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Social interactions do not drive territory aggregation in a grassland songbird

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Abstract. Understanding the drivers of animal distributions is a fundamental goal of ecology and informs habitat management. The costs and benefits of colonial aggregations in animals are well established, but the factors leading to aggregation in territorial animals remain unclear. Territorial animals might aggregate to facilitate social behavior such as (1) group defense from predators and/or parasites, (2) cooperative care of offspring, (3) extra-pair mating, and/or (4) mitigating costs of extra-pair mating through kin selection. Using experimental and observational methods, we tested predictions of all four hypotheses in a tallgrass prairie in northeast Kansas, United States. Grasshopper Sparrow (*Ammodramus saviarum*) males formed clumps of territories in some parts of the site while leaving other apparently suitable areas unoccupied. Despite substantial sampling effort (653 territories and 223 nests), we found no support for any hypothesized social driver of aggregation, nor evidence that aggregation increases nest success. Our results run counter to previous evidence that conspecific interactions shape territory distributions. These results suggest one of the following alternatives: (1) the benefits of aggregation accrue to different life-history stages, or (2) the benefits of territory aggregation may be too small to detect in short-term studies and/or the consequences of aggregation are sufficiently temporally and spatially variable that they do not always appear to be locally adaptive, perhaps exacerbated by changing landscape contexts and declining population sizes.

Key words: breeding systems; conspecific attraction; cowbirds; fitness; relatedness; threat models.

INTRODUCTION

Understanding the causes of distributional patterns is a primary goal of ecology and central to the management of declining species (Sexton et al. 2009). Mobile animals constantly make habitat selection choices that affect survival and reproductive success (Cody 1985). Individual decisions rarely result in random patterns of distribution (Börger et al. 2008). When animals distribute themselves evenly, theory suggests that competition and despotic behavior likely shape space use (Cresswell 1998, Holdridge et al. 2016). Alternatively, clumped distributions suggest either Allee effects or aggregation around nondepreciable resources (Allee 1931, Fretwell and Lucas 1970). Aggregations occur in diverse taxa (Podulka 2004, Varricchio et al. 2008) and often affect reproductive success, but the mechanisms underlying reproductive benefits are rarely known (Lott 1984, Reed and Dobson 1993).

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Insights into the drivers of territory aggregation come from nonterritorial, colonial species forming high-density aggregations around patchily distributed food resources (e.g., Jourdain and Vongraven 2017) or structures required for reproduction (Wittenberger and Hunt 1985, Sachs and Rubenstein 2007). Conspecifics themselves may also act as resources (Stamps 1988), especially in lekking species (Höglund et al. 1995), those that cluster during locomotion (e.g., Andersson and Wallander 2004) or thermoregulation (Gilbert et al. 2010), and those that hunt cooperatively (e.g., Dumke et al. 2018) or breed cooperatively (Koenig and Dickinson 2004). Aggregations can also reduce predation (Hamilton 1971, Valeix et al. 2009). In sum, animal aggregations occur in response to clumped distributions of key resources or because of the fitness benefits of social interactions.

Aggregation is not without costs, however. Large groups sometimes attract predators (e.g., Vulinec 1990) and increase rates of parasitism (e.g., Leu et al. 2010). Aggregations can also seriously degrade habitats (Kerbes et al. 1990) and exacerbate intraspecific competition for food or mates (Sansom et al. 2008). When the costs of aggregation are high, we instead

expect territorial defense (Brown and Orians 1970, Adams 2001).

Even species that defend their own territories sometimes aggregate those territories (Muller 1998, Tarof and Ratcliffe 2004) for some of the same reasons shaping coloniality (Lack 1968). Aggregated territories are often clumped around patchily distributed food or nest sites (Dias et al. 2009, Wakano et al. 2009) or shaped by conspecific interactions (Stamps 1988, Kokko and Rankin 2006). Aggregations of territorial birds have been studied extensively (e.g., Bohórquez and Stiles 2002), typically focusing on physical attributes influencing habitat quality (e.g., Tiainen et al. 1983, Macedo et al. 2018). However, conspecifics can also act as a resource in territorial species via at least four mechanisms.

First, conspecifics sometimes reduce the risk of predation via vocal signaling (Langham et al. 2006, Webster et al. 2018). Similarly, conspecifics can signal other threats, such as brood parasites, which lay their eggs in other species' nests (Lorenzana and Sealy 2001). If group defense against predators and/or brood parasites functions in territory aggregation, individuals in high-density areas would be expected to produce signals alerting neighbors to threats and experience reduced predation or brood parasitism relative to isolated conspecifics.

Second, territorial birds could benefit from aggregation if they facultatively cooperatively care for offspring. Although socially monogamous species typically raise nestlings alone, in some species, adults sometimes help raise young of nearby pairs (Riehl 2013), and this behavior could be facilitated by short interterritory distances. If aggregation functions in the context of facilitating cooperative care, we expect that cooperative care would be most prevalent in the most aggregated territories.

Third, territory aggregation could facilitate mating with individuals outside the pair bond (Emlen and Oring 1977), a behavior that increases genetic diversity of broods (Johnsen et al. 2000). Thus, aggregated territories can function as a "hidden lek" (Wagner 1993, Tarof et al. 2005), with high densities increasing territory attractiveness to females (Hoi and Hoi-Leitner 1997) and opportunities for extra-pair matings (Danchin and Wagner 1997, Wagner 1998). In at least three songbird species, this driver of territory distribution seems plausible; Willow Warblers (*Phylloscopus trochilus*), Gray Catbirds (*Dumetella carolinensis*), and Reed Buntings (*Emberiza schoeniclus*) nesting in high-density areas rear more extra-pair young than do individuals in low-density areas (Bjørnstad and Lifjeld 1997, Ryder et al. 2012, Mayer and Pasinelli 2013). If aggregation increases the likelihood of extra-pair mating, we expect a positive relationship between aggregation and the proportion of extra-pair offspring in nests.

