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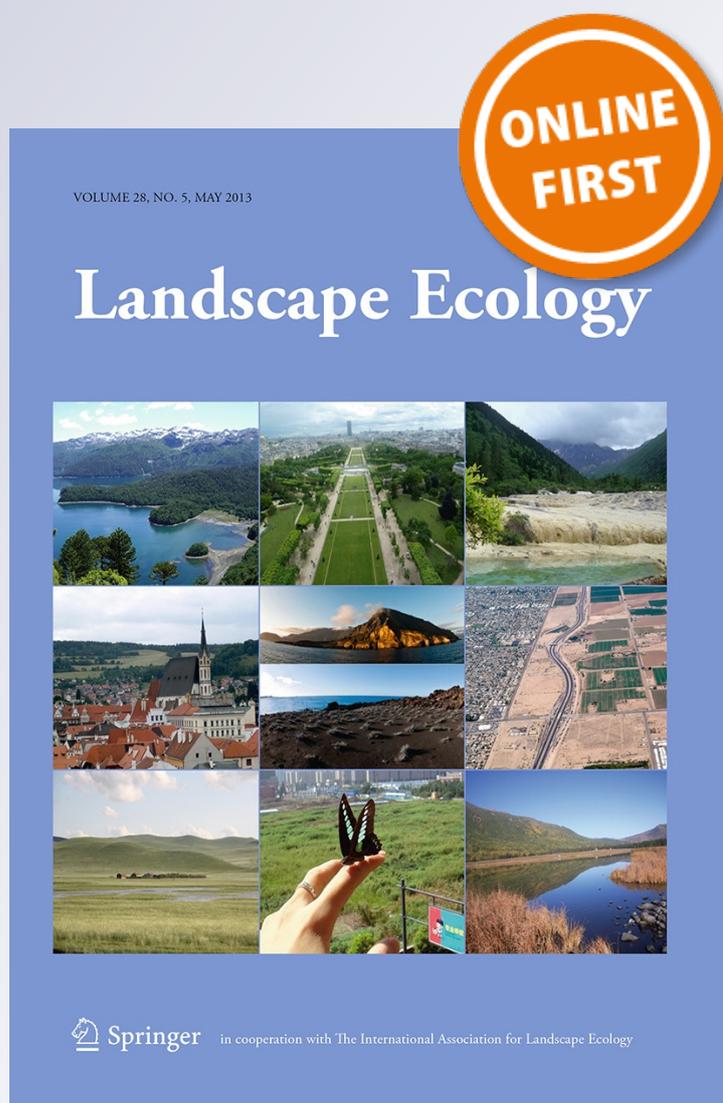
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Broad-scale heterogeneity influences nest selection by Brown-headed Cowbirds

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Abstract Increasing habitat heterogeneity is widely considered to improve conditions for biodiversity. Yet benefits for native species depend on scale and the effect of heterogeneity on key processes influencing survival and reproduction. We examined the relationship between habitat heterogeneity and brood parasitism at multiple scales in a region characterized by (1) relatively high cowbird abundance, (2) high abundance of our focal species, the grassland obligate Grasshopper Sparrow (*Ammodramus savannarum*), (3) variation in the structure and composition of grassland habitats, and (4) a gradient of woodland cover in the landscape matrix. Tree cover at broad scales was found to have the greatest impact on parasitism while factors at finer scales were relatively unimportant. We found that for every 1 % increase in tree cover within 1 km of Grasshopper Sparrow nests, the probability of parasitism decreases by 3 %. Parasitism reduced clutch sizes and the number of

Grasshopper Sparrows fledged, but survival rates were similar between non-parasitized and parasitized nests. Furthermore, simple population projection models indicated that parasitism has the greatest impact at moderate survival levels and can inhibit the resiliency of this population. Our results support the hypothesis that cowbirds prefer forest hosts, which may reduce parasitism rates on grassland birds in heterogeneous landscapes. Collectively, our findings suggest that the effect of cowbird parasitism may be greater for Grasshopper Sparrows than was previously thought.

Keywords Demography · Grasshopper Sparrow · Grasslands · Grazing · Nest survival · Parasitism · Prescribed fire

Introduction

Understanding the consequences of spatial heterogeneity for animal populations has long been a central theme in landscape ecology (Turner 1989). Because many human land uses tend to homogenize vegetation structure and composition, increasing heterogeneity is widely thought to improve conditions for biodiversity (Ostfeld et al. 1997; Fuhlendorf et al. 2006). Yet this relationship is scale-dependent. Increases in habitat heterogeneity may benefit some native species, but prove a detriment to others depending on the response of key processes influencing survival and reproduction.

