



Causes and consequences of avian within-season dispersal decisions in a dynamic grassland environment

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Understanding the causes and consequences of dispersal is key to identifying selective pressures underlying species-level variation in biogeography, metapopulation dynamics and adaptive capacity. We tested the hypotheses that nest predation and/or brood parasitism avoidance drive breeding dispersal decisions and that dispersal functions to reduce subsequent reproductive failure in grasshopper sparrows, *Ammodramus savannarum*, breeding in eastern Kansas, U.S.A. Over 2 years, we monitored the fate of 222 nests and the movements of 144 parents. We established the spatiotemporal patterns of nest success among all nests, then related nest predation and parasitism to subsequent dispersal behaviour and reproductive success. Birds were more likely to disperse following nest predation, but decisions were unaffected by parasitism. Dispersers experienced higher chances of subsequent nest survival than did site-faithful individuals. Although second nests were parasitized less often than were first nests, dispersers did not experience substantially lower parasitism than did site-faithful individuals, suggesting that the challenges of predation and brood parasitism may be solved in different ways. This study represents one of few tests of alternative hypotheses explaining dispersal decisions of songbirds within seasons and represents a rare case study of the consequences of breeding dispersal on subsequent reproductive success. Our results suggest that differences in dispersal tendencies may result from variation in risk-response thresholds rather than alternative causal drivers.

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Dispersal is a trait common to nearly all living organisms and is the process by which gene flow occurs. Consequently, variation in dispersal tendency is critical to our understanding of biogeographical patterns (Choudoir, Barberán, Menninger, Dunn, & Fierer, 2018), metapopulation dynamics (Stacey & Taper, 1992), community assembly (Lowe & McPeck, 2014) and local adaptation (Jönsson et al., 2016). Most animals make natal dispersal movements from birth sites to first breeding sites with large consequences for fitness (Greenwood & Harvey, 1980; Matthysen, 2005). Additionally, in mobile taxa, subsequent dispersal from one breeding site to another is possible and sometimes common (Ronce, 2007). Breeding dispersal allows individuals to track favourable conditions in temporally variable environments and results in connectivity of spatially structured populations over fragmented landscapes (Ronce, 2007). Because movements in and out of populations confound estimates of true survival (Sandercock, 2006), understanding the ecological factors shaping dispersal is critical to

developing accurate demographic models and inferring population trajectories. Furthermore, identifying the drivers of dispersal is important to interpreting geographical and taxonomic variation in site fidelity, evaluating assumptions inherent in ecological theory and making sense of long-term population trends (Acevedo & Fletcher, 2017; Brawn & Robinson, 1996; Greenwood & Harvey, 1982).

As with natal dispersal, breeding dispersal can yield genetic benefits, foremost among them being inbreeding avoidance (Clobert et al., 2012). However, because natal dispersal is more ubiquitous and precedes breeding dispersal in an individual's lifetime, alternative factors dominate explanations for breeding dispersal. As spatial and temporal variability of environmental conditions increases, predictability of local habitat quality declines (McPeck & Holt, 1992; Paradis, Baillie, Sutherland, & Gregory, 1998; Switzer, 1993). Under low predictability, individuals cannot rely on past experience to accurately anticipate future reproductive success or chances of survival. Thus, breeding dispersal is often attributed to habitat variability. Yet the axes of habitat quality most strongly affecting fitness vary according to species-level traits and community context. Factors commonly invoked include food availability (e.g. *Erigone* spiders; Bonte, Lukac, & Lens, 2008), density of

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competitors (e.g. earthworms, *Aporrectodea icterica* and *Dendrobaena veneta*; Mathieu et al., 2010), availability and spatial predictability of breeding sites or mates (e.g. Andouin gulls, *Ichthyetaeus audouinii*: Fernández-Chacón et al., 2013; or grey seals, *Halichoerus grypus*: Weitzman, den Heyer, & Bowen, 2017) and predation or brood parasitism risk (e.g. damselflies, *Calopteryx virgo*: Suhonen, Honkavaara, & Rantala, 2010).

In birds, breeding site fidelity is the norm; even in migratory species, many birds return to the same patches or territories year after year (Cresswell, 2014). However, because birds are so exceptionally mobile, dispersal between breeding seasons can occur frequently (Marzluff, DeLap, Oleyar, Whittaker, & Gardner, 2016). In highly variable environments, some birds even disperse between breeding attempts within the same breeding season; in marshland/coastal breeding species, as many as 65% of individuals switch breeding territories within seasons (Beletsky & Orians, 1987; Stenzel et al., 1994). The rules underlying individual dispersal decisions frequently appear to hinge on nest success, where birds adopt a 'win-stay, lose-switch' strategy (Chalfoun & Martin, 2010). In species as different as goldeneyes, *Bucephala clangula* (Dow & Fredga, 1983), northern flickers, *Colaptes auratus* (Fisher & Wiebe, 2006), and greater flamingoes, *Phoenicopterus roseus* (Nager et al., 1996), birds whose nests are depredated are more likely to move to new breeding locations in subsequent years than those that successfully raise young. The fitness consequences of such movements are far less understood; dispersers often do not experience enhanced subsequent reproductive success relative to site-faithful individuals (Calabuig, Ortego, Cordero, & Aparicio, 2008; Ost, Lehikoinen, Jaatinen, & Kilpi, 2011).

Nest predation is only one of numerous factors affecting reproductive success. Brood parasitism occurs when conspecifics or allospesifics lay eggs in other birds' nests, thereby avoiding energetic and opportunity costs associated with nesting. Parasitism directly reduces host fitness through egg or nestling destruction and/or ejection, and indirectly via competition among nestlings for parental care, potentially reducing future reproductive investment by host parents (Robinson, Rothstein, Brittingham, Petit, & Grzybowski, 1995). Some hosts can discriminate between their own eggs and those of brood parasites (dickcissels, *Spiza americana*: Peer, McCleery, & Jensen, 2018) and will eject or destroy parasite eggs (Hauber et al., 2014). However, egg rejection increases the risk of retaliation by parasites (Abou Chakra, Hilbe, & Traulsen, 2014; Hoover & Robinson, 2007; Peer et al., 2018) and under some conditions, hosts abandon nests following parasitism (Servedio & Hauber, 2006). Thus, brood parasitism risk could influence the decision to stay or leave even in species that routinely raise parasitic young (Chaianunporn & Hovestadt, 2012). Some evidence suggests this is the case; prothonotary warblers, *Protonotaria citrea*, and great reed warblers, *Acrocephalus arundinaceus*, that were parasitized in one year were more likely to nest at new sites the following year (Hoover & Reetz, 2006; Koleček et al., 2015). However, if individuals do not discriminate between successfully fledging host or parasite young, the 'win-stay, lose-switch' strategy may not be evolutionarily stable (Schmidt, 2001), and consequently parasitism and predation may exert different selective pressures on dispersal behaviour.

