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ARE THERE OPTIMAL DENSITIES FOR PRAIRIE BIRDS?

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Abstract. The major forces of food and predation shape fitness-enhancing decisions of birds at all stages of their life cycles. During the breeding season, birds can minimize nest loss due to predation by selecting sites with a lower probability of predation. To understand the environmental and social aspects and consequences of breeding-site selection in prairie birds, we explored variation in nest-survival patterns of the Lark Bunting (*Calamospiza melanocorys*) in the shortgrass prairie region of North America. Over four breeding seasons, we documented the survival of 405 nests, conducted 60 surveys to estimate bird densities, and measured several vegetative features to describe habitat structure in 24 randomly selected study plots. Nest survival varied with the buntings' density as described by a quadratic polynomial, increasing with density below 1.5 birds ha^{-1} and decreasing with density between 1.5 and 3 birds ha^{-1}, suggesting that an optimal range of densities favors reproductive success of the Lark Bunting, which nests semi-colonially. Nest survival also increased with increasing vegetation structure of study plots and varied with age of the nest, increasing during early incubation and late in the nestling stage and declining slightly from mid-incubation to the middle of the nestling period. The existence of an optimal range of densities in this semi-colonial species can be elucidated by the "commodity-selection hypothesis" at low densities and density dependence at high densities.

Key words: avian density; Calamospiza melanocorys; *commodity-selection hypothesis; Lark Bunting; nest survival; Program MARK; shortgrass prairie*

¿Existen Densidades Óptimas para las Aves de Praderas?

Resumen. La disponibilidad de alimento y la depredación son las fuerzas principales que moldean las decisiones que incrementan la adecuación biológica de las aves en todas las etapas de sus ciclos de vida. Durante la estación reproductiva, las aves pueden minimizar la pérdida de los nidos debido a la depredación mediante la selección de sitios con una menor probabilidad de depredación. Para entender los aspectos ambientales y sociales y las consecuencias de la selección de los sitios de anidación en las aves de pradera, exploramos la variación en los patrones de supervivencia de los nidos de *Calamospiza melanocorys* en la región de pradera de pastos cortos de America del Norte. A lo largo de cuatro estaciones reproductivas, documentamos la supervivencia de 405 nidos, realizamos 60 muestreos para estimar las densidades de las aves y medimos varios aspectos de la vegetación para describir la estructura del hábitat en 24 parcelas de estudio seleccionadas al azar. La supervivencia del nido varió con la densidad de *C. melanocorys* siguiendo la forma de un polinomio cuadrático, incrementando con una densidad menor a 1.5 aves/ha y disminuyendo con una densidad de entre 1.5 y 3 aves/ha, sugiriendo que un rango óptimo de densidades favorece el éxito reproductivo de los individuos de *C. melanocorys*, los cuales nidifican de modo semi-colonial. La supervivencia del nido también incrementó con un aumento en la estructura de la vegetación de las parcelas de estudio y varió con la edad del nido, incrementando a principios de la incubación y al final del período de pichón y disminuyendo suavemente desde mediados de la incubación hasta la mitad del período de pichón. La existencia de un rango óptimo de densidades en esta especie semi-colonial puede ser entendida a través de la "hipótesis de selección de bienes de consumo" a bajas densidades y por denso dependencia a altas densidades.

INTRODUCTION

The major forces of food and predation shape the fitness-enhancing decisions of birds at all stages of their life cycles and ultimately determine lifetime reproductive fitness. During the breeding season, the influence of predation on fitness is particularly great, accounting for >80% of nest loss on average (Martin 1993) and >90% of nest loss for birds of shortgrass prairie (Yackel Adams et al. 2007). At several scales (landscape, habitat, territory, and nest site), birds can minimize nest predation by selecting breeding sites with a lower probability of detection by predators; several studies have sought to identify the environmental cues, landscape features, and vegetation structure of favorable habitats and nest sites (Martin 1993, Davis 2005, Fontaine and Martin 2006).