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A key process limiting productivity for many bird species is brood parasitism (Ortega 1998). In North America, female Brown-headed cowbirds (*Molothrus ater*) reduce host productivity by removing eggs and nestlings, and destroying nests to initiate re-nesting attempts, thus creating opportunities for future parasitism (Granfors et al. 2001; Peer 2006). In the heterogeneous landscape mosaics of the Midwestern U.S., parasitism rates on forest songbird nests are inversely correlated with forest cover within a 10-km radius (Robinson et al. 1995; Thompson et al. 2000). Thus parasitism becomes less frequent as broad-scale heterogeneity decreases, presumably because the distance cowbirds can travel to breeding areas is limited by their requirement for open foraging sites. Cowbirds in the Midwest and eastern U.S. also demonstrate a clear preference for forest hosts over species nesting in habitats with less complex structure, such as oldfields, shrublands, or grasslands (Hahn and Hatfield 1995; Strausberger and Ashley 1997; Robinson et al. 2000; Thompson et al. 2000). Underscoring this pattern, Robinson (1999) note that parasitism is not a significant problem for grassland birds in habitats with structures less complex than forests.

One might reasonably expect that parasitism rates for grassland birds would increase further west with decreases in forest cover and forest host species. Indeed, studies in the Great Plains have shown grassland species to be parasitized at more than twice the frequency of their conspecifics in the Midwest (Peer et al. 2000 and references therein). In landscapes dominated by grasslands, parasitism rates have been shown to correlate positively with proximity to woody vegetation (Davis and Sealy 2000; Koford et al. 2000; Patten et al. 2006, 2011). Yet other work in this region has shown little to no effect of such patch-scale habitat heterogeneity (Jensen and Cully 2005), similar to studies examining the relationships between local variability in habitat features and parasitism of forest bird nests (Gates and Gysel 1978; Brittingham and Temple 1983; Robinson and Wilcove 1994; Thompson et al. 2000; Hannon et al. 2009).

It is possible that variable responses to local habitat heterogeneity are driving substantial variation in parasitism rates for grassland birds in the Great Plains over fairly narrow spatial extents. For example, researchers in North Dakota, the heart of the cowbird's range, have documented parasitism rates for grassland birds ranging from 0.01 to 12.0 % (Grant et al. 2006;

Pietz et al. 2009). Studies conducted in the Flint Hills of Kansas and Oklahoma reported parasitism rates of grassland obligate species that varied from 6.5 % to 80.0 % (Jensen and Cully 2005; Patten et al. 2006, 2011). There is evidence to suggest that the effect of heterogeneity at local scales must be considered in light of broader patterns of habitat variability. Over recent decades, tree encroachment has become widespread in extensive portions of the Great Plains (Grant et al. 2004; Engle et al. 2008), and this phenomenon may exert a strong influence on parasitism rates in grasslands (Pietz et al. 2009).

We examined the relationship between parasitism rates and habitat heterogeneity at multiple scales in a region characterized by (1) relatively high cowbird abundance, (2) high abundance of our focal species, the grassland obligate Grasshopper Sparrow (*Ammodramus savannarum*), (3) variation in the structure and composition of grassland habitats, and (4) a gradient of woodland cover in the landscape matrix (Pillsbury 2010; Hovick et al. 2011). We predicted that woody habitat features at local scales would correlate positively with parasitism rates. Yet because grassland patches in our study system are relatively small, we predicted that the primary driver would be the amount of woodland cover in the surrounding landscape. The first objective of our study was to examine the influence of local- and landscape-level heterogeneity on the probability of parasitism. Our second objective was to explore the consequences of parasitism on demographic patterns for this host species.

Methods

Study site

The study was conducted on nine pastures, ranging from 22.5 to 37 ha in size and located in the Grand River Grasslands, Ringgold County, Iowa. About 80 % of this region remains in native and non-native grasslands, although woodlands and row-crop fields are common in drainages and river bottoms. On average, the landscape matrix surrounding research pastures comprised 12 % row-crops, 62 % grassland, and 24 % woody vegetation (Pillsbury 2010). While woodlands do comprise a large part of the surrounding landscape, woodland vegetation is not in the form of forest stands, but is patchily distributed and

encroaching in private lands that lack prescribed fire. Dominant native herbaceous species included rough dropseed (*Sporobolus clandestinus*), sedges (*Carex* spp.), and Baldwin's ironweed (*Veronica baldwinii*) (McGranahan 2008). Common exotic species included tall fescue (*Festuca arundinacea*), black medick (*Medicago lupulina*) and Kentucky bluegrass (*Poa pratensis*).