Midcontinental grasslands of North America are one of the most dynamic environments on earth, shaped and maintained by fire, grazing by large herbivores and variable rainfall (Knapp & Smith, 2001). The combined effects of climatic variability and disturbance regimes result in dramatic changes in habitat attributes within and between years (Knapp, Briggs, Hartnett, & Collins, 1998; Wiens, 1974). Associated with this interannual unpredictability, Great Plains grassland-dependent bird species exhibit far lower site fidelity than is typical in more predictable forested environments

(Jones, Dieni, Green, & Gouse, 2007). Mounting evidence suggests that in addition to between-year movements, grassland-dependent birds respond to their temporally dynamic environments by routinely dispersing between breeding attempts within seasons (Herse, Estey, Moore, & Boyle, 2017; Hobson & Robbins, 2009). Although such movements could be shaped by vegetation per se (via the availability of suitable nest sites), or bottom-up processes influencing other axes of habitat quality, it is likely that changing vegetation structure affects the key determinants of reproductive success. Ground-nesting grassland birds in North America's tall-grass prairie experience high rates of nest predation (McNew, Hunt, Gregory, Wisely, & Sandercock, 2014). Furthermore, tallgrass prairies lie at the core of the historical distribution of brown-headed cowbirds, *Molothrus ater* (hereafter, cowbirds), and the incidence of nest parasitism can be as high as 92% for some species and sites (Jensen & Cully, 2005). Given the importance of both predation and parasitism to avian reproductive success, we hypothesized that these two factors would be dominant drivers of grassland bird within-season breeding dispersal behaviour.

We investigated how the inherent variability of grassland systems affects nest success and how nest predation and brood parasitism shape dispersal decisions in grasshopper sparrows, *Ammodramus savannarum* (Emberizidae), breeding in the Flint Hills of northeast Kansas, U.S.A. This species experiences high rates of both predation and parasitism locally (Hovick et al., 2012; Rivers, Jensen, Kosciuch, & Rothstein, 2010). Within-season breeding dispersal of grasshopper sparrows is remarkably common at this site; roughly half of all territorial males move to new territories midseason, sometimes moving several kilometres (Williams & Boyle, 2018). Although the spatial distributions of territories are shaped by the interactive consequences of fire and grazing, movements are not related to these drivers of grassland dynamics in straightforward ways (Williams & Boyle, 2018).

In this study, we determined nest fates in an experimentally managed landscape to first elucidate the temporal and spatial effects of fire and grazing disturbances on nest survival. We then tested the following predictions relating predation and nest parasitism to dispersal behaviour. If predation avoidance influences within-season breeding dispersal, we predicted that (1) birds would be more likely to disperse following nest failure than after successfully raising first broods. If the timing of predation (relative to nest stage) confers information about relative risk, we predicted that (2) birds would be more likely to disperse if their first nests failed early in the nesting cycle relative to those whose nests failed closer to fledging. If nest parasitism avoidance contributes to explaining dispersal decisions, we predicted that birds whose first nests (3) were parasitized at all or (4) received more cowbird eggs/nest would be more likely to move to new breeding sites than birds that received none or fewer cowbird eggs. To determine the potential fitness consequences of those movements, we predicted that (5) nest success would be greater, (6) nest parasitism incidence would be lower or (7) of lower intensity in comparisons of first and second nests of birds that dispersed between attempts, while we would expect no change in intensity and incidence of parasitism, or in nest success of site-faithful individuals. Finally, (8) nest success measured at the individual level should mirror the benefits of dispersal measured at the population level.

METHODS

Study Species and Area

Grasshopper sparrows are small-bodied (~17 g) passerines that rely on native grasslands year round (Vickery, 1996). Grasshopper sparrows breed from southern Canada, throughout much of the

U.S.A., and in parts of Mexico, the Caribbean and Central America (Vickery, 1996). In midcontinental tallgrass prairies, grasshopper sparrows are migratory and breed at locally high densities in areas that are burned every 1–3 years and grazed at low or moderate intensities (Powell, 2006, 2008). Periodic fires minimize woody vegetation that sparrows avoid (Graves, Rodewald, & Hull, 2010), while permitting dead grass to accumulate, which is used by sparrows for nesting (Frey, Jensen, & With, 2008). Grazing produces bare patches of ground used for foraging (Vickery, 1996). Grasshopper sparrows mainly consume arthropods during breeding, preferring grasshoppers, arachnids, beetles, hemipterans and caterpillars (Joern, 1988; Kaspari & Joern, 1993).

Grasshopper sparrows begin returning to northeast Kansas in late March or early April, with males establishing and defending territories soon after arrival. Females arrive after males and select mates in April from among the territorial males (Vickery, 1996). Birds start laying their first clutches in early May. Grasshopper sparrows build domed nests of grasses on the ground in clumps of forbs or grass. Females incubate four to five eggs following laying of

the penultimate egg. At our site, ~48% of nests also contain one to three parasitic eggs (Rivers et al., 2010). Although grasshopper sparrows accept cowbird eggs, we have found parasitic eggs buried under nesting material, indicating that they are capable of distinguishing parasitic eggs from their own. Incubation lasts 10–12 days, and young fledge after 6–9 days (Vickery, 1996). Young disperse away from natal territories a few weeks postfledging (Anthony, Gill, Small, Parks, & Sears, 2013). Males defend territories and sing from perches until early August.

We worked at the Konza Prairie Biological Station, a 3487 ha tract of tallgrass prairie co-owned by Kansas State University and The Nature Conservancy, located ~5 km south of the city of Manhattan (Fig. 1).

