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RESEARCH ARTICLE

Patterns and correlates of within-season breeding dispersal: A common strategy in a declining grassland songbird

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ABSTRACT

Dispersal is a ubiquitous behavior with important consequences for gene flow, demography, and conservation. Some birds engage in between-year breeding dispersal, but the factors shaping variation in this behavior are not well understood. In mid-continental grasslands, preliminary evidence suggested that Grasshopper Sparrows (*Ammodramus savannarum*) dispersed not only between seasons, but also within breeding seasons—an apparently uncommon avian behavior. We studied a population of Grasshopper Sparrows breeding in northeastern Kansas, USA, to document the spatial and temporal patterns of within-season breeding dispersal in an experimentally managed tallgrass prairie from 2013 to 2015. We combined color-band resighting, territory mapping, and radio telemetry to quantify changes in territory density, turnover of territorial males, and dispersal distances. Density of Grasshopper Sparrows varied seasonally in management-specific ways, simultaneously increasing and decreasing in watersheds that differed in management regime. Turnover was unexpectedly high, with over half of territorial males being replaced each month. We documented over a third of males dispersing up to ~9 km between breeding attempts. Our study provides the first comprehensive description of the patterns of within-season breeding dispersal in a grassland songbird. Our results reveal the remarkable prevalence of within-season movement in this system and the relatively large distances over which birds disperse. Such mobility has important implications for survey design and habitat management, as birds select habitat at much larger spatial scales than is generally appreciated. These results also provide foundational information for tests of alternative hypotheses explaining the ecological and evolutionary basis for such movements.

Keywords: grasslands, Konza Prairie, inter-patch movement, intra-season movement, LTER, mid-season habitat shifts, territory switching

Patrones y correlatos de la dispersión adentro de la estación reproductiva: una estrategia común en un ave canora de pastizal en disminución

RESUMEN

La dispersión es un comportamiento ubicuo con consecuencias importantes para el flujo génico, la demografía y la conservación. Algunas aves se embarcan en la dispersión reproductiva entre años, pero los factores que modelan la variación en este comportamiento no están bien entendidos. En los pastizales del medio del continente, la evidencia preliminar sugirió que *Ammodramus savannarum* se dispersó no solo entre estaciones, sino también adentro de las estaciones reproductivas—un comportamiento aparentemente poco común en las aves. Entre 2013 y 2015, estudiamos una población de *A. savannarum* que cría en el noroeste de Kansas para documentar los patrones espaciales y temporales de la dispersión adentro de la estación reproductiva en una pradera de pastos altos manejada experimentalmente. Combinamos el avistaje repetido de anillos de color, el mapeo territorial y la radio telemetría para cuantificar cambios en la densidad territorial, recambio de machos territoriales y distancias de dispersión. La densidad de *A. savannarum* varió estacionalmente según los modos específicos de manejo, con aumentos y disminuciones simultáneas en densidad en las cuencas con diferentes regímenes de manejo. El recambio fue inesperadamente alto, con más de la mitad de los machos territoriales siendo reemplazados cada mes. Documentamos más de un tercio de machos dispersándose hasta ~9 km entre intentos reproductivos. Nuestro estudio brinda la primera descripción completa de los patrones de dispersión adentro de la estación reproductiva en un ave canora de pastizal. Nuestros resultados relevan la notable prevalencia de movimientos adentro de la estación en este sistema y las distancias relativamente largas sobre las cuales las aves se dispersan. Tal movilidad tiene implicancias importantes para el diseño de los muestreos y el manejo del hábitat, ya que las aves seleccionan el hábitat a escalas espaciales mucho más amplias que lo que normalmente se supone. Estos resultados también brindan información fundamental para evaluar hipótesis alternativas que explican las bases ecológicas y evolutivas de estos movimientos.

Palabras clave: cambios de hábitat de mitad de estación, cambios de territorio, LTER, movimiento entre parches, movimiento intra-estacional, pastizales, Pradera Konza

INTRODUCTION

Dispersal, or the permanent movement from one home range to a new one, 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 promotes gene flow between populations and is important for demographic rescue (Ronce 2007). The frequency and distances of dispersal often differ between sexes and age classes (Clobert et al. 2012). Natal dispersal, or the movement from a natal site to the site of first reproduction, is common. Consequently, most theory and empirical data pertain to natal dispersal (Clobert et al. 2012). By contrast, breeding dispersal, or the movement of adults between successive breeding attempts, is far less common, and high breeding-site fidelity is typical of most animals (Switzer 1993, Clobert et al. 2012). However, in highly mobile species, adults sometimes make multiple dispersal movements within and across seasons (Greenwood and Harvey 1982). The factors shaping individual variation in breeding-dispersal behavior are not well understood.

In birds, adults frequently disperse between years (Howlett and Stutchbury 1997, Winkler et al. 2004, Bötsch et al. 2012, Cline et al. 2013, Fernández-Chacón et al. 2013, Ganey et al. 2014, Pearson and Colwell 2014). Those movements are influenced by multiple exogenous and endogenous factors, including habitat quality, food, predation risk, 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). An individual's propensity to disperse can also be positively or negatively influenced by density and nesting success of conspecifics (Pakanen et al. 2011, Fernández-Chacón et al. 2013). High conspecific density can increase competition, leading to increased dispersal (Fernández-Chacón et al. 2013). Conversely, high density may reduce dispersal through conspecific attraction (Doligez et al. 2002), while low density of conspecifics may indicate low-quality habitat (Andrews et al. 2015).

Comparatively few studies have documented or attempted to explain breeding dispersal within seasons, a behavior in which an individual moves between successive breeding sites within a single season. Most within-season breeding-dispersal studies have focused on songbirds breeding in structurally stable forested habitats where this behavior is relatively uncommon; typically about 2–15% of individuals disperse, and dispersal distances are short, involving movements of <1 territory (Drilling and Thompson 1991, Howlett and Stutchbury 1997, Haas 1998, Betts et al. 2008, Cline et al. 2013, Gow and Stutchbury 2013).