Finally, extra-pair mating can have negative consequences for cuckolded individuals in socially monogamous pairs. Males that pursue extra-pair copulations have fewer opportunities to guard mates, resulting in a nest filled with rivals' offspring (Chuang-Dobbs et al.

2001, Brylawski and Whittingham 2004). That paternity cost could be reduced if males aggregate with kin, increasing the likelihood of being cuckolded by relatives (Clutton-Brock 2002). Thus, if extra-pair mating is common, the fourth social mechanism underlying aggregation may be that males mitigate the costs of cuckoldry by aggregating with male kin.

We tested 10 predictions to distinguish amongst these four social drivers of territory aggregation: cooperative defense, cooperative care, extra-pair paternity, and kinship. Grasshopper Sparrows (*Ammodramus saviarum*) are small territorial songbirds (Vickery 1996) that distribute their territories in densities varying from 0.24 territories/ha (Renken and Dinsmore 1987) to >1 territories/ha (Danner et al. 2018). Grasshopper Sparrows select grasslands with patches of sparse vegetation for foraging mixed with clumps of denser vegetation for nesting (Whitmore 1981, Ammer 2003). In tallgrass prairies of northeast Kansas, Grasshopper Sparrows preferentially nest in grazed prairies burned every 2–3 yr (Powell 2008) but leave large areas of seemingly suitable areas unoccupied (Appendix S1: Video S1). Sparrow territory density at our site is not related to food abundance, and within-season dispersal movements are not consistently toward high-density areas (Williams 2016) unlike other regions where this species exhibits conspecific attraction (Andrews et al. 2015).

If sparrows aggregate to (1) facilitate *cooperative defense*, we predicted that, relative to males in low territory-density areas, males in high territory-density areas would (i) be more likely to approach simulated intrusions by nest predators or brood parasites, (ii) have lower approach latency, (iii) be more likely to produce alarm vocalizations in reaction to simulated threats, and (iv) be less likely to have their nests depredated or parasitized. If sparrows aggregate to (2) facilitate *cooperative care* (observed infrequently in this species; Kaspari and O'Leary 1988, Ammer 2003, but see Adler and Ritchison 2011), we predicted that (v) nests having nonparent helpers would be located in areas of high relative territory density than nests without cooperative care. If sparrows aggregate territories to (3) facilitate *extra-pair mating*, (which also occurs in this species; Danner et al. 2018), we predicted that (vi) nests with extra-pair young would be located in areas of high relative territory density. If aggregation (4) facilitates *kin selection*, with related males aggregating to minimize costs of extra-pair mating, we predicted that (vii) the distance between related males' territories would be lower than the distance between unrelated males' territories on average, and (viii) the genetic father of extra-pair young would be more closely related to the cuckolded male than the average pairwise relatedness of all males in the population. Finally, if any of these factors explain aggregation, we predicted that nest success would (ix) be higher in areas of high territory density, and (x) be more dependent on social factors than on structural attributes of the territory or landscape surrounding each nest (i.e., height of

vegetation, distance to the nearest edge, relative cover of herbaceous flowering plants at the nest, and distance to the nearest trees). We tested these predictions using data from 658 territories and 223 nests collected over 3 yr.

METHODS

Study species and site

Grasshopper Sparrows are small (14–20 g) grassland-obligate songbirds that breed across much of the continental United States (Vickery 1996). Grasshopper Sparrows are declining across their range, with losses as large as 4% per year in the central United States (Sauer et al. 2011). Mitigating declines of Grasshopper Sparrows and other grassland-obligate species is a regional and national conservation priority (Vickery et al. 1999). Although generally socially monogamous (but see Small et al. 2009), Grasshopper Sparrows engage in extra-pair mating at some sites, and occasionally, cooperative care (Kaspari and O’Leary 1988, Ammer 2003, Danner et al. 2018). Nests at our site are commonly parasitized by Brown-headed Cowbirds (*Molothrus ater*), a native obligate brood parasite (De Geus and Best 1991).

We studied sparrows from May to August, 2013 to 2015, at the Konza Prairie Biological Station (KPBS; 39.106743, -96.609333), a 3,487-ha site in NE Kansas jointly owned and managed by Kansas State University and The Nature Conservancy. We also worked at the Rannell’s Flint Hills Prairie Preserve, a 1,175-ha site owned by Kansas State University. Because these two properties are adjacent to one another, we consider them to comprise a single site (hereafter collectively “Konza”). The pastures at KPBS are experimentally managed with replicated combinations of prescribed fire (every 1, 2, 3, 4, or 20 yr) and grazing regimes (bison, cattle, and no grazing; Knapp and Seastedt 1998). The cattle-grazed pastures on which we worked were managed with patch-burn grazing on a 3-yr fire rotation (Weir et al. 2013). At Rannell’s, pastures were managed with “intensive early stocking” of steers (Owensby et al. 2008). Konza receives an average of 83.5 cm rainfall annually, and monthly mean temperatures range from -3°C to 27°C (Hayden 1998). We studied sparrows on 18 pastures representing replicated combinations of ungrazed, bison-grazed, and cattle-grazed areas managed in combination with annual, 2-yr, or 3-yr burns. We selected study areas to encompass the range of Grasshopper Sparrow habitat associations at this site (Powell 2008).