Konza Prairie is part of the Long-Term Ecological Research (LTER) network and is experimentally managed with combinations of prescribed fire and grazing in watershed-level treatments (Knapp et al., 1998). We worked on 18 pastures representing replicated combinations of the disturbance regimes that create grasshopper sparrow habitat: year-long bison-grazed or ungrazed

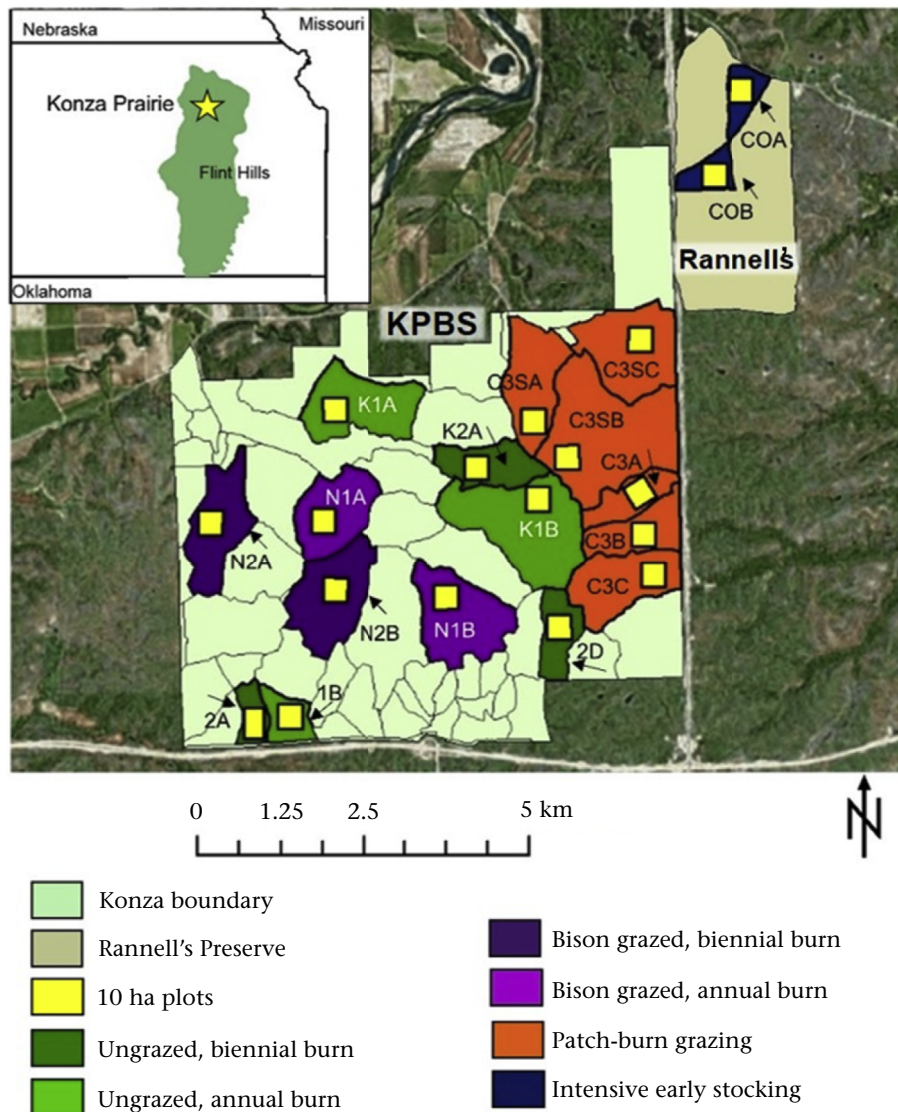


Figure 1. Map showing the Konza Prairie Biological Station (KPBS) and the Rannell's Preserve. Internal boundary lines represent pastures managed with varying grazing and burning regimes. The 18 pastures on which we worked are labeled and shaded by grazing regime; purple represents bison-grazed areas, orange and blue represent cattle-grazed areas, and green represents ungrazed areas. Yellow squares mark locations of 10 ha plots. The inset map locates the study site (star) within the Flint Hills (green shading) in eastern Kansas, U.S.A.

pastures burned annually or every 2 years; pastures grazed by cow–calf pairs and burned rotationally every 3 years (i.e. ‘patch-burn grazing’; [Fuhlendorf & Engle, 2001](#)) and pastures burned annually and grazed under an ‘intensive early stocking’ regime consisting of double-stocking of steers from April to July ([Owensby, Auen, Berns, & Dhuyvetter, 2008](#)). Intensively early stocked pastures were located on the adjacent Rannell’s Flint Hills Prairie Preserve, a 1175 ha tract of tallgrass prairie owned by Kansas State University. We refer to the two preserves collectively comprising our study site as ‘Konza’. Within each pasture, we randomly located a 10 ha plot (316.5 × 316.5 m) located ≥20 m from any road or fence line ([Fig. 1](#)). Prescribed fires occurred in March and April prior to green-up and arrival of most migrant birds.

Nest Searching and Monitoring

Throughout the 2014 and 2015 breeding seasons, we searched for nests by rope dragging ([Higgins, Kirsch, & Ball, 1969](#)), haphazardly flushing females from nests, and behavioural observations. We recorded nest locations using hand-held GPS units (GPSmap 60CSx, Garmin, Olathe, KS, U.S.A.) and placed painted rocks and flags 5 m from the nest to aid in nest relocation. We candled eggs to estimate age ([Lokemoen & Koford, 1996](#)) and counted eggs and/or nestlings of sparrows and cowbirds. We identified cowbird eggs by size and pigmentation, and nestlings based on rictal flange colour. We monitored nests every 2–3 days to determine nest fates. For nests first located posthatching, we estimated nestling age based on developmental stage ([Vickery, 1996](#)). To estimate fail and fledge times, we embedded iButton temperature loggers (Maxim Integrated Products, Sunnyvale, CA, U.S.A.) at the bottom of the nest cup and at paired (ambient) locations ~5 m from the nest under similar vegetation. We programmed iButtons to record temperature at 10 min intervals, assigning nest completion time as the time that nest temperature traces began to track ambient temperature variation.

