



POPULATION-SPECIFIC DEMOGRAPHIC ESTIMATES PROVIDE INSIGHTS INTO DECLINES OF LARK BUNTINGS (*CALAMOSPIZA MELANOCORYS*)

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ABSTRACT.—Many North American prairie bird populations have recently declined, and the causes of these declines remain largely unknown. To determine whether population limitation occurs during breeding, we evaluated the stability of a population of prairie birds using population-specific values for fecundity and postfledging survival. During 2001–2003, we radiomarked 67 female Lark Buntings (*Calamospiza melanocorys*) to determine annual fecundity and evaluate contributing factors such as nest survival and breeding response (number of breeding attempts and dispersal). Collectively, 67 females built 112 nests (1.67 ± 0.07 nests female⁻¹ season⁻¹; range: 1–3); 34 were second nests and 11 were third nests. Daily nest survival estimates were similar for initial and later nests with overall nest survival (DSR¹⁹) of 30.7% and 31.7%, respectively. Nest predation was the most common cause of failure (92%). Capture and radiomarking of females did not affect nest survival. Lark Bunting dispersal probabilities increased among females that fledged young from initial nests and females that lost their original nests late in the season. Conservative and liberal estimates of mean annual fecundity were 0.96 ± 0.11 and 1.24 ± 0.09 female offspring per female, respectively. Given the fecundity and juvenile-survival estimates for this population, annual adult survival values of 71–77% are necessary to achieve a stable population. Because adult survival of prairie passerines ranges between 55% and 65%, this study area may not be capable of sustaining a stable population in the absence of immigration. We contrast our population assessment with one that assumes indirect values of fecundity and juvenile survival. To elucidate limiting factors, estimation of population-specific demographic parameters is desirable. We present an approach for selecting species and areas for evaluation of population stability. Received 14 September 2005, accepted 15 May 2006.

Key words: *Calamospiza melanocorys*, dispersal, fecundity, Lark Bunting, population growth rates, prairie birds, renesting, transmitter effect.

Las Estimaciones Demográficas Poblacionales Específicas Brindan Pistas sobre la Disminución de *Calamospiza melanocorys*

RESUMEN.—Muchas poblaciones de aves de las praderas de América del Norte han disminuido recientemente, y las causas de estas disminuciones permanecen básicamente desconocidas. Evaluamos la estabilidad de una población de aves de pradera usando valores de fecundidad y supervivencia posterior al emplumamiento específicos de la población para determinar si la limitante poblacional se presenta durante el período reproductivo. Entre 2001 y 2003, marcamos con radios a 67

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hembras de *Calamospiza melanocorys* para determinar la fecundidad anual y para evaluar los factores que contribuyen a ésta, como la supervivencia del nido y la respuesta reproductiva (número de intentos reproductivos y dispersión). En conjunto, las 67 hembras construyeron 112 nidos, (1.67 ± 0.07 nidos hembra⁻¹ estación⁻¹; rango: 1–3); 34 fueron segundos nidos y 11 fueron terceros nidos. Las estimaciones de supervivencia diaria de los nidos fueron similares para los nidos iniciales y sucesivos, con una supervivencia general de 30.7% y 31.7%, respectivamente. La depredación de los nidos fue la causa más común de su fracaso (92%). La captura y la marcación con radios de las hembras no afectaron la supervivencia de los nidos. La probabilidad de dispersión de *C. melanocorys* aumentó en las hembras que llegaron a criar pichones en el nido inicial y en las hembras que perdieron sus nidos originales al final de la estación. Las estimaciones conservadoras y liberales de la fecundidad anual media fueron de 0.96 ± 0.11 y de 1.24 ± 0.09 pichones hembra por hembra, respectivamente. Dadas las estimaciones de fecundidad y de supervivencia de los juveniles para esta población, se necesitan valores de supervivencia anual de los adultos del 71% al 77% para alcanzar una población estable. Debido a que la supervivencia de los paserinos de pradera adultos fluctúa entre el 55% y el 65%, esta área de estudio podría no ser capaz de mantener una población estable en la ausencia de inmigración. Comparamos nuestra evaluación poblacional con una que se basa en valores indirectos de fecundidad y supervivencia juvenil. Para dilucidar los factores limitantes, sería importante estimar parámetros demográficos poblacionales específicos. Presentamos un enfoque para la selección de especies y de áreas para evaluar la estabilidad poblacional.

EFFECTIVE CONSERVATION APPROACHES for reversing population declines in birds require understanding the relative importance of limiting factors and the seasons in which they operate during a bird's annual cycle. Establishing a causal link between documented population declines and limiting factors is difficult, particularly with migrants that are exposed to multiple pressures throughout their annual life cycle. Although factors influencing reproductive success are believed to be the primary cause of declines of some Neotropical migrant populations in forested systems (Holmes et al. 1992, Robinson et al. 1995), whether bird populations are limited in summer, in winter, or during migration is largely unknown for most declining migrant species (Sherry and Holmes 1992, Newton 2004). Attaining this information is an initial step toward developing responsive and effective conservation actions.

There have been laudable efforts (Donovan et al. 1995, McCoy et al. 1999) to determine whether particular breeding areas operate as population sources or sinks (*sensu* Pulliam 1988) for declining species, yet these evaluations used assumed values for important but unknown demographic parameters for the species of interest. Reliable approaches to estimating

avian population growth rates require sound demographic data on fecundity, survival, and dispersal (Sillett and Holmes 2002). Fecundity estimates (number of female offspring per female per year) are usually absent from population growth assessments because they require intensive tracking of marked females throughout the breeding season. Most fecundity estimates are indirectly inferred, either from nest survival (Donovan et al. 1995) or by combining nest survival estimates with seasonal-productivity models (Pease and Gryzbowski 1995). It is problematic to infer fecundity from nesting data only, because fecundity estimation is more than the product of clutch size and nest survival (Jones et al. 2005); rather, estimating fecundity also requires some knowledge of the breeding responses that females have after experiencing nest failure or success.

Prairie bird species have experienced the largest population declines of any terrestrial avian group in the past four decades in North America, according to Breeding Bird Survey (BBS) analyses (Knopf 1994, Sauer et al. 2004). To date, little is known about the causes of population declines of prairie birds, though prairie loss and fragmentation on the breeding grounds (Herkert et al. 2003) and control programs on

wintering Dickcissels (Basili and Temple 1999) have been strongly implicated. A step in elucidating the causes of declines is to determine at what time(s) in the annual cycle population limitation is occurring. Despite high interest in factors that influence productivity of declining prairie birds (Vickery and Herkert 2001), whether population limitation is occurring during the breeding season remains unknown for most species. A practical cost-effective approach to this formidable task can be to seek evidence of population limitation where there is reasonable expectation of population stability, such as on breeding grounds in extensive undisturbed habitat (Herkert et al. 2003), but where populations are declining. This would yield great information gain for research dollars spent because we already expect prairie habitats that are disturbed, highly fragmented, or on the periphery of the breeding range to possibly function as population sinks. Additionally, conservation actions may have the best chance for timely success in extensive undisturbed habitats.