Capturing males and calculating centroid density

We surveyed by systematically walking through each pasture following a different path each time, attempting to pass within earshot (~100–200 m depending on wind) of all locations. We located territorial, singing males, noted locations of preferred perches, and returned within about a week to capture them. We

attempted to capture every male sparrow within our study area by luring them into 12 × 3 m, 38-mm mesh nylon mist nests (Ecotone, Gdynia, Poland) using small speakers to broadcast conspecific song (territorial “buzz” song; Soha et al. 2009). We placed a unique combination of three colored plastic leg bands and one numbered aluminum U.S. Fish and Wildlife (USFW) band on each bird. We drew 30–100 L of blood from the brachial vein and stored samples on ice before centrifuging within ~6 h. We stored red blood cells in Queen’s Lysis Buffer at -20°C for up to 1 yr prior to genetic analysis. If birds were not present when we returned to band them, we assumed that they did not have a territory and did not include them in analyses.

We surveyed each pasture every ~8 d (min = 5, max = 17), locating males using binoculars and spotting scopes and identifying them by their leg bands. Using a handheld GPS unit, we recorded 1–20 (~3) locations of each male during each survey. Grasshopper Sparrows in this region often disperse between breeding attempts within a single breeding season (Williams and Boyle 2018). Thus, we split the breeding season into three equal-length periods: “early” (before 2 June), “middle” (2 June–6 July), and “late” summer (after 6 July). We grouped location data (capture and perch locations from surveys) for each individual by time period. We assumed that the recorded locations represented the most defended parts of each territory and averaged those to locate a period-specific territory centroid. Some males held territories during more than one time period; we included spatial data for each time period in which they were present, calculating new centroids to account for shifts in territory locations within season.

To test the *cooperative defense* hypothesis (1), we categorically classified individual males as “unaggregated” or “aggregated” based on distance to the nearest neighbor. Grasshopper Sparrows defend territories with average radii of ~50 m (Smith 1968), so we classified males as “aggregated” or “unaggregated” if their centroid was ≤100 m or >100 m from their closest neighbor’s centroid, respectively.

To test the *cooperative care* (2) and *extra-pair mating* (3) hypotheses, we calculated the territory density around each nest. We plotted centroids in ArcGIS (ESRI, Redlands, California, United States) separately for each time period and generated a 200-m buffer around each centroid. We chose this radius based on observations of male forays 100–200 m from their centroid. We generated a kernel density plot of the centroids and buffers, producing a high-resolution (cell size: 2 × 2m) continuous raster of territories/ha. We then plotted the location of each nest (see below) on the kernel density map for the period in which the nest was initiated, extracted density values at that location, and log-transformed those values. We tested predictions of the *kin selection* (4) hypothesis using a distance metric; we calculated Euclidean distances between centroids of each pair present during each time period using SPAGeDi (Hardy and Vekemans 2002).

Behavioral trials

To test predictions of the *cooperative defense* (1) hypothesis, we simulated territory intrusions in 2013. We randomly assigned aggregated and unaggregated males to receive models of a female Brown-headed Cowbird, a black rat snake (*Elaphe obsoleta obsoleta*) posing as a potential nest predator, or a female House Sparrow (*Passer domesticus*) as a control. We mounted a model 5 m from the focal male's primary perch and covered it with a 1 × 1 m opaque camouflaged cloth. One observer (SMM) hid in vegetation 20 m from the model, sitting as low to the ground as possible and waited 15–40 min until the male acclimated to the presence of the concealed mount and observer. If the male did not return to his territory within 40 min, we postponed the trial until the next day.

We initiated 20-min-long trials by revealing the mount by pulling away the cloth using an attached string. In the trials using the House Sparrow and cowbird mounts, we broadcast audio recordings of contact calls of the corresponding species for 2 min interspersed with 2 min of silence throughout the trial. We recorded locations of all perches used by focal males and all aggressive behaviors such as alarm calls or wing fluttering (Vickery 1996). We conducted all trials between 30 min after sunrise to 10:30 h to control for potential diurnal changes in male attentiveness.

Nest searching and monitoring

In 2014 and 2015 we located nests by observing adult sparrows feeding nestlings, flushing incubating or brooding sparrows opportunistically, or by dragging a weighted ~30-m rope within territories. We recorded the location of each nest using a handheld GPS and marked the nest location 5 m from the nest opening. We captured females by flushing them into mist nets placed <1 m from the nest entrance. We banded, measured, and sampled females as we did males so we could identify females during observations. We visited each nest every 2–3 d and recorded the number of sparrow and cowbird eggs and nestlings. When nestlings were 5–7 d old we measured them, took blood samples for paternity analyses, and banded each with a federal aluminum band. When we found dead nestlings, we collected them and stored them in a –20°C freezer for DNA extraction. We categorized nests as “successful” when both (a) host chicks were ≥7 d old when the nest was completed (mean fledge age at our site), and (b) parents were seen nearby chipping and carrying food after the presumed fledge date. We considered nests as “unsuccessful” if the chicks were <7 d old when the nest was found empty, the nest fledged only cowbird young, the nest cup was destroyed, or we saw no later evidence of parental care. If any eggs or nestlings <7 d old went missing, we counted the nest as partially depredated.

Landscape and vegetation around nests

To compare the relationship between nest success, territory density, and landscape structural attributes (prediction x), we measured vegetation in the immediate vicinity of each nest. Increased vegetation height has been associated with higher daily survival at this site (Klug et al. 2010), so we measured vegetation height at the nest cup using a Robel pole (Robel et al. 1970, Martin et al. 1997). Because forb cover at the nest is often positively related to nest success in grassland birds (McKee et al. 1998), we measured the percentage of forb cover at the nest within a 0.25 × 0.5 m Daubemire frame (Martin et al. 1997) surrounding the nest cup. Predation is often high near habitat edges (Johnson and Temple 1990, Herkert et al. 2003, Renfrew and Ribic 2003), so we used aerial imagery of the site (Google Maps, Mountain View, California, United States) to map the trees and pasture edges (e.g., mowed burn guard, gravel road, or paved highway), and measured linear distances from nests to the closest tree line and edge in ArcMap.

