advantage of the social environment to make habitat selection decisions. Growing evidence suggests that public information plays an important role in shaping post-dispersal settlement decisions (Doligez et al. 2002). However, evidence for conspecific attraction shaping settlement decisions in Grasshopper Sparrows suggests social information is not important, both in relation to density of conspecifics (Chapter 1) and nest success (E. Williams and A. Boyle, unpubl. data).

In conclusion, this study highlights the unexpected result that food availability does not shape habitat selection decisions following within-season breeding dispersal. My results call into question the general expectation about the importance of food in shaping habitat choice and seasonal movements. Access to, and abundance of critical food resources may be very important during periods of high energetic demand, such as fueling prior to migration, during stopover, and molt (Metcalfe and Furness 1984, McCabe and Olsen 2015). Similarly, food may still be one of the central ecological explanations for why birds make long movements over broad geographic scales (Levey 1988, Levey and Stiles 1992). However, food does not seem to be important in shaping within-season dispersal in grassland songbirds, at least at local scales. My study emphasizes that other ecological processes, such as nest predation or nest parasitism risk and nest microhabitat quality, come into play when birds make settlement decisions. My results also demonstrate that habitat managers should not base management prescriptions solely on increasing food resources for maintaining grassland bird populations. Increasing understanding

of the ecological and evolutionary causes and consequences of within-season dispersal and habitat choice in grassland birds will both advance dispersal theory and improve conservation of species living in variable ecosystems.

# Figures and Tables

**Figure 3.1: Map showing the Konza Prairie to the west of Highway 177 and the Rannell's Preserve to the east. Internal boundary lines represent a watershed labeled by name, with specific management regime detailed in the map legend. Locations of 10-ha plots are marked by yellow squares. The inset map displays the location of the study site within the Flint Hills ecoregion (green shading) in eastern Kansas.**
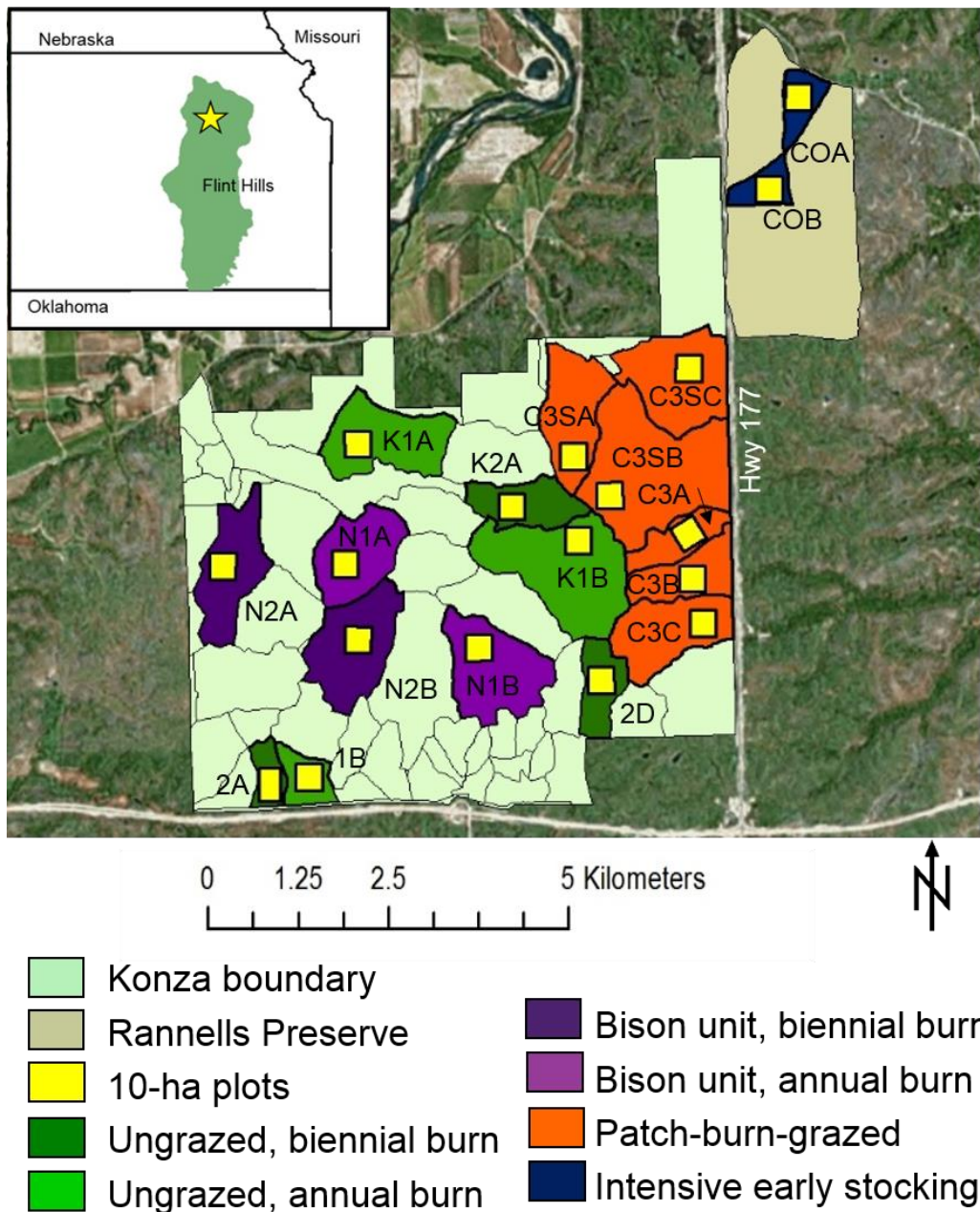
**Figure 3.2: Temporal patterns of prey abundance during the 2014 breeding season at Konza. Prey abundance represents the mean biomass (in grams) per 150 m² (area of transect) of arthropod prey for Grasshopper Sparrows during early, mid, and late season. Prey abundance are depicted as raw, untransformed values.**
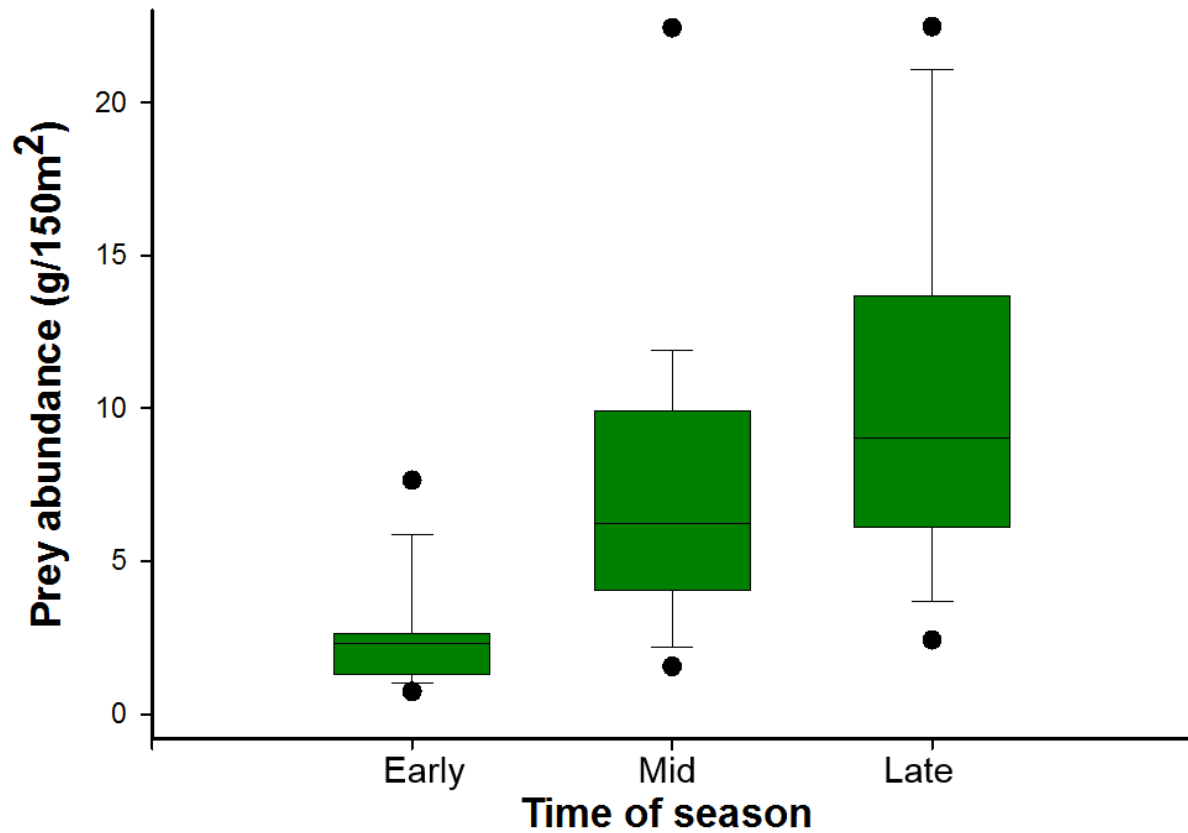