All pastures were managed using grazing and prescribed fire in one of two regimes. The first, referred to as the patch-burn grazed treatment ($n = 5$), attempted to increase habitat heterogeneity by burning one third of each pasture annually. The second, known as the grazed-and-burned treatment ($n = 4$), adopted a more traditional homogeneity-based approach by burning the entirety of each pasture every third year. Rather than analyze the effects of treatments per se, however, we focused on more direct measures of heterogeneity derived from vegetation sampling, as previous work revealed little contrast between the two treatments (Pillsbury et al. 2011). Cattle stocking rates were similar for both treatments on an annual basis, but ranged from 1.10 to 4.24 AUM/ha across the 3 years of our study.

Focal species

The Grasshopper Sparrow is a species of continental concern as a result of population declines near 80 % over the last half century (Panjabi et al. 2005; Sauer et al. 2011). In our study region, the domed nests of this grassland obligate tend to be located on the ground in patchy habitat characterized by bare ground and bunch grasses (Hovick et al. 2012). The cryptic nature of Grasshopper Sparrow nests has been proposed as an explanation for brood parasitism rates that are purported to be low relative to other grassland birds (Vickery 1996). While this may be the case further east, parasitism rates have been shown to vary widely in the grasslands of central North America that comprise the core of this species range as well as that of the Brown-headed Cowbird (Table 1).

Data collection

We searched for nests from 0600 to 1,200 (CDT) from 14 June through 15 July in 2008 and 15 May through 25 July in 2009 and 2010. Most nests were located using systematic rope-dragging, in which a flag was

placed at one end of a 30 m rope every 50 m to ensure complete coverage of research pastures. In the event of a flush, we searched the immediate area extensively. If a nest was not found and the flushed bird showed signs of nesting (i.e., insistent chipping, flailing wing display, short-circular flights), the location was marked as a probable nest site and searched again within 3 days by walking and using flushing sticks (Winter et al. 2003).

When we located nests, the Universal Transverse Mercator (UTM) coordinates were recorded, eggs were candled to determine age (Lokemon and Koford 1996), and flagging was placed low in the vegetation 5 m north and 5 m south of the nest to aid in relocation. Nests were monitored every third day, with more frequent visits near hatching and fledging. During each nest visit we recorded the number and stage of all eggs and nestlings (Ralph et al. 1993). We considered a nest to be successful if ≥ 1 host young fledged. Fledging was subsequently confirmed by observing parental behavior (i.e., alarm calls and feeding).

To determine the effects of fine-scale heterogeneity on parasitism rates, we measured vegetation structure and composition at the nest and in each cardinal direction at a distance of 5 m from the nest using a 0.5 m² quadrat (Hovick et al. 2011). Within the quadrat we visually estimated percent cover of tall fescue, warm-season grasses, cool-season grasses (including tall fescue), forbs, legumes, bare ground, litter, and woody vegetation, and recorded these measurements as the midpoints of the following intervals: 0–5, 6–25, 26–50, 51–75, 76–95, and 96–100 (Daubenmire 1959). Fescue, warm-season grass, and cool-season grass cover were also summed and classified as another variable, total live coverage. Additionally, we recorded visual obstruction at a distance of 4 m from the center of the quadrat and 1 m above ground, noting the height at which the pole was 50 % obscured by vegetation (Robel et al. 1970).