We sought evidence of population limitation on the breeding grounds for a shortgrass prairie species with observed population declines near the center of its breeding range where relatively extensive prairie habitat remains. Northeast Colorado falls near the geographic center of the breeding range of the Lark Bunting (*Calamospiza melanocorys*) and lies within the stratum of the highest bird densities (Sauer et al. 2004). Yet within this area, the BBS trend maps reveal significant population declines (Sauer et al. 2004). Between 1966 and 2003, Lark Buntings have declined annually by 2.5% in Colorado and 2.1% in the High Plains physiographic region (Sauer et al. 2004). We quantified several demographic parameters (nest survival, breeding responses, and fecundity) of radiomarked Lark Buntings breeding within an extensive shortgrass prairie in northeast Colorado during 2001–2003. Using our fecundity and postfledging survival estimates (Yackel Adams et al. 2006) for this population, we modeled population growth rates to determine adult survival values necessary to maintain a stable population. We contrast our population assessment with one that assumes only indirect values of fecundity and juvenile survival. Because radiotransmitters may influence reproductive success (Croll et al. 1996) and nesting behavior (Massey et al. 1988), we also evaluated effects of transmitter attachment on

nest survival by monitoring females with and without transmitters.

METHODS

Study species.—Lark Buntings are large sparrows endemic to the prairies of North America (Shane 2000). Breeding occurs from mid- to late May through early August. Lark Buntings are ground nesters and lay 2–6 eggs per clutch. Both males and females incubate, brood, and care for fledglings. Their nesting cycle (nest building through fledging) requires 23–28 days (2–3 days for nest building, 1 day per egg laid, 11 days for incubation, and 8 days for nestling care). At fledging, parents divide the brood and continue parental care for three weeks (Yackel Adams et al. 2001). Lark Buntings commonly renest after nest failure but are believed to be single-brooded because of extensive early post-breeding migration (Shane 2000); for instance, males and females in northeast Colorado begin flocking and departing as early as late July.

Study area.—In 2001–2003, we quantified nest survival, breeding responses (number of breeding attempts and dispersal), and fecundity of Lark Buntings at three randomly selected 65-ha plots on the Pawnee National Grassland, Weld County, Colorado (40°45'N to 40°41'N, 104°37'W to 104°21'W). In 2002, because severe drought conditions lowered breeding densities, we expanded plots into adjacent lands (455 ha) to increase sample sizes. Study plots were grazed shortgrass prairie typified by buffalograss (*Buchloe dactyloides*), blue grama (*Bouteloua gracilis*), cacti (*Opuntia polyacantha*), forbs, and shrubs such as fourwing saltbush (*Atriplex canescens*) and broom snakeweed (*Gutierrezia sarothrae*). Potential nest predators in the study area include thirteen-lined ground squirrel (*Spermophilus tridecemlineatus*), coyote (*Canis latrans*), swift fox (*Vulpes velox*), long-tailed weasel (*Mustela frenata*), badger (*Taxidea taxus*), striped skunk (*Mephitis mephitis*), bullsnake (*Pituophis melanoleucus*), western hognose snake (*Heterodon nasicus*), and prairie rattlesnake (*Crotalus viridis*).

Locating and monitoring nests.—We systematically searched for initial nests between 20 May and 5 June by dragging a rope between two observers 25 m apart and by observing adult behavior. We marked nests with small wooden stakes at 10 m and 30 m from each nest. We

floated eggs (Westerskov 1950) to estimate nest age (i.e., determine dates of nest initiation and hatching) and included only females that laid their first egg before 3 June to ensure inclusion of initial nests. We checked nests every one to four days until the nest failed or fledged. During the last nest check (day of fledging), we noted signs that would help determine whether young had fledged (parents feeding young or calling in the vicinity, fecal droppings outside the nest—deposited only after young fledge; A. Yackel Adams pers. obs.). Nest attempts were considered successful if at least one nestling fledged from the nest.

Capture, marking, and relocating birds.—We captured females on nests using a modified Potter trap. Each female was measured (mass and wing chord) and banded with federal and color bands (1–2 per bird). We affixed radio-transmitters (BD-2G Model, Holohil Systems, Carp, Ontario) using leg harnesses (Rappole and Tipton 1991). Transmitters weighed 1.35–1.48 g (3–4% of body weight) and had a battery life of 60–70 days.

We tracked females daily to determine fecundity and breeding responses. We located birds using Wildlife Materials TRX-1000S receivers (164–165 MHz band) with hand-held or vehicle-mounted three- and five-element yagi antennas. Range of transmitters was about 600–900 m, depending on terrain. We continued to monitor all birds until death, battery expiration, or departure from the study plot (including a 5-km [2001–2002] or 10-km [2003] buffer around the study plot). We checked signals of missing birds on the study plot daily to learn of possible return. In midseason 2003, we also used fixed-wing aircraft to locate missing females in a 10-km search area around each study plot.

To evaluate breeding responses, we designated females as “re nesting,” “ceased breeding,” or “dispersed” after each nesting attempt. We defined “re nesting” as a subsequent nest (≥ 1 egg) after either an unsuccessful or a successful nest. We considered females to have ceased breeding if they remained on the study plot and did not re nest or if they left the study plot in late July after nest failure or fledgling depredation. Females were designated as dispersed if they were not located on the study plot or the surrounding search area before late July. Field methods were approved by Colorado State University Animal Care and Use Committee (Protocol 01-091A-01).

Data analyses.—We used the nest-survival model in MARK (White and Burnham 1999) to evaluate daily survival rates (DSR) for two subsets of nest data in two analyses. The first analysis evaluated the importance of temporal variation in 2001–2003 by considering nesting attempt (initial vs. subsequent) and time of season for all nests of radiomarked females. The second analysis examined the effect of mark type (radiomarked vs. unmarked females) on nest survival only in 2003. This data subset consisted of females that nested spatially (<150 m) and seasonally (<2 weeks) close to each other. For both analyses, we calculated overall nest survival as DSR¹⁹.