**Figure 3.3: Management-specific patterns of prey abundance in intensive early stocking (IES, blue symbol), ungrazed (green symbol), bison (purple symbol), and patch-burn grazing (orange symbol). Prey abundance represents the mean biomass (in grams) per 150 m² (area of transect) of arthropod prey for Grasshopper Sparrows. Prey abundance values represent raw, untransformed values.**
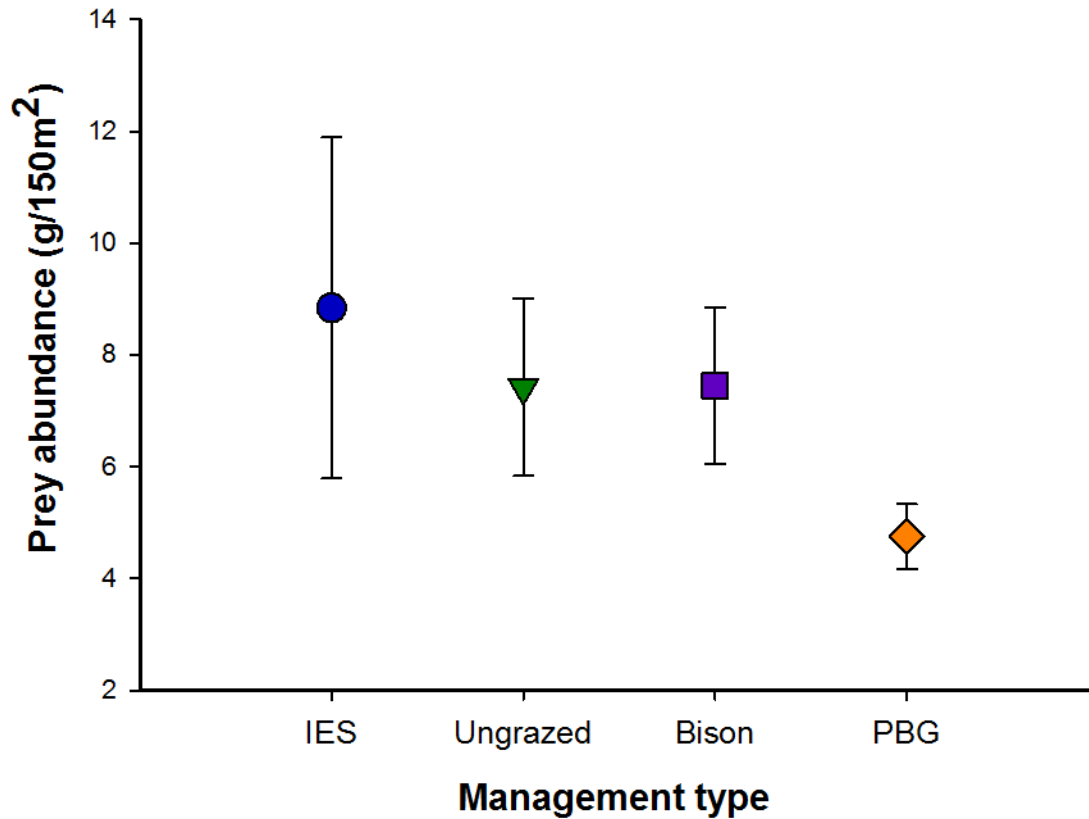
**Figure 3.4: Temporal patterns of prey abundance within each management type in 2014. Prey abundance represents the mean biomass (in grams) per 150 m² (area of transect) of arthropod prey for Grasshopper Sparrows during early, mid, and late season. Values for each time period for each watershed have been connected by lines. Each symbol represents a different watershed. Light green symbols represent watersheds burned in 2014, and dark green symbols represent watersheds not burned in 2014. Numbers above symbols represent mean densities of territorial males/10 ha for each time period. Prey abundance values represent raw, untransformed values. Standard error bars have been removed for clarity.**
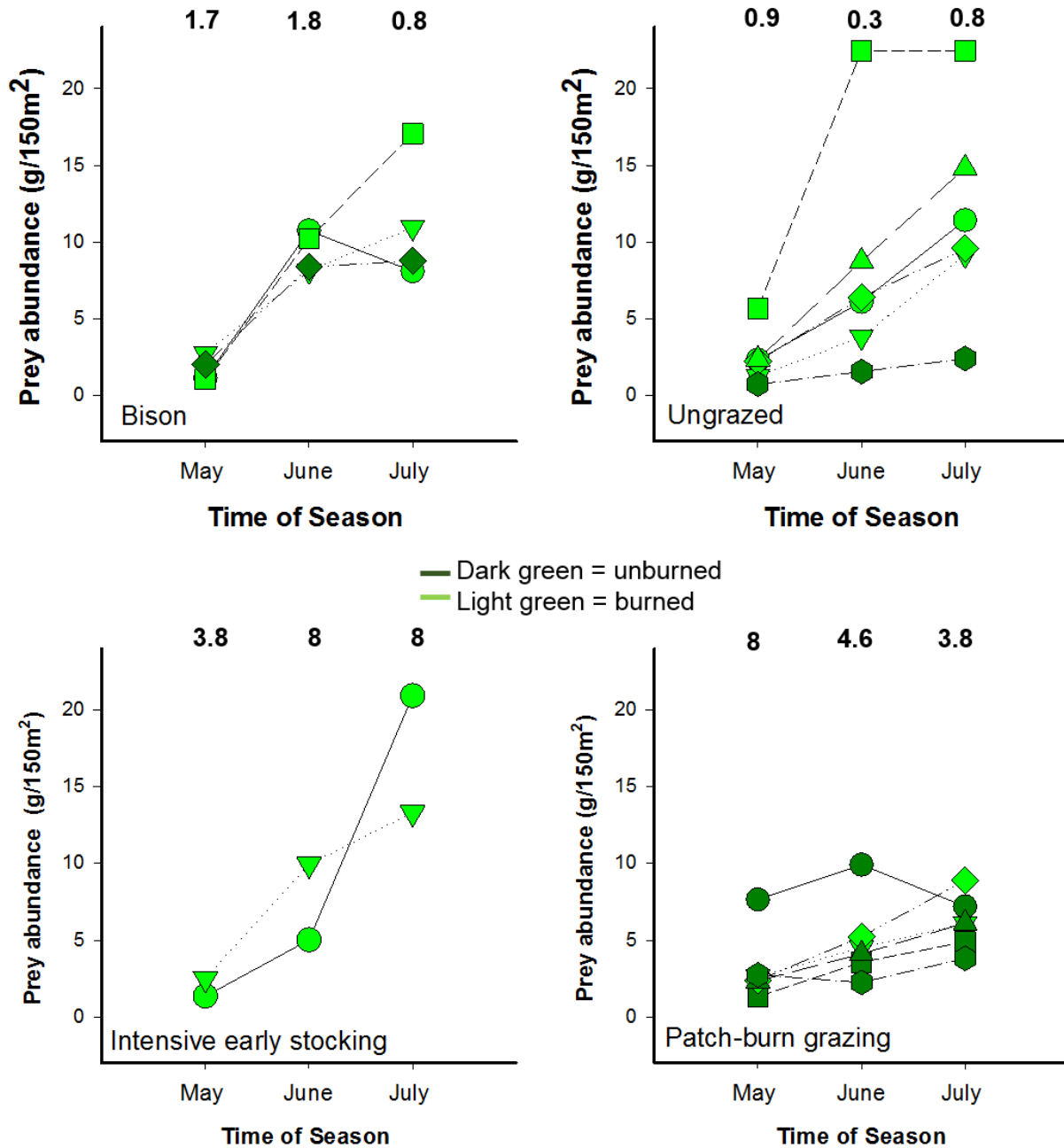


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**Figure 3.5: Relationship between density of territorial males sighted per 10 ha plot and prey abundance ($F_{1, 53} = 0.5$, $P = 0.479$) in 2014. Each dot represents one watershed