To characterize the relationship between parasitism rates and heterogeneity at broader scales, we digitized tree cover around study pastures using 2-m resolution true color orthophotos (U.S. Department of Agriculture 2005) with ArcGIS 9.1 (Environmental Systems Research Institute, Redlands, CA). We chose a maximum distance of 1,000 m because regressions of variance in grass cover and wooded vegetation density against distance from pasture edges showed an asymptote

Table 1 Published rates of Brown-headed Cowbird (*Molothrus ater*) parasitism on Grasshopper Sparrows (*Ammodramus saviannarum*)

State/ province	Nest sample	Parasitism (rate)	Source
Illinois	318	13 (4 %)	Peer et al. 2000
Indiana	41	1 (2.4 %)	Galligan et al. 2006
Iowa	62	2 (3.2 %)	Patterson and Best 1996
Kansas	61	21 (34.4 %)	Jensen 1999
Kansas	18	9 (50 %)	Elliot 1978
Kansas	18	4 (22.2 %)	Hill 1976
Kansas	46	22 (47.8 %)	Rivers et al. 2010
Kentucky	131	0 (0 %)	Giocomo et al. 2008
Manitoba	48	13 (27.1 %)	Davis and Sealy 2000
Minnesota	46	3 (6.5 %)	Johnson and Temple 1990
North Dakota	45	10 (22.2 %)	Koford et al. 2000
Oklahoma	274	18 (6.6 %)	Patten et al. 2011
Ontario	74	7 (8.1 %)	Peck and James 1987

at 1,000 m, beyond which there was no additional uncaptured variance among pastures (Pillsbury 2010). We measured distances from nests to the nearest woody vegetation and to the nearest fence line because both measures are hypothesized to influence parasitism by providing perch sites for cowbirds (Patten et al. 2011).

Productivity measures

To examine the effects of parasitism on host productivity, we focused on three parameters: clutch size differences between parasitized and non-parasitized nests, rates of multiple parasitism, and number of hosts fledged in parasitized and non-parasitized nests. Nests were considered parasitized if they contained ≥ 1 cowbird egg or nestling and experienced multiple parasitism when they contained >1 cowbird egg or nestling. Multiple parasitism can be caused by one female laying multiple eggs or different females laying eggs in the same nest (McLaren et al. 2003). Cowbird eggs were easily distinguished from host eggs because they are larger, have an overall darker appearance, and are speckled across the entire eggshell whereas host eggs are primarily speckled on only one

end. Discerning cowbird nestlings from host nestlings can be done on the basis of size (depending on age), but is more reliably accomplished by examining rectal flanges (gape color); hosts have yellow/orange flanges whereas cowbird flanges are bright white.

Data analysis

We used logistic regression models in Program R (R core development team 2005) to examine the influence of multi-scale heterogeneity on the probability of cowbird parasitism. Each nest was treated as an individual Bernoulli trial and was assigned a zero if it was not parasitized and a one if parasitism occurred. We tested the influence of heterogeneity by running a series of univariate models at each of four spatial scales using parameters that were selected a priori. At each scale, parameters were compared to a null model and then joined in additive models if ΔAIC_c was less than that of the null and within 2 of the best model for the respective scale. Alternatively, if all univariate models at a particular scale were less informative than the null model (i.e., $>\Delta AIC_c$) then no additive models were created for that scale and no parameters from that scale were included in multi-scale models. Parameters that were correlated were not included in the same model (e.g., trees at 500 and 1,000 m). At each scale, model selection was based on Akaike's information criterion, adjusted for small sample sizes (AIC_c), and model weights (Burnham and Anderson 1998). We assessed overall model fit using the global model and a Hosmer–Lemeshow goodness-of-fit test (Burnham and Anderson 2002).

Population projection

We assessed the potential effects of parasitism on Grasshopper Sparrow population viability with a population growth model sensu Donovan et al. (1995). We chose to use this simple method to illustrate the additive effect of cowbirds on population decline of Grasshopper Sparrows. It was not our intent to make a complex model incorporating stochastic events, density dependence, or differential survival based on age classes, but just to elucidate general trends. We used the following two-stage population projection model to assess change in population size through time:

$$N_{A(t+1)} = (N_{At} * S_{At}) + (N_{At} * F_t * S_{Jt}) \quad (1.1)$$

where t is the year of the simulation, N_A is the number of adult breeding females, N_{At} is the number of adult breeding females in year t , S_{At} is the survival of adult females from year t to year $t + 1$, F_t is the mean number of female offspring produced per female in year t , and S_{Jt} is juvenile survival from year t to $t + 1$. We used 1,000 females as a starting population size and projected population growth or decline over 25 years. Empirical adult survival estimates were not available for Grasshopper Sparrows, so we used the mean survival rate ($\bar{x} = 0.537$, $SE = 0.02$, $CI = 0.49\text{--}0.57$) of five grassland-associated species with similar nesting habits (Martin 1995). We used a value of 0.235 ($SE = 0.01$, $CI = 0.13\text{--}0.40$) for juvenile survival that was estimated using daily survival rates that we generated in program MARK after tracking 32 postfledging individuals from this population in 2009 (Hovick et al. 2011). Estimates were made from the two-week period after chicks left the nest at which time daily survival rates stabilized and began to increase. To our knowledge, this is the only estimate for postfledging Grasshopper Sparrow survival; however, it does not account for survival through migration until the following breeding season, and therefore, should be viewed as a best case scenario. We calculated the mean number of females produced by a nesting female each year (i.e., fecundity) using a clutch size estimate of 4 calculated from nests in this study that were not parasitized ($n = 328$), and calculated nest success estimates from this population using program MARK ($S' = 0.22$, $SE = 0.005$, $CI = 0.17\text{--}0.27$; Hovick et al. 2012). Additionally, we used the maximum number of re-nest attempts ($n = 4$) and the maximum number of broods per year ($n = 2$) from the literature (Vickery 1996). When calculating fecundity estimates, we assumed breeding success and number-of-young per brood were equal throughout the season, reproductive output was the same for all age classes, and a 50:50 sex ratio (Donovan et al. 1995). We projected a theoretical population of 1,000 females using the parameters cited above and then generated high and low survival scenarios using the upper and lower confidence bounds of each parameter.

We calculated fecundity estimates using the method followed by Donovan et al. (1995) and McCoy et al. (1999). For example, starting with an initial population of 100 nesting females and incorporating

the parameters described above, there would be 22 females that produce 44 female offspring on their first nest attempt ($100 \times 0.22 \times 4 \times 0.50$). These same 22 females would all attempt a second nest, and 17 of these would fail and 5 would produce 10 female young ($22 \times 0.22 \times 4 \times 0.50$). This same logic can be followed for all 100 breeding females until an individual has two successful broods or four nesting attempts, whichever comes first (Table 2). To account for differences in fecundity between parasitized and non-parasitized individuals, we reduced clutch size by 38.6 % (difference in clutch size between parasitized and non nests, see Table 3) for 28 % of the population.

Results

We located and monitored 440 Grasshopper Sparrow nests during the study period. Parasitism rates varied little across years, with a mean rate of ~ 28 % (range: 24–29 %) for the three breeding seasons. Constant daily survival rates for parasitized and non-parasitized nests were similar during the two nesting stages (parasitized: incubation 0.921, nestling 0.910; non-parasitized: incubation 0.922, nestling 0.914), and the overall probability of a parasitized nest fledging one host offspring was 17.3 % compared with 18.2 % for non-parasitized nests. Clutch sizes in parasitized nests averaged 1.56 fewer host eggs than non-parasitized nests, and nests that were parasitized fledged 1.49 fewer Grasshopper Sparrows. Approximately 47 % of parasitized nests experienced multiple parasitism over the study period (Table 3).

We used 13 parameters in regression analyses to investigate the relationship between heterogeneity at four spatial scales and the probability of parasitism by cowbirds (Table 4). The global model did not differ significantly from observed values, implying that that our model results fit the data (H–L Goodness of Fit, $\chi^2 = 5.09$, $p = 0.75$). Additionally, we found that nests were distributed throughout research pastures without avoidance of woody vegetation near pasture edges (Table 4). At the landscape scale, tree cover within 1,000 m of the nest explained the most variation in cowbird nest selection and it had a negative influence ($\beta = -3.06$ and $SE = 1.02$, 95 % $CI = -5.10$ to -1.12). Parameters investigated at other scales explained less variation than a null model

Table 2 Grasshopper Sparrow fecundity rates for a theoretical population of 100 females experiencing 22 % nest survival, initiating maximum of 4 nest attempts, and producing a maximum of 2 broods annually

Attempt	Nests failed	Nests successful	Fecundity not parasitized	Fecundity 28 % parasitism
1	78	22	44	39
2	78	22	44	39
3	74	21	42	37
4	67	20	40	36
Total			170	151

We assumed that breeding success and number-of-young per brood were constant throughout the season, that reproductive output was the same for all age classes, and there was a 50:50 sex ratio. Fecundity estimates for parasitized nests were calculated using a 38.6 percent reduction in clutch size (see Table 3)

(i.e., intercept only) and thus precluded the creation of multi-scale, additive models (Table 5).