To better evaluate fecundity rates, we modeled the probability of intrayear dispersal as a function of three variables (initial body condition, initial nest fate, and breeding response date) and their interactions with logistic regression using PROC LOGISTIC in SAS (SAS Institute 2000). We evaluated two metrics to assess initial body condition: clutch size (Slagsvold and Lifjeld 1988) and mass*wing chord⁻¹ (Johnson et al. 1985). Clutch size correlates with body condition prior to egg laying in passerines (Slagsvold and Lifjeld 1988, Schluter and Gustafsson 1993), but because it also increases with age in many avian species (Ricklefs 1973), it can reflect more than just body condition. We designated three levels of reproductive fate (nest failed, nestlings fledged and died, and young fledged to independence), but had data sufficient only to evaluate fate at two levels (nest failed and nest fledged) in the global model. We defined “breeding response date” as the day a female was available to breed again (i.e., the day after nest failure, fledgling depredation, or independence of young), with May 22 = 1 (date of first nest).

We evaluated models using Akaike’s Information Criterion (AIC) corrected for small sample size (AIC_c) and when necessary for overdispersion (QAIC_c) (Burnham and Anderson 2002). The relative differences (ΔAIC_c) between each model and the model with the minimum AIC_c value allow for a quick comparison and ranking of candidate models. The model with the smallest ΔAIC_c is the best approximating model of the candidate models, given the data. Akaike weights (w_i) are used to assess the weight of evidence in favor of a model. We also used 95% confidence intervals (CI) of slope

estimates to assess the strength of an effect. Burnham and Anderson (2002) recommended the use of summed Akaike weights (Σw_i) to evaluate the relative importance of variables when a balanced model set is used (e.g., in our balanced model set of 18 total models, each variable appeared in 13 models and each interaction appeared in 5 models). We computed a relative importance measure for each variable and interaction by summing Akaike weights over every model in which that variable or interaction appeared (Akaike weights ≥ 0.40 suggest that a variable is having an effect on the process of interest; G. C. White unpubl. data).

We found slight evidence of overdispersion ($\hat{c} = 1.20$; deviance/degrees of freedom) in the intrayear dispersal data when evaluating the global model (including all variables of interest; clutch + fate + date + [clutch*fate] + [clutch*date] + [fate*date]); therefore, we used QAIC_c for model selection and $\sqrt{\hat{c}}$ to inflate our variances. We built models using clutch size because, in a preliminary analysis, clutch size predicted dispersal much better than mass*wing chord⁻¹ in the global model (Δ QAIC_c of the model including clutch size was 4 units lower than the model including mass*wing chord⁻¹, and the 95% CI of the mass*wing chord⁻¹ slope parameter largely overlapped zero).

Because of model-selection uncertainty (models with Δ AIC_c values < 7 can be plausible), we model-averaged the SAS-generated effect sizes ($\hat{\beta}$, regression coefficients) over the entire set of models with a weighted average based on Akaike weights (Burnham and Anderson 2002). We computed unconditional standard errors for the effect sizes, thereby incorporating model-selection uncertainty into precision estimates, and used the Z distribution to calculate 95% CIs. Because $R^2 < 1$ in logistic regression, we report the proportion of variation explained by a model by using the maximum-rescaled R^2 (\bar{R}^2), where $\bar{R}^2 = R^2/\text{maximum } R^2$ (Nagelkerke 1991).

Fecundity estimation.—We calculated annual fecundity as the number of female offspring produced per breeding female (female offspring per female). We assumed a 1:1 sex ratio (Wheelwright and Seabury 2003, A. S. Chaine unpubl. data) and divided the total offspring per female by 2. To account for uncertainty in renesting of females that dispersed during the study, we calculated fecundity using two methods (Kershner et al. 2004). The first method (hereafter “conservative

estimate”) assumed that we monitored every nest attempt for all radiomarked females, and that dispersed birds did not renest. The second method (hereafter “liberal estimate”) assumed that dispersed birds renested at the same rate and experienced the same nest survival probabilities and productivity as females that did not disperse. We recognize the importance of potential year effects on fecundity (Morrison and Bolger 2002) but were unable to analyze year effects (2001–2003) on fecundity because of small sample sizes in 2001 and 2002.

Stable population assessment.—We estimated annual adult female survival rates required for a stable population using the equation (Pulliam 1988)

$$\lambda = S_a + S_j\beta$$

where λ is the population growth rate, S_a is annual adult survival, S_j is annual juvenile survival separated into components of postfledging survival (S_{jp}), migration (S_{jm}), and overwinter survival (S_{jw}), and β is annual fecundity (female offspring per female). Adult survival necessary to obtain a stable population was, therefore, estimated as

$$S_a = 1 - (S_{jp} S_{jm} S_{jw})\beta$$

To perform our modeling exercise, we specified fecundity values based on point estimates obtained from our conservative and liberal estimates as well as their 95% CIs. We estimated annual juvenile survival as the product of our highest 22-day postfledging survival estimate obtained from this population (0.360 ± 0.08 ; Yackel Adams et al. 2006), a monthly survival probability of 0.81 during migration (Sillett and Holmes 2002), and a monthly winter survival rate of 1.0 (Sillett and Holmes 2002). This estimate, based on the highest survival values in the literature, provides a best-case scenario and yields an annual juvenile survival rate of 0.236. We also calculated the 95% CI for the juvenile survival estimate to provide a range of estimates. All estimates are presented as means \pm SE unless otherwise noted.

RESULTS

We radiomarked 67 female Lark Buntings (12 in 2001, 8 in 2002, and 47 in 2003). Collectively,

these females built 112 nests (1.67 ± 0.07 nests female⁻¹ season⁻¹; range: 1–3), of which 45 were subsequent nests (34 second nests and 11 third nests). Forty-two nests (38%) fledged young. One female removed its transmitter after initial nest failure; we were unable to visually relocate this bird on site or within an extensively searched 200-m radius of its initial nest, so it was considered dispersed. One female died because of transmitter entanglement, which probably caused failure of its initial nest; therefore, we included information from this female only to evaluate the effect of radiomarking females on nest survival.

Reproductive parameters.—Across three years, we monitored 111 nests for 1,193 exposure days in a 79-day interval (22 May–8 August). Breeding was terminated two weeks early during the severe drought of 2002. Clutch size tended to be smaller in subsequent nests than in initial nests, whereas hatching rate was the same (Table 1). Other reproductive parameters of hatchlings per nest, nestling survival per successful nest, fledglings per nest, or fledglings per successful nest were also reduced in subsequent nests; however, 95% CIs for these parameters largely overlapped (Table 1).

