



# Do habitat preferences improve fitness? Context-specific adaptive habitat selection by a grassland songbird

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## Abstract

Animals are predicted to prefer high-quality over low-quality habitats, but adaptive habitat selection is less straightforward than often assumed. Preferences may improve only specific fitness metrics at particular spatial scales, with variation across time or between sexes. Preferences sometimes even reduce fitness. We investigated the context specificity of adaptive habitat selection, studying dickcissels (*Spiza americana*)—a polygynous songbird—as a model. From 2014 to 2015, we measured male and female habitat preferences at two scales (territories and landscape patches) on 21 grassland patches in Ringgold County, Iowa, USA. We tested whether preferences improved four fitness metrics—polygyny, avoidance of brood parasitism by brown-headed cowbirds (*Molothrus ater*), fledgling productivity, and offspring condition. Both sexes preferred territories where offspring attained superior condition and patches where parasitism was infrequent. Females preferred patches where nests produced more fledglings, and in 2014, males on preferred (i.e., early-established) territories attracted more mates and produced more fledglings. However, males on non-preferred (i.e., late-established) territories were more successful in 2015. This inconsistency may have arisen because females were abundant and nest-predation rates were low in May–June 2014, allowing early-settling males to produce many young. In 2015, however, females were more abundant and nests more successful later in the breeding season. Our results show that habitat preferences do not uniformly improve fitness, and some benefits differ between sexes. Moreover, preference–fitness relationships only manifest at specific scales, and annual variation in population and predation dynamics can limit consistency. Detecting adaptive habitat selection thus requires multi-year measurements and careful consideration of relevant scales.

**Keywords** Brown-headed cowbird · Dickcissel · Polygyny · Reproductive success · Scale dependence

## Introduction

Animal habitat preferences are often predicted to improve fitness due to natural selection—a behavior known as adaptive habitat selection (Jaenike and Holt 1991; Chalfoun

and Schmidt 2012). Adaptive habitat selection has been observed in some systems (e.g., Chalfoun and Martin 2007; McLoughlin et al. 2007; Germain et al. 2015), but many studies have found ambiguous cases and counterexamples (e.g., Clark and Shutler 1999; Lloyd and Martin 2005; Mägi et al. 2009; Lamb et al. 2017; reviewed in Chalfoun and Schmidt 2012). Such deviations challenge straightforward predictions in favor of nuanced explorations of how habitat selection mediates fitness.

Mismatches between habitat preferences and habitat quality can arise through ecological traps (Schlaepfer et al. 2002), where sensory cues that historically indicated high-quality habitats now attract animals to degraded areas (e.g., Robertson and Hutto 2007; Lamb et al. 2017). Preferences may also not improve fitness when there is no clear gradient of habitat quality: alternative habitats may offer similar predation risks (Ellison et al. 2013; Embar et al. 2014), or spatiotemporal variability in predator and competitor

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Studies of whether animal habitat preferences enhance fitness are often contradictory. We show that context is key. Preferences improve fitness, but benefits are scale dependent and vary over time.

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assemblages may reduce the value of consistent selection strategies (Filliater et al. 1994; Martin and Martin 2001).

In other cases, however, investigators might fail to detect adaptive habitat selection because they measure only one aspect of fitness. Fitness is a product of many factors, including offspring production, offspring survival, foraging, and adult survival (Johnson 2007). Studies focused on a single fitness metric (e.g., Misenhelter and Rotenberry 2000; Frei et al. 2013) may overlook benefits of habitat preferences to other metrics. This may be particularly common when animals face trade-offs between fitness components during habitat selection (e.g., selecting habitats with low predation risk vs. with high food availability; Heithaus 2005; Utz et al. 2016). Detecting adaptive habitat selection thus requires measuring a suite of fitness metrics (Lloyd and Martin 2005; Chalfoun and Martin 2007; Uboni et al. 2017).

In addition, different fitness components are often mediated by habitat at distinct spatial scales (Chalfoun and Martin 2007; Quinlan and Green 2012). Food availability, for instance, may depend on animal home-range selection (Orians and Wittenberger 1991; McLoughlin et al. 2007), while predation risk depends on the scales of predator search behavior (Tewksbury et al. 2006; Shew et al. 2019). Animals must balance different fitness pressures and, therefore, consider multiple scales during habitat selection. Studies measuring preferences at a single scale (e.g., Lloyd and Martin 2005; Robertson and Hutto 2007) may overlook fitness benefits at other scales.

The complexity of adaptive habitat selection is illustrated by songbird breeding ecology. For instance, selecting high-quality territories may allow male birds to attract more mates (Zimmerman 1966), but avoiding nest predation and brood parasitism can depend more strongly on nest-site or landscape-scale habitat selection (Tewksbury et al. 2006; Maresh Nelson et al. 2018; Shew et al. 2019). Even then, fledgling survival may depend on a different suite of predators, or be more a function of offspring body condition (Jones et al. 2017). In each case, temporal variation in the environment could render the benefits of habitat preferences inconsistent among seasons (Borgmann et al. 2013), and differences in life-history strategies might drive male and female birds to benefit from habitat selection in different ways.

