

DISSERTATION

POPULATION DEMOGRAPHY OF LARK BUNTINGS: POST-FLEDGING SURVIVAL,  
FECUNDITY, AND BREEDING DECISIONS

Submitted by

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## ABSTRACT OF DISSERTATION

### POPULATION DEMOGRAPHY OF LARK BUNTINGS: POST-FLEDGING SURVIVAL, FECUNDITY, AND BREEDING DECISIONS

Grassland bird species have experienced the largest population declines of any terrestrial avian group in the past four decades in North America. Lark buntings (*Calamospiza melanocorys*), endemic to the grasslands of North America, have declined by 2.5% per year in Colorado and 2.1% per year in the High Plains physiographic region between 1966 and 2003. Although reasons for these declines have yet to be elucidated, factors influencing reproductive productivity and juvenile survival on the breeding grounds are among the possibilities. To assess population declines, direct and reliable estimates of survival, fecundity, and dispersal are required. Consequently, I estimated demographic parameters (i.e., post-fledging survival and fecundity) for lark buntings in a relatively extensive (62% grassland remaining within a 21,600 km<sup>2</sup> area) native shortgrass landscape on the Pawnee National Grassland, Colorado in 2001-2003.

In chapter 1, I applied an information-theoretic approach to evaluate factors affecting post-fledging survival of lark buntings. I estimated daily and 22-day post-fledging survival ( $n = 206$ , 82 broods) using radio-telemetry and color bands to track fledglings. For 2001-2002 data, I employed the joint model in program MARK to examine the effects of drought condition, time in season, age, nestling condition (rank, condition index, or brood size), mark type (radio-marked versus band-only), and sex of attending parent on post-fledging survival. Estimated daily survival probabilities ( $\pm$  SE) were higher under normal precipitation (2001:  $0.933 \pm 0.010$ ) and mild drought conditions (2003:  $0.933 \pm 0.013$ ) than during a severe drought (2002:  $0.908 \pm 0.011$ ). Post-fledging daily survival probabilities in 2001 and 2002 were best explained by models that incorporated drought condition, time in season (quadratic trend), ages  $\leq 3$ , and rank  $\times$  drought interaction. Daily survival probabilities were lower under severe drought conditions than in a normal year; the model-averaged coefficient for the additive effect of drought on survival of fledglings was  $\hat{\beta}_{\text{drought}} = -3.99$  (95% CI = -7.94, -0.05). Models also revealed greater survival in mid-season ( $\hat{\beta}_{T^2} = -0.002$ , 95% CI = -0.003, -0.001). Survival was lower for recently-fledged young (ages  $\leq 3$ ) than older fledglings. Rank was an important predictor of fledgling survival only during the severe drought of 2002.

Both mark type and sex of attending parent had no effect on survival. Survival estimates that account for age, condition of young, ecological conditions and other factors are important for parameterization of realistic population models. My results suggest that age-specific estimates can help identify critical time periods within the species' life-cycle, and that species-specific estimates of post-fledging survival are more informative than generalized estimates used in population growth models.

In chapter 2, I evaluated the stability of a breeding population of lark buntings using population-specific values for two demographic parameters, fecundity and post-fledging survival, and quantified breeding decisions of females. I followed 67 radio-marked female lark buntings captured on their initial nests to determine annual fecundity and evaluate factors affecting it, such as nest survival and breeding decisions (re nesting, ceased breeding, dispersal). Collectively, the 67 females built 112 nests ( $1.67 \pm 0.07$  nests per female per season (mean  $\pm$  1 SE); range 1-3) of which 45 were subsequent nests (34 second nests and 11 third nests). Daily nest survival estimates were similar for initial and subsequent nests with overall nest survival (DSP<sup>19</sup>) of 30.7% and 31.7%, respectively. Nest predation was the most common cause of failure (92%). Capture and radio-marking of females did not affect nest survival. Lark bunting dispersal probabilities increased among females that (1) fledged young from initial nests, and (2) lost their initial nest late in the season. Conservative and liberal estimates of mean annual fecundity were  $0.96 \pm 0.11$  and  $1.24 \pm 0.09$  female offspring female<sup>-1</sup>. Given these fecundity estimates along with estimates of juvenile survival obtained for this species, adult survival values of 70-76% are necessary to achieve a stable population. Adult survival estimates for prairie passerines range between 55-65%, indicating that this study area is unable to maintain a stable population in the absence of immigration. My results suggest that population declines of prairie birds are caused, at least in part, by breeding ground phenomena. Further consideration of the quality of breeding areas in the context of the predator communities is clearly needed.

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**CHAPTER 1:**  
**MODELING AVIAN POST-FLEDGING SURVIVAL IN RESPONSE TO DROUGHT**

**INTRODUCTION**

Many biological and ecological factors influence the survival of avian species and modify their population dynamics. Rigorous approaches to survival analysis can evaluate the relative importance of various factors, elucidate potential mechanisms of population declines, and facilitate efforts to reverse these declines. One component of survival, juvenile survival during the first year, can have dramatic effects on population dynamics of passerines, yet remains the least studied component of avian demographics (Gardali et al. 2003). Changes in juvenile survival of song thrushes (*Turdus philomelos*) in Great Britain were sufficient to cause a population decline (Robinson et al. 2004). In general, estimates of avian juvenile survival are largely unavailable, and population modelers have assumed juvenile survival indirectly as a fraction (0.25 to 0.50) of adult survival (Ricklefs 1973, Donovan et al. 1995). Until recently, this assumption has not been evaluated (Anders et al. 1997, Gardali et al. 2003).

Several recent passerine studies relying on radio-telemetry provide survival estimates and evaluations of factors influencing survival during the vulnerable post-fledging period (defined as time between leaving the nest (fledging) and parental independence). Trends in survival relative to post-fledging age, time in season, and body condition (variously defined) have been suggested. Lower survival during the first week post-fledging due to predation was documented in five studies assessing post-fledging age (Sullivan 1989, Anders et al. 1997, Naef-Daenzer et al. 2001). Survival decreased during the breeding season for European starlings (*Sturnus vulgaris*), yellow-breasted chats (*Icteria virens*), and great and coal tits (*Parus major*, *P. ater*) (Krementz et al. 1989, Maxted 2001, Naef-Daenzer et al. 2001), yet seasonal timing had no effect on fledgling survival in wood thrushes (*Hylocichla mustelina*; Anders et al. (1997)). Body condition increased survival probability for European starlings fledging early in the season (Krementz et al. 1989) and for great and coal tits fledging late in the season (Naef-Daenzer et al. 2001), but

not for wood thrushes (Anders et al. 1997) or yellow-eyed juncos (*Junco phaenotus*) (Sullivan 1989).

I estimated annual density and nest survival, and applied an information-theoretic approach to evaluate factors affecting post-fledging survival of a shortgrass prairie bird, lark bunting (*Calamospiza melanocorys*), a species that has declined by 2.1% per year in the High Plains physiographic region between 1966 and 2003 (Sauer et al. 2004). Fortuitously, during my study, birds experienced a broad range of ecological conditions, enabling me to examine the influence of drought on post-fledgling survival. I defined an *a priori* set of 30 models to evaluate potential sources of variation in daily post-fledging survival as a function of drought condition, time in season, post-fledging age, nestling condition, mark type (radio-marked vs. band-only), and sex of attending parent. I compare the performance of my post-fledging survival estimates and a popular indirect estimate used in population modeling.

## **METHODS**

### **Study Area**

During 2001-2003, I quantified densities, nest survival, and post-fledging survival of lark buntings at three randomly selected 65-ha plots on the Pawnee National Grassland, Weld County, northeast Colorado (40° 43' N, 104° 29' W). In 2002, severe drought conditions lowered breeding densities; to increase sample sizes, I expanded plots to a total of 455 ha. Study plots were grazed shortgrass prairie dominated by buffalograss (*Buchloe dactyloides*) and blue grama (*Bouteloua gracilis*). Potential predators include 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*), northern harrier (*Circus cyaneus*), burrowing owl (*Athene cunicularia*), prairie falcon (*Falco mexicanus*), and Swainson's hawk (*Buteo swainsoni*).