In addition to environmental and structural cues, passerines may use social information when selecting breeding sites (Ahlering et al. 2006), and information gained from

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conspecifics, in turn, may increase reproductive fitness. The importance of social cues in habitat selection is described by the "commodity-selection hypothesis" which postulates that breeding aggregations or colonies form as individuals independently select for preferred habitat features (habitat-mediated aggregation) and simultaneously are attracted to birds of the same species (conspecific attraction leading to additive aggregation; Danchin and Wagner 1997). For birds in general, colony sizes can range from only a few nests to more than a million birds, and nest distribution ranges from loosely aggregated to densely packed (Wittenberger and Hunt 1985, Rolland et al. 1998). A corollary of additive aggregation is that some habitat patches may be crowded whereas other favorable habitats remain unused, a pattern long noted by ornithologists (Lack 1968, Stamps 1986).

In this article we explore variation in nest-survival patterns to understand the social aspects and consequences of breeding decisions made by prairie birds, with a focus on the Lark Bunting (*Calamospiza melanocorys*), whose populations that are declining throughout Colorado (Sauer et al. 2006). It breeds in loose aggregations and is considered semicolonial or colonial while nesting (Lack 1968, Wittenberger and Hunt 1985, Shane 2000). Over four breeding seasons, we quantified nest survival, bird densities, and vegetative features at 25 randomly selected study sites. Here we examine nest survival of Lark Buntings relative to intrinsic (nest age), extrinsic (habitat structure), and social (densities of conspecifics and other grassland birds) factors. We discuss the implications of our findings for recent theoretical developments in social breeding in birds and conservation approaches.

METHODS

STUDY AREA

From mid-May to late July, 1997–1999 and 2001, we surveyed grassland birds and monitored nests in and near the Pawnee National Grassland, northeastern Colorado (40° 43′ N, 104° 29′ W), in a moderately fragmented landscape composed of shortgrass prairie (62%), irrigated and nonirrigated crops (29%), and Conservation Reserve Program (CRP) fields (8%). We randomly selected 24 study sites (64.7 ha or one quarter section; boundaries determined by quarter-section lines of the Public Land Survey), including 16 shortgrass prairie sites and eight CRP sites on U.S. Forest Service land accessible by road. Prairie study sites were dominated by xeric grasses such as buffalograss (*Buchloe dactyloides*) and blue grama (*Bouteloua gracilis*) with occasional shrubs of four-winged saltbush (*Atriplex canescens*) and broom snakeweed (*Gutierrezia sarothrae*). CRP sites were vegetated primarily with exotic grasses such as smooth brome (*Bromus inermis*), intermediate wheatgrass (*Agropyron intermedium*), and crested wheatgrass (*A. cristatum*). Potential nest predators include the thirteen-lined ground squirrel (*Spermophilus tridecemlineatus*), coyote (*Canis latrans*), swift fox (*Vulpes velox*), long-tailed weasel (*Mustela frenata*), bullsnake (*Pituophis melanoleucus*), western hognose snake (*Heterodon nasicus*), and Burrowing Owl (*Athene cunicularia*).

FIELD PROCEDURES

We conducted our research at 16, 16, 20, and 8 sites per year in 1997, 1998, 1999, and 2001, for a total of 24 unique sites and 60 site-year combinations. At each site, we surveyed all grassland birds along point transects at 12 (occasionally 6) points 300 m apart from 05:30 to 09:30 MDT, between 21 May and 9 June, avoiding inclement weather. All birds detected by sight or sound were recorded within intervals of 0–25 m, 25–50 m, 50–75 m, 75–100 m, and 100–150 m. We searched all sites systematically for nests by dragging a rope between two observers 25 m apart and by observing adults' behavior. To determine incubation stage, we floated two eggs by using a modified technique of Westerskov (1950), and we recorded the number, age, and status of eggs and nestlings at 2- to 4-day intervals until nests were empty. During the last nest check, we noted signs of fledging (parents feeding young or calling in vicinity, fecal droppings outside of nest; Yackel Adams et al. 2006). Nests were active from 18 May to 24 July. We sampled the vegetation structure and composition of grassland patches along the point transects between 21 May and 11 June. We visually estimated the percent cover of grasses, sedges, forbs, shrubs, cacti, and bare ground within plots of radius 5 m and measured grass height and vegetation density at distances of 1, 3, and 5 m from the point in one direction (east). We recorded vegetation density as the number of vegetation hits on a 1-cm-diameter pole at intervals of 0–5, 5–10, 10–20, and 20–30 cm above ground. We constructed several vegetation-structure variables for use in the analyses.