The interplay of fitness metrics, spatial scales, temporal variation, and sex differences may render adaptive habitat selection context specific. We sought to detangle this specificity by studying how habitat preferences at two spatial scales influenced four fitness metrics over two years in a migratory songbird of North American grasslands—the dickcissel (*Spiza americana*). We quantified preferences of male and female birds among territories and landscape patches, and then tested whether birds in preferred habitats experienced improvements in polygynous mate attraction, rates of brood parasitism by brown-headed cowbirds

(*Molothrus ater*), fledgling productivity, and offspring body condition. We predicted that dickcissels would benefit from habitat preferences, but sought to determine which fitness components improved in each sex, and which spatial scales governed each fitness metric. In addition, we examined whether benefits of occupying preferred habitats were consistent between breeding seasons.

## Methods

### Focal species

Dickcissels are an ideal species in which to evaluate adaptive habitat selection. They inhabit many types of grasslands (e.g., prairies, grazed pastures, old-fields), but densities and reproductive success vary among patches, suggesting that habitat preferences may relate to fitness (Zimmerman 1971). The fact that dickcissels exhibit facultative polygyny (i.e., some males pair with multiple females, some with one female, and others attract no mates) accentuates differences in individual male fitness and provides a metric of female preferences among territories (Zimmerman 1966; Sousa and Westneat 2013a). Finally, because dickcissels have low rates of site fidelity (10–49% of males return to their territories between years; Fletcher et al. 2006; Zimmerman and Finck 1989), annual habitat choices may be based not only on settlement decisions made in prior years, but also on conditions in the current year.

### Study area

We investigated dickcissel habitat preferences and reproductive success in 2014–2015 on seven pastures (17.6–41.1 ha in area) in the Grand River Grasslands of Ringgold County, Iowa, USA (map of pastures in Online Resource 1). This 62,000-ha region is characterized by high levels (~70%) of herbaceous land cover, interspersed with row-crop fields and woodlands (Duchardt et al. 2016). The average daily temperature from May to Aug was 21.0 °C in 2014 and 21.6 °C in 2015 (National Climatic Data Center 2019). Total May–Aug rainfall was 28.8 inches in 2014 and 27.4 inches in 2015 (National Climatic Data Center 2019). There were more pronounced differences in monthly climate data (Online Resource 2).

Our pastures were spaced at an average pairwise distance of 5.96 km (range 0.7–13.3). Each pasture was divided into three patches (21 patches total, 3.5–15.6 ha) demarcating management units (Online Resource 3). Two pastures were treated with patch-burn grazing, wherein one patch has been burned each year on a rotating basis and cattle have been stocked each year from Apr to Oct. The other five pastures have been burned every 3–5 years, with two pastures grazed

and three ungrazed. Two patches in one of these grazed pastures were treated with glyphosate herbicide in fall 2014 to control an invasive grass (tall fescue; *Schedonorus arundinaceus*). One of these treated patches was drilled with a high-diversity native seed mix in spring 2015. Differential management among patches has generated divergent plant and bird communities (Duchardt et al. 2016), so we considered patches as distinct replicates.

### Measuring habitat preferences

To document settlement patterns, we mapped dickcissel territories from 07-May to 13-Aug in 2014 and 08-May to 22-Aug in 2015. To aid mapping, we captured as many singing males as possible via targeted mist-netting with recorded playbacks, marking each with a unique combination of color bands and a numbered, aluminum band from the United States Geological Survey. We mapped territories on each pasture every 3–7 days ( $\bar{x} \pm \text{SD} = 4.9 \pm 1.4$  d) for a total of 18–23 (median = 20) surveys per pasture per year (Sousa and Westneat 2013a; Joos et al. 2014). Survey routes and pasture survey order varied among mapping rounds to reduce sampling bias (Bibby et al. 2000). Surveys were conducted between 0500 and 1300 h, and not during precipitation or high wind. Surveyors recorded band combinations and throat markings of each male to aid individual identification, and conducted focal observations ( $9.4 \pm 6.1$  min) of each male in each survey, using a GPS to mark all perches ( $3.4 \pm 1.8$  perches per focal observation).

We only considered males territorial if observed in  $\geq 2$  surveys. Perches recorded in different surveys were only considered part of the same territory if at least one was within 30 m of a perch used by the same male in another survey. Territory tenure was the number of days between the male's first detection and the day after last detection. We drew territory boundaries in ArcMap10.5 [ESRI, Redlands, CA, USA], grouping points based on bands, throat markings, perch proximity, and simultaneous sightings of males (Bibby et al. 2000). Boundaries were minimum convex polygons around all perches where an individual male sang or was seen with a female ( $28.7 \pm 17.6$  perches recorded per territory).

We quantified male territory preferences based on the relative order in which territories were first established (Sergio and Newton 2003; Joos et al. 2014). Territories seen in the first survey round were assigned Settlement Rank = 1 (most preferred); territories appearing in the second round, Settlement Rank = 2; and so forth. Multiple males sometimes established territories in the same location in a given year (overlap > 50%), with later males either displacing existing territory holders or resettling abandoned areas. In these cases, we assigned territories settled later the same rank as the earliest territory established

in the same location (Joos et al. 2014) because the area within the later-established territories was more preferred than an unmodified rank would indicate. Although we cannot distinguish whether preferences were a function of site fidelity or habitat characteristics, settlement rank indicates which territories males prioritized.

We quantified relative preferences of males among patches based on the maximum territory density recorded on each patch each year (Chalfoun and Martin 2007). Territories overlapping two patches were considered half territories in each patch. Maximum densities were greater on patches with an early date of first settlement, so we considered density as a reliable indicator of preference (GLM:  $F_{1, 31} = 12.53$ ,  $p = 0.001$ ,  $R^2 = 0.288$ ,  $\beta_{\text{First Territory Date}} = -0.008 \pm 0.002$  SE).