### **Field Procedures**

I characterized vegetation structure and composition of study plots by sampling 15 points at 50-m intervals along a randomly placed 700-m transect in early August. At each point, I estimated percent cover of grasses and sedges, forbs, and bare ground within a 20 × 50-cm frame (Daubenmire 1959). I measured grass and forb heights at 5, 25, and 45 cm along the center line of the frame and maximum heights of grasses and forbs within the frame.

Between 6-13 June 2001-2003, I estimated density of breeding male lark buntings with distance

sampling (Buckland et al. 1993). I conducted 18 point transects annually (6 per plot) and an additional 42 point transects in the expanded plots of 2002. I spaced points systematically at 300 m along a grid with a random first start.

I systematically searched for nests between 22 May-8 August by dragging a rope between two observers 25 m apart and by observing adult behavior. I floated eggs (Westerskov 1950) to estimate hatching date. I checked nests every 1-4 days until failure or fledging. During the last nest check (day of fledging), I noted signs to indicate fledging (parents feeding young or calling in the vicinity, fecal droppings outside of the nest).

During the nestling period, I captured adult birds using a modified Potter trap, fitted them with color and USFWS bands, and affixed radio transmitters (BD-2G Model, Holohil Systems Limited, CAN) 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.

In 2001-2002, I weighed (nearest 0.5 g) and measured (wing chord; nearest 0.5 mm) nestlings at 4-7 days post-hatching to avoid premature fledging; nestlings were banded with color and USFWS bands. At post-fledging age 0 (day 0 = first day out of the nest) to age 4, I hand-caught one to two randomly selected fledglings per brood and equipped them with a transmitter (BD-2 Model, Holohil Systems Limited, CAN) using a wing harness of elastic nylon to allow for growth of wings and pectoral muscles. Transmitters weighed 1.05-1.09 grams (4-5% of body weight) and had a battery life of 35 days. In 2003, nestlings were not handled, banded, or radio-marked (unmarked fledglings).

I tracked radio-marked and band-only fledglings daily in 2001 and 2002 and every other day in 2003 (unmarked fledglings) to determine survival, movement, and vegetation use. I located birds using Wildlife Materials TRX-1000S receivers (164-165 MHz band) with hand-held or vehicle-mounted three- and-five element yagi antennae. Range of transmitters was approximately 600 to 900 m depending on terrain. In 2003, aerial tracking via fixed winged aircraft occurred mid-season. I located band-only (2001-2002) and unmarked (2003) fledglings by tracking the radio-marked parent and watching parent-offspring interactions (e.g., feeding or leading young). I observed color bands on band-only fledglings to obtain individual identity. For unmarked fledglings I recorded the number of young associated with a radio-marked parent. Location of the young was documented with associated vegetation (i.e., grass, forb, shrub,

and cactus).

I obtained resightings of live individuals and recoveries of dead fledglings. A resighting consisted of either 1) the physical resighting of marked young, or 2) repeated food deliveries and alarm calling by parents in a particular location. A dead recovery consisted of 1) recovering a body or its remains, 2) recovering a damaged transmitter, or 3) behavioral evidence that a radio-marked parent was no longer feeding young. Because parents are very attentive to young for the first three weeks post-fledging, they provided a reliable behavioral clue for assessing survival of the young. When a parent appeared to be caring for fewer young than observed previously, I watched the parent for an additional hour to establish evidence that a fledgling(s) had died. I tracked adults daily that were no longer caring for young until they left the search area which included a 1.6 km (2001-2002) or 3 km (2003) buffer around the study plot. Young of parents that were no longer located within the search area during the dependency period (22 days) were considered dead. I regularly recovered the physical remains of radio-marked fledglings, and on several occasions the remains of band-only fledglings, either by a careful search of the vegetation surrounding the natal area on the day of fledgling or by watching a marked parent unable to deliver food to a particular location (I noted that parents would attempt to deliver food to the remains of a dead fledgling for several hours). I continued to monitor all birds until death, battery expiration, or departure from the search area. I checked signals of missing birds daily to discover possible return.

Evidence suggesting cause of mortality included cleanly plucked feathers (raptor predation), nibbled feather ends and chewed body parts (mammalian predation), transmitters found in scat containing high concentrations of uric acid (snake predation), and intact bodies (starvation/exposure). My field methods were approved by the Colorado State University Animal Care and Use Committee (Protocol 01-091A-01).

### **Data Analyses**

I calculated densities of male lark buntings for each year in Program DISTANCE, v. 3.5 (Thomas et al. 1998) using the six robust models suggested by Buckland et al. (1993:46). These models included the uniform key function with cosine and simple polynomial expansion series, the half normal key function with cosine and hermite polynomial expansion series, and hazard rate key function with cosine and simple polynomial expansion series. I examined detection functions for each study plot and year and pooled

detections when appropriate to obtain annual densities. I examined  $\chi^2$  values for each model to test for adequate fit ( $P > 0.05$ ). I used the nest survival model available in program MARK (White and Burnham 1999) to estimate daily survival probabilities (DSP) of lark buntings. I calculated overall nest survival as DSP<sup>19</sup> (lark buntings averaged 11 incubation days and 8 nestling days in this study).

For 2001 and 2002 post-fledging survival data, I modeled survival as a function of group and individual covariates using the Burnham Joint Model (joint live and dead recovery encounters; Burnham Both in program MARK) and evaluated models using Akaike's Information Criterion (AIC; Akaike 1973) corrected for small sample size (AIC<sub>c</sub>; Burnham and Anderson 2002). Overdispersion (lack of independence of fledglings in the brood) was likely not important because parents split the brood upon leaving the nest and then kept those young in separate locations. Further, a chi-squared goodness of fit test that examined brood size and number of known surviving young during a 22-day period produced an overdispersion estimate  $< 1$  ( $\hat{c} = \chi^2/df = 0.582$ ;  $\chi^2 = 5.82$ ,  $df = 10$ ).

I also used the joint model to estimate post-fledging survival in 2003; I did not combine these data with 2001-2002 because I tracked young less frequently (2-day intervals) and did not collect individual covariates in 2003. The joint model is a combination of the Cormack-Jolly-Seber model and the band recovery models of Brownie et al. (1985). Because the joint model estimates more parameters than either model alone, it increases flexibility, precision, and information about biology and sampling processes (Nasution et al. 2001). The joint model provides estimates of: 1) survival ( $S$ ); 2) resighting probability of live individuals ( $p$ ); 3) probability of recovery of dead individuals ( $r$ ); and 4) probability that an individual remains in the study area (fidelity) and available for recapture ( $F$ ).