A PRIORI MODELS

Our primary interest was in evaluating the role of bird density in nest survival. Because nest age and habitat structure also can influence nest survival, we included these categories of variables in our set of candidate models to account for as much additional variation as possible. Information from the scientific literature in support of inclusion of these variables is as follows. In some species of grassland birds, daily survival varies linearly with nest age (Dinsmore et al. 2002, Davis 2005, Lloyd and Martin 2005), yet in others a cubic polynomial best describes the effect of nest age (Davis 2005, Grant et al. 2005). Responses to vegetation structure can be highly variable, yet nest survival can increase with increasing nest concealment (Winter et al. 2005, Davis 2005). In general, birds are most abundant in habitats with high productivity (Bock and Jones 2004), although this relationship does not hold in areas of recent habitat disturbance. As an alternative to a linear trend, we also evaluated a quadratic trend of bird density on nest survival

STATISTICAL ANALYSES

Because predators may be attracted to areas of high bird densities regardless of bird species, we evaluated whether to use densities of Lark Buntings only or densities of all grassland birds; in all analyses we evaluated the linear and quadratic forms. We defined "grassland birds" as ground-nesting grassland doves and passerines, including the Mourning Dove (*Zenaida macroura*), Horned Lark (*Eremophila alpestris*), Cassin's Sparrow (*Aimophila cassinii*), Brewer's Sparrow (*Spizella breweri*), Lark Sparrow (*Chondestes grammacus*), Lark Bunting, Grasshopper Sparrow (*Ammodramus savannarum*), McCown's Longspur (*Calcarius mccownii*), Chestnut-collared Longspur (*C. ornatus*), and Western Meadowlark (*Sturnella neglecta*). We classified birds into detection guilds of subtle (Cassin's Sparrow, Brewer's Sparrow, Lark Sparrow, Grasshopper Sparrow) and obvious (often detected by prominent song or flight display: Mourning Dove, Horned Lark, Lark Bunting, McCown's Longspur, Chestnut-collared Longspur, Western Meadowlark). We estimated densities of grassland birds for each year and site (sampling unit) by using the Multiple Covariates Distance Sampling (MCDS) analysis procedures in DISTANCE v. 4.1 (Thomas et al. 2003); this analysis accounts for detection variability due to covariates (e.g., observer and habitat structure) and calculates estimates with maximum precision. We modeled the probability of detecting grassland birds and Lark Buntings as a function of radial distance, observer, plot vegetation variables, and detection guild by using four robust models suggested by Buckland et al. (2001). Because fitting the detection function with multiple covariates is computationally difficult, building model sets with forward stepwise selection (adding covariates one at a time) is recommended for MCDS (Thomas et al. 2003). We first evaluated four recommended models (half-normal key function with cosine and hermite polynomial expansion series and hazard-rate key function with cosine and simple polynomial expansion series) with no covariates (constant model) and selected the best model with Akaike's information criterion (AIC; Burnham and Anderson 2002). We selected the best model from among univariate models by using seven vegetation-structure variables: AvgGhgt (average grass height), PercGS (percent cover of grasses and sedges), PercFSb (percent cover of forbs and shrubs), PercVeg (percent cover of grasses, sedges, forbs, and shrubs), AvhtVeg (AvgGhgt × PercVeg), HitsVeg (vegetation hits × PercVeg), and Overall (AvgGhgt × Hits × PercVeg). We constructed a balanced model set with all combinations of the selected vegetation covariate, observer, and detection guild (for all grassland birds). To minimize bias from model-selection uncertainty, we model-averaged avian densities for model sets with closely competing models (i.e., models with $\Delta AIC < 7$).