We considered nests to be successful if at least one grasshopper sparrow or cowbird chick fledged, typically confirmed by sightings of the fledgling(s), or of parents carrying food or alarm calling near completed nests. When we could not confirm fledging, we assumed the nest was successful if contents disappeared at fledging age (~8 days), we resighted putative nest parents ‘chipping’ nearby and the nest remained intact. We recognize that a small percentage of nests could be wrongly coded as successful using these field methods. However, subsequent nest video camera data from this system indicated that we correctly distinguished between successful and depredated nests in 37 of 38 cases. We assumed nests failed as a result of predation when contents disappeared from nests prior to the expected fledging date and we detected no adult activity nearby. We used direct evidence (e.g. intact dead nestlings, flooded nests) and the timing of failure relative to heavy rainstorms (≤6 h) to classify nests as failing because of weather. A small fraction were trampled by grazers, failed by researcher disturbance or abandoned for unknown reasons.

Coding Nesting Attempts

To test predictions regarding the fitness consequences of dispersal (prediction 8), we compared the fates of nests that were found prior to within-season movements (predispersal) and following within-season movements (postdispersal) in two ways. When we located more than one nest of the same individual within seasons, we evaluated fates of paired, presumed first and second, nests directly. However, for most individuals, we located only one nest per season. We also sometimes found unmarked territorial males appearing on plots for the first time and initiating new nests as late as July or early August. Those later nests likely

reflected second (or later) breeding attempts following within-season breeding dispersal events. Therefore, we categorized nests as either ‘first’ or ‘second’ based on the following calculations. As the typical laying to fledging period lasts 24 days, we used first egg dates of 30 April in 2014 and 11 May in 2015 to calculate the earliest dates that a five-egg nest could successfully fledge, as 23 May 2014 and 4 June 2015. We allowed at least 1 week for birds to disperse and establish a new territory and another week to build a nest; thus 8 June 2014 and 18 June 2015 represent the earliest possible clutch initiation dates for second nests following the successful fledging of a first brood. Because parents feed fledglings, we added another week to the later date of 18 June and assigned 25 June as the latest date in both years for which nests could plausibly represent first attempts of the season. We thus divided the season into two halves, with the nests of a given individual initiated prior to 25 June coded as ‘first’ nests and later nests coded as ‘second’ nests.

We recognize that nests initiated earlier than 25 June may well reflect re-nesting attempts by females whose true first nests failed. Thus, an unknown fraction of nests coded as first attempts were likely second attempts and some ‘second’ nests may represent a third or subsequent nesting attempt made by an individual that season. Violations of this assumption do not influence the interpretation of our results, however, because our predictions assess behavioural responses to prior nesting success (regardless of the attempt) and consequences of those responses for subsequent nest survival. If anything, violation of this assumption would reduce our power to detect relationships between predation, parasitism and dispersal, rather than inflate it.

For individuals inferred to have dispersed following early nesting attempts, we cannot rule out the possibility that some individuals may have died or abandoned reproduction for that year. Several lines of evidence suggest that most birds that disappeared likely dispersed, however. First, given the frequency of within-season breeding dispersal to known locations within our study area (33%) and the large areas of suitable habitat surrounding our site, we suspect that many individuals established territories in areas we did not survey and that they initiated a second (or later) brood elsewhere ([Williams & Boyle, 2018](#)). Second, unmarked territorial males appeared on study plots later in the breeding season at similar frequencies to those that disappeared, which we inferred as having dispersed. Thus, it is therefore probable that disappearances reflect within-season movements rather than individual mortalities or the cessation of breeding activities. Furthermore, we used behavioural cues to assess mating status of each male in every survey ([Rivers, Althoff, Gipson, & Pontius, 2003](#)). Based on observations directly indicating nesting behaviour or the incidence of vocalizations functioning in the context of pair bonds ([Lohr, Ashby, & Wakamiya, 2013](#)), we estimate pairing success to be as high as 97% for males in this population (E. J. Williams, personal observation). Thus, it seems unlikely that birds that disappeared early in the season would forgo further mating opportunities when the chances of establishing a new pair bond are high.

A final consideration is that, due to the low return rates in this population, only 3% of nests in 2015 belonged to individuals included in our 2014 data set and we opted to include all nests in our analyses. Since our objective was to examine the drivers of within-season breeding dispersal, we treated each individual/year independently in our analyses and included all males for which we could assign dispersal status. However, we recognize that if dispersal propensity is repeatable within individuals, including both years’ data for these few individuals is a form of pseudoreplication. To determine whether including all data from these individuals influenced our results, we ran analyses both with and without the 2015 nests and report the resulting minor differences.

Dispersal Behaviour

We assessed dispersal behaviour via ~weekly resighting surveys supplemented by radio telemetry (described in Williams & Boyle, 2018) and used both methods to assign dispersal status of putative parents of nests. We captured grasshopper sparrows in mist nets (Ecotone, Gdynia, Poland) and placed a numbered U.S. Geological Survey band and a unique combination of three coloured leg bands on each adult. We systematically searched within the 10 ha plots and resighted birds opportunistically elsewhere within focal watersheds every week (mean \pm SD = 8.4 \pm 3.1 days, range 6–17 days), recording two to eight locations of territorial males each survey. On 19 male parents, we affixed 0.52–0.56 g radiotransmitters with ranges of 0.8–1.6 km. Transmitters and harnesses weighed \leq 4% body mass. We confirmed the location of these males every 2 days, and when they disappeared from initial territories, we searched until we relocated them, or for 2 weeks over a \geq 5 km radius. We failed to locate three tagged birds, inferring them to have died or dispersed beyond our search radius.

We considered males to have dispersed if they (1) displayed territorial behaviour \geq 100 m away from the centroid of their original territory or nest location, or (2) were not resighted on or near their initial territory \geq 1 week after their nest failed or fledged. We chose a 100 m cutoff because territory sizes are 43 m (\pm SE 2 m) in diameter at Konza. Thus, our 100 m spatial scale is comparable to the 2 \times territory radius commonly applied in other studies (Becker, Roeder, Husak, & Murphy, 2018; Paxton, Sogge, Durst, Theimer, & Hatten, 2007). Conversely, we considered birds to be site-faithful if they remained territorial within 100 m of their original territory or nest $>$ 1 week after the nest failed or fledged.