We measured female territory preferences based on territory polygyny levels; territories selected by more females were considered more preferred (Orlans and Wittenberger 1991). Polygyny level was the maximum number of simultaneously active nests on the territory (Sousa and Westneat 2013a). We located nests by observing adult behaviors (Martin and Geupel 1993), dragging a rope across pastures (Higgins et al. 1969), and noting incidental flushes. We visited nests every 1–3 days after discovery to record the number of dickcissel and brown-headed cowbird eggs and nestlings (Ralph et al. 1996). Nests empty before chicks were  $\geq 7$  days old—the age at which they are able to fledge—were considered depredated (hatch = day 1). Nests were considered successful when  $\geq 1$  nestling fledged. We confirmed fledging based on parental behavior.

To determine territory polygyny levels, we calculated nest initiation dates—i.e., date of first egg laid in each nest, following Maresh Nelson et al. (2018)—and noted nest end dates from monitoring data. Matching nests with territories based on nest locations and interactions of females with males, we determined how many nests were simultaneously active on each territory. However, we deemed it likely that we failed to find nests in some territories (22 of 193 territories), specifically in territories with no known nests where we observed a female in  $\geq 2$  surveys or saw parents feeding fledglings. We increased the polygyny level for these territories by one.

We estimated female patch preferences by dividing the total number of nests built on each patch each year by the total number of territories on the patch (nest–territory ratios; Zimmerman 1971). We divided nest abundances by territory abundances, rather than by patch area, because patch selection by females is constrained by mate availability. Nest–territory ratios were greater in patches where the first nest was initiated earlier, suggesting that these ratios reveal similar preference patterns compared to female settlement timing (GLM:  $F_{1, 27} = 7.03$ ,  $p = 0.013$ ,  $R^2 = 0.207$ ,  $\beta_{\text{First Nest Date}} = -0.012 \pm 0.004$  SE).

## Measuring reproductive success

We measured multiple fitness metrics: mate attraction, cowbird parasitism rates, fledgling productivity, and nestling body condition. We evaluated mate attraction by males based on territory polygyny levels (see above) and quantified parasitism by the presence or absence of cowbird eggs or nestlings in nests (Benson et al. 2010).

We quantified fledgling productivity by males as the total number of dickcissels fledged from each territory (territory productivity; Sousa and Westneat 2013a). In the seven cases where we observed parents feeding fledglings from a nest we did not find, we assumed these nests had each produced two dickcissel chicks—the median number fledged from successful nests—and added these to the productivity of the respective territories.

Evaluating fledgling productivity by females required a different approach since fledglings from polygynous territories could be the offspring of multiple females. We thus counted how many dickcissels fledged from individual nests that produced at least one fledgling (nest productivity). We included nests from which only cowbirds fledged in this analysis, counting them as having produced zero dickcissel fledglings (Benson et al. 2010). Because dickcissels rarely

build additional nests after producing a successful brood, nest productivity is likely a good estimate of annual fledgling productivity by individual females (Walk et al. 2004).

To quantify nestling body condition, we weighed chicks and measured their tarsus lengths 4–6 days after hatching (hatch = day 1). We then regressed mass vs. tarsus length (GLM:  $F_{1, 214} = 629.37$ ,  $p < 0.001$ ,  $R^2 = 0.746$ ;  $\beta_{\text{Tarsus}} = 1.11 \pm 0.04$  SE) and calculated an index of body condition for each chick as its residual from this linear relationship (Vitz and Rodewald 2011). This metric has been shown to influence post-fledging survival of dickcissels (Jones et al. 2017), and using it allowed us to control for variation in mass due to nestling age and frame size.

## Data analysis

We conducted seven analyses to investigate adaptive habitat selection by dickcissels (Table 1). Analyses related fitness metrics (response variables) to male and female habitat preferences at the territory and patch scales (explanatory variables). All analyses were performed in SAS 9.4 using PROC GLIMMIX [SAS Institute, Cary, NC, USA]. Analyses of cowbird parasitism risk used a binomial distribution. We chose a distribution for the other fitness metrics

**Table 1** Analyses of adaptive habitat selection by male and female dickcissels

Analysis	Unit of replication	Territory/patch preference metrics (fixed effects)	Reproductive metrics (response variables)
(a) Male habitat preferences and mate attraction	Territory	Settlement rank/maximum territory density in the patch containing the territory	Territory polygyny level <sup>a</sup>
(b) Male habitat preferences and brood parasitism	Nest	Settlement rank of the territory/maximum territory density in the patch where the nest was built	Nest parasitized? (Y/N) <sup>b</sup>
(c) Female habitat preferences and brood parasitism	Nest	Polygyny level in the territory/nest–territory ratio in the patch where the nest was built	Nest parasitized? (Y/N) <sup>b</sup>
(d) Male habitat preferences and fledgling productivity	Territory	Settlement rank/maximum territory density in the patch containing the territory	Territory productivity <sup>c</sup>
(e) Female habitat preferences and fledgling productivity	Nest	Polygyny level in the territory/nest–territory ratio in the patch where the nest was built	Nest productivity <sup>a,d</sup>
(f) Male habitat preferences and nestling body condition	Nestling	Settlement rank of the territory/maximum territory density in the patch where the nestlings were reared	Nestling condition <sup>e</sup>
(g) Female habitat preferences and nestling body condition	Nestling	Polygyny level in the territory/nest–territory ratio in the patch where the nestlings were reared	Nestling condition <sup>e</sup>