To calculate daily nest-survival probabilities of Lark Buntings, we used the robust nest-survival model in MARK Version 4.3 (White and Burnham 1999), which uses generalized linear modeling based on a binomial likelihood. On the basis of Baicich and Harrison (1997), we used 12 days and 8 days for the duration of the incubation and nestling periods, respectively. For nests of uncertain fate (5.9% of 405 nests), the final observation interval was censored and nests were coded as successful, as recommended by Manolis et al. (2000). Nests of unknown age (6.4% of 405 nests; all occurred in 1997 and 1998) were assigned the average initial age of nests.

Because of the large number of potential variables under consideration, we conducted preliminary analyses to determine which of two to several possible metrics of each category of predictive variables (nest age, habitat structure, bird density) to carry forward to the final set of candidate models. Within each category, we selected the variable with the greatest influence on nest survival by choosing the univariate model (including quadratic or cubic polynomial forms, both of which included the lower-order terms) with the lowest AIC_c. We chose nest age from among linear, quadratic, and cubic polynomial forms and bird density from linear and quadratic forms. Habitat-structure variables included PercGS, PercFSb, PercVeg, AvgGHgt, MedGHgt (median grass height), HitsGS (number of hits of grasses and sedges), HitsFSb (number of hits of forbs and shrubs), HitsVeg, and constructed variables AvhtGS (AvgGHgt × PercGS), AvhtFSb (AvgGHgt × PercFSb), AvhtVeg, and Overall. If the constant model outperformed the best model in a category but the difference in AIC_c was less than 2, we included the variable in more inclusive models, assuming such a variable had some (albeit little) predictive power.

We built a balanced model set by using the selected metric from each of three categories of predictive variables (nest age, habitat structure, and bird density) for a total of seven models plus a constant model. We evaluated the influence of these three categories of variables on survival of Lark Bunting nests by using the ΔAIC_c and regression coefficients with confidence intervals (CI). Reported values are means or regression coefficients ± 1 SE.

RESULTS

We conducted 60 bird surveys and monitored 405 Lark Bunting nests during our 4-year study. Densities, clutch sizes, and numbers of young per successful nest averaged 1.0 birds ha^{-1} (±0.10, range 0–2.9), 4.5 (±0.04, 95% CI = 4.5, 4.6, n = 325), and 3.7 (± 0.1, 95% CI = 3.5, 3.9, n = 138), respectively. Daily nest survival and overall nest success across the entire study period were 0.937 (±0.004, 95% CI = 0.929, 0.944) and 0.272, respectively. The metrics selected during the preliminary analyses to be carried forth to the more inclusive model set were nest age (cubic polynomial), habitat structure (median grass height; MedGHgt), and bird density (quadratic polynomial of Lark Bunting density). The AIC_c values for the cubic polynomial model of nest age were 13.051, 15.050, and 23.200 units lower than AIC_c values of the linear, quadratic, and

TABLE 1. Nest age, habitat structure, and Lark Bunting density strongly influenced survival of 405 Lark Bunting nests on the Pawnee National Grassland and vicinity, northeastern Colorado, 1997–2001, as indicated by model-selection results. Analysis performed in program MARK. Models are listed beginning with the best-fitting model and sorted by Akaike's information criterion adjusted for small sample size (ΔAIC_c). Also shown for each model are the number of parameters (K) and model weight (w_i), which indicates the relative likelihood of each model given the model set and which collectively sum to 1 for the entire model set.

Nest-survival model[a]	ΔAIC_c	K	w_i
Nest age^3 + Habitat structure[b]	0	5	0.499
Nest age^3 + Habitat structure + Lark Bunting density^2	1.084	7	0.290
Nest age^3	2.591	4	0.137
Nest age^3 + Lark Bunting density^2	3.804	6	0.074
Habitat structure	16.985	2	0.0001
Habitat structure + Lark Bunting density^2	17.260	4	0
S. (constant model)	21.782	1	0
Lark Bunting density^2	22.455	3	0