during early (orange symbols), mid (blue symbols), or late (green symbols) periods during the breeding season. Prey abundance values represent raw, untransformed values. Standard error bars have been removed for clarity.**
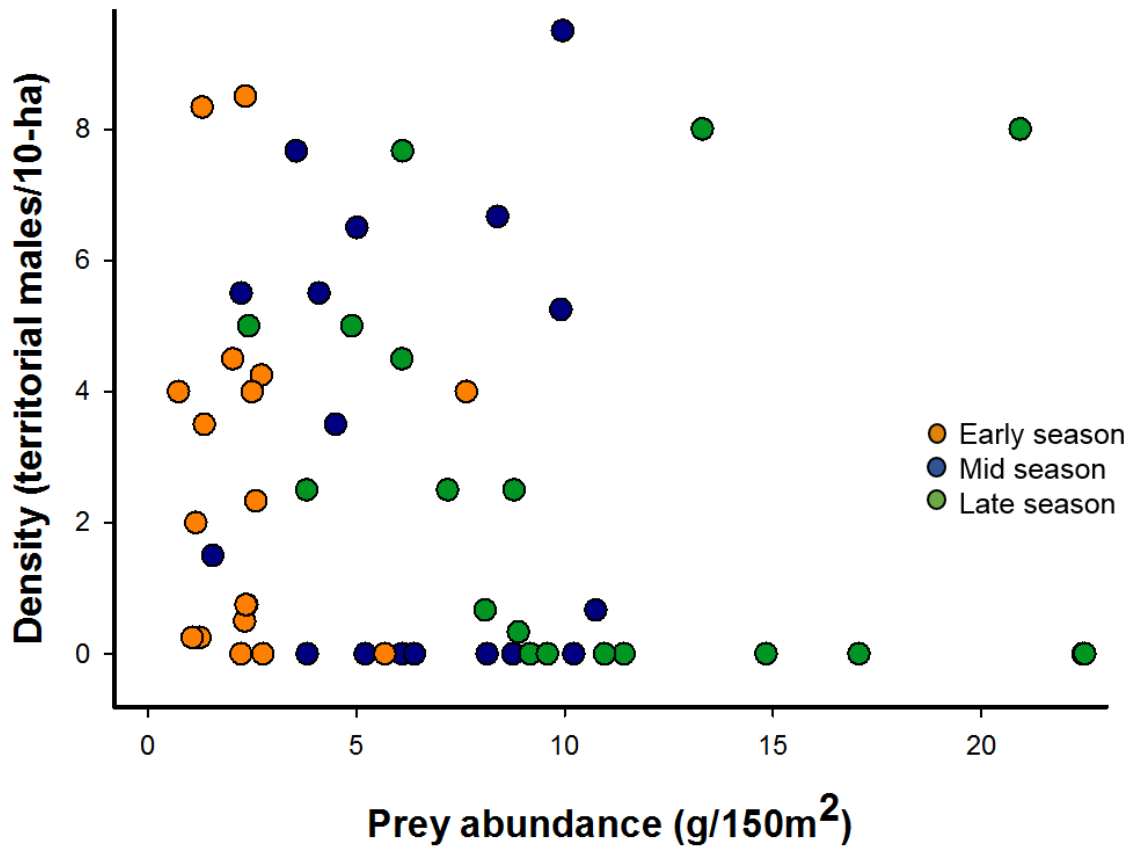
**Figure 3.6: Relationship between density of territorial males sighted per 10 ha plot and prey abundance ($F_{1, 35}$ = 0.1, $P$ = 0.7617) in 2014, within plots that contained Grasshopper Sparrows. Each dot represents a watershed in bison (purple symbols), patch-burn grazed (orange symbols), intensive early stocking (blue symbols), and ungrazed (green symbols) management. Prey abundance values represent raw, untransformed values. Standard error bars have been removed for clarity.**
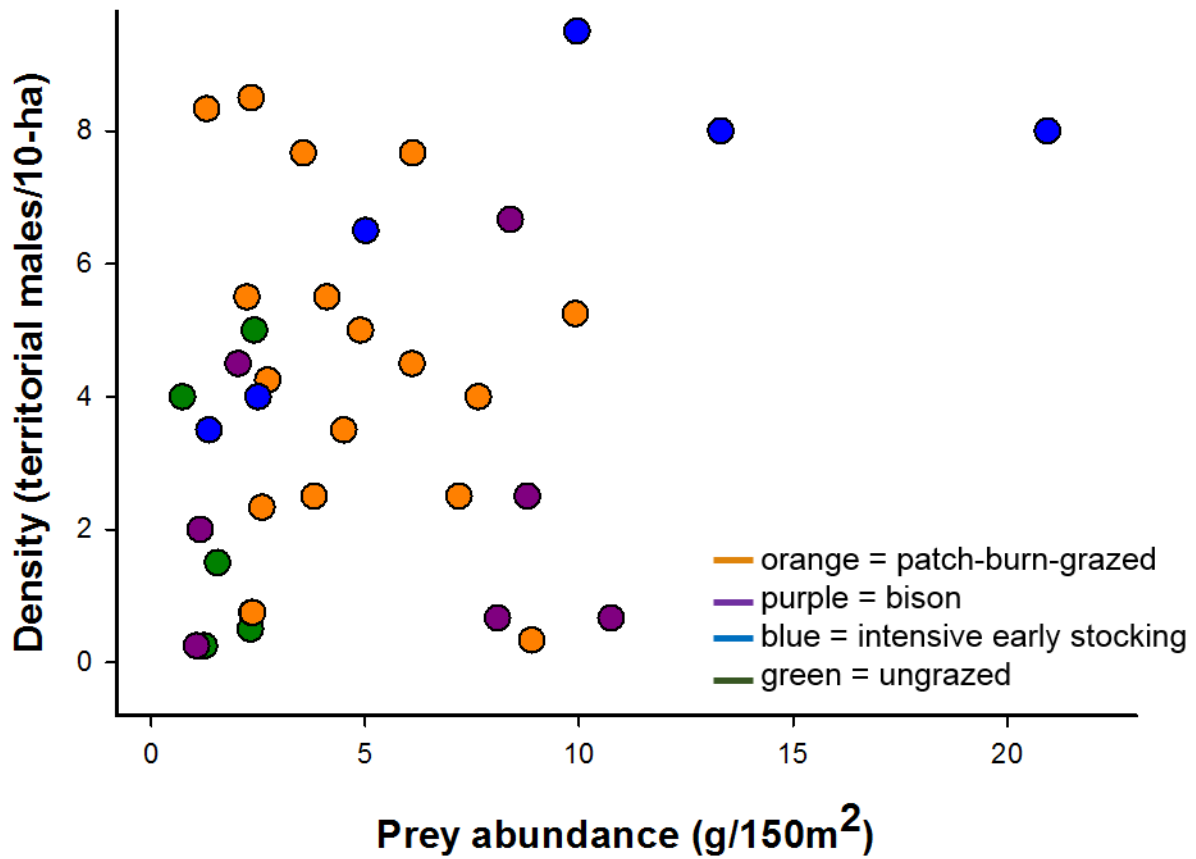
**Figure 3.7: Association between prey abundance and change in density of Grasshopper Sparrows within different management regimes in 2014.** Change in density (± SE) represents the calculated difference between mean density (territories/10 ha plot) during early or mid-season and mean density during mid-season to late season, respectively. Prey abundance values represent raw, untransformed values. Negative values represent a decline in number of territorial males between time periods, whereas positive values present an increase in number of territorial males between time periods.