Observing cooperative care

To test the prediction that aggregation facilitates cooperative care (v), we observed as many nests as possible (given logistical constraints) that survived to the nestling stage in 2014 and 2015. We observed nests using a 25–60 × 88 mm spotting scope for 30–90-min periods daily between hatching and either fledging or failure. We observed birds from a small (~1 × 1 × 1.5 m) blind placed ≤30 m from the nests between 0600–1100 h. When winds exceeded ~20 kph, we instead hid in bushes to minimize disturbance from flapping blind materials. We recorded the identity of each adult visiting the nest, timing of visits, and behavior of adults ≤30 m of the nest including feeding, singing, interspecific interactions, perching, and removing fecal sacs.

DNA amplification

We used DNA microsatellites previously used to genotype Grasshopper Sparrows to determine the relatedness of nestmates, between adult males and their nestlings, and between pairs of adult males. We extracted DNA from blood samples using a Qiagen DNeasy Blood and Tissue kit (Qiagen, Venlo, Netherlands) and a modified version of the Qiagen protocol (Appendix S1). We amplified DNA at up to five microsatellite loci (Appendix S1: Table S1, Dawson et al. 1997, Gibbs et al. 1999, Bulgin et al. 2003). We included an M13 sequence on the front of each forward primer to add a post-PCR fluorescent tag (Selkoe and Toonen 2006).

We ran PCR reactions at 11.3-μL volumes including 1.3 μL of 20 g/μL DNA, 1.80 μL water, 2.26 μL of 1X Taq buffer, 1.13 μL of 2.5 mM MgCl₂, 1.13 μL of 0.2 nM deoxynucleotide triphosphates, 1.13 μL of bovine serum albumin, 2.034 μL of 0.9 M betaine, 0.565 μL of

0.5 M forward and reverse primers, 0.226 μL of 0.2 M M-13 primer tag, and 0.113 μL of 5X Promega GoTaq Flexi polymerase (Piertney and Höglund 2001). We amplified loci using thermal conditions established for sparrows: 94°C for 3 min, 32 cycles of 94°C for 30 s, annealing temperature for 40 s, 72°C for 40 s, then a final extension step of 72°C for 10 min. We labeled the M13 tags with fluorophore dyes and genotyped samples using an ABI sequencer (Selkoe and Toonen 2006).

Establishing relatedness and paternity

Using GeneMarker (Soft Genetics, LCC, Pennsylvania, United States), we established the genotype of each individual by identifying the base pair length of each allele. We identified possible null alleles using MicroChecker (Van Oosterhout et al. 2004) and determined heterozygosity at each locus using SPAGeDi (Hardy and Vekemans 2002; Appendix S1: Table S2). Because some loci were not in Hardy-Weinberg equilibrium, we calculated the pairwise relatedness value ‘ r ’ (Queller and Goodnight 1989) for males occupying the site during the same third of the year. For the test of prediction vii, each datum represents a unique, pairwise comparison between two males present in the same time period. We used MLRelate (Kalinowski et al. 2006) to calculate the likelihood that nestmates were full- or half-siblings and the likelihood that nestlings were sired by attending social males. We identified the most likely father of each extra-pair nestling using MLRelate and compared the distances between territories of the social and genetic males.

Nest success models

To test predictions ix and x, we compared competing models of daily nest survival using a hierarchical approach. First, we evaluated candidate models to determine the temporal factors that best accounted for variation in nest success due to the inherent variability in grassland ecosystems (Hayden 1998). These models assessed variation in daily nest survival by year, date (linear and quadratic), and a year \times time interaction. Second, we determined the landscape attributes most strongly associated with nest success by evaluating all additive and interactive combinations of vegetation height at the nest, percent forb cover, distance to the nearest edge, and distance to the nearest tree line, z -transforming continuous variables. Third, we tested the simple prediction that territory density was positively related to nest success (ix), evaluating models in which daily survival varied by density and density² (to account for the possibility that nest success was highest at moderate densities; Vickery et al. 1992) relative to a constant model. We compared models using Akaike’s information criterion adjusted for small sample size (AIC_c; Anderson and Burnham 2002). Finally, we evaluated all additive and interactive combinations of the factors included within the top two ΔAIC_c of top-ranked models

from each of the temporal, landscape, and density model sets. We did not restrict this candidate set based on *a priori* expectations because the inherent temporal and spatial variability of the system made it difficult to predict which combinations of factors were likely to be most biologically meaningful. We analyzed nest success with the *RMark* package (Laake 2013) implemented in R (R Development Core Team 2013), which uses a maximum-likelihood approach and a logit-link function to estimate daily nest survival (Dinsmore et al. 2002). We prepared figures with *ggplot2* (Wickham 2016). All data tables and code underlying these analyses are deposited at Dryad (<https://doi.org/10.5061/dryad.3xsj3tx9w>).

RESULTS

Over 3 yr we color-banded 658 adult males and determined territory centroids of ~263 males/year (201 in 2013, 266 in 2014, and 322 in 2015). Within each time period, we analyzed spatial distributions of 57–164 centroids (mean: 118). Some males held territories in >1 time period (32 in 2013, 62 in 2014, and 77 in 2015). We conducted 225 territory surveys, 214 of which resulted in spatial data for at least one banded, territorial male. Grasshopper Sparrow males were not evenly distributed during any period of any year. Territory density varied from 0 to 2.32 territories/ha, and the location of high-density aggregations differed between time periods and years (Appendix S1: Fig. S1). Mean density surrounding nests was 0.77 (SD \pm 0.57) territories/ha (Appendix S1: Fig. S2), with 75% of the nests located where density was <1.01 territories/ha.