Theoretical models predict that we should see greater prevalence of dispersal of all types in spatially and temporally variable habitats where predictability of habitat quality is low (Roff 1975, McPeek and Holt 1992, Switzer 1993). Species that depend on variable habitats may adopt a mobile strategy, whereby sequential habitat-selection decisions respond to changing local environmental conditions. In grassland ecosystems, disturbances of fire, grazing, and plant succession create a dynamic landscape within and between seasons. Habitat management of grassland ecosystems often mimics natural sources of disturbance through prescribed burning and grazing by large ungulates (Fuhlendorf et al. 2009), which creates a mosaic of habitats in which plant growth, composition, and structure vary in response to fire intensity and grazing pressure (Fuhlendorf et al. 2010). Coupled with this structural and compositional heterogeneity, high intra- and inter-annual variability in rainfall and temperature distinguish grasslands as particularly dynamic environments (Knapp et al. 1998, Gherardi and Sala 2015). The interactions between natural disturbance processes, variable climate, and dramatic phenological changes within growing seasons influence all ecological drivers of habitat quality, which would be predicted to result in highly dynamic habitat selection and movement patterns of grassland-obligate animals.

Evidence of within-season breeding dispersal in grassland birds is largely anecdotal, and little is known about how often or why this behavior occurs. Some grassland-obligate migratory birds, including Henslow's Sparrow (*Ammodramus henslowii*) and Baird's Sparrow (*A. bairdii*), are described as shifting in and out of territories and defending new, distant areas later in the season (Green 1992, Green et al. 2002, Herkert et al. 2002). Life-history accounts for both Henslow's and Baird's sparrows recount disappearances of singing males with establishment of new males in the same territories (Green et al. 2002, Herkert et al. 2002, Rodewald 2015). In the grassland-breeding Sedge Wren (*Cistothorus platensis*), it is likely that all individuals disperse within the season, apparently breeding sequentially in widely separated regions during the same summer (Bedell 1996, Herkert et al. 2001, Hobson and Robbins 2009). Preliminary evidence from a population of Grasshopper Sparrows (*A. savannarum*) in the Flint Hills of eastern Kansas, USA, revealed that some Grasshopper Sparrows remained faithful to single territories the entire summer, whereas others held multiple, successive territories located up to several kilometers from one another. These anecdotes suggest that within-season breeding dispersal may be common in grassland songbirds, but no study to date has described the patterns and correlates of such behavior. A better understanding of this behavior is a necessary step in identifying the ecological drivers of such movements. Quantifying rates of dispersal could also

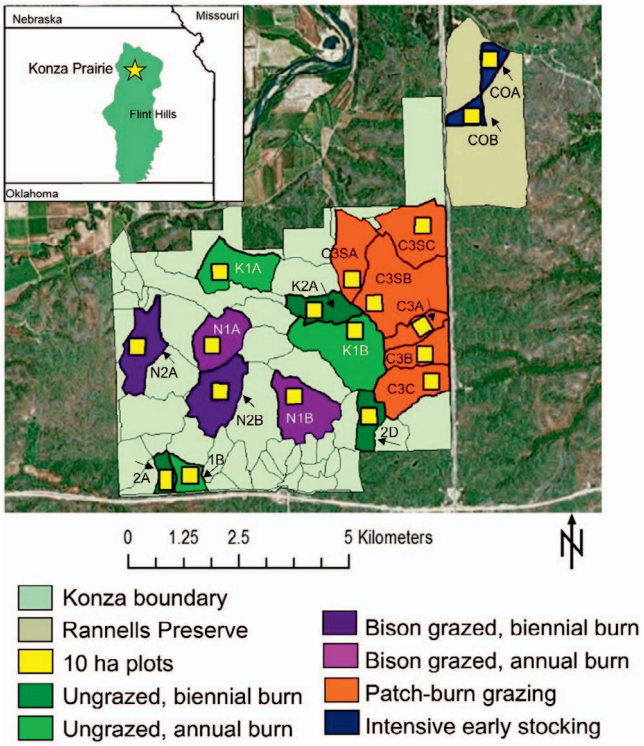

FIGURE 1. Map showing the Konza Prairie to the west of Kansas Highway 177 and Rannells Flint Hills Prairie Preserve to the east. Internal boundary lines represent units managed with varying grazing and burning regimes. The 18 units in which we studied Grasshopper Sparrows are labeled and colored according to management regime (purple = bison-grazed areas; orange and blue = cattle-grazed areas; darker shades of green = ungrazed areas). Areas of the Konza Prairie not included in this study are in pale green. Within focal units, 10 ha study plots are marked by yellow squares. Inset map displays the location of the study site (star) within the Flint Hills ecoregion (green) of eastern Kansas.

improve estimates of survival of imperiled grassland songbirds by accounting for the portion of apparent survival attributable to dispersal (Sandercock 2006). Finally, describing the patterns of within-season breeding dispersal can inform survey design, because distances traveled reveal the spatial scales at which habitat should be studied and conserved.

In order to provide a comprehensive description of the spatial and temporal patterns of within-season breeding dispersal in a declining grassland songbird, we studied Grasshopper Sparrows breeding in tallgrass prairie in the Flint Hills region of eastern Kansas during the 2013–2015 breeding seasons. We used 3 approaches to describe the frequency, magnitude, and spatiotemporal patterns of within-season breeding dispersal, measuring (1) changes in territory density, (2) territory turnover, and (3) movements of marked individuals via territory surveys, resighting of marked individuals, and radio telemetry. We related temporal and spatial patterns of territory density and turnover to time of season, year, density of conspecifics, and rangeland management practices of 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 United States, Mexico, the Caribbean, and parts of Central and South America (Vickery 1996). The subspecies *A. s. perspallidus* is migratory and breeds across the western half of North America. In tallgrass prairies of the Great Plains, Grasshopper Sparrows are commonly found on land burned every 1–3 yr and managed with low-intensity cattle grazing (Powell 2006). Arthropods comprise 70% of the Grasshopper Sparrow diet during breeding, largely consisting of grasshoppers, hemipterans, arachnids, beetles, and caterpillars (Joern 1988). The quantity and community composition of arthropod prey are strongly affected by fire and grazing (Jonas and Joern 2007). Burning every 1–3 yr allows intermediate amounts of dead grass to accumulate that sparrows use for nesting, and grazing produces barer patches used for foraging (Powell 2008).

Grasshopper Sparrows arrive in northeastern Kansas as early as mid-March, and males typically establish territories in mid-April. Pairs begin forming in late April, and clutch initiation begins soon afterward. Grasshopper Sparrows build domed nests of soft grasses and roots on the ground, at the base of overhanging grasses or forbs. Clutches typically contain 4–5 eggs, with females beginning incubation after laying the penultimate egg. Breeding attempts take 24–26 days from laying to fledging. Males defend territories and sing from conspicuous perches until early August (E. J. Williams and W. A. Boyle personal observation).