I hypothesized that six factors explained variation in post-fledging survival (2001-2002). (1) Drought conditions. Post-fledging survival is lower during severe drought because of reduced food availability. During a severe drought in North Dakota in 1988, grasshopper densities and nesting productivity of grassland birds declined (Fowler et al. 1991, George et al. 1992). (2) Time in season. Post-fledging survival would be highest mid-season because fledglings from these nests would have greater food availability and better nestling condition than those young fledging early or late in the season. Grasshoppers, the main prey fed to young, in northern Colorado typically decrease throughout the summer, after peaking in late June or mid-July (Capinera and Sechrist 1982, Przybyszewski and Capinera 1990). (3)

Post-fledging age. Newly-fledged young (ages 0-3) would have the lowest survival rates because they are developing locomotion skills and feathers; at this age, they sit motionless in vegetation between movements (Yackel Adams et al. 2001). Young are capable of short runs by ages 3-4 and short flights (0.5-25 m) by ages 4-6. (4) Nestling condition. Post-fledging survival would decrease as nestling condition decreases. I considered three metrics of nestling condition (rank, body condition, and brood size) and used  $AIC_c$  to select the best predictor for subsequent models. Rank was calculated during 4-7 days post-hatching by dividing each sibling's mass by the mass of the heaviest nestling (e.g., if the largest nestling in a brood weighed 20 g, its rank would be 1.00 (20/20), whereas a sibling of 18 g would have a rank of 0.90 (18/20). Body condition was estimated as the residual from the linear regression of mass on wing chord; this metric corrects for differences in mass from overall body-size variation and allows measurements of nestlings to occur over several days. Brood size was the number of young recorded during the last nest check (day before fledging). I assumed rank would be an important predictor of survival because lark buntings hatch asynchronously but fledge on the same day, leaving the smallest nestlings at a possible disadvantage. I did not expect brood size to have a strong effect because both parents provision young. (5) Sex of attending parent. Matriarchal brood units would have higher fledgling survival than patriarchal brood units because female lark buntings are more cryptic and appear more cautious when feeding young. At fledging, lark bunting parents divide the brood and maintain these stable brood units during the parental care period (at least 20 days; Yackel Adams et al. 2001). (6) Mark type. No measurable differences in survival rates exist between radio-marked and band-only fledglings because transmitters are lightweight and compact.

I estimated survival during the first three weeks post-fledging; individuals that survived beyond 22 days were censored. For my 2001-2002 data, I standardized 11 June as day 1 and numbered all tracking occasions (survival day) sequentially until 16 August, for a total of 67 occasions. In 2003, using a different data structure than in 2001 and 2002, resightings and dead recoveries were summarized into 13 occasions: pre-fledging, age 0, age 1, ages 2-3, 4-5, 6-7, 8-9, 10-11, 12-13, 14-15, 16-17, 18-19, and age 21. Survival estimates are modeled using a logit link function. I present post-fledging model-averaged daily survival probabilities (DSP)  $\pm$  SE, slope estimates, and associated 95% confidence intervals (CI). Additionally, I calculated a 22-day survival estimate, assuming a constant daily survival probability within each year (calculated as  $DSP^{22}$ ) and as the model-averaged product of 22 daily survival probabilities under the best-

case (mid-season survival), worst-case (early season), and average-case (using the mean for rank and time in the season) scenarios to compare these estimates among the three years and with those available in the literature. I computed the variances of 22-day survival periods using the delta method (Seber 2002) and obtained model-averaged variance-covariance matrices based on Burnham and Anderson (2004).

I modeled  $p$  (resighting probability) as a function of mark type because I assumed that resightings of radio-marked young would be easier to obtain than those of band-only young (located by watching parent-offspring interactions). Because my use of physical as well as behavioral evidence enabled me to obtain 100% of dead recoveries, I fixed  $r = 1$ . Also, because adults usually kept young within 800 m of the natal area during the first 3 weeks after fledging, I assumed 100% site fidelity and fixed  $F = 1$ .

## **RESULTS**

The shortgrass prairie region entered a drought cycle of varying severity during the course of my study. In 2001, precipitation levels in northeast Colorado were fairly normal with only a few weeks of abnormally dry conditions, 2002 was classified as a severe drought, and 2003 had mild drought conditions (National Drought and Mitigation Center 2003). Annual precipitation in 2002 was 50-70% below the 1961-1990 average (Pielke et al. 2004). In response, grasses diminished by 25% in cover and 46% in height during the severe drought, but rebounded under the mild drought conditions of 2003 (Table 1.1).

In the three study plots, I detected 102 male lark buntings in 2001, 2 in 2002, and 92 in 2003. In 2002, I detected an additional 50 buntings from the expanded study areas. Density estimates in 2001 and 2003 were similar and much greater than in 2002 (Table 1.2). I monitored 377 lark bunting nests across a 78-day interval (22 May-8 August). Number of young fledged per successful nest was  $2.69 \pm 0.12$  ( $n = 51$ ),  $3.00 \pm 0.17$  ( $n = 32$ ), and  $3.00 \pm 0.15$  ( $n = 47$ ) in 2001, 2002, and 2003, respectively. Causes of nest failure were predation (92.3% of 248 failed nests), inclement weather (4.4%), nest desertion (2.0%), and cattle activity (1.2%). Daily nest survival estimates were slightly higher in 2001 and 2003 than in 2002 (Table 1.2), although the 95% confidence intervals for the three years overlapped. Overall nest survival (DSP<sup>19</sup>) was 28.5%, 18.9%, and 24.2% for the three years, respectively.

### **Post-fledging Survival**

From 11 June to 16 August, I tracked 206 fledglings from 82 broods for 22 days after fledging. Radio-transmitters were applied to 38% (26 of 69) of fledglings in 2001 and 47% (46 of 98) of fledglings in

2002; fledglings were tracked for a total of 1,477 bird-days, including 757 days for radio-marked fledglings and 720 days for band-only young. Average mass at age 0 was similar between years (2001:  $21.80 \text{ g} \pm 0.72 \text{ SE}$ ,  $n = 51$  and 2002:  $21.69 \pm 0.39$ ,  $n = 22$ ). By age 4, however, young were 2.5 g heavier in 2002 (2001:  $25.80 \pm 0.78$ ,  $n = 18$  and 2002:  $28.3 \pm 0.51$ ,  $n = 27$ ). Wing chords were similar across years for both ages 0 and 4 (age 0 in 2001:  $41.00 \text{ mm} \pm 1.14 \text{ SE}$ ,  $n = 16$  and 2002:  $41.24 \pm 0.67$ ,  $n = 49$ ; and age 4 in 2001:  $58.57 \pm 0.75$ ,  $n = 14$  and 2002:  $60.06 \pm 0.72$ ,  $n = 27$ ).

In 2001, I monitored 12 fledglings throughout the entire 22-day observation period and 11 young during part of this period. I recovered remains of 21 individuals and inferred death for 25 (ages 0-11) via adult behavior. In 2002, I monitored 15 fledglings throughout the entire 22-day period and 16 for part of the period. I recovered remains for 29 individuals and inferred death for 38 (ages 0-4). Predation was the primary cause of fledgling mortality (78% of 50 recovered fledglings) followed by exposure or starvation (18%), and harness entanglement (4%). Of predation events, I assumed seven were by raptors, seven by mammals, and one by snake in 2001, and eight by raptors, 14 by mammals, and two by snakes in 2002.

Daily post-fledging survival estimates from the drought condition model were similar and slightly higher in 2001 and 2003 than in 2002 (Table 1.2); however, 95% confidence intervals for the three years overlapped. Post-fledging survival (calculated as DSP<sup>22</sup>) was 0.217 in 2001, 0.121 in 2002, and 0.216 in 2003. For the average-case scenario, the model-averaged product of the 22-day survival was  $0.360 \pm 0.08$  in 2001 and  $0.276 \pm 0.08$  in 2002. Survival for the best-case scenario was  $0.433 \pm 0.14$  in 2001 and  $0.511 \pm 0.10$  in 2002, and for the worst-case scenario survival was  $0.154 \pm 0.10$  in 2001 and  $0.018 \pm 0.02$  in 2002.

Post-fledging daily survival probabilities in 2001 and 2002 were best explained by models that incorporated effects of drought condition, time in season (quadratic trend), post-fledging age (ages  $\leq 3$ ), and rank  $\times$  drought interaction (Table 1.3). Drought condition had a negative effect on fledgling survival ( $\hat{\beta}_{\text{drought}} = -3.99$  [SE = 2.01, 95% CI = -7.94, -0.05]). Models with quadratic trends on survival in season received strong support and showed greater fledgling survival in mid-season than early or late season ( $\hat{\beta}_{T_2} = -0.002$ , SE = 0.001, 95% CI = -0.003, -0.001; Table 1.3). Models with a linear temporal trend received no support (the top model containing a linear trend on season had a  $\Delta\text{AIC}_c = 15.61$ ; Table 1.3).