Cooperative defense hypothesis

We performed 24 behavioral trials in 2013 with males in 9 unaggregated and 15 aggregated territories. We found no evidence to support the *cooperative defense* (1) hypothesis; aggregated males did not approach models any more closely than did unaggregated males (prediction i) (Fig. 1A; cowbird: $t_4 = 0.4$, $P = 0.727$; snake: $t_3 = 1.1$, $P = 0.351$; control: $t_3 = 0.1$, $P = 0.950$), and their approach latency did not differ (prediction ii; Fig. 1B; cowbird: $t_5 = -0.1$, $P = 0.943$; snake: $t_9 = -0.9$, $P = 0.383$; control: $t_4 = -0.6$, $P = 0.554$). Likewise, males in aggregated territories were not more likely to vocalize (“chip”) in response to threat models compared to males in unaggregated territories (prediction iii; $\chi^2 = 0.2$, $df = 1$, $P = 0.631$).

We used all 223 nests to determine whether high territory density was associated with reduced predation or brood parasitism (prediction iv). Of those, 152 were inferred to have been depredated and 86 were parasitized. The proximity of neighboring males did not confer any protection from predation or brood parasitism. The likelihood of partial or complete nest predation (Appendix S1: Fig. S3a) was not related to the density of male sparrow territories near the nest ($t_{114} = -1.7$, $P = 0.094$).

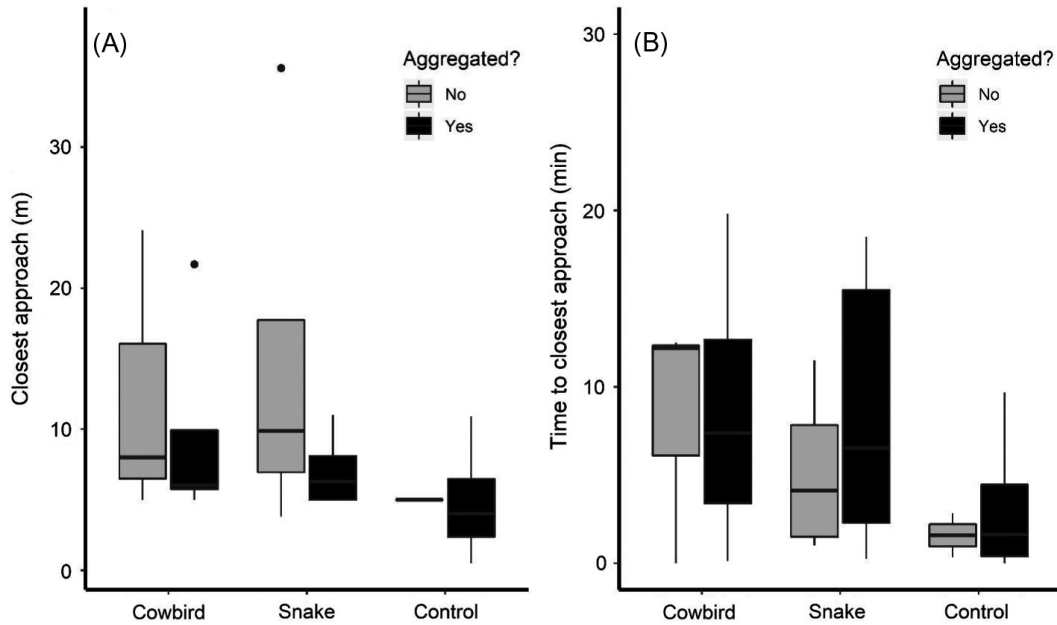


FIG. 1. Aggregation did not affect sparrow responses to cowbird, snake, and control threat models. The closest approach distance to threat models (A) was not different between aggregated (black boxes) and unaggregated males (gray boxes; parasite: $t_4 = 0.4$, $P = 0.727$; snake: $t_3 = 1.1$, $P = 0.351$; control: $t_3 = 0.1$, $P = 0.950$), nor was the latency to approach (B) after the model was uncovered (parasite: $t_5 = -0.1$, $P = 0.943$; snake: $t_9 = -0.9$, $P = 0.383$; control: $t_4 = -0.6$, $P = 0.554$).

Similarly, parasitized nests (Appendix S1: Fig. S3b) were surrounded by an average of 0.2 more territories/ha than unparasitized nests ($t_{204} = -2.2$, $P = 0.028$).

Cooperative care

We observed 44 nestling-stage nests for a total of 106 h to assess whether nests with helpers were located in higher-density areas than others (prediction v). Despite previous evidence of cooperative feeding at this site (unpublished data), we only observed nest parents feeding, removing fecal sacs, or brooding nestlings.

Extra-pair mating

We genotyped 118 nestlings, social males at 29 nests, and 393 other territorial males. We found evidence of high rates of extra-pair paternity; of 33 nests for which we genotyped nestlings, 16 (48.5%) contained at least one extra-pair nestling and 18.6% of all nestlings were sired by an extra-pair male. Six nests (18.2%) contained more than one extra-pair young. Contrary to prediction (vi), nests containing extra-pair young tended to be located in areas with lower rather than higher density relative to nests with no extra-pair young (Fig. 2; $F_{2,30} = 2.1$, $P = 0.146$).