We studied Grasshopper Sparrows at the Konza Prairie Biological Station, a 3,487 ha tract of tallgrass prairie co-owned by Kansas State University and The Nature Conservancy, ~5 km south of the city of Manhattan (Figure 1). The Konza Prairie is a long-term ecological research site experimentally managed with fire and grazing in watershed units (Knapp et al. 1998). Core treatments include year-long bison grazing or no grazing, and prescribed fires every 1, 2, 4, or 20 yr. Six additional watersheds at Konza are patch-burn grazed in 2 replicate sets. Patch-burn grazing involves a 3 yr rotational burn regime in combination with warm-season cattle grazing (Fuhlendorf and Engle 2001). We also studied Grasshopper Sparrows at Rannells Flint Hills Prairie Preserve, a 1,175 ha tract of tallgrass prairie owned by Kansas State University,

TABLE 1. Watershed names, burn intervals, management regimes, total number of color-banded birds marked per watershed for all years combined (2013–2015), densities of Grasshopper Sparrows per year, and turnover of territorial males per year in our study area in eastern Kansas, USA. Density values represent the mean (± SE) of maximum densities for early-, mid-, and late-season periods for each 10 ha plot (see text). Raw turnover values were calculated for early- to mid-season (E–M) and mid- to late-season (M–L) periods. Burn interval is the number of years between fires. Management types include ungrazed (U), patch-burn grazing (P), intensive early stocking (I), and bison-grazed (B).

				2013			2014			2015		
Watershed name	Burn interval (yr)	Management type	Birds marked (*n*)	Turnover (%) E–M	Turnover (%) M–L	Density (*n*)	Turnover (%) E–M	Turnover (%) M–L	Density (*n*)	Turnover (%) E–M	Turnover (%) M–L	Density (*n*)
1B	1	U	0	0	0	0 ± 0	100	0	0.33 ± 0.33	100	0	0.33 ± 0.33
2A	2	U	11	100	0	0.67 ± 0.67	100	0	0.33 ± 0.33	0	0	0 ± 0
2D	2	U	67	67	75	1.33 ± 0.33	71	38	5.67 ± 1.45	100	100	1 ± 0
C3A	3	P	84	33	33	1.67 ± 0.33	76	100	6.67 ± 0.33	73	100	7 ± 4
C3B	3	P	89	54	42	4 ± 0.58	9	64	6.33 ± 0.33	58	80	6.33 ± 2.33
C3C	3	P	95	37	57	4.67 ± 0.67	30	53	9.67 ± 2.33	75	68	6.67 ± 1.33
C3SA	3	P	56	100	78	2.33 ± 0.33	100	100	1 ± 0.58	29	63	5.33 ± 0.67
C3SB	3	P	117	100	20	1.67 ± 0.33	60	42	9.33 ± 1.76	50	37	8.33 ± 0.88
C3SC	3	P	19	100	100	1 ± 0	50	38	7.33 ± 0.33	60	100	1.67 ± 0.33
COA	1	I	79	38	50	5 ± 0	9	67	8.67 ± 0.67	43	63	13.33 ± 2.03
COB	1	I	67	38	45	5.33 ± 0.67	43	44	10 ± 1	53	53	15.33 ± 0.33
K1A	1	U	0	100	0	0.33 ± 0.33	0	0	0 ± 0	0	100	0.33 ± 0.33
K1B	1	U	7	50	33	1 ± 0	100	0	0.67 ± 0.67	50	100	2.33 ± 0.88
K2A	2	U	19	46	42	3 ± 0.58	0	0	0.00 ± 0.00	100	60	2 ± 1
N1A	1	B	9	67	100	2 ± 0	100	0	2.67 ± 0.67	67	67	2.33 ± 0.88
N1B	1	B	19	0	100	1 ± 0	100	0	0.33 ± 0.33	100	75	2.67 ± 1.20
N2A	2	B	3	50	0	1.67 ± 0.33	0	0	0 ± 0	60	43	2 ± 0
N2B	2	B	46	43	0	3 ± 0	30	64	8 ± 1	23	75	3.33 ± 0.33

located adjacent to Konza Prairie Biological Station (Figure 1). Rannells Preserve includes pastures managed under an "intensive early stocking" regime consisting of annual burning and double stocking of steers from April to July (Owensby et al. 2008). Prescribed burns in our study areas all took place in March and April, prior to green-up and arrival of most migrant birds. We included sites at Rannells Preserve to study Grasshopper Sparrow responses to intensive early stocking, because this management regime is the predominant rangeland management within the Flint Hills and is not represented on the Konza Prairie. We hereafter refer to the 2 reserves comprising our research site collectively as "Konza."

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

Grasshopper Sparrow breeding densities vary in native grasslands, with maxima of 1 territory ha^{-1} reported in grazed prairies burned every 1–3 yr (Powell 2006, Rahmig et al. 2009). Accordingly, we studied Grasshopper Sparrows on watershed units that encompass burn–grazing dynamics that may affect patterns of territory density, movement, and habitat-selection decisions throughout the breeding season (Table 1). We selected 18 watershed units in replicated combinations of (1) bison grazing ($n = 4$) or no grazing ($n = 6$), burned either annually or every 2 yr; (2) intensive early stocking ($n = 2$); and (3) patch-burn grazing (2 sets of 3 units, each unit burned completely every 3 yr; $n = 6$). We randomly located a 10 ha plot (316.5 × 316.5 m) within each unit, located ≥20 m from any road or fence line (Figure 1).

Individual Capture, Resighting, Territory Surveys, and Radio Telemetry

We captured male Grasshopper Sparrows in mist nets (Ecotone, Gdynia, Poland) from late April until early August. We placed nets near primary song perches within territories and lured birds using song playbacks. We placed a numbered federal band and a unique combination of 3 colored leg bands on each individual. We 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 detected only when flushed from nests, we did not include females in quantitative analyses; their cryptic behavior means that we undoubtedly missed

most females during resighting efforts and, thus, could only poorly estimate density, turnover, and dispersal distances. However, we report anecdotal information on females when available.

During breeding, males sing and use flight and wing displays to defend territories. Males sing from prominent perches, often singing ~45 times hr^{-1} (Lohr et al. 2013). We considered males territorial if they sang the territorial "buzz" song, performed perched wing displays or flutter-flights, or initiated aggressive chases with other males (Vickery 1996, Soha et al. 2009). We considered males mated if they sang the "warble" song associated with pair-bond formation (Lohr et al. 2013) or acted nonaggressively with another nonsinging bird that we presumed to be female (Smith 1959, Vickery 1996). The relative frequency with which males sing the warble song type tends to increase over the sequence of pair bonding, nest building, incubation, and nestling brooding. We confirmed mating status via vocalization type on multiple days, and in the majority of cases we visually confirmed pairing status; we never found nests belonging to males that we had observed only singing the territorial song.