We categorized nests as 'predispersal' if we located them prior to a parent's movements and as 'postdispersal' when they were located on second territories following dispersal movements. We also coded nests as 'postdispersal' if the individual appeared for the first time on our intensively surveyed plots after 25 June and were assumed to have dispersed from elsewhere on or off our study area. Although both males and females sometimes dispersed, and potentially, both parents of the same nest may have behaved differently following nest success or failure, we could typically only assign movement status for the male due to the difficulty of resighting secretive females. However, 3% of nests represented females that dispersed between nesting attempts. We ran analyses without the nests of dispersing females and found qualitatively identical results. Thus, we present the results based on the full data set.

Analyses

We first evaluated the underlying temporal patterns and consequences of habitat variability on nest survival using all nests found in both years ($N = 222$ nests; Supplementary Material, Table S1). We used the nest survival procedure of the program MARK (v.6.2; White & Burnham, 1999) implemented in RMark (Laake & Rexstad, 2008). Program MARK uses a maximum likelihood approach and the logit link function to estimate daily survival probabilities (Dinsmore, White, & Knopf, 2002; White & Burnham, 1999). 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 equally parsimonious (Burnham & Anderson, 2002). We extrapolated daily nest survival estimates to a 24-day incubation to fledging exposure period and estimated variances using the delta method (Powell, 2007). We tested models including all combinations of the additive effects of grazing treatment (bison, cattle, no grazing), burned in current year (yes or no), clutch initiation date and year (2014 and 2015). To account for potential

nonlinearity of seasonal trends, we evaluated models that included clutch initiation date as a quadratic term. Additionally, we explored how landscape and seasonal effects might depend on year by evaluating models including interactions between year and each of the other variables, alone and in combination (Supplementary Material, Table S2).

We then tested predictions of the predation and parasitism risk hypotheses to explain within-season breeding dispersal decisions by including dispersal in nest survival models. Although, in nature, dispersal is the inferred response to nest failure and this modelling approach reverses the inferred causality of this relationship, we used this approach because it accounts for the imperfect detection of nests and seasonal variation in nest survival (Dinsmore & Dinsmore, 2007). Modelling dispersal probability as a function of whether or not the nest failed could inflate subsequent inferences made from these results due to the inherent biases associated with this method (White & Burnham, 1999). Thus, we first determined whether birds were more likely to disperse following nest failure (prediction 1) by restricting our data set to first nests ($N = 82$; Table S1) for which we could classify parents as having subsequently dispersed or who remained site-faithful, excluding nests that failed because of human interference. We included the spatiotemporal factors included in the top model identified in the previous step, and evaluated whether dispersal behaviour improved model fit.

To determine whether the timing of nest predation affected dispersal decisions (prediction 2), we modelled the likelihood of dispersal (yes/no) as a function of nest age at time of failure in first nests ($N = 82$; Table S1) using logistic regression. To determine whether parasitism incidence (coded as a binary variable, prediction 3) affected dispersal decisions, we compared the proportion of first nests parasitized in birds that subsequently dispersed ($N = 24$ of 45 first nests; Table S1) versus those that remained site-faithful ($N = 21$ of 37 first nests; Table S1) using likelihood ratio chi-square tests. To determine whether intensity of parasitism affects dispersal (prediction 4), we modelled the number of cowbird eggs in first nests as a function of subsequent dispersal behaviour using a GLM with a Poisson distribution and a log link function.

To determine whether dispersal within seasons might function to reduce nest predation and/or parasitism, we first tested the prediction (5) that dispersers increase their chances of nest success following dispersal, including all nests for which we could classify parents as having dispersed or remained site-faithful from direct observations of new territory locations, new birds appearing midway through the season or telemetry data, coding nests as either first or second attempts ($N = 82$ first nests, 62 second nests; Table S1). We constructed nest survival models in RMark, accounting for the spatiotemporal variables identified in step 1, and evaluated the explanatory power of an interaction between dispersal status and nest number. Using the same nests, we determined whether dispersal was associated with reduced parasitism risk (prediction 6), modelling parasitism as a binary response in a GLM using a logit link and testing for an interaction between dispersal status and nest number. Similarly, we modelled the number of parasitic eggs in response to the same predictor variables as in prediction 6 in a GLM using the log link function (prediction 7). Finally, we explored the individual consequences of dispersal in those individuals for which we located two nests within the same season, coding birds as dispersers or site-faithful individuals ($N = 19$ individuals, 38 nests). We calculated daily nest survival estimates for each nest and, using those values as our response variable, constructed a GLMM including individual as a random effect and evaluated the explanatory power of the dispersal status \times nest number interaction. We conducted all analyses in R 3.3.3 (R Development Core Team, 2017).

Ethical Note

All research was conducted under approved ethical animal care and use protocols (Kansas State University No. 3260) and research permits from the North American Bird Banding Laboratory (No. 23836), Konza Prairie Biological Station (No. 202, No. 254) and the Kansas Department of Wildlife, Parks, and Tourism (SC-106-2013, SC-110-2014, SC-037-2015). We took several steps to minimize stress to birds during banding and radiotransmitter attachment. We watched mist nets continuously until capturing targeted territorial birds, which reduced time in mist nets to typically <3 min. Two experienced observers processed birds as soon as they were captured within ~50 m of the capture location, minimizing handling time. For birds receiving transmitters, we used pre-threaded harnesses to quickly attach tags and, if needed, reduced the number of measurements taken so as not to increase the total handling time.

RESULTS

We found and monitored 222 nests ($N = 115$ in 2014, 107 in 2015); 40 were known first or second nests and 182 were inferred based on laying date. Nests received an average (\pm SE) of 0.73 ± 0.07 cowbird eggs. Nests failed as a result of predation ($N = 111$), cowbird parasitism (via ejection of whole clutches, destruction of eggs or nestlings; $N = 6$), human disturbance ($N = 17$), weather ($N = 5$), abandonment for unknown reasons ($N = 5$) and livestock ($N = 2$).

Spatiotemporal Correlates of Nest Survival

Overall raw nest success was 34% (37% in 2014, 33% in 2015). Daily nest survival (\pm SE) across the entire breeding season for both years was 0.89 ± 0.01 (all nests, $N = 222$), with nest survival higher in 2014 (0.91 ± 0.01 ; $N = 115$ nests) than in 2015 (0.86 ± 0.01 ; $N = 107$ nests). Extrapolated across the entire 24-day nesting period, grasshopper sparrow young had a 7% chance of surviving to fledge (0.0664 ± 0.0002). Thirty-nine per cent of nests contained at least one cowbird egg. The combination of spatiotemporal variables that best explained variation in daily nest survival (for all nests ($N = 222$)) were grazing treatment, year and their interaction; no other model was $\leq 2 \Delta AIC_c$. The top model had a model weight of 0.315, which was nearly 3.2 times the support of the next model (Table S2). In 2014, daily nest survival estimates were similar among grazing treatments, whereas in 2015, survival was generally lower, and dramatically so in bison-grazed pastures relative to cattle-grazed and ungrazed areas (Fig. 2).