Nest attempt (initial vs. subsequent) and time of season did not influence nest survival. Univariate models incorporating these two effects had far less AIC_c weight than the constant-only model (0.21, 0.21, and 0.58, respectively), and the 95% CIs were centered on zero in the model containing that effect ($\beta_{\text{attempt}} = 0.03$, 95% CI: -0.47 to 0.52; $\beta_{\text{time of season}} = -0.001$, 95% CI: -0.02 to 0.02). Daily nest survival estimates for initial and subsequent nests (Table 1)

yield overall nest survival (DSR¹⁹) of 30.7% and 31.7%, respectively. Predation was the major cause of failure in both initial and subsequent nests (87.5% of 39 and 97% of 30 failed nests, respectively). Other failures for initial nests were attributable to nest desertion (5%) and inclement weather (7.5%), and other failures of subsequent nests were attributable to inclement weather (3%).

To evaluate the effects of mark type (radiomarked vs. unmarked females), we identified a subset of nests from 2003 in a 58-day period (22 May–18 July); the subset included 84 nests of radiomarked (exposure days = 869) and 62 nests of unmarked (exposure days = 612) females. Clutch size was similar for radiomarked (4.36 ± 0.14) and unmarked (4.43 ± 0.17) females. We found no evidence that capture and radiomarking of females affected nest survival; confidence intervals for daily survival probabilities of radiomarked females (0.930 ± 0.01 , 95% CI: 0.911 to 0.946) and unmarked females (0.927 ± 0.01 , 95% CI: 0.904 to 0.947) largely overlapped. The constant model had greater AIC_c weight than the model incorporating mark effect (0.73 and 0.27, respectively), and the effect of mark type was essentially zero ($\beta_{\text{mark type}} = -0.03$, 95% CI: -0.45 to 0.38).

Breeding responses.—Renesting occurred for 7 of the 27 (30%) females that successfully fledged young from an initial nest (Fig. 1). Two of these seven birds renested after successfully raising young to independence (at least 21 days). The remaining five females renested after their offspring were depredated 3–13 days postfledging. Five of the seven second nests failed. Four of these failures occurred

TABLE 1. Reproductive parameters for initial and subsequent nests (second and third attempts combined) of Lark Buntings on the Pawnee National Grassland, northeast Colorado, 2001–2003.

Parameter	Initial nests			Subsequent nests		
	Mean ± SE	95% CI	n	Mean ± SE	95% CI	n
Daily nest survival	0.94 ± 0.01	0.92–0.96	66	0.94 ± 0.01	0.92–0.96	45
Clutch size	4.62 ± 0.10	4.42–4.82	66	4.02 ± 0.14	3.75–4.30	45
Hatch rate ^a	0.86 ± 0.03	0.81–0.92	39	0.85 ± 0.05	0.76–0.94	25
Hatchlings per nest attempt	3.77 ± 0.14	3.50–4.04	39	3.40 ± 0.21	2.99–3.81	25
Nestling survival per successful nest ^b	0.86 ± 0.04	0.78–0.95	27	0.79 ± 0.07	0.65–0.93	15
Fledglings per nest	1.33 ± 0.21	0.93–1.74	66	0.87 ± 0.21	0.46–1.27	45
Fledglings per successful nest	3.26 ± 0.15	2.97–3.55	27	2.60 ± 0.29	2.03–3.17	15

^aProportion of fully incubated eggs that hatched, a function of infertility and embryonic mortality.

^bProportion of hatchlings that survived to fledging, a function of starvation, inclement weather, and partial predation.

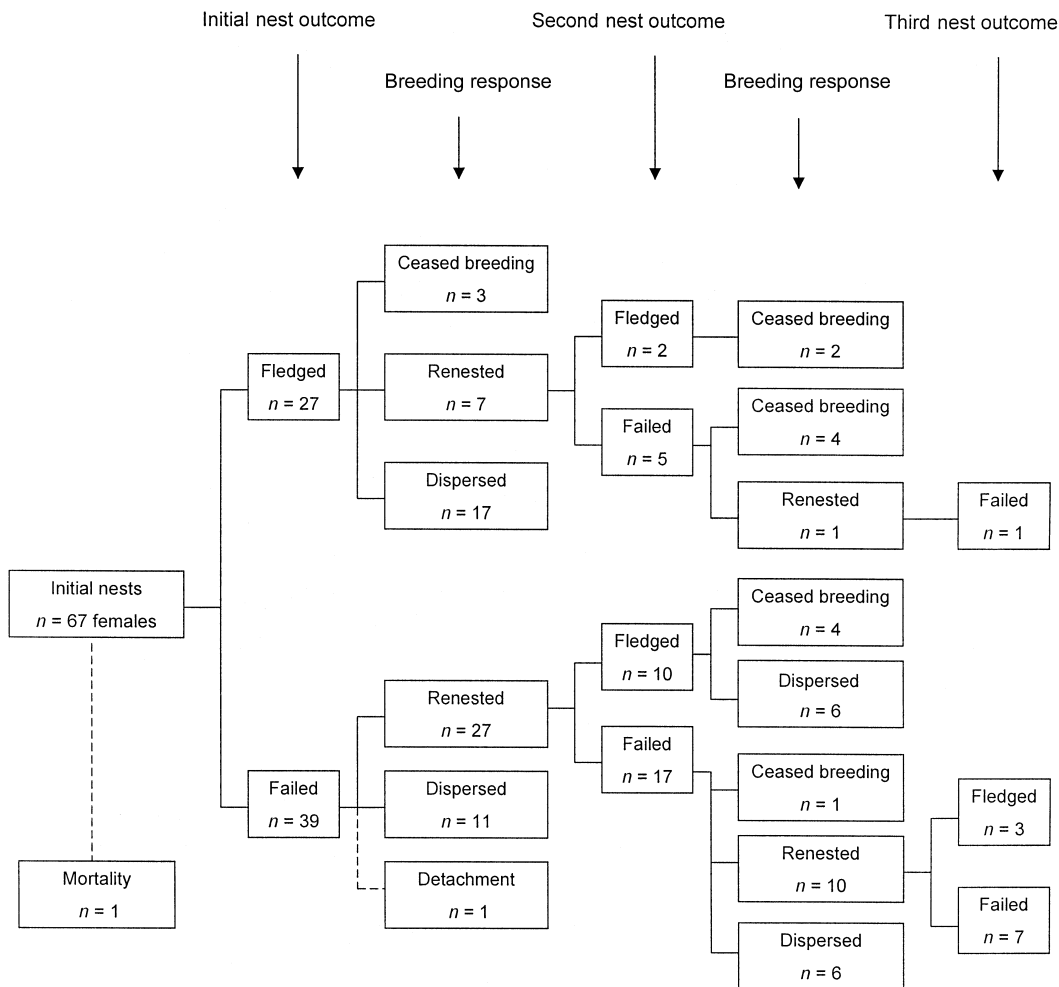


FIG. 1. Nest outcome and breeding responses of 67 female Lark Buntings during the 2001–2003 breeding seasons on the Pawnee National Grassland in northeast Colorado.