Models with lower survival for recently fledged young (ages  $\leq 3$ ) received substantial support (Table 1.3). As expected, coefficient estimates were negative and large, especially for ages 0 and 1 ( $\hat{\beta}_{\text{age}0} = -3.10$  [SE = 0.40, 95% CI = -3.88, -2.32],  $\hat{\beta}_{\text{age}1} = -2.40$  [SE = 0.42, 95% CI = -3.21, -1.58],  $\hat{\beta}_{\text{age}2} = -0.85$  [SE = 0.60, 95% CI = -2.03, 0.32],  $\hat{\beta}_{\text{age}3} = -1.28$  [SE = 0.51, 95% CI = -2.29, -0.27]). The addition of post-fledging age 4 to the general model produced a positive slope estimate ( $\hat{\beta}_{\text{age}4} = 0.57$  [SE = 1.04, 95% CI = -1.05, 2.62]), as illustrated by the effect of age on nestling survival for heaviest fledglings in mid-season 2001 (Figure 1.1). This pattern was consistent among all drought condition, rank, and time-in-season combinations. The most general model incorporating post-fledging age as a continuous variable, not specifying the first 3 days out of the nest, received no support ( $\Delta\text{AIC}_c = 90.61$ ,  $w_i = 0$ ; Table 1.3).

Rank of young within a nest varied (mean = 0.876; range 0.340-1.00) as did condition (mean  $\pm 1$  SD =  $-0.002 \pm 1.01$ , range -2.40-3.51) and brood size (mean  $\pm 1$  SD =  $3.31 \pm 0.798$ , range 1-4). In a preliminary analysis of nestling condition, rank predicted fledgling survival better than condition or brood size; the  $\Delta\text{AIC}_c$  of the most general model including rank was 9 units lower than general models including the other two metrics. Rank was an important predictor of fledgling survival only during the severe drought of 2002, as indicated by a rank  $\times$  drought interaction. In 2002 only, survival increased with nestling rank (heaviest nestlings had the highest rank; Figure 1.2) with  $\hat{\beta}_{\text{rank } 2002} = 3.80$ , SE = 1.59, 95% CI = 0.68, 6.93 versus  $\hat{\beta}_{\text{rank } 2001} = -0.47$ , SE = 1.38, 95% CI = -3.18, 2.23.

Models incorporating mark type (radio-marked versus band-only) of fledglings received no support; the confidence interval for the effect of mark type was essentially 0 in all models containing that effect. Even though mark type had no effect on fledging survival, as expected it did have a strong influence on recapture probability. Recapture probabilities were higher for radio-marked fledglings ( $\hat{p}_{\text{radio-marked}} = 0.98$ , SE = 0.01, 95% CI = 0.96, 0.99) than for band-only fledglings ( $\hat{p}_{\text{band-only}} = 0.86$ , SE = 0.01, 95% CI = 0.83, 0.88) in 2001-2002. Recapture probabilities for unmarked fledglings in 2003 ( $\hat{p}_{\text{unmarked } 2003} = 0.88$ , SE = 0.02, 95% CI = 0.83, 0.91) were similar to estimates of band-only fledglings in 2002.

Upon fledging the parents divided the brood and remained as distinct brood units during the

tracking period, with the exception of one fledgling which switched from male to female care at post-fledging age 5. In the two years, I observed 47 matriarchal (24 in 2001 and 23 in 2002) and 32 patriarchal (15 in 2001 and 17 in 2002) brood units. There was little support for an additive effect of sex of attending parent on fledgling survival; the confidence interval largely overlapped zero in all models containing that effect.

Microhabitat use by fledglings was similar between years; in 1464 tracking occasions, fledglings sought shelter in shrubs (63%), grasses (22%), cacti (6%), forbs and fences (each 3%), and bare ground and trees (each 1%). I found young in grass with no overhead cover during the cool hours of the morning and in shrubs during the warm hours of the day. Adults cared for young at least three weeks after fledgling and stayed within 1,600 m of the natal area (typically within 800 m). Independence occurred between ages 20-28. Ten of 27 fledglings tracked through the 22-day period remained in the area after independence but were no longer associated with the attending adult. The time of independence for the other 17 fledglings was unknown; nine disappeared between ages 21 and 31 on the same day as their attending adults. In the remaining eight cases, I lost the transmitter signal from the adult or fledgling between ages 21 and 30.

## **DISCUSSION**

I used an information-theoretic approach to evaluate hypothesized sources of variation in post-fledging survival of lark buntings using the joint model of program MARK. Post-fledging survival was higher mid-season, increased with age, and increased with rank during the severe drought of 2002. Survival was not influenced either by mark type or sex of attending parent.

*A priori*, I predicted higher mid-season survival due to higher expected densities of grasshoppers in mid-season. Two plausible mechanisms inversely relate food availability to predation risk: 1) well-fed young would beg less thereby attracting fewer predators (Mumme 1992); and 2) parents could devote more time to fledgling defense (e.g., I occasionally witnessed adults chasing away thirteen-lined ground squirrels and mobbing foxes in the vicinity of fledglings). Fledglings may also experience decreased predation risk mid-season due to the abundant production of young from alternate prey species (Sundell et al. 2003), e.g., recently weaned thirteen-lined ground squirrels. Another possibility for high mid-season survival could be from changes in predator numbers and predator phenology (Naef-Daenzer et al. 2001), but I have no information to adequately assess this possibility.

Survival of lark bunting fledglings increased with age, with lowest survival the first few days out of the nest, consistent with other studies (Sullivan 1989, Anders et al. 1997, Naef-Daenzer et al. 2001). Predation, the primary cause of fledgling mortality (78%), was likely correlated with developmental behaviors associated with different ages. Recently fledged young followed parents through vegetation, often tripping and getting caught in grass or on cactus spines. Young would often tire and briefly sit exposed until they were able to proceed; when under cover, young sat motionless and were easily captured by hand.

Nestling condition (rank) was important as a predictor of survival only during the severe drought, suggestive of competition for food among nest mates under food stress. The rank  $\times$  drought interaction illustrates the need to use caution when interpreting survival estimates obtained only under “normal” environmental conditions (Anders et al. 1997, Maxted 2001) or when only largest young are radio-marked (e.g., Coen and Lindell 2004). I think my rank  $\times$  drought interaction was due to a reduction of the bunting’s main prey (viz., grasshoppers). Although I did not quantify grasshoppers, I noted fewer throughout the 2002 breeding season and similarly low grasshopper densities occurred during a severe drought in North Dakota (Fowler et al. 1991). Early termination of lark bunting breeding in 2002 was likely due to low food availability (DeSante and Baptista 1989). Finally, greatly reduced lark bunting densities were consistent with other studies of grassland birds during severe drought (George et al. 1992). In early to mid-May of the severe drought, lark buntings were numerous; in late May a large exodus of these birds occurred, probably in response to reduced food availability.

My observation of no measurable effect of transmitter attachment on survival of fledglings is consistent with the only two available studies (Powell et al. 1998, and Naef-Daenzer et al. 2001). Powell et al. (1998) found that immature radio-marked wood thrushes had return rates to breeding grounds similar to that of band-only individuals; body mass upon return was also similar between the two groups. Naef-Daenzer et al. (2001) found no survival difference between radio-marked and color-marked great and coal tit fledglings. While mark type did not affect post-fledging survival during the 22-day period, five older birds ( $>$  age 21) caught their lower mandibles in the wing harness ligature, possibly while preening. I therefore encourage use of the leg harness (Rappole and Tipton 1991) as an attachment method on fledglings whenever possible (e.g., Anders et al. 1997, Coen and Lindell 2004, Kershner et al. 2004);

however, this method did not work with young of my study species (i.e., young had difficulty walking and tended to fall backwards).