Each row summarizes one of seven analyses examining whether habitat preferences at territory and patch scales improve components of reproductive success

<sup>a</sup>Modeled with a Poisson distribution

<sup>b</sup>Modeled with a binomial distribution. Only nests that survived to incubation were included in these analyses. Cowbirds typically parasitize nests during the laying phase, so nests that did not survive to incubation did not have an equal opportunity to be parasitized

<sup>c</sup>Modeled with a negative binomial distribution

<sup>d</sup>Only nests that survived to fledging were included in this analysis

<sup>e</sup>Modeled with a Gaussian distribution

by testing whether a Gaussian, negative binomial, or Poisson distribution yielded the lowest  $AIC_c$  score. We only accepted distributions yielding ratios of Pearson Chi-squared  $df^{-1} < 1.2$  to avoid overdispersion (Littell et al. 2006). We used likelihood-ratio tests to decide whether to include ‘Pasture’, ‘Year’, or ‘Pasture  $\times$  Year’ as random effects in each analysis. We tested for non-independence between territories defended by the same male by conducting a likelihood-ratio test on models including ‘MaleID’ as a random effect. This random effect never improved model fit, so we did not retain it in any case. However, we did include ‘NestID’ as a random effect in analyses of nestling condition to account for non-independence among siblings.

In all analyses, we conducted a two-stage model selection process to relate fitness to habitat preferences. We used Maximum Likelihood (adaptive quadrature) parameter estimation to compare models with differing fixed effects. In Stage 1, we selected fixed effects by comparing  $AIC_c$  scores of models including covariates to a random-effects-only model. Covariates represented variables that may have influenced fitness but were not strictly related to habitat preferences (e.g., temporal variables, nest contents, etc.). We considered a covariate supported if its respective model contributed to the cumulative top 90% of model weights, as long as it also had model weight greater than the random-effects-only model (Burnham and Anderson 1998, p. 127). Random variables and selected covariates were included in all Stage-2 models.

In Stage 2, we related fitness metrics to habitat preferences. Candidate model sets for analyses of male preferences included ‘Settlement Rank’ and ‘Maximum Territory Density’, our metrics of male territory- and patch-scale preferences. Analyses of female preferences included models for ‘Territory Polygyny level’ and ‘Nest–Territory Ratio’, our parallel metrics of female preferences. To evaluate the consistency of preference–fitness relationships from 2014 to 2015, Stage-2 model sets also included interactions between each preference metric and ‘Year’.

For each Stage-2 analysis, we compared  $AIC_c$  scores of candidate models to a base model with only random effects and covariates. We considered models supported if they contributed to the cumulative top 90% of weights in their respective model set and were ranked above the base. We computed predicted values of fitness metrics across observed ranges of preference metrics, holding covariates at average values (Shaffer and Thompson 2007). We generated 85% confidence intervals around predicted values since  $AIC_c$  selects variables at this level (Arnold 2010).

In two analyses—the comparison of male preferences to territory polygyny levels and territory productivity—each territory represented one unit of replication. However, there were many locations where multiple territories occupied the same space (at different times) within a breeding season.

Thus, to avoid pseudoreplication, we only included the territory with the longest tenure occupying a given location, and thereby excluded 37 territories from those analyses.

## Results

### Data structure and annual variability

We used data from all seven pastures in 2015 but excluded one in 2014 because dickcissels vacated it after an intense June storm. In 2014, we used 3235 of 3737 recorded perches to map 107 territories. We only included 83 of these territories in territory-scale analyses, however, since 24 overlapped  $> 50\%$  with other territories of longer tenure. In 2015, we mapped 86 territories—using 2303 of 2486 recorded perches—but excluded 13 from territory-scale analyses due to overlap. We banded 42 males in 2014, 13 of which returned in 2015 (site-fidelity rate = 30.1%). We banded an additional 11 males in 2015.

Males and females colonized the study region more quickly and at higher densities in 2014 than 2015, although dickcissels continued breeding later into 2015 (Fig. 1, Table 2). From May–June, the male–female ratio was lower in 2014 than 2015, indicating a relatively high abundance of females early in 2014 (Online Resource 4). This pattern reversed in July, when the male–female ratio was lower in 2015. Fledgling productivity and polygyny rates (Online Resource 5) were relatively low in 2015, but cowbird parasitism was less frequent that year (Table 2).