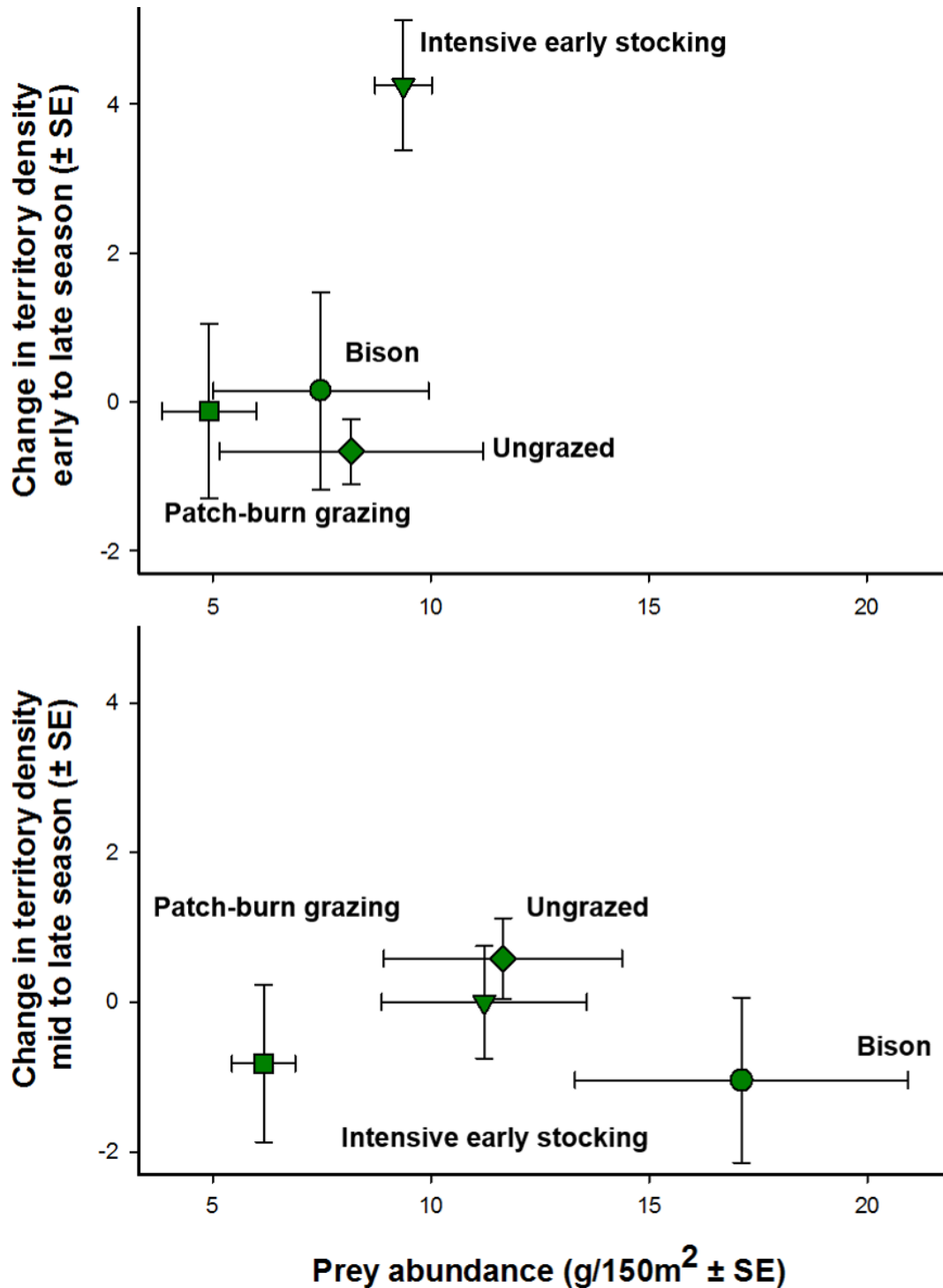
**Figure 3.8: Association between prey abundance and residual TRIG ($F_{1, 184} = 4.0$, $P = 0.046$) of Grasshopper Sparrows in 2014. Each dot represents an individual bird. Residuals of concentration of TRIG were calculated after accounting for capture time, capture date, and fat score. Prey abundance represents mean biomass (in grams) per 150 m² (area of transect) of arthropod prey for Grasshopper Sparrows during early, mid, and late season. Prey abundance