Why Disperse?

We modelled the fates of 82 first nests belonging to either site-faithful parents (i.e. birds that subsequently remained on the same territories; $N = 37$) or dispersers (i.e. those that subsequently departed; $N = 45$). After accounting for the spatiotemporal variables identified in the full data set, we found overwhelming support for dispersal status improving fit to our data (prediction 1; Table 1).

The model including only grazing, year and their interaction had a ΔAIC_c of 19.8 and model weight of 0.0003, whereas the top model including dispersal status had a model weight of 0.658. In analyses that excluded the seven nests from 2015 sired by males represented in the 2014 data set, the relative support for a dispersal-only model and the model including dispersal, year, grazing treatment and their interaction were reversed, with the dispersal-only model being 0.95 ΔAIC_c values lower than the top model in Table 1 ($N = 75$

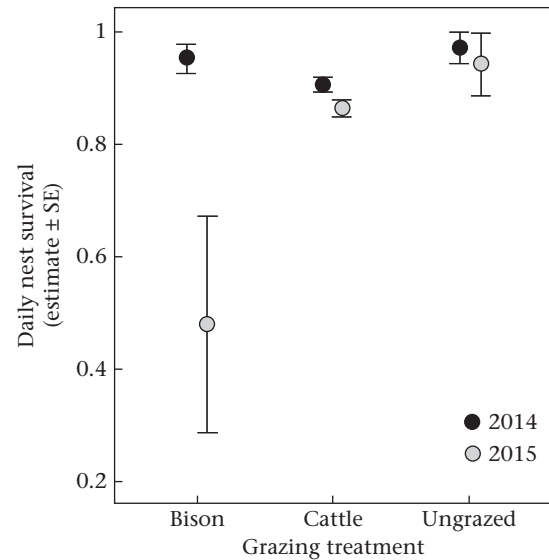


Figure 2. Spatiotemporal factors affecting daily survival estimates of grasshopper sparrow nests at Konza Prairie. Values are from the top model including grazing treatment, year, and their interaction. Estimates from 2014 are depicted in black and 2015 in grey.

Table 1

Models of daily nest survival of first nests of grasshopper sparrows at Konza Prairie, 2014–2015

Model	K^a	ΔAIC_c^b	AIC_c^c	w_i^d
Dispersal + grazing + year + grazing×year	7	0	313.88	0.658
Dispersal	2	1.20	315.08	0.354
Grazing + year + grazing×year	6	19.77	333.65	0.000
Constant	1	21.09	334.97	0.000

^a Number of parameters.

^b ΔAIC_c : difference in the AIC of the next model versus the best-fit model.

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

^d w_i : model weight, calculated as $\exp(-1/2 \times \Delta AIC_c)$ divided by the sum of this quantity for all models.

first nests). Extrapolated over the 24-day nesting period, individuals that later dispersed experienced ~15 times lower nest survival in their first nest attempts (predispersal) than did birds that remained on territories (0.0290 ± 0.0003 versus 0.4546 ± 0.0143 ; Table 2).

Furthermore, birds were more likely to disperse if their nests failed earlier in the nesting cycle (prediction 2); the odds of dispersing increased 1.21 times for each day earlier that the nest failed (likelihood ratio: $\chi^2 = 26.0$, $P < 0.0001$). First nests of birds that subsequently dispersed ($N = 45$ first nests) were parasitized at similar frequencies as first nests of site-faithful birds ($N = 37$ first nests; 53.3% versus 56.8%, respectively; likelihood ratio: $\chi^2 = 0.1$, $P = 0.757$; prediction 3; Fig. 3b). Similarly, the number of cowbird eggs deposited in first nests was not related to subsequent dispersal behaviour of host parents (likelihood ratio: $\chi^2 = 0.2$, $P = 0.657$; prediction 4).

Does Dispersal Reduce Risk of Nest Predation or Brood Parasitism?

Dispersal yielded clear reproductive benefits; daily nest survival of second nests was >12% higher than first nests for dispersers (Fig. 3a; $N = 43$ second nests versus 45 first nests). The model including only dispersal status, first versus second nest, and their interaction was the top fitting model, with a model weight of 0.826

Table 2

Estimates of daily survival of first nests (prior to movements) and second nests (following movements) of grasshopper sparrows that dispersed and those that remained on initial territories (site-faithful)

Attempt	Dispersal status	Daily survival rate			Period survival ^a	
		Estimate	SE	Variance	Estimate	Variance
First (45)	Disperser	0.8628	0.0197	0.0004	0.0290	0.0003
First (37)	Site-faithful	0.9677	0.0106	0.0001	0.4546	0.0143
Second (43)	Disperser	0.9297	0.0145	0.0002	0.1738	0.0042
Second (19)	Site-faithful	0.9250	0.0228	0.0005	0.1541	0.0083

Sample sizes are shown in parentheses.

^a Estimate of daily survival rate and error extrapolated to the 24-day exposure period (nest initiation to fledging) using the delta method.

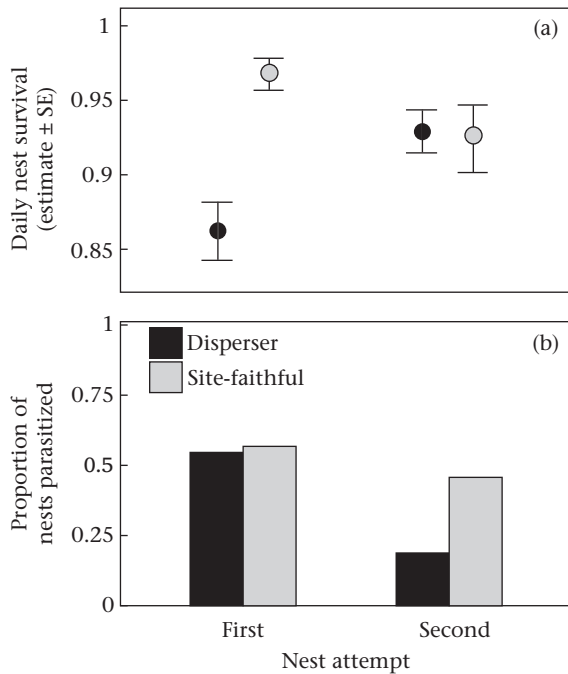


Figure 3. (a) Daily nest survival and (b) proportion of nests parasitized in first and second nests of dispersers (black) and site-faithful (grey) grasshopper sparrows breeding at Konza Prairie, 2014–2015.