### **Low Survival**

My 22-day survival of 0.217, 0.120, and 0.217 in 2001-2003, respectively, and average-case survival scenarios in 2001 (0.360) and 2002 (0.276) are lower than most estimates for other North American passerines. Three-week survival of wood thrushes and eastern meadowlarks (*Sturnella magna*) was 0.423 and 0.680 ((Anders et al. 1997, Kershner et al. 2004). Further comparisons are difficult because survival is measured over varying time intervals. My low survival estimates are consistent with Ricklefs' (1973) observation that species with short nestling periods (e.g., lark buntings) generally have lower post-fledging survival than species with longer nestling periods and whose young fledge in a more developed state. Estimates available subsequent to Ricklefs' observation roughly follow this trend; for example, verdin (*Auriparus flaviceps*) have a long nestling period (21 days) and a relatively high fledgling survival rate of 0.783 over 28 days (Austin 1977); yellow-eyed juncos have a short nestling period (10 days) and a low survival rate of 0.321 over 42 days (Sullivan 1989). However, over a seven-week period, European starlings with a long nestling period (21-23 days) and wood thrushes with a short nestling period (12-15 days) had similar survival rates (0.429 [Kremetz et al. 1989] and 0.423 [Anders et al. 1997], respectively). Additional empirically determined estimates of post-fledging survival are needed to adequately test this correlation. If Ricklefs' observation proves generalizable, then such estimates could be useful in making predictions about post-fledging survival of unstudied species.

Drought conditions are not anomalous in the shortgrass ecosystem (Doesken et al. 2003), suggesting that my low survival rates are not unusual for the area. I also think it is improbable that radios on adults hampered their abilities to adequately provision young. There were no observable limitations with capture or delivery of prey, nor were adults noticeably distracted by the presence of the transmitter. Neudorf and Pitcher (1997) found that short-term transmitter application to female hooded warblers (*Wilsonia citrina*) did not affect their ability to feed and care for nestlings (transmitter weight was 7-8.5% of body mass).

### **Evaluation of Indirect Estimate of Juvenile Survival of 0.31**

Sensitivity analyses from several population growth models for migratory passerines (Thompson

1993, Powell et al. 1999, Powell et al. 2000) demonstrate that models are sensitive to the estimate of juvenile survival. A small difference in juvenile survival may produce a substantial effect on the outcome of population growth models. Demographic models of neotropical migrants often assume an indirect estimate of juvenile survival of 0.31 (Donovan et al. 1995, Robinson et al. 1995, Faaborg et al. 1998). My 22-day survival estimates suggest that juvenile survival during the first year may be considerably lower than 0.31. I estimated annual juvenile survival as the product of my post-fledging survival estimates (using 2001-2002 average-case scenarios) and a mean winter survival rate of 0.680, a liberal estimate based on juvenile warbler species (Holmes et al. 1989). My survival estimates of 0.360 and 0.276 in 2001 and 2002, respectively, yield annual juvenile survival rates of 0.245 and 0.188, well below 0.31. I advocate the use of a range of juvenile survival values (Gardali et al. 2003) for modeling population dynamics unless a species-specific survival estimate incorporating important periods (i.e., post-fledging, independence, migration, and winter) is available.

The choice of which juvenile survival estimate to apply to source-sink models is important because their performances vary depending on other demographic parameters used in the model. To illustrate this, I performed calculations using juvenile survival estimates from my average-case scenario estimate in 2001 and the indirect estimate of 0.31. Source-sink estimation followed Pulliam's model (1988), where the population is determined to be producing individuals at replacement levels if recruitment (mean number of female offspring/female/year  $\times$  juvenile survival) equals adult mortality (1 - adult survival). I used a mean annual fecundity of 1.2 based on my liberal estimate obtained for this species (Chapter 2), and a mean annual adult mortality of 0.38 (Donovan et al. 1995). Using my juvenile survival estimate, I calculated recruitment as 0.294 ( $1.2 \times 0.245$ ; fecundity  $\times$  juvenile survival), which is well below 0.38 (adult mortality), thereby indicating a sink population. Using the value of 0.31 instead, the resulting recruitment is 0.372, still indicating a sink population. However, at a slightly higher estimate for fecundity (1.25), the two juvenile survival estimates yield opposing designations; the 0.31 juvenile survival estimate indicates a population source whereas my juvenile survival estimate indicates a sink.

## **CONSERVATION IMPLICATIONS**

Grassland bird species have experienced the largest population declines of any terrestrial avian group in the past four decades in North America (Knopf 1994, Sauer et al. 2004). Lark buntings declined

by 2.5% per year in Colorado and 2.1% per year in the High Plains physiographic region between 1966 and 2003 (Sauer et al. 2004). For management to be effective in reversing population declines in grassland birds, the ultimate factors underlying the declines must be identified and addressed. Although reasons for these declines have yet to be elucidated, factors influencing reproductive success and juvenile survival appear to be prominent mechanisms in this area. As with my post-fledging survival estimates, my overall nest survival estimates (19-29%) are at the low end of reported nest survival estimates (25-50%) for grassland birds (Vickery et al. 1992, Martin 1995). Large tracts of relatively intact grasslands (such as the Pawnee National Grassland) are generally thought to function as source habitats (Perkins et al. 2003). However, the current low productivity of lark buntings suggests the need to further consider the quality of the breeding area in the context of the predator communities it currently supports. My finding of lower post-fledging survival during the severe drought warrants concern for grassland bird populations if drought conditions become more frequent and severe in North American prairie regions, as predicted by some climate models (IPCC 2001, Alley et al. 2003).

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Table 1.1. Mean vegetation structure and composition  $\pm$  SE (95% confidence intervals) of the Pawnee National Grassland, Weld County, Colorado, during the breeding season (2001-2003).

Vegetation variable	2001 normal conditions	2002 severe drought	2003 mild drought
Percent cover bare ground	18.9 $\pm$ 1.8 (15.4, 22.4)	34.5 $\pm$ 2.2 (30.1, 38.9)	36.0 $\pm$ 2.7 (30.7, 41.3)
Percent cover grasses and sedges	56.9 $\pm$ 2.2 (52.7, 61.2)	42.9 $\pm$ 1.8 (39.4, 46.5)	50.7 $\pm$ 3.2 (44.5, 56.9)
Percent cover forbs	6.6 $\pm$ 0.7 (5.2, 7.9)	0.8 $\pm$ 0.1 (0.5, 1.0)	7.5 $\pm$ 2.0 (3.5, 11.4)
Maximum grass height (cm)	21.4 $\pm$ 0.7 (20.0, 22.9)	14.8 $\pm$ 0.7 (13.4, 16.2)	25.0 $\pm$ 1.9 (21.4, 28.6)
Mean grass height (cm)	10.5 $\pm$ 0.5 (9.5, 11.5)	5.7 $\pm$ 0.4 (5.0, 6.5)	10.3 $\pm$ 0.9 (8.5, 12.1)
Maximum forb height (cm)	14.8 $\pm$ 1.0 (12.9, 16.7)	7.3 $\pm$ 0.5 (6.3, 8.4)	13.9 $\pm$ 1.3 (11.4, 16.4)
Mean forb height (cm)	8.3 $\pm$ 0.4 (7.6, 9.0)	5.3 $\pm$ 0.6 (4.1, 6.6)	8.6 $\pm$ 1.1 (6.4, 10.7)

Table 1.2. Annual estimates of density (model averaged, see methods), daily nest survival, and daily post-fledging survival (assumes a constant daily survival rate for each year) for lark buntings on the Pawnee National Grassland, Weld County, Colorado, for 2001-2003. All estimates  $\pm$  SE with 95% CI (profile likelihood confidence intervals computed for survival estimates) on the following line.