values represent raw, untransformed values. Standard error bars have been removed for clarity.**
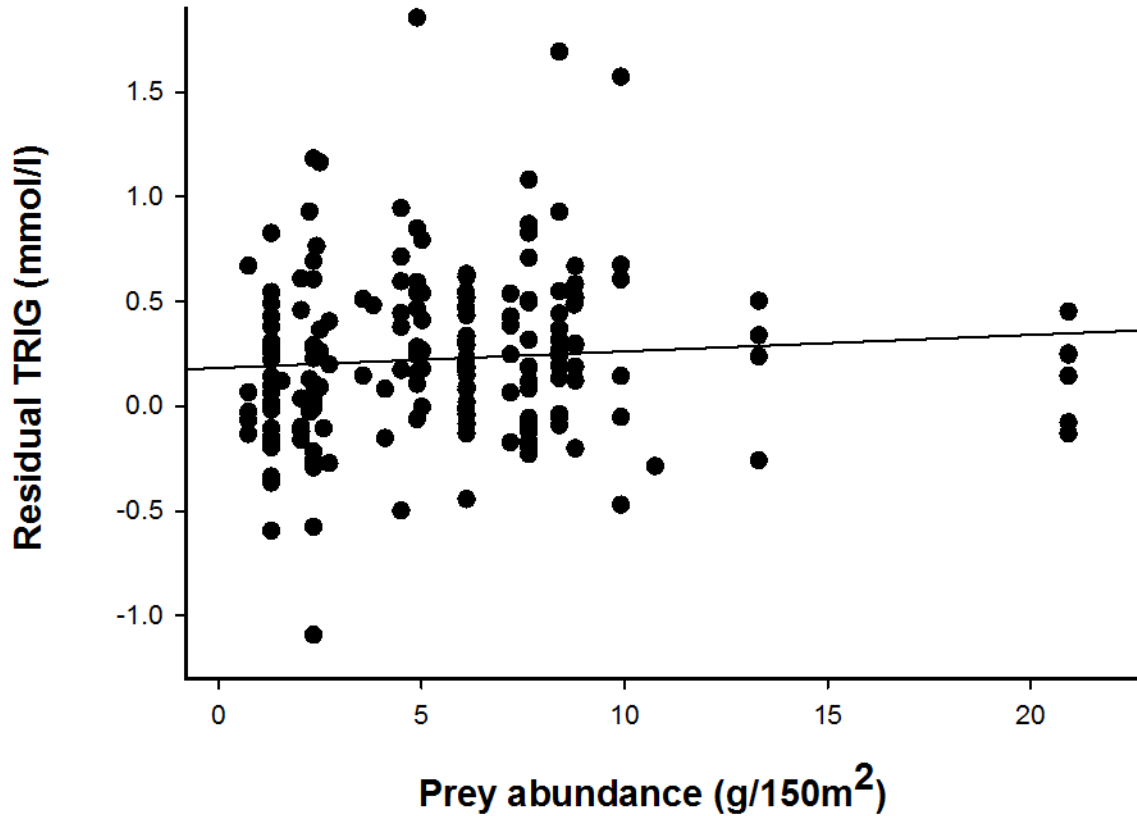
**Figure 3.9: Temporal patterns of residual TRIG within each management treatment during the 2013–2015 breeding seasons. Residuals of concentration of TRIG were calculated after accounting for capture time, fat score, and year. Each symbol represents the mean residual TRIG for a specific watershed. Light green symbols represent burned watersheds and dark