To verify that dispersal movements were occurring between breeding attempts, we characterized male reproductive status using a slightly modified rank-scale index (Rivers et al. 2003). We classified a male as 1 if he sang only the territorial "buzz" song; 1.5 if he sang the warble song, indicating he was mated; 2 if we saw 2 birds together acting nonaggressively; 3 if we observed an individual giving alarm calls or carrying nesting material; 4 if we observed evidence of nestlings, such as food-provisioning behavior; and 5 if we 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 determining reproductive status of species with cryptic behavior (Vickery et al. 1992).

To determine seasonal changes in density, turnover of territorial males, locations of postdispersal territories, and dispersal distances, we exhaustively surveyed the 10 ha plots every week (mean ± SD = 8.4 ± 3.1 days; range: 6–17 days) and resighted color-banded birds regularly, but less comprehensively, elsewhere within focal watersheds. We recorded 2–8 locations within and at the margins of territories each time we resighted a marked individual using hand-held GPS units (GPSmap 60CSx; Garmin, Olathe, Kansas). We also mapped territory locations of both banded and unmarked individuals on printed aerial maps of plots during each survey. We surveyed 1 or 2 plots between 0600 and 1100 hours for 45 min to 3 hr each. We avoided having the same observer survey the same plot consecutively, and we alternated surveying each plot during earlier and later periods in a morning. Observers traversed plots following a different track during each survey, in such a way that they covered the entire 10 ha area and passed within <75 m of all points within the plot. Singing Grasshopper Sparrows were typically audible at distances of >200 m, and the majority of territorial males could be heard singing from any point within the 316.5 × 316.5 m plot. Observers used 20× spotting scopes or 8× binoculars to determine whether each male was color-banded and, if so, they identified the individual via color-band combination.

In addition to color-band resighting, we used radio telemetry to determine postdispersal territory locations and dispersal distances. We fitted males ($n = 19$) with radio transmitters using a figure-8 leg harness (Rappole and Tipton 1991). In 2014 we used 0.52 g BD-2 VHF radio transmitters (Holohil Systems, Carp, Ontario, Canada); in 2015 we used 0.56 g PicoPip Ag376 VHF radio transmitters (Lotek Wireless, Newmarket, Ontario) that transmitted over longer distances (0.8 km in 2014 vs. 1.6 km in 2015). Transmitters and harnesses weighed ~0.7 g (4% body mass; mean ± SE = 17.40 ± 0.16 g of birds fit with transmitters). Transmitters of similar size induced no measurable negative effects on similarly sized songbirds (Rae et al. 2009, Streby et al. 2013).

Because our objective was to establish when and where individuals dispersed rather than to collect detailed data on movement tracks, we located individuals every 2 days using 3-element folding Yagis and portable handheld radio receivers (R-1000, Communications Specialists, Orange, California, USA; Biotracker Receiver, Lotek Wireless). When birds disappeared from the territories on which we tagged them, we searched ~42 hr $bird^{-1}$ over a 2 wk period (~6 hr day^{-1} every 2 days) on foot and using a car-mounted omnidirectional antenna (Lotek Wireless). We searched systematically within a ≥5 km radius from the last known location, and opportunistically elsewhere during territory surveys. We relocated 7 of 10 lost birds, several of which were relocated far (>1.2 km) from their previous territory. We assumed that the remaining 3 radio-tagged birds either died or dispersed beyond our study site. The maximum dispersal distance we could have detected within our study site was 11.1 km (longest straight-line distance between watersheds 2A to COA; Figure 1). However, many shorter-distance dispersal distances could have gone undetected due to the spatial configuration of our study plots. The 3 lost birds were not included in estimates of dispersal distance.

Analyses

We present 3 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 defending ≥2 territories in succession within seasons. These methods made different assumptions about the fate of undetected birds that serve to bracket estimates of true dispersal. Our

turnover metrics assume that all birds disappearing from plots dispersed rather than died, whereas estimates based on direct observations assume that only the individuals we detected in new locations dispersed and that all others died. For estimates based on resighting, we considered males to have dispersed if they (1) displayed territorial behavior $\geq$100 m away from the centroid of their original territory or nest location or (2) were not resighted at their initial territory $\geq$1 wk after their nest failed or fledged. We chose a 100 m cutoff because Grasshopper Sparrow territories range in size from 40 to 90 m in diameter across the breeding range (Delany et al. 1995, Vickery 1996, Jones et al. 2007) and are, on average ($\pm$ SE), 43 $\pm$ 2 m in diameter at Konza. Thus, a shift of 100 m represents a movement of $>$2 territories. Conversely, we considered individuals site faithful if they (1) continued to display territorial behavior within 100 m of their original territory or nest or (2) were resighted again on their initial territory $>$1 wk after the nest failed or fledged.

Seasonal changes in density. To measure spatial and temporal variation in density, we divided each season into early-, mid-, and late-season time periods; each of these periods could feasibly encompass a complete breeding attempt. Within each period, we conducted 3–5 surveys. The dates of the periods varied slightly among years because of differences in timing of surveys and our attempts to balance the number of surveys per plot between periods. Across years, the early-season period began during April 30–May 3 and ended during June 1–6; mid-season began during June 2–7 and ended during July 1–5; and late-season began during July 2–6 and ended during July 29–August 3. We calculated territory density in each period as the maximum number of unique territorial males detected during a survey within each 10 ha plot. We calculated changes in density between periods by subtracting the number of territories in one period from that in the previous period.

Although we attempted to locate every territorial male within plots on every survey, some birds were likely not detected because of weather (e.g., temperature or wind) that affects bird behavior and the ability of observers to detect birds. Thus, we explored different approaches for calculating density to determine whether results were sensitive to low counts attributable to weather or observer effects. We calculated the mean number of unique territorial males and the mean of the 2 highest surveys within each period. The spatial and temporal patterns of these alternative metrics were very similar to maximum counts; thus, we report only the maximum density results because they represent our best estimate of the number of territories simultaneously active on each plot during each part of the season.