late in the breeding season, precluding a third attempt. One female initiated a third nest on 2 July 2003. Of the 39 females that failed during their initial nests, 27 (69%) remained in the area to re-nest a second time (Fig. 1). Seventeen of the 27 second nests failed, and 37% of the 27 females re-nested a third time. Females re-nested promptly. First eggs were laid in new nests 6 ± 0.52 days (range: 4–17 days) after nest failure and 6 ± 1.7 days (range: 1–14 days) after death or independence of young. Birds typically re-nested in proximity to previous nests. Mean distance between initial and second nests was 119 ± 25.88 m (range: 19–672 m, only 3 nests >490 m), initial and third nests 96.09 ± 20.87 m (range: 13–300 m, only 1 nest >130 m),

and second and third nests 83.91 ± 24.01 m (range: 30–280 m, only 1 nest >130 m).

Fourteen birds were designated as “ceased breeding.” Twelve of these left the study area after nest failure or fledgling depredation in late July (18 July–24 July), making it unlikely that they would re-nest at another site. The other two birds remained on site after they ceased breeding (Fig. 1). One of these females, after caring for a fledgling until independence (which occurred on 10 July 2002), remained on site for an additional 14 days without evidence of re-nesting. The other female successfully fledged two nests, but in neither case did the fledglings achieve independence. She lost her last fledgling on 14 July 2003 and remained on site through 3 August 2003.

Of the 27 females that successfully fledged young from an initial nest, 17 (63%) dispersed from the study area (Fig. 1) between 4 June and 10 July. Eleven dispersed within two days after fledgling depredation (0–16 days postfledging). The remaining six females dispersed alone or with fledglings after having cared for them 22 days postfledging. Of the 39 females that failed on their initial nest, 11 (28%) immediately dispersed from the study area (Fig. 1) between 1 June and 2 July. Of the 27 birds that renested, 6 females dispersed immediately after the second nest failed; another 6 females dispersed after fledgling depredation (0–13 days postfledging).

Each female that dispersed from the study area was located at least once after nest failure or fledgling depredation, which suggests that all left the area with a functional transmitter. We were able to locate one female with her 21-day-old fledgling in a small flock of Lark Buntings 5.3 km from her initial nest on 10 July; the other dispersed females were not detected via ground or aerial searches within 5 km (2001 and 2002) and 10 km (2003) of the study plots.

Intrayear dispersal probability was best explained by models that incorporated effects of initial nest fate and breeding response date (hereafter “response date”) and the interaction between these variables. Dispersal probabilities increased for females with successful initial nests, as indicated by a negative coefficient ($\hat{\beta}$) for this variable in the best model and its model-averaged estimate (Table 2). Although response date alone had no effect, the interaction between fate and response date was an important predictor of dispersal (Table 2). Females whose initial

nests failed later in the season had a higher probability of dispersal. The 95% CI on the effect estimate for the interaction between fate and response date did not include zero (95% CI: 0.01 to 0.15) in the top model but slightly overlapped zero with its modeled average estimate (Table 2). Relative importance (Σw_i) confirmed strong support for fate, response date, and fate*response date, and indicated almost no support for clutch size and its interactions between fate and response date, which had substantially smaller summed weights (<0.40; Table 2). The top and global model maximum-rescaled $R^2 = 0.31$ and 0.40, respectively.

Annual fecundity.—For conservative estimates of fecundity (assuming that dispersed birds did not renest), 63.5 female young were produced from the 42 fledged nests. Mean annual fecundity was 0.96 ± 0.11 female offspring female⁻¹ (range: 0–3 female young). Liberal estimates assumed that dispersed females renested at the same rate as nondispersed females (92% [34 of 37] for second nests and 50% [11 of 22] for third nests) and that they experienced the same subsequent nest survival (31.7%) and productivity from fledged nests (1.3 female young). Liberal estimates, by adding 18 additional female young to the population, increased the mean annual fecundity to 1.24 ± 0.09 female offspring female⁻¹.

Adult survival needed to obtain stable population.—We calculated the range of annual female survival necessary to maintain a stable population (Table 3) using our point estimates for fecundity and juvenile survival (Yackel Adams et al. 2006) and their associated 95% CIs. Assuming the

TABLE 2. Estimated relative importance values (summed QAIC_c weights; Σw_i), top model, and model-averaged effect sizes ($\hat{\beta} \pm SE$), and 95% confidence intervals (CI) from logistic regression analysis of initial body condition (clutch size), initial nest fate (fate), response date (date) and their interactions on intrayear dispersal of Lark Buntings in northeast Colorado, 2001–2003 ($n = 62$). Estimates presented for fate represent the failure of the initial nest.

Variable	Σw_i	Top model		Model averaged	
		$\hat{\beta} \pm SE$	95% CI	$\hat{\beta} \pm SE$	95% CI
Intercept	–	–0.17 ± 2.00	–1.35 to 3.81	–0.88 ± 5.22	–11.12 to 9.36
Fate	0.90	–3.24 ± 1.26	–6.18 to 1.05	–1.78 ± 2.22	–6.14 to 2.58
Date	0.64	0.00 ± 0.03	–0.07 to 0.07	0.03 ± 0.07	–0.11 to 0.17
Fate*date	0.45	0.08 ± 0.03	0.01 to 0.15	0.06 ± 0.05	–0.03 to 0.15
Clutch size	0.37	–	–	0.37 ± 0.69	–0.98 to 1.72
Clutch size*fate	0.13	–	–	–0.24 ± 0.42	–1.07 to 0.59
Clutch size*date	0.07	–	–	–0.01 ± 0.01	–0.03 to 0.02

TABLE 3. Adult survival estimates of female Lark Buntings necessary to maintain a stable population (in bold), assuming specific estimates for fecundity and juvenile survival with 95% confidence intervals (CI).