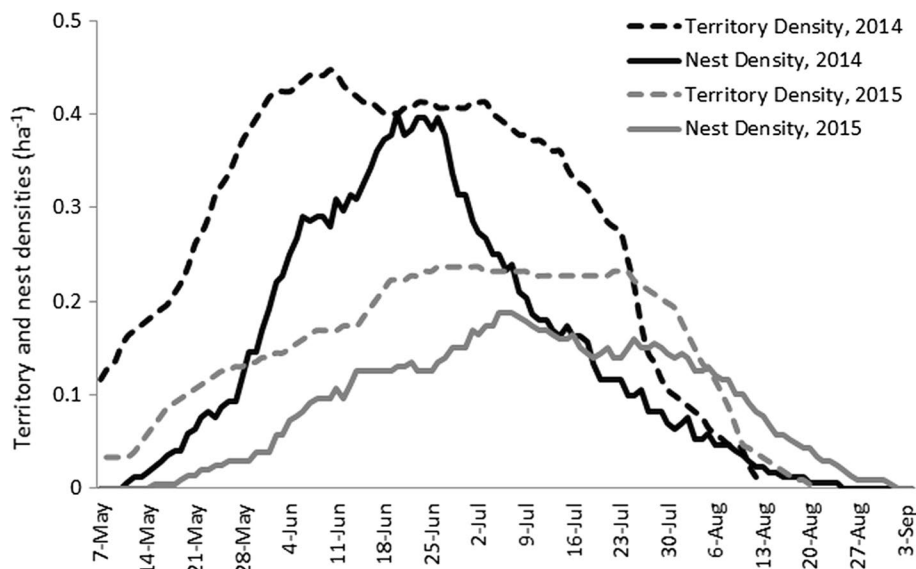
### Male habitat preferences and mate attraction

Territory polygyny level increased with tenure ( $\beta_{\text{Tenure}} = 0.022 \pm 0.005$  SE); males attracted more mates by holding territories for longer. Controlling for tenure, the interaction between territory settlement rank and year was the best-supported habitat-preference model (Table 3a). Males in territories settled earlier in the season achieved marginally greater polygyny in 2014, while males in territories settled later attracted more mates in 2015 (Fig. 2a). Territories in high-density patches consistently achieved greater polygyny levels ( $\beta_{\text{Max Density}} = 0.416 \pm 0.201$  SE; Fig. 2b).

### Habitat preferences and cowbird parasitism

Nests initiated later in the season were less likely to be parasitized ( $\beta_{\text{Initiation Date}} = -0.036 \pm 0.010$  SE). Controlling for nest initiation date, neither male nor female territory preferences influenced parasitism risk, but patch preferences of both sexes ranked above their respective base models (Table 3b, c). Nests in patches with high territory density (Fig. 3a) and with high nest–territory ratios (Fig. 3b) were

**Fig. 1** Densities of dickcissel territories (dashed) and nests (solid) in 2014 (black) and 2015 (gray), across all study pastures in Ringgold County, IA, USA. Densities calculated as the total number of territories and nests known each day divided by total area surveyed each year (2014: 18 patches, 171.8 ha; 2015: 21 patches, 206.8 ha). Territory densities smoothed between surveys



**Table 2** Dickcissel abundance, reproductive success, and phenology in the Grand River Grasslands of Ringgold County, IA, during the 2014–2015 breeding seasons

Metric	2014	2015
Pastures (patches) sampled	6 (18)	7 (21)
Territories observed	107	86
Territory size, ha ( $\bar{x} \pm SD$ , median)	0.75 $\pm$ 0.91, 0.51	1.01 $\pm$ 0.84, 0.87
% Territories polygynous (i.e., > 1 concurrent nest)	29.4%	11.5%
Nests found (+ estimated nests not found)	149 (+ 7)	59 (+ 15)
Successful nests (+ est. successful nests not found)	46 (+ 3)	13 (+ 4)
Dickcissel chicks fledged (+ est. fledglings not found)	113 (+ 6)	31 (+ 8)
Avg. nest productivity (i.e., fledglings per successful nest)	2.18	2.16
Avg. territory productivity (i.e., fledglings per territory)	1.09	0.44
Dickcissel nestlings measured	140	42
% Nests parasitized by cowbirds	50.4%	36.5%
Cowbird fledglings produced	34	3
Average date of territory establishment	27-May	14-June
Date of first nest initiation	11-May	15-May
Date of peak nest density	20-June	05-July
Date of final male departure	12-August	20-August
Date of final nest-cycle completion	24-August	01-September

less likely to be parasitized ( $\beta_{\text{Max Density}} = -0.800 \pm 0.542$  SE;  $\beta_{\text{Nest-Territory Ratio}} = -0.888 \pm 0.449$  SE).

### Habitat preferences and fledgling productivity

Territory productivity—our metric of fledgling productivity by males—was greater in territories where more nests were built ( $\beta_{\text{Total Nests}} = 0.429 \pm 0.147$  SE). Controlling for this, the best-supported preference model was the interaction between territory settlement rank and year (Table 3d). More dickcissels fledged from territories settled earlier in the season in 2014. In 2015, however, territories settled later produced more fledglings (Fig. 4a). Territories in patches

with high territory density consistently produced more fledglings ( $\beta_{\text{Max Density}} = 0.657 \pm 0.365$  SE; Fig. 4b).

Nest productivity—our metric of fledgling productivity by females—was unrelated to territory-scale preferences (Table 3e). In contrast, nest productivity tended to be greater in patches preferred by females ( $\beta_{\text{Nest-Territory Ratio}} = 0.184 \pm 0.119$  SE; Fig. 5).