Parameter	2001	2002 <sup>a</sup>	2003
	normal conditions	severe drought	mild drought
Density (male lark buntings per ha)	1.62 $\pm$ 0.21 (1.19, 2.05)	0.03 $\pm$ 0.02 (0.01, 0.11)	1.46 $\pm$ 0.19 (1.08, 1.84)
Daily nest survival rate	0.936 $\pm$ 0.007 (0.923, 0.948) <i>n</i> = 141	0.916 $\pm$ 0.011 (0.893, 0.936) <i>n</i> = 83	0.928 $\pm$ 0.007 (0.914, 0.940) <i>n</i> = 153
Daily post-fledging survival probability	0.933 $\pm$ 0.010 (0.913, 0.950) <i>n</i> = 69, 28 broods	0.908 $\pm$ 0.011 (0.886, 0.928) <i>n</i> = 98, 30 broods	0.933 $\pm$ 0.013 (0.905, 0.954) <i>n</i> = 39, 24 broods

<sup>a</sup> Estimate for the 3 original study plots with a pooled detection function across years. The density estimate of expanded plots was 0.17  $\pm$  0.04 (0.10, 0.24).

Table 1.3. Model selection results (30 *a priori* models) from program MARK with probability of a live resighting ( $p$ ) a function of mark type, probability of a dead recovery ( $r$ )=1, and fidelity ( $F$ ) = 1 for post-fledging survival of lark buntings, Pawnee National Grassland, Weld County, Colorado, 2001-2002. Models with the lowest  $AIC_c$  are considered best based on the data, and  $\Delta AIC_c$  is the difference in  $AIC_c$  between the current model and the top model (Burnham and Anderson 2002).  $K$  is the number of parameters in each model and  $w_i$  represents Akaike's model weight.

Post-fledging survival models <sup>a</sup>	$K$	$AIC_c$	$\Delta AIC_c$	$w_i$
Drought + Ages $\leq 3 + T^2 + (\text{Rank} \times \text{Drought})$	13	1343.37	0.00	0.43
Drought + Ages $\leq 3 + \text{Parent} + T^2 + (\text{Rank} \times \text{Drought})$	14	1344.82	1.46	0.21
Drought + Ages $\leq 3 + \text{Mark type} + T^2 + (\text{Rank} \times \text{Drought})$	14	1345.30	1.93	0.16
Drought + Ages $\leq 3 + \text{Parent} + \text{Mark type} + T^2 + (\text{Rank} \times \text{Drought})$	15	1346.77	3.40	0.08
Ages $\leq 3 + \text{Rank} + T^2$	11	1347.59	4.22	0.05
Drought + Ages $\leq 3 + \text{Rank} + T^2$	12	1348.34	4.97	0.04
Ages $\leq 3 + \text{Rank} + \text{Parent} + \text{Mark type} + T^2$	13	1350.17	6.80	0.01
Drought + Ages $\leq 3 + \text{Rank} + \text{Parent} + \text{Mark type} + T^2$	14	1351.37	8.01	0.01
Drought + Ages $\leq 3 + T^2$	11	1352.49	9.12	0.01
Drought + Ages $\leq 3 + \text{Parent} + \text{Mark type} + T^2$	13	1355.67	12.30	0.00
Drought + Ages $\leq 3 + T + (\text{Rank} \times \text{Drought})$	12	1358.98	15.61	0.00
Drought + Ages $\leq 3 + (\text{Rank} \times \text{Drought})$	11	1359.22	15.85	0.00
Drought + Ages $\leq 3 + \text{Mark type} + (\text{Rank} \times \text{Drought})$	12	1360.62	17.25	0.00
Drought + Ages $\leq 3 + \text{Mark type} + T + (\text{Rank} \times \text{Drought})$	13	1360.74	17.38	0.00
Drought + Ages $\leq 3 + \text{Parent} + (\text{Rank} \times \text{Drought})$	12	1361.13	17.76	0.00
Drought + Ages $\leq 3 + \text{Parent} + \text{Mark type} + (\text{Rank} \times \text{Drought})$	13	1362.54	19.17	0.00
Drought + Ages $\leq 3 + \text{Parent} + \text{Mark type} + T + (\text{Rank} \times \text{Drought})$	14	1362.56	19.20	0.00
Drought + Ages $\leq 3 + \text{Rank}$	10	1362.77	19.41	0.00
Ages $\leq 3$	8	1365.47	22.11	0.00
Drought + Ages $\leq 3$	9	1366.30	22.93	0.00

continued

Table 1.3. Continued.

Post-fledging survival models <sup>a</sup>	$K$	$AIC_c$	$\Delta AIC_c$	$w_i$
Drought + Ages $\leq 3$ + $T$	10	1366.47	23.11	0.00
Drought + Ages $\leq 3$ + Rank + Parent + Mark type + $T$	13	1366.48	23.12	0.00
Drought + Ages $\leq 3$ + Parent	10	1368.14	24.78	0.00
Drought + Ages $\leq 3$ + Mark type	10	1368.33	24.96	0.00
Drought + Ages $\leq 3$ + Parent + Mark type + $T$	12	1370.08	26.71	0.00
Drought + Age <sub>cont</sub> + $T^2$ + (Rank $\times$ Drought)	9	1431.02	87.65	0.00
Drought + Age <sub>cont</sub> + Parent + Mark type + $T^2$ + (Rank $\times$ Drought)	11	1433.98	90.61	0.00
Drought + Parent + Mark type + $T^2$ + (Rank $\times$ Drought)	10	1452.78	109.41	0.00
Drought + Age <sub>cont</sub>	5	1455.21	111.84	0.00
Drought + (Rank $\times$ Drought)	6	1468.27	124.91	0.00

<sup>a</sup>Survival is modeled as a function of the following covariates: post-fledging age (Age<sub>cont</sub>) is a continuous individual covariate referring to the number of days since fledgling (up to 22 days), with the first day out of the nest as age 0; Ages  $\leq 3$  modeled the first three days out of the nest separately as: age 0, age 1, age 2, and age 3; sex of the attending parent (Parent); radio-marked or band-only marked fledglings (Mark type); nestling condition as measured by (Rank), calculated by dividing each sibling's mass by the mass of the heaviest nestling; a linear trend ( $T$ ), representing a linear change in survival over time; a curvilinear trend ( $T^2$ ); and an interaction between rank and drought (Rank  $\times$  Drought). Models with Ages  $\leq 3$  also included Age<sub>cont</sub> and  $T^2$  models included  $T$ .

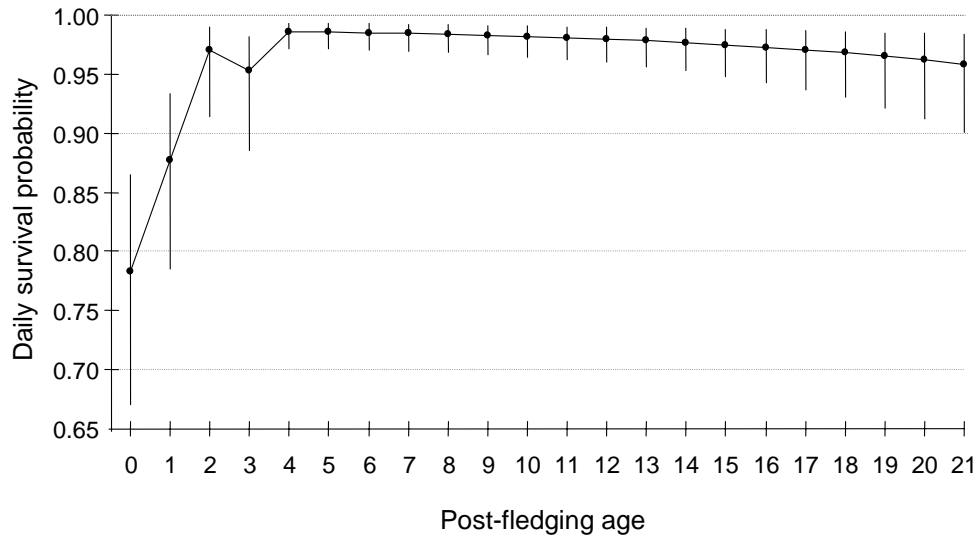


Figure 1.1. Model-averaged daily survival probabilities and 95% confidence intervals for lark bunting fledglings of rank 1 (heaviest young within a brood) during mid-season (4 July-25 July 2001) on the Pawnee National Grassland, Weld County, Colorado. Post-fledging age represents the number of days since fledging, with age 0 as the first day out of the nest.