Because tree cover in the landscape matrix surrounding pastures was the most influential measure of heterogeneity in determining the probability of nest parasitism; we used logistic regression to examine how this probability varied with tree cover, and included confidence intervals that were calculated using the delta method (Powell 2007; Fig. 1). Additionally, we calculated odds ratios for the 1,000 m tree cover model using parameter slope, which showed that a 1 % decrease in tree cover resulted in a 3 % increase in the probability of parasitism.

Simple population growth models exhibited exponential declines over 25 years for the low survival scenario, modest declines for the actual population estimates (i.e., estimates derived from this population),

and exponential increases under the high survival scenario (Table 6). Assuming no immigration and no parasitism, Grasshopper Sparrows experienced a decline of nearly 80 % to 194 breeding females. However, when survival estimates were high, this population exceeded its carrying capacity by producing nearly 4 million individuals over 25 years. This latter project is unrealistic given that conditions are unlikely to be ideal for 25 consecutive years, but is useful in underscoring the resilience of Grasshopper Sparrow populations when survival parameters are high. Additionally, these projections illustrate the potential additive impacts of cowbird parasitism when survival parameters are low—a more likely scenario for the population examined during this study.

Discussion

Consistent with our predictions, heterogeneity at the broadest spatial scale had the greatest impact on cowbird parasitism rates and parameters measured at finer scales were relatively unimportant. Increases in tree cover within 1 km of Grasshopper Sparrow nests were strongly associated with a decreased probability of parasitism. Heterogeneity in grasslands resulting from tree or shrub cover is typically viewed in a negative context (Johnson and Temple 1990; Koford et al. 2000; Patten et al. 2011), yet our findings are similar to the pattern of reduced parasitism rates for grassland birds with increases in tree cover reported in the northern Great Plains (Pietz et al. 2009). This difference is likely a function of scale. Typically, the relationship between woody vegetation and nest parasitism in grasslands has been viewed through the

Table 3 Demographics for Grasshopper Sparrow nests monitored in Ringgold County, IA, USA

Years	Rate BHCO	Clutch	Clutch-P	BHCO	MP rate (%)	Fledglings	Fledglings-P
2008	24 (18/75)	3.93 ± 0.12 (57)	2.94 ± 0.27 (18)	1.72 ± 0.29 (18)	50 (9/18)	3.59 ± 0.22 (29)	2.63 ± 0.53 (8)
2009	>29 (74/255)	4.01 ± 0.07 (181)	2.36 ± 0.13 (74)	1.62 ± 0.10 (74)	>44 (33/74)	3.32 ± 0.21 (41)	1.57 ± 0.17 (14)
2010	>29 (37/127)	4.17 ± 0.09 (90)	2.49 ± 0.19 (37)	1.68 ± 0.14 (37)	>51 (19/37)	3.19 ± 0.22 (26)	1.67 ± 0.24 (9)
All	>28 (129/457)	4.04 ± 0.18 (328)	2.48 ± 0.10 (129)	1.65 ± 0.07 (129)	>47 (61/129)	3.36 ± 0.12 (96)	1.87 ± 0.18 (31)

Rate BHCO percentage of nests parasitized by Brown-headed Cowbirds, Clutch the mean clutch size ± SE of nests that were not parasitized, Clutch-P the mean clutch size ± SE of nests that were parasitized, BHCO eggs the mean number ± SE of Brown-headed Cowbird eggs deposited per parasitized nest, MP rate the percentage of parasitized nests experiencing multiple parasitism (>1 cowbird egg or chick), Fledglings the mean number ± SE of host young to fledge in nests that were not parasitized, and Fledglings-P the mean number ± SE host young to fledge in nests that were parasitized. All parenthetical values refer to the number of nests used to calculate these descriptive statistics

Table 4 Parameters selected for inclusion in logistic models predicting the probability of parasitism by Brown-headed Cowbirds in Ringgold County, IA, USA