	Survival	Conservative fecundity estimate			Liberal fecundity estimate		
		Lower CI	Estimate	Upper CI	Lower CI	Estimate	Upper CI
Annual Juvenile		0.75	0.96	1.18	1.06	1.24	1.42
Lower CI	0.138	0.90	0.87	0.84	0.85	0.83	0.80
Estimate	0.236	0.82	0.77	0.72	0.75	0.71	0.67
Upper CI	0.335	0.75	0.68	0.61	0.64	0.59	0.53

Note: The conservative fecundity estimate assumed that dispersed females did not renest, and the liberal estimate assumed that females that dispersed renested at the same rate, and experienced the same nest survival probabilities and productivity, as females that remained on study plots. Annual juvenile survival was calculated as the product of the highest 22-day postfledging-survival estimate obtained from this population over a four-year period (0.360 ± 0.08 ; Yackel Adams et al. 2006), a monthly survival probability of 0.81 during migration (Sillett and Holmes 2002), and a monthly winter survival rate of 1.0 (Sillett and Holmes 2002).

conservative fecundity estimate of 0.96 female offspring female⁻¹ and annual juvenile survival of 0.236, annual adult survival must be 77% to achieve a stable population. Using the liberal fecundity estimate of 1.24 female offspring female⁻¹ and annual juvenile survival of 0.236, annual adult survival must be 71% to achieve a stable population.

DISCUSSION

We evaluated the stability of a breeding population of prairie birds using population-specific values for two demographic parameters. Whereas assumptions of fecundity and postfledging survival (a component of juvenile survival; see above) are commonly based on indirect estimates from the scientific literature, we were able to quantify these parameters for our study population. For the Lark Bunting in Colorado, our demographic analysis revealed that population declines are attributable, in part, to events on the breeding grounds. Adult survival rates necessary to maintain this population of Lark Buntings (0.71–0.77; Table 3) are greater than estimates of annual adult survival of small passerines (0.40–0.62; Martin 1995, Sillett and Holmes 2002) and ground-nesting species in grassland-shrub habitat (0.55; Martin 1995), which indicates that this population may not be self-sustaining without immigration. As we illustrate below, differing assumptions of these demographic parameters yield not only opposing conclusions about when and where population limitation occurs, but undoubtedly would lead to disparate conservation approaches.

Deriving population-specific values for important demographic parameters in population models is critical for assessing causes of population declines.

To illustrate the importance of using population-specific values, we contrast our findings with assumed values obtained from the literature for two demographic parameters, fecundity and juvenile survival. Using our population-specific values, Lark Bunting adult survival of 0.71–0.77 is necessary to sustain the population without immigration. If we substitute only the indirect estimate of annual juvenile survival commonly used in the literature (0.31; Donovan et al. 1995, Faaborg et al. 1998), adult survival of 0.62–0.70 is required for a stable population. If we assume that prairie birds produce an average of 1.5 broods (Martin 1995) and use our population-specific values for juvenile survival, adult survival of 0.54–0.64 is necessary. If indirect values for both fecundity (1.5 broods) and juvenile survival (0.31) are assumed, adult survival necessary to sustain the population is only 0.42–0.55. Clearly, final interpretations about population stability depend on the assumed input to the models (Jones et al. 2005).

To maintain population stability with an assumed adult survival of 0.55 (Martin 1995), Lark Buntings require high fecundity (1.29) and high juvenile survival (0.35). This scenario is probably unrealistic for our population, because it is more likely that (1) the true rate for fecundity approaches our conservative estimate (0.96; see below) and (2) annual juvenile survival does not exceed 0.24. True annual juvenile survival is probably at or below 0.236, because this

estimate incorporates the highest annual post-fledging survival in this species in a four-year period (Yackel Adams et al. 2001, 2006). Further, the only mark–recapture estimate available for annual juvenile survival for a migrant bird is 0.25 (Gardali et al. 2003). This estimate may be biased high, because it fails to include mortality between fledging and independence, a time when fledging mortality is known to be high (Yackel Adams et al. 2001).

Our study underscores the need for robust reliable estimates of adult survival (e.g., Cilimburg et al. 2002, Sillett and Holmes 2002, Dinsmore et al. 2003) for passerine populations. Because we lack a direct adult survival estimate for this species, our interpretation may be problematic. First, we must assume that reported survival estimates adequately represent the species, sex, and habitat of interest. Second, and more importantly, current survival estimates for passerines are based on return rates or mark–recapture; both methods tend to underestimate survival because they fail to distinguish mortality from permanent dispersal (i.e., estimates reflect apparent survival, not actual survival). Return rates produce even more biased survival estimates than those obtained by mark–recapture, because they do not account for resighting or recapture probabilities (Nichols 1992). The accuracy of both methods depends largely on the degree of philopatry of individuals in the population (Sillett and Holmes 2002) and the size of the search area (Cilimburg et al. 2002); if capture probability is high or the search area is large, bias in the survival estimates may be minimized. To adjust the conservative estimates of adult survival, McCoy et al. (1999) added 0.1 to published estimates of adult survival. Cilimburg et al. (2002) found that survival probabilities increased by 6.5–22.9% (0.02–0.11) when information on dispersed birds located by expanding the search area was included; this suggests that the 0.1 adjustment is reasonable in some cases and low in others. If we adjust adult survival estimates for ground-nesting prairie birds (0.55; Martin 1995) by 0.1, the annual survival rate for Lark Buntings becomes 0.65, still below what is required for a stable population based on reasonable fecundity and juvenile survival values for this population (Table 3).

Factors influencing fecundity.—Fecundity in avian species is profoundly reduced by high nest-predation rates. As found in other prairie

passerine studies, low fecundity in our population of Lark Buntings resulted from high rates of nest predation (Granfors et al. 1996) and the limited ability to double-brood (Kershner et al. 2004, Walk et al. 2004). Our conservative fecundity estimate of 0.96 female offspring female⁻¹ falls between conservative estimates for prairie species: 0.61 for Dickcissels (*Spiza americana*; Walk et al. 2004) and 1.27 for Eastern Meadowlarks (*Sturnella magna*; Kershner et al. 2004). Our liberal estimate of 1.24 is similar to the liberal estimate reported for Eastern Meadowlarks (1.36; Kershner et al. 2004). Annual fecundity estimates of other non-prairie passerines range more broadly, from 0.5 to 2.2 (Nolan 1978, Holmes et al. 1992, Budnik et al. 2000, Morrison and Bolger 2002, Sedgwick 2004).

Fecundity estimation is strongly influenced by assumptions regarding reneating (Grzybowski and Pease 2005). Birds may compensate for low nest survival by persistently reneating (Pease and Grzybowski 1995, Schmidt and Whelan 1999), but how many nests a female will initiate during a breeding season must be determined. In our study, Lark Buntings initiated up to three nests per season, which is consistent with a color-marked Lark Bunting population (J. B. Barna and A. S. Chaine unpubl. data). Reneating attempts typically occurred 6 days after failure (4–5 days is the shortest physiologically possible interval for passerines; Scott et al. 1987). Reneats had similar survival probabilities as initial nests but smaller clutches. Despite reduced clutch sizes, reneating efforts increased fecundity, because 15 of 45 reneats fledged young.