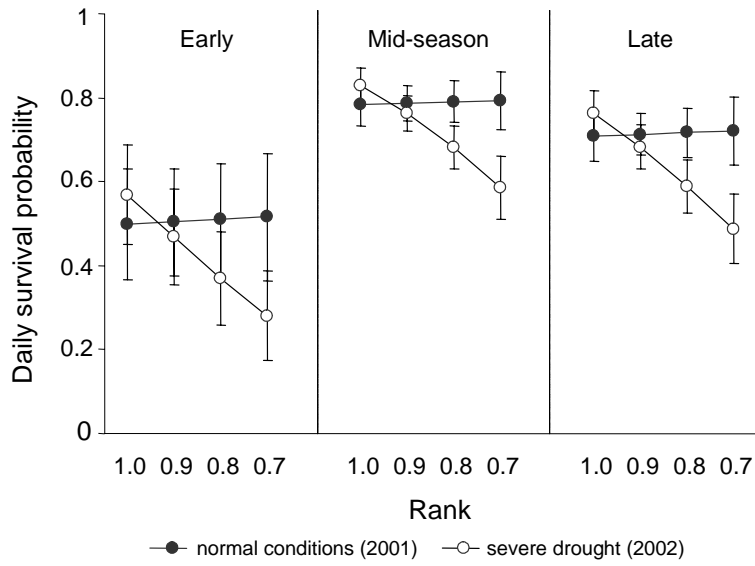


Figure 1.2. Daily survival probabilities of newly-fledged lark buntings on the Pawnee National Grassland, Weld County, Colorado, vary as a function of time in season and rank  $\times$  drought interaction, illustrated for post-fledging age 0. Rank was calculated by dividing each sibling's mass by the mass of the heaviest nestling. All estimates are model averaged  $\pm$  SE. Early season begins 12 June, mid-season 4 July, and late season 26 July.

## **CHAPTER 2:**

### **FECUNDITY AND BREEDING DECISIONS OF LARK BUNTINGS: IMPLICATIONS FOR POPULATION DECLINES**

#### **INTRODUCTION**

Many North American bird populations have suffered significant declines over the last four decades (Peterjohn and Sauer 1999, Sauer et al. 2004). Effective conservation approaches for reversing population declines in birds require understanding the relative importance of limiting factors and the seasons 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. Collectively, pressures in breeding grounds, wintering grounds, and migratory stopovers can include habitat loss, habitat alteration, fragmentation, aerial spraying of insects, and exposure to contaminants (DeGraaf and Rappole 1995). Although factors influencing reproductive success are thought 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, winter, or migration is largely unknown for most declining migrant species (Sherry and Holmes 1992). Attaining this information is an initial step toward the development of responsive and effective conservation actions.

There have been laudable efforts to determine if particular breeding tracts operate as population sources or sinks (Pulliam 1988) for declining species, yet these evaluations have assumed values for important but unknown demographic parameters for the species of interest (Donovan et al. 1995, McCoy et al. 1999). Reliable approaches to estimating avian population growth rates require sound demographic data on fecundity, survival, and dispersal. 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. Therefore, most fecundity estimates are indirectly inferred, either from nest survival (Dececco et al. 2000) or, less frequently, through combining nest survival estimates with seasonal-productivity models (Pease and Gryzbowski 1995). It is problematic to infer fecundity from a

sample of nests because fecundity estimation is more than the product of clutch size and nest survival (Pease and Gryzbowski 1995, Thompson et al. 2001). Estimating fecundity requires knowledge of breeding decisions females make 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 (Knopf 1994, Sauer et al. 2004), but when population limitation occurs is unknown for most species. Between 1966 and 2003, lark buntings (the state bird of Colorado) have declined annually by 2.5% in Colorado and 2.1% in the High Plains physiographic region (Sauer et al. 2004). To elucidate whether breeding events contribute to declines of these prairie birds, I quantified several demographic parameters (nest survival, breeding decisions, and fecundity) of radio-marked lark buntings breeding within an extensive shortgrass prairie in northeast Colorado. Using fecundity and post-fledging survival estimates for this population (Chapter 1), I modeled population growth rates to determine adult survival values necessary to maintain a stable population ( $\lambda = 1$ ). Because radio transmitters may influence reproductive success (Croll et al. 1996) and nesting behavior (Massey et al. 1988), I also evaluated transmitter attachment on nest survival by monitoring females with and without transmitters.

## **METHODS**

### **Study Species**

Lark buntings are large sparrows (length 14-18 cm; mass 30-51 g) endemic to the prairies of North America (Shane 2000). Adults typically breed in grasslands and shrub-steppe of the high plains (Shane 2000) but also use hay meadows (Maher 1974) and Conservation Reserve Program (CRP) grasslands (Howard et al. 2001). Males arrive in Colorado in early May, with females arriving a few days later (Creighton 1971). Breeding occurs from mid-to-late May through early August. Lark buntings are ground nesters and will lay 2-6 eggs per clutch (mean = 4.0; Strong and Ryder 1971). Both males and females incubate, brood, and care for fledglings. Their nesting cycle (nest building through fledging) requires approximately 23-27 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 an additional 3 weeks (Yackel Adams et al. 2001). Lark buntings commonly renest after nest failure but are thought to be single brooded due to extensive early postbreeding migration (Shane 2000); for instance, males and females in northeast Colorado begin flocking and departing as early as late July.

## Study Area

During 2001-2003, I quantified nest survival, breeding decisions, 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, I expanded plots into adjacent lands (455 ha) to increase sample sizes. Study plots were grazed shortgrass prairie typified by short and mid-grasses, including buffalograss (*Buchloe dactyloides*), blue grama (*Bouteloua gracilis*), threeawn (*Aristida longiseta*), western wheatgrass (*Agropyron smithii*), and needleandthread grass (*Stipa comata*), and by cacti (*Opuntia polykantha*), forbs, small patches of yucca (*Yucca glauca*), and shrubs such as fourwing saltbush (*Atriplex canescens*), broom snakeweed (*Gutierrezia sarothrae*), and rabbitbrush (*Chrysothamnus nauseosus*). Potential nest predators present on 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 the prairie rattlesnake (*Crotalus v. viridis*).

## Field Procedures

I systematically searched for initial nests between 20 May-5 June by dragging a rope between two observers 25 m apart and by observing adult behavior. I marked nests with a small wooden stake at 10 m and 30 m from each nest. I floated eggs (Westerskov 1950) to estimate nest age (i.e., determine dates of nest initiation, hatching) and included only females that laid their first egg before 3 June to ensure inclusion of initial nests. Every 1-4 days, I checked nests until they failed or fledged. During the last nest check (day of fledging), I noted signs that would help determine if young fledged (parents feeding young or calling in the vicinity, fecal droppings outside of the nest [deposited only after young fledge; AYA personal observation]). Nest attempts were considered successful if at least one nestling fledged from the nest.

I captured females on nests using a modified Potter trap (designed by J. B. Barna and A. S. Chaine, University of California, Santa Cruz, USA). Each female was measured (mass and wing chord) and banded with USFWS and color bands (1-2 per bird; Darvac, A. C. Hughes, London, UK). I affixed radio transmitters 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 (BD-2G Model, Holohil Systems Limited, CAN).

I tracked females daily to determine fecundity and breeding decisions. I located birds using Wildlife Materials TRX-1000S receivers (164-165 MHz band) with hand-held or vehicle-mounted three- and five-element yagi antennae. Range of transmitters was ca 600 to 900 m depending on terrain. I 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). On a daily basis, I checked signals of missing birds on the study plot to learn of possible return. In mid-season 2003, I also used fixed-wing aircraft to locate missing females in a 10-km search area around each study plot.