Grasshopper Sparrow abundances vary across different burn intervals and grazing regimes (Powell 2006, 2008), and relative abundance may reflect gradients of habitat quality important in shaping dispersal decisions. Thus, we related density to spatial and temporal correlates to infer the importance of habitat quality in shaping movements in a series of generalized linear models with territory density modeled with a Poisson distribution. Because we had only 3 yr of data (2013–2015), we included year as a fixed effect in all models (Gelman 2005, Gelman and Hill 2007). We first analyzed density as a function of time period (i.e. early-, mid-, or late-season; model 1). We then explored the relationship between density and land-management regime, independent of time of season, modeling density as a function of grazing (cattle, bison, none), fire (burned in current year or not), and the interaction of those 2 factors (model 2). We added temporal effects to the management-only model by including time period (model 3). Finally, we evaluated whether temporal changes in density within seasons operated interactively with the management regime by adding a 3-way interaction to this model (i.e. grazing*fire*time; model 4). We did not consider interactions between year, time period, and management effects, because of sample-size limitations and the complexity of interpreting model effects. Our sample size for these models was $n = 162$ (18 plots surveyed during the 3 periods over the 3 breeding seasons). We analyzed models using the "glm" function in R package "lme4" (Bates et al. 2014). We determined which of the above models provided a better fit to our data using an information-theoretic approach (Burnham and Anderson 2003). We 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 to equally parsimonious (Burnham and Anderson 2003).

Turnover of territorial males within plots. Even on plots where density remained fairly constant, the identity of territory holders changed. Thus, the turnover of territorial males provides a second metric useful for quantifying dispersal tendency. We calculated turnover using a modified equation from Brown and Kodric-Brown (1977): (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). Since turnover is a unitless number, varying continuously between 0 and 1 (i.e. 0.5 represents half of territorial individuals turning over), we multiplied values by 100, presenting turnover values as percentages. We calculated turnover between early- and mid-season periods, and between mid- and late-season periods, each year. We counted a male as present in a given period if he was detected during any of the surveys conducted during that period. If a male moved $>$100 m but remained within the 10 ha plot, we still counted him as present (i.e. not replaced by another male). Although this criterion differs from that used to estimate dispersal distances, we chose to

quantify turnover in this way to provide inference relevant to studies of unmarked birds. Studies of habitat selection frequently estimate the relative abundance of birds within fixed areas rather than obtaining spatially explicit individual-level data. Thus, our turnover metric estimates the degree to which studies of unmarked birds underestimate the prevalence of dispersal in and out of plots. If an unbanded male defended the same perches in a similar area overlapping that of a previous period, we considered that bird to be the same individual. However, if an unbanded male appeared in a previously unoccupied area, or if an unbanded male was replaced by a banded male or vice versa, we considered that territory to have turned over. Only males exhibiting territorial behavior (reproductive index $\geq$1) were considered in calculations of turnover. Although this metric assumes that birds leaving plots dispersed rather than died, our criteria are somewhat conservative, in the sense that we did not include males that dispersed short distances within plots in turnover calculations.

Because we were interested in assessing spatial and temporal variation in turnover, we restricted analyses to plots in which we detected $\geq$2 territorial males at some point during the season. We then followed the same modeling approach described previously for density, first exploring the temporal and spatial patterns independently, and then evaluating generalized linear models (GLMs) that included a 3-way interaction between grazing, fire, and time of season. Because turnover values were not normally distributed, we fitted models using a quasi-binomial distribution to account for the overdispersion in our data (Bolker 2008). The sample size for turnover models was $n = 73$ because we excluded 35 observations of plots that had $<$2 territorial males at some point during the study. We used function "glm" in R package "lme4" (Bates et al. 2014). Because the quasi-likelihood is not a true likelihood, we could not use likelihood ratio tests for model inference; we instead reported F statistics for each model (Bolker 2008). We ranked each model using differences in quasi-AIC and calculated the ΔqAIC as the difference in deviance divided by the estimate of the overdispersion parameter, φ (Burnham and Anderson 2004).

Role of conspecific attraction. Dispersal decisions may be positively related to the density of conspecifics; in Illinois, Grasshopper Sparrows moved into sites later in the season where territorial songs were broadcast from speakers (Andrews et al. 2015). Alternatively, dispersal and density may be negatively related if competition for food or nesting sites leads individuals to leave. Furthermore, this relationship may also not be linear; high densities could lead to increased dispersal due to competition, and low densities could also lead to increased dispersal if low density signals low-quality habitat. Thus, we tested for both linear and quadratic relationships between dispersal and density. We related plot-level seasonal changes in density and turnover metrics to territory density measured in the pre-turnover period in GLMs including transition period (early- to mid-season, mid- to late-season) and year as a fixed effect.

Known movements of marked birds. We measured the Euclidean distance between the centroids of territory locations of birds that defended different territories during different parts of the season. For females with known nest locations, we measured the distance between nests. For females observed at new territories at which we did not locate new nests, we measured the distance between resight locations. We present raw dispersal distances, which likely underestimate true dispersal-distance kernels, because we did not account for the truncation of estimates due to sampling a finite area (Baker and Geupel 1995). We conducted statistical analyses using R 3.3.3 (R Core Team 2017). We present means ± SE for all results and considered values with $\alpha \leq 0.05$ to be significant.

RESULTS

Seasonal Changes in Density

We captured and color banded 647 males and 132 females in 2013–2015 (total = 779); 198–236 adult males were banded each year. We detected (captured and/or resighted) 203 color-banded individuals in 2013, 349 in 2014, and 390 in 2015. These numbers include all marked individuals that we knew to be present in a given year, including both newly banded individuals and returning individuals banded in previous years that we recaptured and/or resighted. In 2013, densities of Grasshopper Sparrows ranged from 0 to 6 territories/10 ha (2.20 ± 0.51 territories/10 ha); in 2014, densities ranged from 0 to 14 territories/10 ha (4.27 ± 0.51 territories/10 ha); and in 2015, densities ranged from 0 to 17 territories/10 ha (4.46 ± 0.51 territories/10 ha).

Density of Grasshopper Sparrows differed across the season, with higher densities during early- and late-season periods (likelihood ratio, $\chi^2 = 10.3$, df = 2, $P = 0.006$; Table 2, model 1). The relationship between density and grazing treatment depended on fire regime (Table 2, model 2; grazing*fire effect test: likelihood ratio, $\chi^2 = 31.7$, df = 2, $P < 0.001$), with both recently burned and unburned cattle-grazed watersheds having the highest densities (Figure 2). The combination of time of season, grazing, fire, and the interaction of grazing and fire explained the most variation in Grasshopper Sparrow density (Table 2, model 3), with ~19 times the support of the treatment-only model. With the exception of the no grazing*fire interaction, the confidence intervals for the beta estimates of all other explanatory variables in the model did not overlap zero (Table 3). Both grazing and burning had positive effects on density; burned, cattle-grazed plots increased by 0.77

TABLE 2. Models explaining the variation in density of Grasshopper Sparrow territories in our study area in eastern Kansas, USA. Management effects include grazing (cattle, bison, none) and fire (burned in current year or not). Temporal effects include time of season (early-, mid-, and late-season periods). All models include year as a fixed effect.