Kin selection

Under the *kin selection* hypothesis (4), we predicted (vii) that males would aggregate with kin to reduce costs

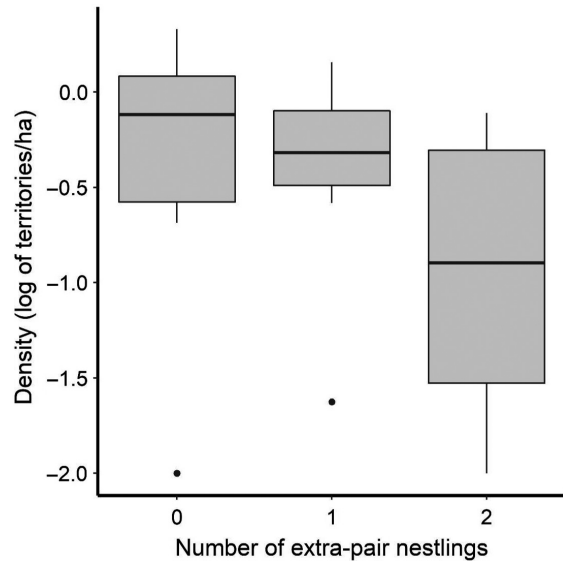


FIG. 2. The number of extra-pair young was not related to territory density. Nests with two extra-pair offspring tended to occur in areas with fewer nearby males, although the difference was not statistically significant ($F_{2,30} = 2.1$, $P = 0.146$). We estimated territory density using a kernel density model, log-transformed the data for analyses, and back-transformed for visualization.

of extra-pair paternity, resulting in a negative relationship between distance separating territories and pairwise relatedness. We calculated 24,350 pairwise comparisons of the relatedness coefficient r representing all combinations of genotyped males occupying the prairie during

each third of each year. As predicted, as interterritory distance decreased, male relatedness increased, but this relationship explained less than 0.03% of the variation in the data set. Thus, we interpret this result to be biologically insignificant; the effect size was so small and variation so large that we deem the relationship to be uninformative and conclude that kin selection is unlikely to explain aggregation in our system (Fig. 3; $P = 0.002$, $r^2 = 0.0003$).

We predicted (viii) that cuckolded males would locate territories close to kin. Results were consistent with this prediction; fathers at nests containing extra-pair nestlings were more closely related to neighbors than they were to other males in the population (Appendix S1: Fig. S4; $t_{1,701} = -8.1$, $P < 0.001$). We identified the likely fathers of the extra-pair offspring and calculated their relatedness to the cuckolded fathers, predicting that males would raise offspring of kin rather than the offspring of other birds. The distribution of relatedness values was not different from the overall population, suggesting that males were not cuckolded by relatives more often than expected (Appendix S1: Fig. S5; Kolmogorov–Smirnov test, $D = 0.2$, $P = 0.217$).

Correlates of nest success

Overall daily survival rate of nests was ~ 0.9 , but because daily nest survival varied by year (Appendix S1: Table S3), we included additive and interactive

combinations of year in subsequent analyses. We predicted that nest success (ix) would increase as territory density increased, and (x) would be more influenced by conspecific density than landscape factors. Territory density alone was weakly and negatively associated with nest success, contrary to prediction (Appendix S1: Table S3), although the confidence intervals overlapped zero ($\beta = -0.243$, -0.588 to 0.102). When we assessed landscape structural factors alone, distance from nest to edge, distance to tree line, percent forb cover, and vegetation height were all associated with variation in nest success. The association between density and nest success varied by year; the top model included only a density \times year interaction, which carried 13.1% of the model weight (Appendix S1: Table S4). In 2015, the relationship between nest success and territory density was positive, but the reverse was true in 2014 (Fig. 4). The difference between years in the relationship between density and nest success was mainly manifest at low densities; at < 0.25 territories/ha, daily nest survival in 2014 was approximately 8% higher than in 2015. When extrapolated over a 21-d nesting attempt, this difference is substantial; 10.9% of nests at low densities would be predicted to fledge young in 2014, compared to a mere 1.5% in 2015.

Our results were consistent with the prediction (x) that nest success would be more strongly associated with variation in density than it was to landscape attributes. However, in addition to the density \times year interaction,

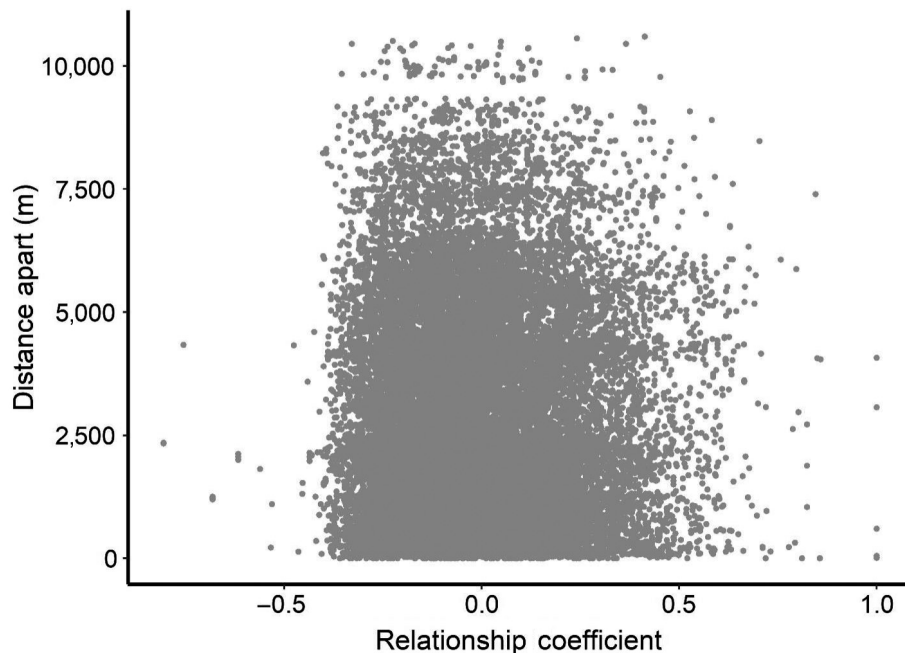


FIG. 3. Relationship between male sparrows' genetic relatedness and the geometric distance between their territories. Each data point is a pairwise comparison of genetic relatedness (Queller and Goodnight's r) of males that held territories during the same third of the year. The relatedness between pairs was negatively related to the distance between those sparrows' territory centroids ($P = 0.002$), but this relationship explained $\leq 0.03\%$ of the variance in the data.