(prediction 5; Table 3; $N = 144$ nests: 82 first nests, 62 second nests).

The top model had ~5.8 times the support of the next best model that included spatiotemporal variables, or the model lacking the interaction term. The chance of nests surviving the 24 days from incubation to fledge increased from 0.0290 ± 0.0003 in first nests of dispersers to 0.1738 ± 0.0042 in second nests of dispersers, whereas in site-faithful individuals, the chances of successfully

fledging young decreased from first to second nests (0.4546 ± 0.0143 versus 0.1541 ± 0.0083 ; Table 2).

Although the risk of parasitism was generally lower in second nests, the chances of being parasitized did not decline significantly more for dispersers relative to site-faithful individuals (whole model including dispersal status, nest attempt and their interaction, likelihood ratio: $\chi^2 = 17.1$, $P = 0.0007$; dispersal status * nest attempt, likelihood ratio: $\chi^2 = 0.5$, $P = 0.466$; $N = 144$ first and second nests; prediction 6). The incidence of parasitism dropped from 53.3% to 18.6% in dispersers, and from 56.8% to 46.2% in site-faithful birds (Fig. 3b). Likewise, parasitism intensity declined by similar amounts in second nests of both dispersers and site-faithful birds (whole model: likelihood ratio: $\chi^2 = 13.4$, $P = 0.0003$; dispersal status * nest attempt: likelihood ratio: $\chi^2 = 0.9$, $P = 0.344$; prediction 7). Nests received between zero (59.8%) and four cowbird eggs (2.8%), with a median of one cowbird egg in first nests and zero eggs in second nests. This reduction in parasitism rate and intensity for dispersers and site-faithful birds was not due to an overall seasonal decline in parasitism risk. There was no association between the proportion of nests parasitized and week of nest initiation ($F_{1,10} = 1.3$, $P = 0.278$), nor an association between the mean number of cowbird eggs in nests and nest initiation date ($F_{1,222} = 0.03$, $P = 0.858$). Population-level benefits of dispersing were reflected in the chances of nest success for the 19 individuals for whom we found both first and second nests and could assign dispersal status (prediction 8). Accounting for repeated measures of individuals as a random effect, daily nest survival of dispersers increased from 0.7416 ± 0.0707 to 0.8435 ± 0.0464 from first to second nests, while daily nest survival of site-faithful birds decreased slightly from 0.9361 ± 0.0226 to 0.8926 ± 0.0359 (dispersal status * nest attempt: $F_{1,17} = 30.8$, $P < 0.0001$). Extrapolated over the 24-day period, these differences were substantial. Among this same set of individuals, the nest success of dispersers increased by 22% (0.0168 ± 0.0021 in second nests versus 0.0007 ± 0.0050 in first nests), whereas the success of site-faithful individuals decreased by 32% (0.0654 ± 0.0013 in second nests versus 0.2050 ± 0.0005 in first nests).

Table 3

Models of daily survival of first and second nests of grasshopper sparrows breeding at Konza Prairie, 2014–2015

Model	K^a	ΔAIC_c^b	AIC_c^c	w_i^d
Dispersal + attempt + dispersal × attempt	4	0	534.72	0.826
Dispersal + attempt + dispersal × attempt + grazing + year + grazing × year	9	3.51	538.23	0.142
Dispersal	2	7.02	541.73	0.025
Dispersal + grazing + year + grazing × year	7	9.52	544.24	0.007
Constant	1	16.73	551.45	0.000
Grazing + year + grazing × year	6	19.35	554.07	0.000

^a Number of parameters.

^b ΔAIC_c : difference in the AIC of the next model versus the best-fit model.

^c AIC_c : Akaike's information criterion adjusted for small sample sizes, calculated as the deviance + $2K$ + a correction term.

^d w_i : model weight, calculated as $\exp(-1/2 \times \Delta AIC_c)$ divided by the sum of this quantity for all models.

DISCUSSION

Our results provide strong evidence that within-season breeding dispersal decisions in our focal species are shaped by predation risk but not parasitism avoidance. Furthermore, those movements are associated with reduced risks of nest predation in subsequent nesting attempts. Our findings are notable because although dispersal appears to be shaped by risk across multiple avian lineages (Botsch, Arlettaz, & Schaub, 2012; Fisher & Wiebe, 2006; Forero, Donazar, Blas, & Hiraldo, 1999; Jackson, Rohwer, & Nolan, 1989), detecting payoffs of those decisions has been more elusive (Chalfoun & Schmidt, 2012). In many species, dispersers are subsequently no more successful than site-faithful individuals, potentially due to the costs of movements themselves (Ost et al., 2011). Furthermore, when dispersal does yield reproductive benefits, those often accrue to a subset of individuals in a population, with benefits varying by sex (e.g. Friedrich, Hunt, Catlin, & Fraser, 2014; Terraube, Vasko, & Korpimäki, 2015) or land cover type (e.g. Marzluff et al., 2016). Due to the secretive behaviour of female grasshopper sparrows, we were rarely able to determine whether pairs divorced or remained with mates. Thus, our results are consistent with birds making either better habitat selection or mate selection choices following initial nest failure, or both. Not only were sparrows more likely to disperse following nest predation than if they were initially successful, those decisions were also nuanced by the timing of failure; birds were most likely to disperse if their nests failed early in the nesting cycle. Although we did not measure the predator community to assess whether subsequent nesting attempts occurred in areas with fewer predators, our results imply that grasshopper sparrows use fine-scale local, year-specific information to assess risk and thus respond adaptively to that risk.