Model	k [a]	Deviance [b]	ΔAIC_c [c]	w_i [d]
Model 3: time + grazing + fire + grazing*fire	10	336.2	0.0	0.94
Model 2: grazing + fire + grazing*fire	8	341.4	5.9	0.05
Model 4: time + grazing + fire + time*grazing + time*fire + grazing*fire + time*grazing*fire	20	328.8	9.6	0.01
Model 1: time	5	483.6	283.7	0.00

[a] Number of parameters used in each model.
[b] Calculated as $-2\ln L$, 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. The lowest AIC_c value is 693.9, from model 3. ΔAIC_c = difference in the AIC_c of the next model compared to the best-fitting model.
[d] Model weight, calculated by the exp(–1/2 *ΔAIC_c) divided by the sum of this quantity for all models.

territories/10 ha, on average, across the season (Table 3). We found no evidence that seasonal effects depended on management regime (Table 2, model 4; grazing*fire*time effect test: likelihood ratio, $\chi^2 = 7.1$, df = 4, $P = 0.13$).

Turnover of Territorial Males within Plots

Overall raw mean turnover of territorial males among all years and watersheds was 52 ± 4%, indicating that the identity of over half of territory holders changed every month. These monthly turnover estimates indicate that ~75% of males changed territories at some point during the season. Among plots, turnover ranged from no turnover (0% turnover; Table 1) to complete territory turnover (100% turnover; Table 1) across the season. The year-only model (variation in turnover explained by year) had the lowest ΔqAIC (3.22), indicating that none of the other models evaluating spatial and temporal effects both independently and interactively had strong support. Thus, the temporal and spatial effects of time of season, grazing, fire, and the interactions of these factors explained negligible variation in turnover.

Role of Conspecific Attraction

The relationship between seasonal changes in territory density and previous territory density was curvilinear; quadratic models fit our data better than linear models (quadratic model: $\Delta AIC_c = 0.0$, $w_i = 0.99$ vs. linear model: $\Delta AIC_c = 10.2$, $w_i = 0.01$). Birds dispersed out of plots that had very low and (especially) very high territory densities, and dispersed into plots with intermediate densities (Figure 3). Thus, we cannot rule out conspecific attraction or competitive interactions in shaping turnover among plots.

Known Movements of Marked Birds

Nine of 19 males fitted with radio transmitters established new territories 120–1,229 m from initial territories (491 ± 17 m; median = 334 m). An additional 7 remained on initial territories throughout the breeding season. We presumed that the remaining 3 males either died or moved to areas that we did not access within or beyond our study site.

Among the 647 marked territorial males, 33% ($n = 213$) were observed defending second territories ≥100 m from the territory on which we initially detected them, whereas 42% ($n = 272$) were observed at the same territory on which we initially detected them. The remaining 25% include males that either dispersed or died. Of the dispersers, 181 (85%) either had a known nest or a reproductive index (RI) score ≥1.5. The remaining 32 males had an RI of 1, indicating only territorial "buzz" singing; 18 of those were observed only once following initial capture, reducing our ability to confirm breeding status through repeated visits. Thus, although the majority of birds that were confirmed to have dispersed did so between breeding attempts, 14 of 181 (8%) males that switched territories may not previously or subsequently have attracted a mate. Dispersal tendency of territorial males was similar among years (24% in 2013, 36% in 2014, and 38% in 2015). Dispersal distances based on resighting ranged from the minimum value (under our criteria) of 101 m to 8,940 m (695 ± 54 m; median = 197 m; Figure 4). Over half of dispersal distances were ≤400 m, and 4% moved >5 km between territories. Forty-eight percent of males moved distances equivalent to 2–4 territories away from previous territories (Figure 4). Mean and median dispersal distances estimated using resighting and radio telemetry were similar, suggesting that our survey protocols were sufficiently extensive and intensive to minimize bias associated with using each method.

We noted dispersal for 7 females that traveled 144–1,321 m. Of those, 4 were detected at subsequent nests; 2 of those 4 changed locations following nest failure, divorcing from mates that were not resighted again. One of the latter remained with her mate following nest abandonment during incubation, and both partners changed territories