Scale/parameter	Mean (SE)	Range	Definition
Landscape			
Trees_100	4.57 (0.003)	0–39	Percent tree cover within 100 m of nest
Trees_500	18.66 (0.005)	1–49	Percent tree cover within 500 m of nest
Trees_1000	23.72 (0.005)	7–44	Percent tree cover within 1,000 m of nest
Pasture			
Dist_fence	82.56 (2.25)	3–219	Distance from a nest to the nearest fence in meters
Dist_wood	103.61 (2.93)	16–315	Distance from a nest to the nearest woody plant in meters
Five meter			
Robel_5	3.72 (0.05)	1–8	Vertical obstruction (height) of vegetation 5 m from nest
Bare_5	11.93 (0.52)	0–63	Percentage of bare ground 5 m from nest
Litter_5	68.56 (0.92)	13–98	Percentage of litter cover 5 m from nest
Total_veg_5	115.76 (1.17)	29–205	Percentage of total biomass coverage 5 m from nest
Nest			
Robel	3.75 (0.05)	0–8	Vertical obstruction (height) of vegetation at nest
Bare	6.51 (0.46)	0–38	Percentage of bare ground at nest
Litter	77.53 (0.93)	0–98	Percentage of litter cover at nest
Total_veg	116.03 (1.41)	38–214	Percentage of total biomass coverage at nest

Table 5 Logistic regression models used to examine Grasshopper Sparrow nest selection by Brown-headed Cowbirds in Ringgold County, IA, USA

Scale	Model	AIC _c	Weight
Landscape	$y = b_0 + \text{trees}_{1000}^a$	0.00	0.51
Landscape	$y = b_0 + \text{trees}_{500}$	0.20	0.46
Landscape	$y = b_0$	6.40	0.02
Landscape	$y = b_0 + \text{trees}_{100}$	7.20	0.01
Pasture	$y = b_0$	0.00	0.53
Pasture	$y = b_0 + \text{dist}_{\text{fence}}$	1.40	0.26
Pasture	$y = b_0 + \text{dist}_{\text{woody}}$	1.90	0.21
5 m	$y = b_0$	0.00	0.32
5 m	$y = b_0 + \text{Robel}_5$	0.10	0.30
5 m	$y = b_0 + \text{total}_{\text{live}}_5$	1.50	0.15
5 m	$y = b_0 + \text{bare}_5$	1.90	0.12
5 m	$y = b_0 + \text{litter}_5$	2.00	0.11
Nest	$y = b_0$	0.00	0.40
Nest	$y = b_0 + \text{Robel}$	1.70	0.17
Nest	$y = b_0 + \text{bare}$	1.90	0.15
Nest	$y = b_0 + \text{litter}$	2.00	0.14
Nest	$y = b_0 + \text{total}_{\text{live}}$	2.00	0.14

See Table 4 for parameter definitions

^a AIC_c for best model = 512.38

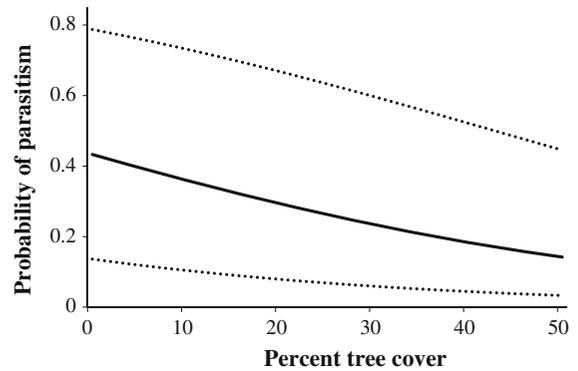


Fig. 1 Logistic regression curve (lines) and 95 % confidence intervals (dotted lines) relating the probability of parasitism to percent tree cover within 1,000 m of a Grasshopper Sparrow nest in Ringgold County, IA, USA

lens of perch proximity rather than as a broad-scale phenomenon (Johnson and Temple 1990; Patten et al. 2006).

In more extensive grasslands of the Great Plains, a lack of focus on the influence of woodlands may be justified. Woodland patches of sufficient size to provide habitat for cowbird hosts may not exist or may be too distant from grassland sites to exert an

effect. For example, researchers in the central and southern Great Plains did not detect a decrease in parasitism associated with proximity to tree cover (or ratio of grassland to forest) within 5 and 10 km of study sites (Jensen and Cully 2005). However, relatively few studies examining tree coverage and host selection by cowbirds exist for the Great Plains, and examination of factors at finer-scales is more common (Clotfelter 1998; Larison et al. 1998; Patten et al. 2011).