[a] Variable forms used in models: nest age^3 = cubic polynomial of nest age; habitat structure = median grass height; Lark Bunting density^2 = quadratic polynomial of Lark Bunting density.
[b] AIC_c value for the top model was 1140.35.

constant models, respectively. Univariate models of all habitat-structure variables tested yielded ΔAIC_c values >2× that of the model of best fit, median grass height. A model using the quadratic polynomial of Lark Bunting density revealed an AIC_c similar (ΔAIC_c = 0.351) to that of the linear form even with the cost of an additional parameter for the quadratic polynomial. Density of all grassland birds did not influence the Lark Bunting's nest survival (β = 0.0004, SE = 0.962, 95% CI = −0.120, 0.121).

Nest age strongly influenced survival of Lark Bunting nests: it appeared in all of the best-fitting models, and its 95% confidence intervals did not span zero for any terms of the polynomial (Tables 1 and 2). In the set of balanced models, the large ΔAIC_c of the strongest model without nest age, 16.985, provides further evidence of the strength of this variable. Nest survival increased with nest age during early incubation and late in the nestling stage and declined slightly between mid-incubation and the middle of the nestling period (Fig. 1A)

TABLE 2. The strength of the relationship between survival of Lark Bunting nests (n = 405) and nest age, habitat structure, and grassland bird density in a shortgrass prairie in northeast Colorado, 1997–2001. The regression coefficients (β), SE, and 95% confidence intervals (95% CI) are from the best-fitting model containing the parameter.

Parameter	β	SE	95% CI
Nest age	0.237	0.061	0.118, 0.358
Nest age^2	−0.024	0.008	−0.040, −0.009
Nest age^3	0.0008	0.0003	0.0002, 0.0013
Habitat structure (median grass height)	0.027	0.013	0.001, 0.052
Lark Bunting density	0.919	0.522	0.104, 1.943
Lark Bunting density^2	0.317	0.188	0.686, 0.051