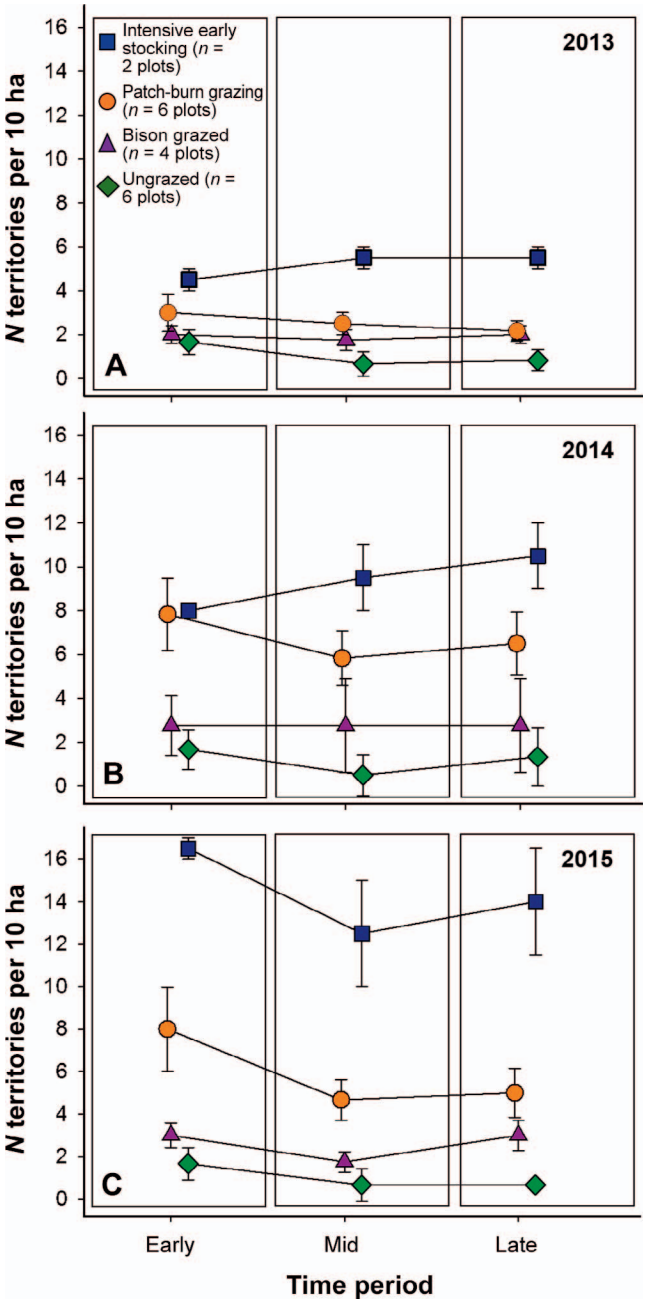

FIGURE 2. Temporal variation in density of territorial male Grasshopper Sparrows in 10 ha plots (i.e. maximum number of territories per plot per management type) in the 2013–2015 breeding seasons in our study area in eastern Kansas, USA. Means (± SE) for each period (early-, mid-, and late-season) of each management regime are connected by lines.

together; the other remained with her mate and switched territories following a successful nest. The remaining 3 females (not detected at postdispersal nests) were resighted >1 mo after their original nest cycle was completed. Two of those females' first nests successfully fledged young, and the other failed as a result of weather.

DISCUSSION

We have provided multiple lines of evidence of a remarkably high prevalence of within-season breeding-dispersal behavior in Grasshopper Sparrows. Over a third of all marked males were detected defending new territories >100 m from previous territories, with some dispersal distances several kilometers between territories. Despite intensive resighting and radio-telemetry efforts, we undoubtedly failed to detect many dispersal events, especially those beyond the boundaries of our site. Thus, our direct observations of dispersal distance represent minima. Over half of territories changed ownership each month, indicating that even the high direct estimates of dispersal tendency from telemetry and resighting likely underestimate the prevalence of this behavior. Consequently, given the different assumptions regarding the fate of unseen birds inherent in each metric, true dispersal tendency likely lies between ~33% and 75%. The consistency of multiple lines of evidence strongly suggests that within-season breeding dispersal is a very common behavioral strategy in this system.

Local densities of Grasshopper Sparrows varied consistently among years according to fire and grazing regime, but the temporal trajectories differed by land use (Figure 2). Both cattle treatments (intensive early stocking and patch-burn grazing) had the highest densities in each year (Figure 2). Fire and grazing treatment reliably predict increases in density over the season (Table 3). Our data are consistent with previous studies at Konza and elsewhere, in which high densities of Grasshopper Sparrows were reported in cattle-grazed areas subject to a short fire-return interval (Powell 2008, Rahmig et al. 2009, Hovick et al. 2012, 2014). Interestingly, although densities of Grasshopper Sparrows in some plots remained fairly constant over the season (e.g., bison-grazed plots in 2014; Figure 2), high turnover on those same plots indicates that the identity of individuals was changing (Table 1). Such patterns suggest that density metrics may be misleading proxies for habitat quality in studies of unmarked birds. Although density was somewhat predictable from management regime (i.e. grazing and/or burning), and likely reflects the availability of vegetation structures suitable for foraging (e.g., bare patches of ground; Powell 2008) and nesting (e.g., dense clumps of vegetation), proximate cues used by sparrows to assess habitat quality may not predictably reflect true quality, leading to dispersal and high turnover.

High turnover in plots with high densities implies that while some birds are perceiving habitat as no longer suitable, others perceive the same area as a good place to settle. Simultaneous emigration and immigration can be explained by unpredictable patterns of nest predation and decision rules based on prior nest success (Fontaine and

TABLE 3. Beta estimates and 95% confidence intervals (CI) for each explanatory variable included in the top model explaining variation in density of Grasshopper Sparrow territories in our study area in eastern Kansas, USA. Management effects include grazing (cattle, bison, none) and fire (burned in current year or not), and temporal effects include time of season (early-, mid-, and late-season periods). Year (2013–2015) is included in all models as a fixed effect.

Explanatory variable	β	95% CI
Intercept	1.01	0.61 to 1.37
Grazing (none)	0.43	0.09 to 0.81
Time (mid-season)	−0.32	−0.52 to −0.12
Time (late-season)	−0.20	−0.39 to −0.01
Fire (yes)	−0.70	−1.13 to −0.27
Year (2014)	0.69	0.47 to 0.91
Year (2015)	0.71	0.49 to 0.93
Grazing*fire (cattle, yes)	0.77	0.29 to 1.23
Grazing*fire (none, yes)	−0.65	−1.34 to 0.02

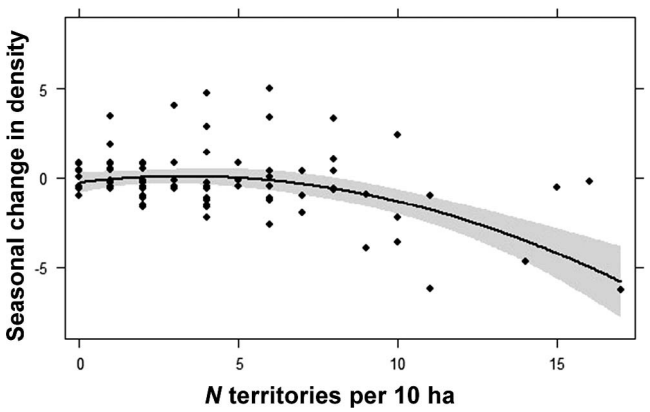

FIGURE 3. Seasonal change in density of territorial male Grasshopper Sparrows in 10 ha plots (i.e. maximum number of territories per plot) in relation to previous density on those plots in the 2013–2015 breeding seasons in our study area in eastern Kansas, USA. Values above zero on the *y*-axis indicate increases in density over the season, and values below zero indicate decreases in density. The shaded region represents the 95% confidence interval around the fitted quadratic relationship.

Martin 2006, Chalfoun and Schmidt 2012). Birds frequently disperse following nest predation (Powell and Frasch 2000, Hoover 2003), while others may settle in the same areas without a priori knowledge of risk.

Turnover of territory holders was high in all 3 years, but our analysis of the relationships between turnover and habitat variables suggests that turnover is not predictable on the basis of land use. The combination of management and seasonal effects explained only about a quarter of the variation in turnover. Low predictability of turnover may mean that underlying ecological drivers of dispersal behavior such as food abundance and predation risk may not vary in temporally consistent ways or be strongly affected by land use under the range of conditions we studied.