Grasshopper sparrows were less successful in avoiding subsequent brood parasitism than predation following dispersal, consistent with results from other systems (common magpie, *Pica pica*, parasitized by great spotted cuckoo, *Clamator glandarius*: Molina-Morales, Martínez, & Avilés, 2012). Although birds apparently learned to reduce their chances of parasitism over the season, dispersers were not clearly more successful in reducing the incidence of brood parasitism. However, it is worth noting that the sample sizes of nests that were parasitized for dispersers and site-faithful individuals were small and our data suggest a potential decline in parasitism intensity for birds that dispersed relative to those that remained site-faithful. The fact that dispersal mitigates the costs of predation but not parasitism could be explained in several ways. (1) The fitness costs of brood parasitism varies among species and costs may be relatively small for grasshopper sparrows. Exploratory analyses of our nest success data revealed that models including cowbird parasitism had low explanatory power, similar to results of other grassland birds (Hovick & Miller, 2013). (2) Grasshopper sparrows may incur substantial fitness costs of parasitism, but not recognize those costs. If parents do not distinguish between their own and cowbird chicks, then they may not respond adaptively to variation in parasitism risk (Schmidt, 2001). Although we do not know whether the birds in our study accurately detected parasitism, we think this unlikely because anecdotal evidence (i.e. egg-burying behaviour) suggests that grasshopper sparrows are capable of distinguishing between their own and parasitic eggs. (3) The fitness costs of parasitism may be high and parents may accurately assess those costs, but the spatial distribution of risk (unpredictable or spatially uniform) may render dispersal an ineffective means to avoid future parasitism. Because second nests were parasitized less intensely than first nests (regardless of laying date), our data strongly support this alternative—birds find ways to minimize parasitism, but not via dispersal. (4) Avoidance of

parasitism may be constrained by other selective pressures. At our study site, nests located in grazed pastures were more likely to be parasitized than those in ungrazed areas, but ungrazed vegetation was rarely selected by this species, likely because it is poor foraging habitat for this species (Rahmig, Jensen, & With, 2009; Sutter & Ritchison, 2005).

The similarity of causes and correlates of between-year dispersal movements (i.e. habitat variability and elevated propensity to disperse following nest failure) and within-season dispersal measured in this study is notable for two reasons. First, we know little about within-season dispersal because it is infrequently studied. Our results are relevant to explaining the sometimes substantial variation in dispersal propensity among populations (Stevens, Turlure, & Baguette, 2010), and leads to the prediction that site fidelity and reproductive success should be strongly correlated among populations, or within populations among years. We would expect that in populations with high nest success, individuals should exhibit high site fidelity to breeding sites (between years) and to territories (within years). Estimating population-level metrics of nest success and site fidelity are both costly and time-intensive. If the associations between these attributes are strong enough, it may be possible to make inferences about one process based on data from the other, when only one data source is available. Second, these results imply that the 'win-stay, lose-switch' strategy may operate differently among populations with differing dispersal propensity. In species that vary in dispersal propensity, individuals in highly dispersive populations may disperse in response to lower risk thresholds (Bonte & Doherty, 2017; Clobert, Le Galliard, Cote, Meylan, & Massot, 2009) rather than qualitatively different causal factors. Variation in risk-response thresholds have been proposed to explain differences in migratory strategies in birds (Ramenofsky, Cornelius, & Helm, 2012), but the substantial knowledge on the proximate causes of avian migration has rarely been applied to dispersal behaviour (Cote et al., 2017). If populations differ in risk-response thresholds, a testable prediction would be that more site-faithful populations should exhibit smaller effect sizes in the relationship between dispersal propensity and timing of nest failure (i.e. bolder, or less risk-averse behaviour). Quantitative evidence supporting such a threshold model for dispersal in wild birds would constitute a major advance in animal movement ecology.

Both the high propensity to disperse and the high rates of nest failure we report have implications for the conservation of declining grassland species. We are certainly not the first to report low nest success of tallgrass prairie-nesting birds (e.g. Herkert et al., 2003; Stauffer, Diefenbach, Marshall, & Brauning, 2011), but even by grassland standards, our estimates are low (7% of nests surviving to fledge). Furthermore, brood parasitism rates are exceptionally high in this region (Jensen & Cully, 2005). Such high predation and parasitism is noteworthy given that the Flint Hills contain the largest remaining tracts of unplowed tallgrass prairie on the continent and are therefore considered a stronghold for threatened species (U. S. Fish and Wildlife Service, 2010; With, King, & Jensen, 2008). The interannual variation in associations between grazing practices and risk of nest failure point to spatial and temporal unpredictability in the associations between proximate cues (i.e. vegetation structure) and underlying risk. Consequently, the same disturbance regimes will result in different vegetation structure and, potentially, different predation pressures in different years due to interannual climatic variation. Thus, solutions must involve preserving habitat heterogeneity at small enough spatial scales to permit short-distance dispersal between breeding attempts, which may be crucial to preserve birds' abilities to respond to year-specific shifting mosaics of risk.

Dispersal of grasshopper sparrows is an example of both condition- and phenotype-dependent behaviour (sensu Clobert et al., 2009); movements appear to be a result of prior experience and objective risk, and individual quality, in that nest site selection shapes future dispersal behaviour. Furthermore, these within-season dispersal movements are informed and plastic (Kesler, Walters, & Kappes, 2010; Ward, 2005). In other words, birds appear to make movement decisions based on both their shifting endogenous state and season-specific environmental cues that provide useful information regarding their chances of future success (Nathan et al., 2008; Robertson, Fletcher, & Austin, 2017). In variable environments where the relationship between exogenous cues and ultimate fitness payoffs change from year to year, within-season dispersal may be more efficient than between-season dispersal for making adaptive habitat selection choices and represent more informed decisions. If correct, this result highlights the importance of temporal and spatial scale-dependence of dispersal for relating movement to demographic processes (Doligez, Cadet, Danchin, & Boulinier, 2003; Rushing, Dudash, & Marra, 2015). When proximate cues reliably predict factors affecting fitness over only very short temporal scales, movements may appear to be less informed than in environments where cues are more temporally consistent. Likewise, that variability likely results in greater incongruence between causal factors shaping departure decisions and the consequences of subsequent settlement choices.

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Declaration of Interest

None.

Supplementary Data

Supplementary data to this article can be found online at <https://doi.org/10.1016/j.anbehav.2019.06.009>.

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