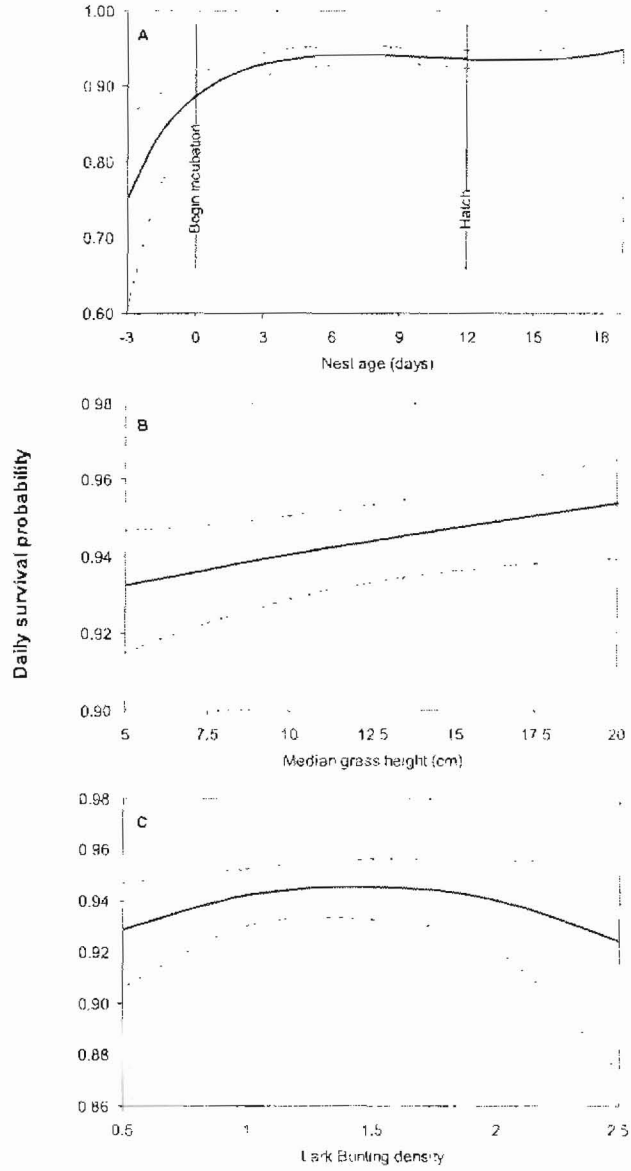

FIGURE 1. Predicted daily survival probabilities of Lark Bunting nests in relation to (A) nest age (days), (B) median grass height, and (C) Lark Bunting density on the Pawnee National Grassland and vicinity, northeastern Colorado, 1997–2001. Estimates and 95% confidence intervals (dashed lines) were generated by the logistic regression equation from the top models (Table 1) containing the effect. To generate the figures in panels B and C, and A and C, respectively, we assigned a nest age of 9 days and median grass height of 10 cm (the weighted median)

Habitat structure as characterized by median grass height also strongly influenced survival of Lark Bunting nests; it appeared in the best-fitting model, and its 95% CI did not span zero (Tables 1 and 2). Nest survival increased with increasing vegetation height (Fig. 1B). Median height of grass in the study plots averaged 12.2 cm (± 6.0 SD).

Lark Bunting density also strongly influenced nest survival but to a lesser degree than did nest age and habitat structure. As a quadratic polynomial, Lark Bunting density appeared in the second best-fitting model, the 95% CIs were highly asymmetric around zero (Tables 1 and 2), and the 90% CI did not overlap zero (linear term: 0.061, 1.778; quadratic term: −0.627, −0.008). A negative regression coefficient of the quadratic term signifies a curve that is concave downward. The best-fitting model including Lark Bunting density suggests that at low densities, nest survival increased with density, but as densities exceeded 1.5 birds ha^{-1}, nest survival declined (Fig. 1C). Despite the important role of nest age on survival of Lark Bunting nests, models without nest age similarly indicate the great importance of Lark Bunting density on nest survival. In fact, in models including only habitat structure and Lark Bunting density, the 95% CI for both density terms no longer span zero (linear term: 0.017, 2.062; quadratic term: −0.741, −0.004).

DISCUSSION

Variation in nest survival stems from the effects of intrinsic and extrinsic factors, from inherent variation that occurs across the nesting cycle combined with environmental and social influences. Although there are several possible mechanisms of nest failure, including predation, starvation, disease, and direct mortality from weather, we suspect that the preponderance of failures during this study was due to predation. Although we were unable to ascertain exact cause of nest failure with 2- to 4-day intervals between nest visits, in a separate study in the same region, Yackel Adams et al. (2007) were able to determine with daily nest checks that 92% of nest failure was due to predation. Furthermore, starvation is generally manifested in partial brood loss rather than in loss of an entire brood within a few days.

For some species of grassland birds, effects of nest age take the form of cubic polynomial models rather than of quadratic, linear, or constant models (Davis 2005, Grant et al. 2005, Davis et al. 2006, this study). A common component of the cubic age effects is a decline in nest survival from mid-incubation to 1 or 2 days post-hatching, and in this study survival of Lark Bunting nests declined between mid-incubation and the middle of the nestling period. Potential explanations include increased parental activity revealing the location of nests to predators (Conway and Martin 2000), increased cues and activity at the nest when young are newly hatched, and additive exposure to risk from various factors (Grant et al. 2005). Survival of Lark Bunting nests increased in the middle of the nestling period, a time when older nestlings are silent when intruders approach. Extrinsic features such as habitat structure also contribute to patterns of nest survival. The positive relationship between nest survival and grass height at both spatial scales may reflect increasing nesting cover that reduces detection by predators (Martin 1993) and differing abundances of predators. In Colorado, thirteen-lined ground squirrels, the primary nest predators at our study sites, were sparse in the tall (>25 cm) grasses associated with CRP fields (0.34 ha^{-1} vs 1.83 ha^{-1} in shortgrass prairie; T. R. Stanley, pers. comm.).