### Habitat preferences and nestling body condition

Nestlings measured later in the day were in superior body condition ( $\beta_{\text{Time of Day}} = 0.156 \pm 0.032$  SE). Controlling for time of day, territory settlement rank was the best-supported

**Table 3** AIC tables comparing territory- and patch-scale habitat preferences of male and female dickcissels to reproductive metrics

Model	# Parameters	Deviance	$\Delta AIC_c$	Model weight ( $\omega$ )
(a) Male habitat preferences and territory polygyny levels <sup>a</sup>				
Settlement rank $\times$ year	6	354.10	0	0.500
Max. territory density	4	359.89	1.42	0.236
Base model (tenure)	3	362.81	2.22	0.158
(b) Male habitat preferences and cowbird parasitism <sup>b</sup>				
Max. territory density	4	202.70	0	0.445
Base model (initiation date)	3	204.84	0.05	0.434
(c) Female habitat preferences and cowbird parasitism <sup>b</sup>				
Nest–territory ratio	4	201.55	0	0.518
Base model (initiation date)	3	204.84	1.21	0.283
(d) Male habitat preferences and territory productivity <sup>c</sup>				
Settlement rank $\times$ year	7	373.29	0	0.860
Max. territory density	5	383.37	5.72	0.049
Base model (total nests)	4	385.54	5.75	0.049
(e) Female habitat preferences and nest productivity <sup>d</sup>				
Nest–territory ratio	2	225.31	0	0.411
Base model (no Covariates)	1	227.69	0.25	0.363
(f) Male habitat preferences and nestling body condition <sup>e</sup>				
Settlement rank	4	562.66	0	0.675
Settlement rank $\times$ year	6	560.33	1.97	0.252
Base model (time of day)	3	570.37	5.60	0.041
(g) Female habitat preferences and nestling body condition <sup>e</sup>				
Territory polygyny level	4	565.70	0	0.449
Nest–territory ratio	4	567.23	1.52	0.210
Base model (time of day)	3	563.41	2.00	0.165

Sub-tables correspond to analyses in Table 1. Only base models—which include supported random effects and covariates—and more highly ranked models are shown. See Online Resource 6 for complete AIC tables

<sup>a</sup>Models include territory tenure as a covariate and ‘Pasture  $\times$  Year’ as a random variable

<sup>b</sup>Models include nest initiation date as a covariate and ‘Pasture’ as a random variable

<sup>c</sup>Models include the total number of nests built on the territory as a covariate and ‘Pasture  $\times$  Year’ as a random variable

<sup>d</sup>Models include no random variables or covariates

<sup>e</sup>Models include time of nestling measurement as a covariate and ‘NestID’ as a random variable

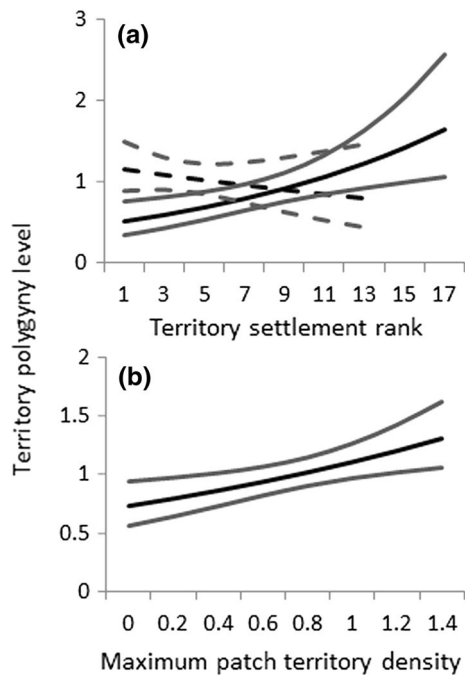
male-preference model (Table 3f). Nestlings attained superior condition when reared in territories established earlier in the season ( $\beta_{\text{Settlement Rank}} = -0.067 \pm 0.023$  SE; Fig. 6a). Though the interaction between settlement rank and year also received some support, inter-annual differences in nestling condition were weak, so we did not consider the interaction informative (Table 3f).

In the analysis of female habitat preferences, again controlling for time of day, both territory polygyny levels and patch nest–territory ratios received support (Table 3g). Nestlings reared in territories with high polygyny levels ( $\beta_{\text{Polygyny Level}} = 0.266 \pm 0.122$  SE; Fig. 6b) and nestlings reared in patches with high nest–territory ratios

( $\beta_{\text{Nest–Territory Ratio}} = 0.250 \pm 0.139$  SE; Fig. 6c) attained superior condition.

## Discussion

Our study provides a complex portrait of adaptive habitat selection. Dickcissel habitat preferences improved every metric of reproduction we measured—polygyny, cowbird parasitism, nestling body condition, and nest and territory productivity—but every relationship was context dependent. Habitat preferences only improved reproduction at particular spatial scales, and relevant scales of preference differed among fitness metrics (Chalfoun and Martin 2007).

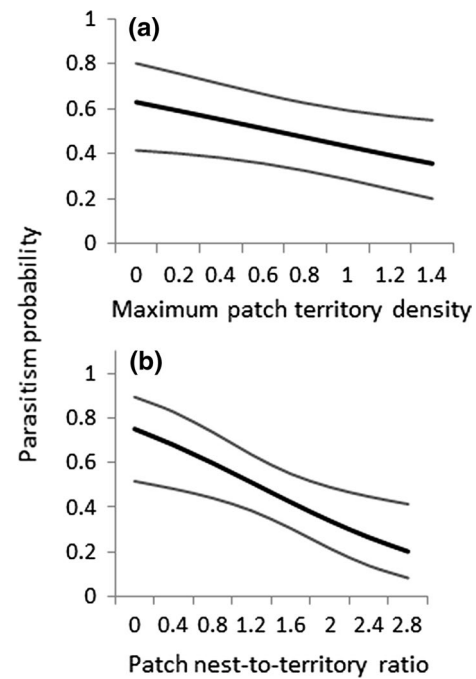


**Fig. 2** Territory polygyny level as a function of **a** territory settlement rank (dashed=2014; solid=2015) and **b** maximum patch territory density. Estimates derived from Generalized Linear Mixed Models (GLMMs) using a Poisson distribution, with ‘Pasture×Year’ as a random effect and territory tenure as a covariate ( $N=156$  territories). Estimates are for a territory defended for 45 days. Error bars are 85% CI