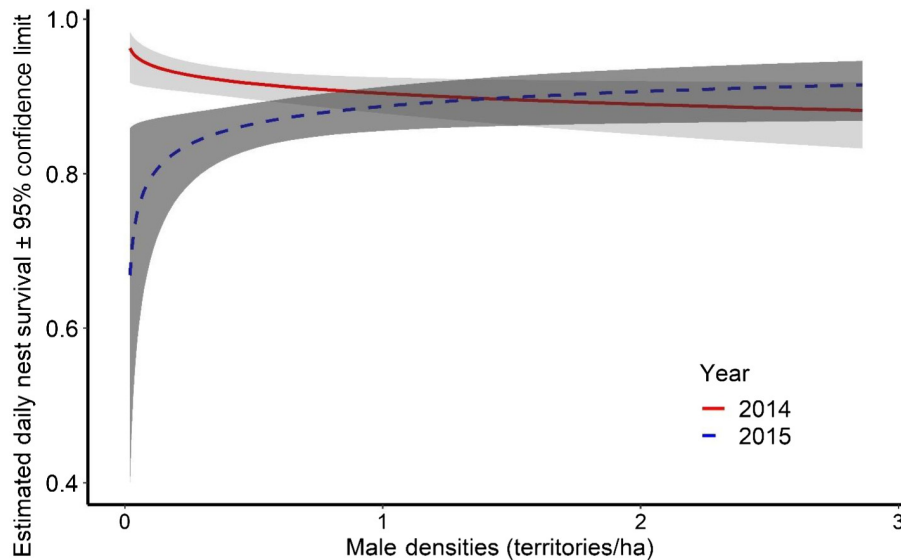


FIG. 4. Estimated effect of male territory density on daily nest survival rate for 2014 (red solid line) and 2015 (blue dashed line), with shaded 95% confidence intervals. The density \times year interaction in the top models was calculated using log-transformed data, which we then back-transformed for visualization. In areas with territory densities of 0.25 centroids/ha (half the average territory density), estimated daily nest survival was 8.7% higher in 2014 than in 2015.

five of seven top models also included an additive effect of one landscape or temporal variable: percent forb cover, vegetation height, distance to the nearest edge, distance to the nearest tree line, or time of year. Nevertheless, the confidence limits around the beta values for each of these variables overlapped zero (Appendix S1: Table S5). One competitive model included an edge \times year \times density interaction. At average distances to edge (109 m) daily nest survival was 6.3% higher in 2014 than in 2015 (Appendix S1: Fig. S6). Although confidence intervals overlapped, the edge \times density interactions suggest that nests farther from edges had lower daily nest survival than nests closest to edges when located in areas of high territory densities. However, nests in areas of low territory densities experienced no edge effects (Appendix S1: Fig. S7).

DISCUSSION

We observed large variation in Grasshopper Sparrow territory densities and the location of high-density areas varied within and among years (Appendix S1: Fig. S1, VideoS1). Because these sparrows are highly mobile (Williams and Boyle 2018), we expected the locations of territories to reflect adaptive choices relevant to nest success or other components of fitness. We tested multiple predictions of four potential social drivers of territory aggregation involving hundreds of territories and nests, experimental behavioral trials, and the largest genetic analysis to date for this species. We found no evidence in support of the *group defense*, *cooperative care*, *extra-pair mating*, or *kin selection* hypotheses. Furthermore, nests

in aggregated territories were not consistently more successful than those in more isolated territories.

The *cooperative defense* hypothesis predicted (i–iii) that males in high-density aggregations would respond more readily to predator and parasite models, but our behavioral trials suggest that male sparrows in aggregations do not respond aggressively to simulated threat any more frequently than do sparrows in more isolated territories. It is possible that the benefits of aggregation result not from *per capita* increases in alarm responses, but rather from the increase in the sum total of warnings resulting from more birds warning of approaching predators (Manser 2001, Templeton and Greene 2007). However, depredated nests were not located in areas of lower density than were successful nests, suggesting that even if birds do receive social information they are not able to use it to reduce nest predation. Furthermore, nests parasitized by Brown-headed Cowbirds were located in areas with higher territory densities than unparasitized nests, suggesting that cowbirds may benefit from aggregations to increase nest-searching efficiency (Krištofik et al. 2010). This relationship suggests that aggregation may actually be detrimental because brood parasitism reduces the number of host fledglings in this system.

Alternatively, the *cooperative care* hypothesis predicted that sparrow nests located in high-density areas would experience more extra-pair cooperative care, as more helpers would be available to assist with nestling care. In over a hundred hours of observation, we witnessed no extra-pair helpers, suggesting that the incidence of such behavior is extremely rare or absent in our population and apparently varies among populations of

this species. At our site, cooperative care cannot explain territory aggregation.

Under the *extra-pair mating* hypothesis, we predicted that nests in areas of high territory density would have higher rates of extra-pair paternity. This expectation is consistent with the “hidden lek” theory (Wagner 1993) and data from Grasshopper Sparrows elsewhere where extra-pair young were most frequent in nests located in high-density areas (Danner et al. 2018). In contrast, territory density and extra-pair young were not positively associated. In this study, males in high-density areas may dedicate more time to mate-guarding in the presence of reproductive competitors (Møller 1991, Thusius et al. 2001). However, overall territory densities at Konza were lower (mean 0.77 territories/ha) rather than higher than those in the previously studied population (Danner et al. 2018, i.e., ~0.64–1.44 territories/ha). Thus, differences in density cannot explain population-level differences in extra-pair paternity, and generally are inconsistent with extra-pair mating opportunities shaping aggregation patterns.