Fecundity estimation is also strongly affected by the number of broods raised each year (Pulliam 1988, Schmidt and Whelan 1999). Although Martin (1995) reports that prairie birds raise an average of 1.5–2 broods per year, data from our study and others (Kershner et al. 2004, Walk et al. 2004) indicate that this estimate is too high and may lead to overestimation of reproductive output. With the 43–45 days required to raise a chick to independence, Lark Buntings can raise a maximum of two broods if they begin breeding early in the 90-day breeding season and are successful in both nesting attempts; they do not seem to overlap first and second broods. We documented only two females successfully raising two broods, though we were unable to follow all Lark Buntings that raised first broods to independence. Six

Lark Buntings left the site (>10 km) after 21 days of parental care; three of these left with their young and probably did not breed again during the season. The breeding response of extending parental care and forgoing additional nest attempts may be determined by high nest-predation rates and low probability of fledging a second brood (Walk et al. 2004).

How representative are our fecundity estimates? – Despite the drought during our study, for several reasons we believe that our estimates of nest survival and reproductive output are reasonable for this population and provide reliable

fecundity estimates. First, although our overall nest survival estimate (31%) is at the low end of reported nest survival estimates for prairie birds (25–50%; Vickery et al. 1992, Martin 1995), it is similar to or greater than nest survival estimates for Lark Buntings from 1997 to 2001 at randomly selected plots on the Pawnee National Grassland (S. K. Skagen unpubl. data; Fig. 2A) under varying amounts of annual precipitation, represented as the percentage of deviation from a 29-year mean (Fig. 2B; Western Regional Climate Data Center [see Acknowledgments]). Annual precipitation from 1997 to 2001 varied

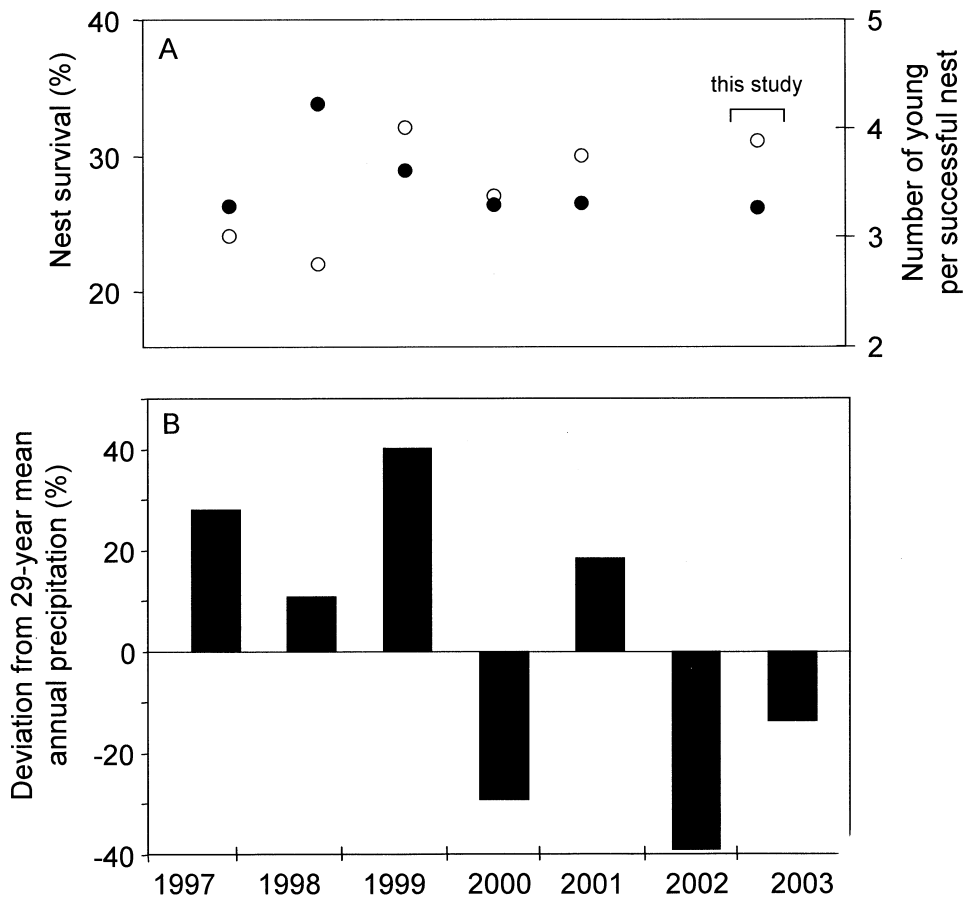


FIG. 2. (A) Overall nest survival (open circles) and number of young per successful nest (closed circles) documented during the present (2001–2003) and previous studies (1997–2001) of Lark Buntings on the Pawnee National Grassland, northeast Colorado, under varying amounts of precipitation. (B) Deviation from mean annual precipitation based on a 29-year (1976–2004) climate record obtained from the Western Regional Climate Data Center (see Acknowledgments) for the Pawnee National Grassland. Long-term precipitation (mean \pm SD) is 32.9 ± 8.2 cm. Sample sizes for nests and successful nests, respectively, are 1997: 64, 25; 1998: 66, 18; 1999: 92, 51; 2000: 29, 14; 2001: 143, 58; and present study: 66, 27.

from 40% above average in 1999 to 29% below average in 2000. Also, the number of young produced per successful nest during this study is similar to estimates in previous years (Fig. 2A). Second, although the shortgrass prairie region entered a drought of varying severity during our study (relatively normal precipitation conditions, severe drought, and mild drought in 2001, 2002, and 2003, respectively), drought conditions are common to the shortgrass ecosystem. In fact, the eastern plains of Colorado are characterized as being almost always in, or on the verge of, drought (Doesken et al. 2003). And finally, even though most of our fecundity data are from 2003, a mild drought year, the overall conditions during 2003 as reflected by vegetation structure, Lark Bunting densities, and postfledging survival were similar to conditions in 2001 (a year of normal precipitation) and different from the severe drought of 2002 (Yackel Adams et al. 2006).

There was also no evidence that use of transmitters biased our fecundity estimates. We detected no measurable effect of transmitters on nest survival when comparing females with and without transmitters, which is consistent with the results of Granfors et al.'s (1996) study of Eastern Meadowlarks. Radiomarked Lark Buntings had no observable limitations with copulations or capture and delivery of prey to young, which is consistent with Neudorf and Pitcher's (1997) finding that applying transmitters to female Hooded Warblers (*Wilsonia citrina*) did not affect their ability to feed nestlings. Similarly, there was no measurable effect of transmitters on survival of fledglings during the study from which the postfledging survival estimates were derived (Yackel Adams et al. 2006).