Moreover, male and female birds faced different limitations. Whereas male habitat preferences at both the territory and patch scales enhanced fledgling productivity, productivity by females was only improved by patch-scale preferences. Adding to this complexity, male territory preferences only improved mate attraction and fledgling productivity in one year of the study—evidence of temporal variation in adaptive habitat selection (Mosser et al. 2009).

We acknowledge we could not examine whether the quality of individual adults influenced fitness, and thus whether preference–fitness relationships were in part a product of high-quality birds occupying preferred habitats (Hasselquist 1998). However, another study found few impacts of male dickcissel traits on annual reproduction, suggesting this may not be an issue (Sousa and Westneat 2013b). We also note that we were unable to follow birds across their entire lifespans, and thus test whether preferences improved lifetime fitness (McLoughlin et al. 2007). Despite these caveats, multiple signals of adaptive habitat selection manifested in the 2 years of our study.

One of the strongest lines of evidence was that territories preferred by males, and both territories and patches preferred by females, produced offspring in superior body condition. Increasing fledgling mass improves



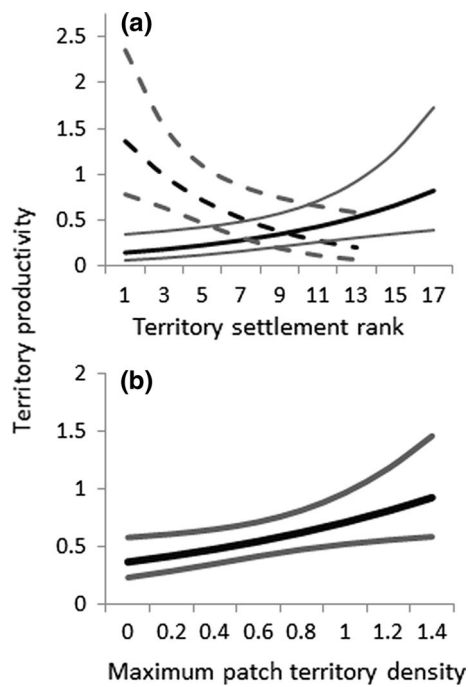
**Fig. 3** Probability a nest will be parasitized by brown-headed cowbirds as a function of **a** maximum patch territory density and **b** patch nest–territory ratio. Estimates derived from GLMMs using a binomial distribution, with ‘Pasture’ as a random effect and nest initiation date as a covariate ( $N=181$  nests). Estimates are for nests initiated on 23-Jun. Error bars are 85% CI

post-fledging survival in dickcissels (Suedkamp Wells et al. 2007; Jones et al. 2017), so habitat preferences likely enhanced parental fitness through offspring recruitment. The mechanisms by which dickcissels identified habitats beneficial to nestling growth are unclear, but they may prefer habitats containing abundant arthropods or vegetation associated with high food availability (Orians and Wittenberger 1991; Germain et al. 2015).

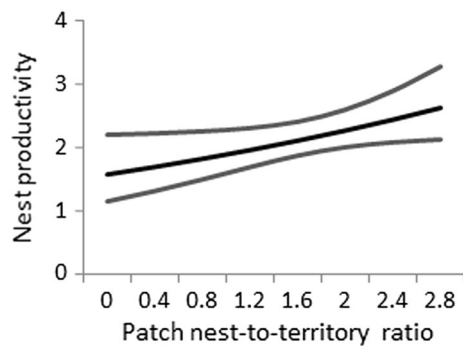
Potential evidence for adaptive habitat selection also emerged in that males and females preferred patches where cowbird parasitism was infrequent. Escaping parasitism enhances fitness as brood parasites increase parental energy costs and reduce offspring condition and productivity (Hoover and Reetz 2006). Our results would constitute evidence of adaptive patch selection if dickcissels detect and avoid cowbirds during settlement (Forsman and Martin 2009). However, it is instead possible that nests in patches with high dickcissel density were parasitized less often because cowbirds could not lay eggs in all nests. In this scenario, it would be unclear whether dickcissels settled near each other to reduce parasitism—a form of adaptive habitat selection—or whether low parasitism rates were a by-product of clustering for another purpose.

Additional research is needed to determine whether dickcissels actively avoid cowbirds at the patch scale, but our