green symbols represent unburned watersheds. Numbers above symbols represent mean densities of territorial males/10 ha for each time period. Standard error bars have been removed for clarity.**
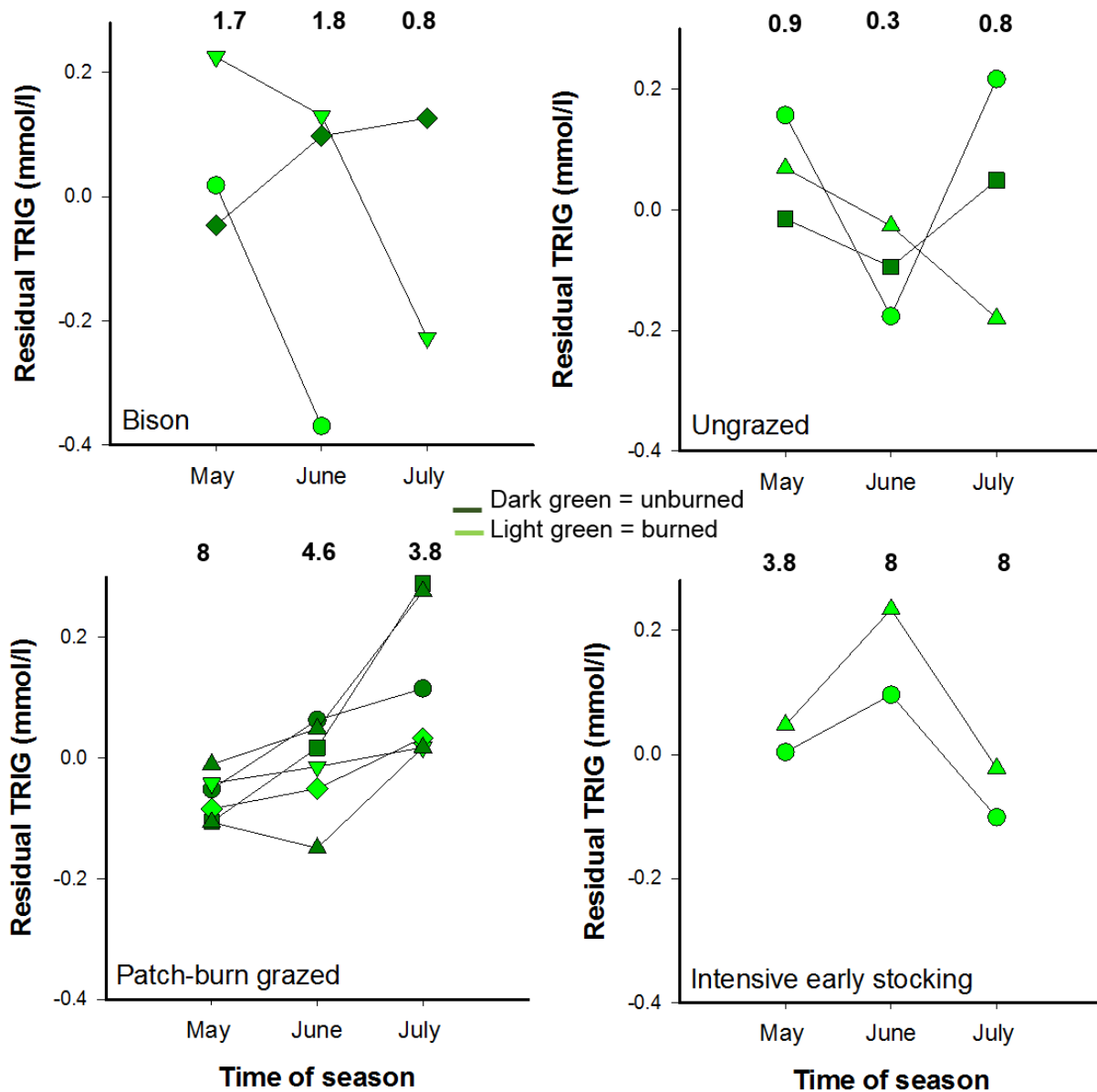
**Figure 3.10: Temporal patterns of the association between density and residual TRIG ($F_{2,}$ $_{536}$ = 8.7, $P$ = 0.0002) of Grasshopper Sparrows during the 2013–2015 breeding seasons at Konza. Each dot represents an individual bird. Residuals of concentration