Conservative versus liberal fecundity estimates.—Because the reproductive output of dispersed birds is unknown, we present two estimates of fecundity based on differing assumptions of re-nesting responses made by females after dispersing 5–10 km. Judging from the relative support for the underlying assumptions, we give greater credence to our conservative estimate. For the conservative estimate, we assumed that dispersed females did not re-nest. We found no evidence of dispersed females re-nesting within 10 km, and Kershner et al. (2004) and Walk et al. (2004) reported no further breeding activity of dispersed female Eastern Meadowlarks ($n = 7$) and Dickcissels ($n = 2$), respectively. For our

liberal estimate, we assumed that dispersed females re-nest at the same rate and experience the same productivity as females that remain on site. There is no direct evidence to support the second assumption; however, passerine studies that examined within-site breeding dispersal between years (as reviewed in Bélichon et al. 1996) have noted that productivity is often similar between new and old territories.

Demographic consequences of female dispersal during the breeding season.—The response to disperse during the breeding season will have a strong effect on fecundity, but whether it is advantageous is not well understood (Brawn and Robinson 1996) and remains “the most prominent missing piece of the songbird demographic puzzle” (Cilimburg et al. 2002:787). Lark Bunting dispersal probabilities increased among females that (1) fledged young from initial nests, as found in other studies (Jackson et al. 1989, Howlett and Stutchbury 1997, Kershner et al. 2004), and (2) lost their initial nest late in the season.

Three hypotheses have been posited to explain dispersal behavior of females that successfully fledge young, two of which address the tradeoff between breeding on-site and moving to a new breeding area while sufficient time exists. The first hypothesis, that dispersal allows females to avoid older fledglings and increase the probability of raising another brood (Jackson et al. 1989, Howlett and Stutchbury 1997), is not supported by our study. Of 17 dispersing females, only 3 left independent young behind, 3 departed with nearly independent young, and 11 dispersed after fledglings were depredated. Three females re-nesting in the study area did so after raising young to independence. Nor does our study support the second hypothesis, that dispersal after fledging young allows the female to avoid breeding in an area of depleted food resources (Greig-Smith 1982). We found no evidence that food resources were depleted in our study area. Many females chose to re-nest in the area, which indicates that resources were adequate for egg production and females readily obtained grasshoppers before departing. A third plausible explanation for late-season dispersal is that dispersal after fledging young allows females to cease breeding and begin premigratory maintenance (Kershner et al. 2004). We offer an additional hypothesis: that dispersal after fledging young enhances female

survival and lifetime fecundity, thereby providing greater advantage than attempts to rear a second brood.

A plausible explanation for early-season dispersal of female Lark Buntings after depredation of their fledglings from initial nests is that during a predation event, the portion of the brood being provisioned by the male generally is not simultaneously depredated; therefore, males are unavailable to renest because they continue to care for their brood units. Lark Buntings are predominantly monogamous (Shane 2000). Dispersal may also be related to site fidelity (Walk et al. 2004). For instance, Lark Buntings in their first breeding season may continue to disperse until they successfully fledge young to independence, and then develop fidelity to the successful site. Lark Buntings renesting nearby after failed attempts may remain because they fledged young in this location the previous year. Bollinger and Gavin (1989) found that 49% of female Bobolinks (*Dolichonyx oryzivorus*) returned to high-quality sites, whereas 24% of females returned to low-quality sites. Passerines exposed to experimental nesting failure returned less often than those experiencing nesting success (Haas 1998).

Conservation implications.—Our results suggest that population declines in Lark Buntings are caused in part by breeding-ground phenomena (fecundity influenced by high rates of predation and the species' limited ability to double-brood). Factors determining breeding success and annual productivity of three other migrant species also had important effects on population growth rates (Nolan 1978, Holmes et al. 1992, Sherry and Holmes 1992). Our findings justify directing further research efforts and initial conservation actions to the breeding grounds but do not eliminate the need to quantify factors influencing overwinter survival.

Although large prairie patches are generally associated with higher avian productivity than fragments (Johnson and Temple 1990, Winter and Faaborg 1999, Herkert et al. 2003), our data suggest that an extensive shortgrass prairie (62% native prairie within a 21,600 km² area; Howard et al. 2001) is unlikely to sustain Lark Buntings in the absence of immigration. Our findings highlight the need to extend conservation actions beyond the acquisition and protection of large habitat patches, but also to evaluate breeding areas in the context of the predator

communities and to seek understanding of the myriad factors affecting predation rates. Predator-prey communities can be altered by changing land-use practices, habitat loss, and habitat fragmentation; such changes can, in turn, modify nest encounter rates, nest vigilance and defense, and predator search effort and strategy.

The use of population-specific values for the breeding demographic parameters, rather than generalized estimates from the scientific literature, allowed us to more thoroughly evaluate the stability of our study population. Investment in the field effort necessary to obtain species- and population-specific estimates of breeding demographic parameters is desirable when asking whether breeding-ground phenomena contribute to population declines. Because it is not feasible to obtain this information for every declining species across the entirety of its range, we need an approach for selecting species and areas in which to evaluate population stability.

To narrow focus for obtaining population-specific estimates of breeding demographic parameters, one should first choose (1) species with relatively restricted breeding ranges (or whose population centers are fairly restricted within a broad range) and (2) areas with observed population declines. To further narrow the geographic scope, one should target areas with a reasonable expectation of population stability and where conservation actions may have the best chance of success. For example, we might expect that populations are more likely stable (1) in areas with high abundances (Bock and Jones 2004), often near the centers of the breeding ranges (Brown et al. 1995; but see Channell and Lomolino 2000) and (2) in locations with extensive remaining habitat (Robinson et al. 1995, Herkert et al. 2003). Using this approach for declining prairie species (Sauer et al. 2004), for example, one might initially target southeast Colorado and central North Dakota for evaluations of population stability of Cassin's Sparrow (*Aimophila cassinii*) and Chestnut-collared Longspur (*Calcarius ornatus*), respectively, both Partners in Flight Species of Continental Importance (Rich et al. 2004). If demographics suggest a stable or source population in regions of high abundances and extensive habitat, and yet populations are declining, phenomena elsewhere in the breeding range or outside of the breeding season are implicated

in observed declines. If demographics suggest a declining or sink population in areas that should be among the best habitats for the species, phenomena on the breeding grounds are responsible, at least in part, for the population declines. In the latter case, as we found with Lark Buntings in northeast Colorado, investigations into proposed limiting factors that would affect the core breeding grounds are warranted.

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