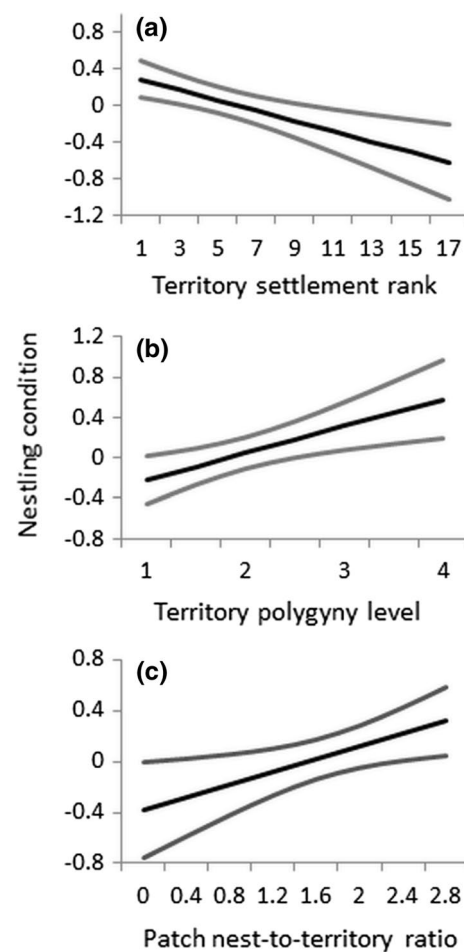
**Fig. 4** Territory productivity (i.e., total dickcissels fledged from a territory) as a function of **a** territory settlement rank (dashed=2014; solid=2015) and **b** maximum patch territory density. Estimates derived from GLMMs using a negative binomial distribution, with ‘Pasture×Year’ as a random effect and total number of nests built in each territory as a covariate ( $N=156$  territories). Estimates are for a territory in which only one nest is built. Error bars are 85% CI



**Fig. 5** Nest productivity (i.e., number of dickcissels fledged from a nest that produces at least one fledgling) as a function of patch nest-to-territory ratio. Estimates derived from a GLMM using a Poisson distribution ( $N=59$  nests). No random effects included. Error bars are 85% CI

results clearly show that territory preferences did not reduce parasitism. This scale-specific limitation may exist because parasitism is mediated by landscape patterns at broad spatial scales (i.e., woodland cover; Pietz et al. 2009; Maresh Nelson et al. 2018).

We also observed scale-dependency with respect to nest productivity—the number of dickcissel chicks that fledged



**Fig. 6** Nestling condition as a function of **a** territory settlement rank, **b** territory polygyny level, and **c** nest-to-territory ratio in the patch where the chick is reared. Estimates derived from GLMMs using a Gaussian distribution, with ‘NestID’ as a random effect and time of day each nestling was measured as a covariate ( $N=182$  nestlings). Error bars are 85% CI

from successful nests. Despite being a key component of female reproduction, only female patch-scale preferences improved nest productivity. This pattern may stem from the fact that only patch-scale preferences reduced brood parasitism. Successful dickcissel nests produced fewer host fledglings when parasitized (Maresh Nelson et al. 2018), so the fact that females did not—or could not—discriminate among territories based on parasitism risk may have prevented them from preferring high-productivity territories.

In contrast to females, males engaged in adaptive territory selection with respect to fledgling productivity and mate attraction—albeit inconsistently. In 2014, early-arriving males selected high-quality territories where they attracted multiple females and produced many fledglings. Late-arriving males were relegated to lower-quality areas unless they took over an established territory (Aebischer et al. 1996;

Joos et al. 2014). Despite this evidence for adaptive territory selection in 2014, however, males in preferred territories performed poorly in 2015.

We offer two hypotheses to explain this reversal. First, nest survival rates were high early in 2014 and decreased over time, but were low early in 2015 and increased over time (Maresh Nelson et al. 2018). These patterns could have allowed early-arriving males to produce more fledglings in 2014, but fewer in 2015. The cause of this variable predation dynamic is uncertain, but it might have resulted from temporal variation in predator foraging behaviors or communities between years (Borgmann et al. 2013). Differences in climate between study years may have contributed to this variation: early-season nest success is often poor for grassland birds when precipitation levels are high (Zuckerberg et al. 2018), and rainfall in May was greater in 2015 than in 2014 (6.8 in vs. 3.7 in; National Climatic Data Center).

A second explanation for this annual inconsistency may stem from variability in dickcissel population dynamics. Females began arriving earlier and in higher abundances in 2014 relative to 2015, reducing mate competition for early males and increasing early-season fledgling productivity. In 2015, female abundance peaked much later in the summer. Thus, early males faced intense mate competition, and late-arriving males may have performed better in 2015 since many early males abandoned their territories after several weeks of attracting no mates.

Temporal variability in preference–fitness relationships underscores a key limitation to adaptive habitat selection: reproduction is mediated in part by factors animals cannot evaluate while selecting habitat. Other authors have noted that microhabitat preferences with respect to nest-site selection may be of little adaptive value due to unpredictable predation risk (e.g., Filliater et al. 1994), and our data suggest that inter-annual variability in predation dynamics may also limit adaptive territory selection. Moreover, to our knowledge, our study is the first to suggest that annual variability in mate competition may reduce the benefits of habitat preferences.

The context specificity of adaptive habitat selection presents logistical challenges for ecologists. Our study illustrates that fitness components are only enhanced by habitat preferences at particular spatial scales. If investigators quantify preferences at scales irrelevant to measured components, preferences may appear unrelated to fitness. Because relevant scales are often unknown a priori, we recommend measuring preferences at multiple scales. Similarly, since our results show that some fitness metrics can be more strongly affected by habitat selection than others, we suggest measuring multiple metrics and urge authors to evaluate how preference–fitness relationships vary over time to discern the mechanisms underlying adaptive

habitat selection. Finally, we recommend examining relationships on a sex-specific basis. Males and females are subject to different life-history constraints, and may, thus, vary in habitat-selection strategies.

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## Compliance with ethical standards

**Conflict of interest** The authors declare that they have no conflict of interest.

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