The *kin selection* hypothesis predicted that if males settled near relatives, cuckolded males could mitigate costs of extra-pair paternity by raising nestlings that contribute to their inclusive fitness (Grafen 1984). However, male relatedness explained very little variation in the physical distance between territories. Because Grasshopper Sparrows seek nearby extra-pair mates (Webster et al. 2001), these data are not consistent with kin selection. In analyses limited to pairs of males that raised extra-pair young and the male that sired them, pairs were not more closely related to one another than expected by chance. Thus, mitigating extra-pair paternity through kinship also cannot explain aggregation of male Grasshopper Sparrow territories.

If aggregations of male territories function adaptively in the context of increasing reproductive output, we predicted a positive relationship between nest success and aggregation, and that this relationship would be stronger than relationships between nest success and physical landscape attributes. However, the relationship between nest success and density was both weak and negative, and reproductive pay-offs of aggregation varied among years. In retrospect, the inherent variability of grassland systems (Winter et al. 2005) make this result unsurprising, but implies that aggregation does not consistently benefit nor compromise nest success.

In sum, not only did we find no evidence for any of the hypotheses for aggregation we considered, but also found no evidence for the putative fitness benefits of territory aggregation. Although it is possible that we did not measure the relevant aspects of the landscape shaping nest success, such a possibility does not alter our conclusions regarding the relationship between density and nest success. We are left with two alternative explanations for territory aggregation. First, aggregation may function to increase survival at later life-history stages. Aggregation could reflect decisions of adult sparrows that prioritize survival and future reproductive potential

over the current breeding effort (Hinde et al. 2010, Dudeck et al. 2018). For example, males could locate territories in areas with high food availability to minimize energetic costs of foraging (Stephens and Krebs 1986, Esler et al. 2007). We think this unlikely at this site, however, as sparrow settlement decisions are unrelated to food availability (Williams 2016). Likewise, aggregated territories may be safer for adults (especially incubating females) rather than for eggs or nestlings if adults evade predation by responding to conspecifics’ warnings (Seppanen et al. 2007). However, we see no evidence supporting this alternative either; despite recording 26 nest predation events on camera, we have never recorded predation of brooding females (unpublished data). Finally, aggregation may increase the survival of juveniles that form small flocks between fledging and migration. Flocking can increase foraging efficiency (Porter and Sealy 1982, Munk 1995) and reduce predation (e.g., Dolan and Butler 2006), and aggregated territories may facilitate flock formation. However, the most isolated territories were only ~2 km from aggregation hotspots, distances unlikely to restrict flocking of independent juveniles who move >100 m/d (Small et al. 2015). Thus, none of the additional lines of evidence suggest that territory aggregation results from survival benefits accruing to alternative life-history stages in this system.

Second, it is possible that there are indeed social benefits of aggregation, even though we did not detect them. Given the inherent variability of grassland systems and the behavioral flexibility of these birds, it is possible that such benefits accrue in some years and contexts, but not in others, and this study spanned a period when the benefits were absent or too small to detect. If the costs of aggregation are low, even marginal benefits of social interactions that operate only in some years could explain patterns of conspecific attraction. Such an alternative could explain why aggregation appears not to be currently or consistently adaptive in this population. It was reasonable to assume we would detect an adaptive function, given the mounting evidence that conspecific attraction affects settlement decisions in a variety of territorial birds (Ward and Schlossberg 2004, Ahlering et al. 2006), including our focal species (Andrews et al. 2015). However, the abiotic conditions favoring grasslands are notoriously variable and the animals that depend upon such habitats exhibit tremendous behavioral flexibility. Against this background of variability, tremendous anthropogenic changes have occurred across the species’ range in the last two centuries. If the benefits of aggregation are context-dependent, it is therefore plausible that they might be influenced by the dramatically altered area and fragmentation of the Great Plains or by diminished local population sizes. In the eastern United States, prairies historically occurred in relatively isolated patches, and grassland birds may have depended on conspecific attraction to locate breeding habitats (Reed and Dobson 1993, Askins et al. 2007). However, in areas that historically consisted of unbroken expanses

of tallgrass prairie, the same may not have been true. Now, only 4% of the tallgrass prairie remains, and much of it is managed intensively for cattle production, reducing habitat quality for breeding birds (Samson et al. 2004). Mobile grassland species may settle on what they perceive to be high-quality habitat, but altered land use may influence nest predation risks such that historic cues result in poor habitat choices. Additionally, the presence of conspecifics may have been beneficial at historical sparrow population sizes, attracting densities that could support social interactions at a scale that yielded fitness benefits, but as populations have declined, those densities are unattainable (Reed 1999).

Territory aggregations often provide insight into resource needs and reflect conspecific interactions in mobile species (Macedo et al. 2018), but as results of this study show, it is not safe to assume aggregation functions in such ways. In a rapidly changing world, studies of animal space use should consider the costs and benefits associated with clustering around social resources as well as important environmental resources. However, aggregation may yield only small fitness benefits that are hard to detect but that nonetheless outweigh negligible costs, and those benefits may influence only one of a variety of life-history stages. Finally, a growing challenge for ecologists will be to determine how behaviors shaped by past selective regimes operate in dramatically altered landscape and population contexts.

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SUPPORTING INFORMATION

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DATA AVAILABILITY

Data and code are available on Dryad: <https://doi.org/10.5061/dryad.3xsj3tx9w>