Social factors also contribute to variation in nest survival. Our study suggests that nest survival is maximized at an intermediate range of Lark Bunting density, indicating the existence of selective pressures exerted from both directions of low and high group sizes. What proximate and ultimate forces encourage aggregation and, in turn, limit colony size? According to the commodity-selection hypothesis (Danchin and Wagner 1997), breeding colonies form because of habitat-mediated aggregation and conspecific attraction. Preferred habitat features may include the presence of adequate food and vegetation for shading and protecting nests from wind and predators (With and Webb 1993). Adaptive advantages leading to conspecific attraction include sexual selection, information gathering (on food, safety, and the general quality of breeding sites), and improved predator defense (groups detect and mob predators more effectively).

With respect to sexual selection, aggregation allows access to higher quality mates and extra-pair copulations, which in some species are beneficial to females and older males (Morton et al. 1990, Danchin and Wagner 1997, Hoi and Hoi-Leitner 1997). Female Lark Buntings choose characteristics of males associated with males' total fitness, and extra-pair fertilization, which can be beneficial to females, accounts for 25% of Lark Bunting young in Colorado (Chaine and Lyon 2008). Conspecifics may gain fitness-enhancing information by observing the choices, behavior, and breeding performance of neighbors (Danchin et al. 2004), as occurs in Blue Tits (*Cyanistes caeruleus*) that make emigration decisions based on the quantity of fledglings raised in a given breeding area (Parejo et al. 2007). Lark Buntings may gather information gathering about breeding areas when young fledge from nests. On several occasions, as we observed young actively or recently fledging from nests, neighboring buntings moved into the vicinity, watched, and vocalized, possibly assessing the number and condition of young. Finally, mutual defense from predators attracts conspecifics to breed in loose colonies; this idea is supported by a comparative analysis of 320 avian species revealing coloniality to be strongly correlated with exposure of nests to predators (Rolland et al. 1998). We observed groups of buntings mobbing the swift fox, a primary predator in the area.

Density-dependent factors can limit bird densities (Fretwell 1972), as evidenced in the Black-throated Blue Warbler

(*Dendroica caerulescens*; Rodenhouse et al. 2003). Density dependence can result from an increase in competition for optimal nesting sites, interference among conspecifics, and attraction of predators. Bachelor and mated male Lark Buntings augment the need for mate-defense behaviors by attacking females during egg laying (A. Chaine, pers. comm.); we noted many attacks that involved several males chasing and copulating with females. Bachelors are prevalent in Colorado, ranging from 23% to 45% of males (Pleszczynska and Hansell 1980, Chaine and Lyon 2008). Predation may reduce nest survival at high bunting densities if high nest densities attract predators to an area by increasing predators' encounter rate and thus their foraging efficiency (Fretwell 1972:128, Schmidt 1999).

The capacity for density dependence is generally not considered when habitat quality for breeding passerines is evaluated. Conservation efforts require metrics for evaluation of habitat quality so that high-quality habitats can be targeted for conservation and so management practices can be evaluated in terms of success in improving habitat quality. Over the past two decades, despite warnings by Van Horne (1983), bird density and abundance often have been used as surrogates for reproductive output to indicate habitat quality (Bock and Jones 2004, Johnson 2007). Disconnects between abundance and fecundity, or habitats with high bird densities and low reproductive success, when discovered, are generally explained in the context of ecological traps (i.e., recently altered environments in which animals preferentially settle in habitat on the basis of formerly reliable cues but within which they experience reduced fitness relative to other available higher-quality habitats; Schlaepfer et al. 2002, Robertson and Hutto 2006). Implicit assumptions of ecological traps are that birds consider primarily environmental rather than social cues to assess quality of breeding habitats, and habitat quality has the greatest effect on reproductive output of all possible factors.

Relationships between densities and nest survival of prairie birds are variable, however, ranging from positive (Winter et al. 2005) or no relationship to negative (Vickery et al. 1992); at times nest survival is highest at medium densities (this study, Vickery et al. 1992). Our study suggests, as an alternative explanation for disconnects between bird densities and fecundity, that selective pressures are exerted from both directions of low and high group sizes. We suspect the nonlinear pattern we report here may be common, but it has remained undetected because of the constraints of early quantitative techniques that did not easily allow the examination of multiple correlates of nest survival.

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