The seasonal changes in density were related to prior densities of conspecifics in a curvilinear fashion; with too many or too few neighboring territories, Grasshopper Sparrows were more likely to disperse. High densities of Grasshopper Sparrows may deplete resources within particular patches, and the birds may then redistribute themselves in relation to available resources (Fretwell and Lucas 1970). Conversely, low densities of Grasshopper Sparrows may indicate low-quality habitat. Our findings somewhat contradict experimental evidence of conspecific attraction in which birds dispersed into areas with high perceived densities (Andrews et al. 2015). Differences between sites may explain differences in results; in Illinois, suitable habitat is limited and interspersed within a matrix of corn and soybean fields, whereas the Konza Prairie is located amid large areas of unplowed tallgrass-prairie habitat totaling >25,000 km^2 (With et al. 2008). Thus, one possibility is that social information may become more important to settlement decisions when habitat is scarce. Alternatively, if overall densities in Illinois correspond to our lowest-density sites, birds may be responding to conspecifics in similar ways across their range.

The prevalence of within-season dispersal documented here may be more typical of grassland-dependent birds than of forest-dwelling birds. In North America, the data are scant; only 2 studies have documented within-season breeding dispersal in grassland-obligate birds, in Dickcissels (*Spiza americana*; Walk et al. 2004) and Burrowing Owls (*Athene cunicularia*; Catlin and Rosenberg 2008). Another study documented "nomadism" in Sedge Wrens (Hobson and Robbins 2009). In these cases, a third to

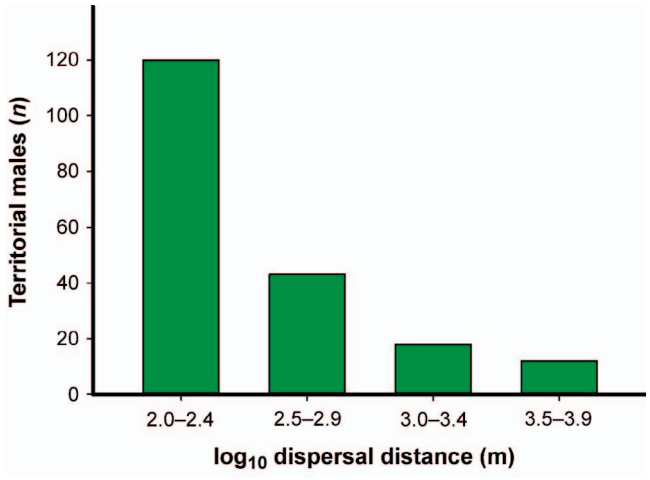

FIGURE 4. Histogram of within-season breeding-dispersal distances of territorial male Grasshopper Sparrows in our study area in eastern Kansas, USA. Dispersal distances have been log transformed to facilitate visualization of distances from 100 to 9,000 m.

nearly all individuals in the population dispersed within the season over long distances (22–806 m in Dickcissels, 55–2,802 m in Burrowing Owls, and potentially all individuals over hundreds of kilometers in Sedge Wrens; Walk et al. 2004, Catlin and Rosenberg 2008, Hobson and Robbins 2009). Several studies of birds in similar habitats elsewhere in the world describe changes in abundance and distribution of unmarked birds. Potentially, such studies might represent examples of within-season breeding dispersal, although they were not described as such by the authors of those studies. In the savannas and shrublands of sub-Saharan Africa, 3 species engage in "itinerant breeding" or within-season dispersal (Jaeger et al. 1986, Grégoire and Cherry 2007, Bötsch et al. 2012). In Europe, many species that were once associated with grasslands are now largely restricted to hay fields and farmland, and several are notable for within-year patterns of changes in abundance and distribution, including Eurasian Skylark (*Alauda arvensis*), Ortolan Bunting (*Emberiza hortulana*), Cirl Bunting (*E. cirlus*), Corn Bunting (*E. calandra*), and Woodlark (*Lullula arborea*) (Dale et al. 2006, Brambilla et al. 2012). Distances between breeding sites for these species appear to be roughly comparable to those in Grasshopper Sparrows, ranging from 28 to 70 km between breeding locations (Jaeger et al. 1986, Dale et al. 2006, Grégoire and Cherry 2007, Catlin and Rosenberg 2008, Hobson and Robbins 2009, Bötsch et al. 2012, Brambilla et al. 2012). Thus, evidence from 3 continents corroborates the idea that within-season breeding dispersal may be a common but not widely recognized strategy of grassland-dependent birds. Such a pattern, if it exists, would be consistent with spatial and temporal heterogeneity selecting for mobile strategies that enable animals to track constantly moving targets of habitat quality. The dimensions of habitat quality these birds may be tracking, however, are currently unknown.

Our study reveals several important insights applicable to the study of breeding dispersal in birds generally. First, our data are consistent with theoretical models that suggest high mobility in spatially heterogeneous and temporally dynamic landscapes (McPeek and Holt 1992, Switzer 1993). Second, the relative importance of conspecific attraction to settlement decisions may be context specific, and responses appear to differ among regions, population densities, or landscape configuration. From the standpoint of study design, our results highlight the fact that dispersal may go unnoticed without systematic resighting of marked individuals over whole breeding seasons. The densities of breeding birds can remain constant, while the identities of territory holders change once or more over a single breeding season. The high territory turnover we report here, even in areas of high density, implies that density alone does not capture the complexity of habitat-selection decisions made by individuals. High densities may often be sustained by movements of birds that depend on patches managed under alternative land use for part of the breeding season. Our results also emphasize the utility of incorporating large spatial scales into study design, given that the incidence of within-season breeding dispersal may be falsely attributed to mortality if dispersal movements are large in relation to the size of the study area. Consequently, our results can inform conservation as well, because high mobility may increase grassland birds' ability to locate isolated patches of high-quality habitat and to colonize newly created or restored habitat.

This description of the incidence and patterns of within-season breeding dispersal sets the stage for future empirical tests of the ecological and evolutionary causes of within-season breeding dispersal. The underlying axes of habitat quality that likely influence dispersal are predation risk, food availability, and nest microhabitat. Direct tests of these ecological processes may provide insight into the factors most important in shaping variation in individual decisions to disperse between breeding attempts and postdispersal settlement choices. Increasing understanding of the factors that explain variation in dispersal behavior, both within and among species, is critical for testing theoretical predictions formulated largely in the context of less mobile organisms, and for improving the conservation of declining species.

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Data deposits: The data we collected for this project have been archived in the Konza Prairie LTER Data Portal (Dataset CBS: http://www.konza.ksu.edu/knz/pages/data/Knzdsdetail.aspx?datasetCode=CBS01).

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