of TRIG were calculated after accounting for capture time, fat score, and year. Density represents the mean number of territorial males sighted per 10 ha plot within each time period. Panel A displays early season (green symbols), panel B displays mid-season (blue symbols) and panel C displays late season (orange symbols).**
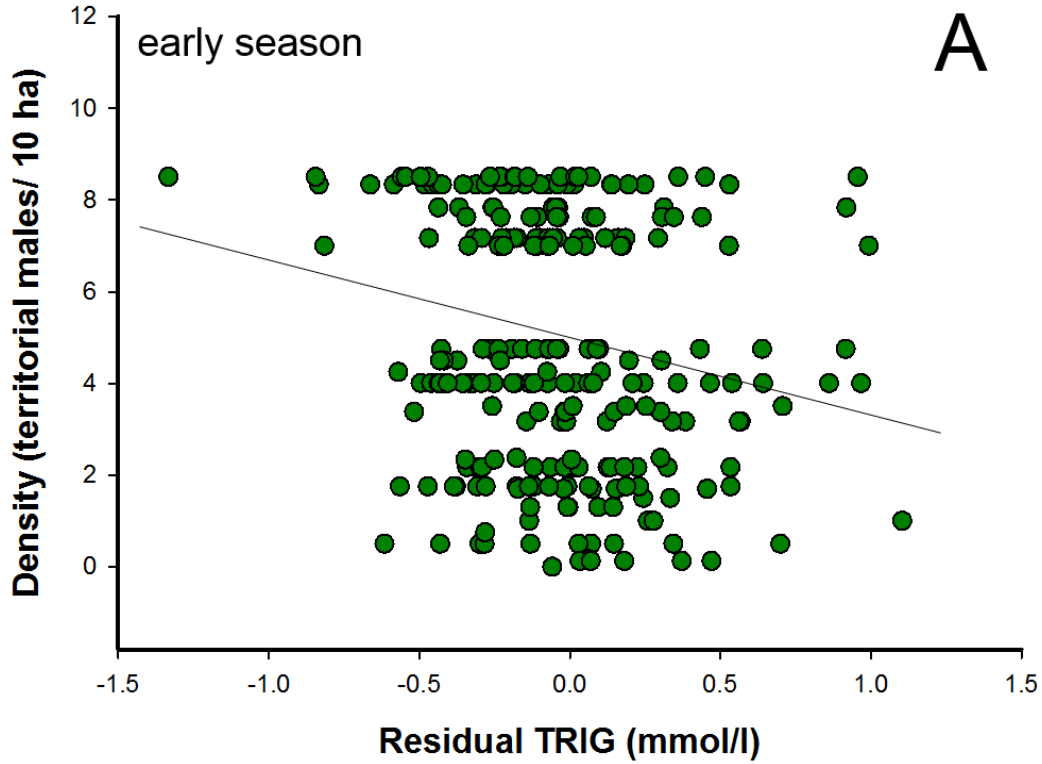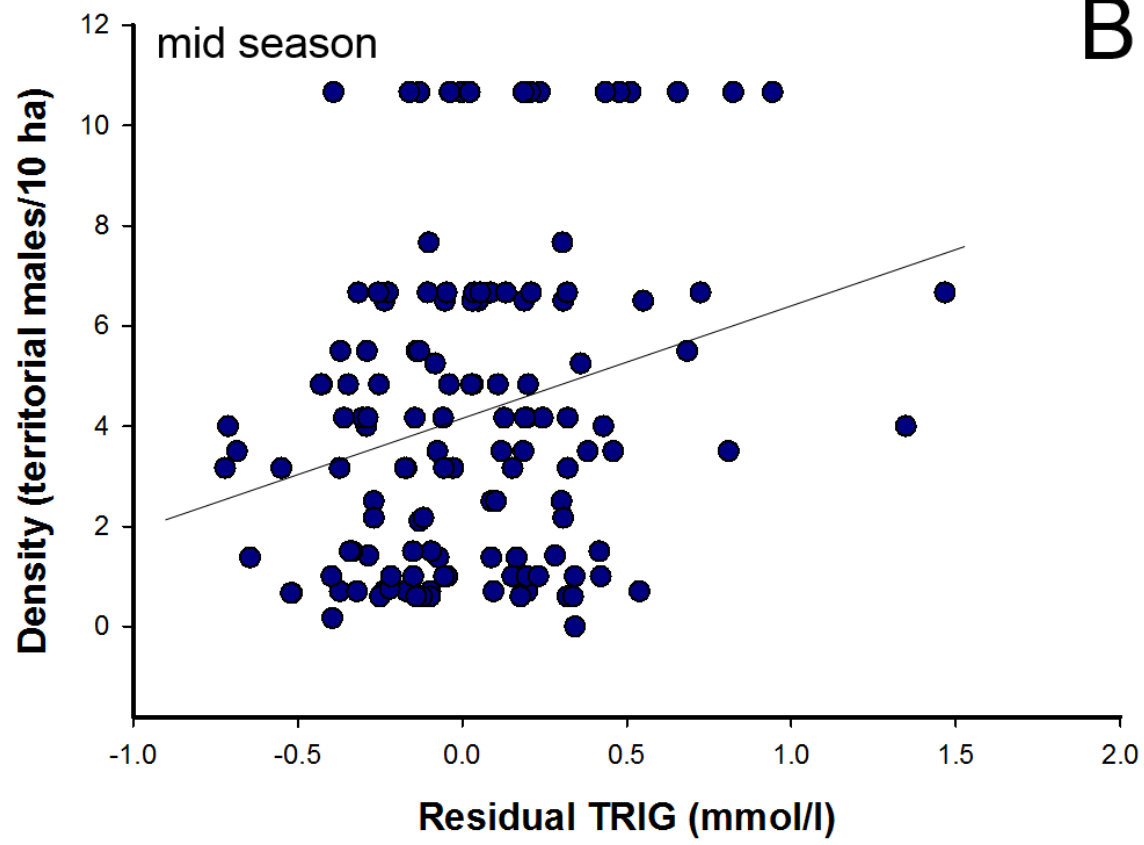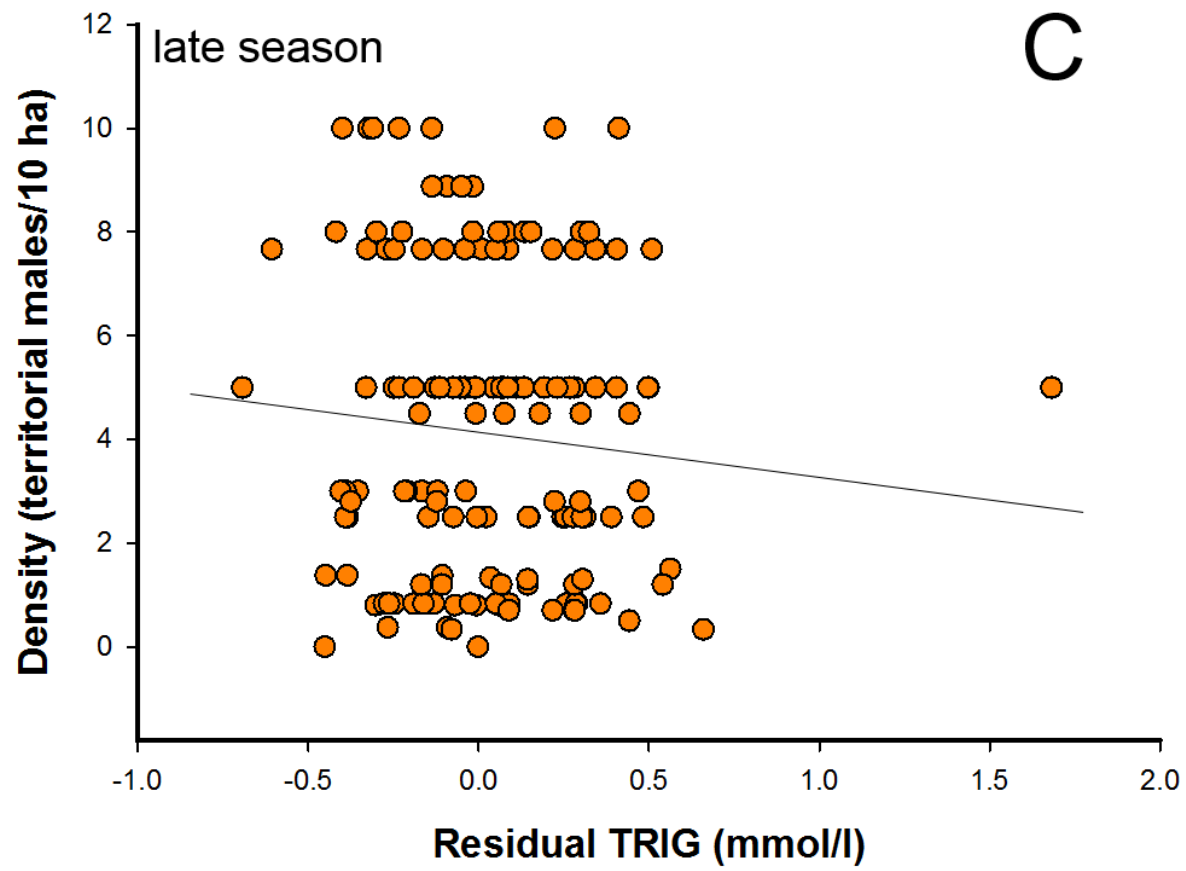
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