In our study, none of the parameters measured at finer scales were strongly associated with selection pressure on nests by cowbirds. A partial explanation for these results could be the general availability of perch sites in our research pastures which is related to the amount of woody shrubs and small pasture sizes (Pillsbury, unpublished data). All pastures had exterior fencing and many had a substantial coral berry (*Symphoricarpos orbiculatus*) component, both of which can act as perch sites for cowbirds. This finding contrasts with patterns of host selection by cowbirds reported for the southern Great Plains. There, 17 host species nesting in tallgrass prairie were more likely to experience parasitism near grassland patch edges and parasitism was strongly related to perch proximity (Patten et al. 2011). Such results are likely a function of limited perch sites (i.e., woody vegetation) in grasslands of the southern Great Plains compared to the highly heterogeneous structure of the Midwest region where our study took place.

Regional variation in the factors driving host selection by cowbirds is not surprising given the extreme variation in landscape composition. Moreover, cowbird population densities vary greatly across their range (Sauer et al. 2011) and are likely to

influence host selection and rates of parasitism. In general, our results fit the pattern of a decrease in parasitism rates on Grasshopper Sparrows from the north-central Great Plains to areas further east. We speculate that the lack of extensive woodlands in many parts of the northern and central Great Plains causes cowbirds to restrict their search image to grassland birds. Further east, as landscape-scale heterogeneity increases and woodlands become more prevalent, cowbirds are able to target species with more easily detectable nesting structures than those of most grassland birds. In the Midwest, for example, cowbird parasitism increased as forest cover increased and in landscapes with relatively less forest, parasitism decreased while songbird productivity increased (Cox et al. 2012). This pattern could be of major consequence to the songbirds in the future as woody vegetation is increasing throughout the Great Plains and portions of the Midwest (Grant et al. 2004; Engle et al. 2008).

Parasitism exerted a negative influence on Grasshopper Sparrow demography in our study. Parasitized nests had smaller clutch sizes and lower fledging rates than non-parasitized nests. Additionally, nearly half of the nests in this study experienced multiple parasitism events, indicating that individual cowbirds repeatedly visit the same nest or that cowbirds may rely on the behavior of conspecifics to locate nests (Rivers et al. 2012). Collectively, these findings suggest that the effect of cowbird parasitism may be greater for Grasshopper Sparrows than was previously thought (Robinson et al. 2000, Patten et al. 2011) and may be contributing to declines in Grasshopper Sparrow populations (Sauer et al. 2011). Further, the degree to which the loud continual begging of cowbird chicks

Table 6 Projected change (i.e., lambda) in the number breeding females present in a theoretical population of Grasshopper Sparrows after 5, 15, and 25 years given low, actual (i.e., estimated from our study population), and high survival parameters, and with an initial population size of 1000 individuals

Model	S_A	S_J	F	F_{BHCO}	No parasitism			28 % parasitism		
					5	15	25	5	15	25
Low	0.499	0.132	1.4	1.24	0.15	0.02	0.00	0.13	0.02	0.00
Actual	0.537	0.235	1.7	1.51	0.72	0.52	0.52	0.56	0.32	0.32
High	0.575	0.409	2	1.78	5.24	27.51	27.51	3.76	14.11	14.11

The low and high survival scenarios were estimated using the upper and lower confidence bounds from survival estimates using the study population or the best available estimates from the literature

S_A adult survival, S_J juvenile survival, F fecundity of a population without parasitism, F_{BHCO} fecundity of a population experiencing 28 % and a 38.6 % reduction in clutch size (i.e., the reduction observe in our study population)

attracts nest predators is largely unknown and could be contributing to the relatively low nest survival rates in this study.

Even if parasitized nests do not attract nest predators more than non-parasitized nests, our projection models suggest that parasitism rates negatively affected the population of our focal species at low and moderate survival scenarios, exacerbating population declines often attributed to nest predation and habitat loss. Despite models showing this is a sink population in the absence of parasitism given the survival parameters we recorded, with high survival parameters the population quickly rebounded. It seems that the additive effects of parasitism and predation during moderate survival years poses the greatest potential for negative population-level impacts. Still, given that rates of nest predation are high in our study area, the effect of cowbird removal efforts may be negligible for this population over the long term (Sandercock et al. 2008). Additionally, the probable association between mesopredators and tree cover may override any positive effects associated with decreased parasitism rates (Renfrew and Ribic 2003). A more general approach to reducing parasitism by eliminating foraging areas that attract high densities of cowbirds (e.g. cattle feedlots) and managing for extensive grassland-dominated landscapes may be a beneficial management solution that could reduce parasitism rates on Grasshopper Sparrows and benefit grassland birds broadly (Shaffer et al. 2003).

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