To evaluate breeding decisions, I designated females as renested, ceased breeding, or dispersed after each nesting attempt. I defined renested as a subsequent nest ( $\geq 1$  egg) within the study area after either an unsuccessful or successful nest. I considered females as ceased breeding if they remained on the study plot and did not renest or if they left the study plot in late July following nest failure or fledgling depredation. Females were designated as dispersed if they were not located on the study plot and surrounding search area prior to late July. The field methods used in this study were approved by the Colorado State University Animal Care and Use Committee (Protocol 01-091A-01).

### **Data Analyses**

I used the nest survival model in program MARK (White and Burnham 1999) to evaluate daily survival probabilities (DSP) 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 in season. Because nest survival can vary between years, I also evaluated nesting attempt and time in season by using only 2003 nesting data (75% of nesting data). The second analysis examined the effect of mark type (radio-marked versus unmarked females) on nest survival in 2003. This data subset consisted of both radio-marked and unmarked females that nested spatially ( $< 150$  m) and seasonally ( $< 2$  weeks) close to each other. For both analyses, I calculated overall nest survival as the daily survival rate raised to 19 ( $\text{DSP}^{19}$ ) because lark buntings averaged 11 incubation days plus 8 nestling days during this study.

I modeled the probability of intra-year dispersal ( $P_{\text{dispersal}}$ ) as a function of three variables (initial body condition, initial nest fate, and decision date) and their interactions with logistic regression using PROC LOGISTIC in program SAS (SAS Institute 2000). I evaluated two metrics to assess initial body condition: clutch size (Slagsvold and Lifjeld 1988) and the ratio of body mass (g) divided by wing chord

(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), clutch size reflects more than just body condition. I designated four levels of reproductive fate (failed in egg stage, failed in nestling stage, fledged and died, and fledged to independence) but had sufficient data only to evaluate fate constrained at two levels (nest failed and nest fledged). I defined decision date as the day a female was available to make a decision (i.e., the day after nest failure, fledgling depredation, or parental independence of young) with May 22 = 1 (date of first nest).

I evaluated all models using Akaike's Information Criterion (AIC; Akaike 1973) corrected for small sample size ( $AIC_c$ ) and when necessary for overdispersion ( $QAIC_c$ ; Burnham and Anderson 2002). The relative differences ( $\Delta AIC_c$ ) 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  $\Delta AIC_c$  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. I also used 95% confidence intervals (CI) of slope estimates to assess the strength of an effect. Burnham and Anderson (2002:167) recommend the use of summed Akaike weights ( $\Sigma w_i$ ) to evaluate the relative importance of variables when a balanced model set is used (e.g., in the logistic regression analysis each variable appeared in 13 models and each interaction appeared in 5 models). I computed a relative importance measure for each variable by summing Akaike weights over every model in which that variable appeared (Akaike weights of  $\geq 0.40$  suggest that a variable is having an effect on the process of interest (G. C. White, unpublished data)).

Because of model-selection uncertainty (models with  $\Delta AIC_c$  values  $< 7$  might be plausible), I 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 2002:253). I computed unconditional standard errors for the effect sizes, thereby incorporating model-selection uncertainty into precision estimates, and used the  $Z$  distribution to calculate 95% confidence intervals (CI). Because  $R^2 < 1$  in logistic regression, I 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).

I calculated annual fecundity as the number of female young produced per female. I assumed a 1:1 sex ratio (Wheelwright and Seabury 2003) and divided the total number of young produced per female by

two. To account for uncertainty in renesting of females that dispersed during the study, I calculated fecundity using two methods (Kershner et al. 2004). The first method (hereafter, conservative estimate) assumed that I monitored every nest attempt for all radio-marked females, and that dispersed birds did not renest. The second method (hereafter, liberal estimate), attempted to account for the uncertainty in fledging success of dispersed females on population productivity, and assumed that dispersed birds renested at the same rate and experienced the same nest survival probabilities and productivity as females that did not disperse.

I estimated annual adult female survival rates required for a stable population based on the equation (Pulliam 1988)

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

where  $\lambda$  is the population growth rate,  $S_a$  is annual adult survival,  $S_j$  is annual juvenile survival, and  $\beta$  is annual fecundity (female offspring female<sup>-1</sup>). Adult survival necessary to obtain a stable population was therefore estimated as

$$S_a = 1 - S_j\beta.$$

To perform this modeling exercise, I specified fecundity values based on point estimates obtained from conservative and liberal estimates, as well as their respective confidence intervals (lower and upper end estimates) to provide intervals that would include worst-and best-case scenarios. I estimated annual juvenile survival as the product of lark bunting post-fledging survival (22 days) obtained from this population (Chapter 1) and a mean winter survival rate of 0.680 (Holmes et al. 1989); this estimate, based on juvenile warbler species, is liberal because it does not include migratory periods. My 22-day post-fledging survival estimate of  $0.360 \pm 0.08$  in 2001 (under normal precipitation) yields an annual juvenile survival rate of 0.245. I also calculated the lower and upper ends of the 95% CI for the juvenile survival estimate to provide a range of estimates that would include worst-and best-case survival scenarios. All estimates are presented as mean  $\pm$  standard error (SE) unless noted otherwise.

## **RESULTS**

I radio-marked 67 female lark buntings (12 in 2001, 8 in 2002, and 47 in 2003). Collectively, these females built 112 nests ( $1.67 \pm 0.07$  nests per female per season; 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 her transmitter after initial nest failure; I was unable to visually relocate this bird on site or within an extensively searched 200-m radius of her initial nest, so she was considered dispersed. One female died due to transmitter entanglement, which probably caused failure of her initial nest; therefore, I included information from this female only to evaluate the effect of radio-marking females on nest survival.

### **Reproductive Parameters**

I monitored 111 nests for 1193 exposure days across a 79-day interval (22 May-8 August). Clutch size tended to be smaller in subsequent nests than in initial nests while hatching rate was the same (Table 2.1). 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, confidence intervals for these parameters largely overlapped (Table 2.1).

Nest attempt (initial vs. subsequent) and time in season did not influence nest survival. Models incorporating these effects received no support (Table 2.2); the confidence intervals were centered on zero in the model containing that effect ( $\hat{\beta}_{\text{attempt}} = 0.03$ , 95% CI = -0.47, 0.52;  $\hat{\beta}_{\text{time in season}} = -0.001$ , 95% CI = -0.02, 0.02). Daily nest survival estimates for initial and subsequent nests (Table 2.1) yield overall nest survival (DSP<sup>19</sup>) of 30.7% and 31.7%, respectively. In 2003 only, daily survival estimates were slightly lower for initial ( $0.918 \pm 0.01$ , 95% CI = 0.887-0.941,  $n = 46$ ) than for subsequent ( $0.941 \pm 0.01$ , 95% CI = 0.916-0.961,  $n = 37$ ) nests. This provides slight support for including the effect of nest attempt (0.38  $\Delta\text{AIC}_c$  units below the best model, a constant model) on nest survival; the confidence intervals for the slope estimate of nest attempt barely included zero ( $\hat{\beta}_{\text{attempt}} = 0.35$ , 95% CI = -0.18, 0.89).

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 due to nest desertion (5%) and inclement weather (7.5%), and for subsequent nests, inclement weather (3%).

In 2003, I monitored 84 nests of radio-marked (exposure days = 869) and 62 nests of unmarked (exposure days = 612) females across a 58-day interval (22 May-18 July). Clutch size was similar for radio-marked ( $4.36 \pm 0.14$ ) and unmarked ( $4.43 \pm 0.17$ ) females. I found no evidence that capture and radio-

marking of females affected nest survival; confidence intervals for daily survival probabilities of radio-marked females ( $0.930 \pm 0.01$ , 95% CI = 0.911-0.946) and unmarked females ( $0.927 \pm 0.01$ , 95% CI = 0.904- 0.947) largely overlapped. The constant model had greater  $AIC_c$  weight than the model incorporating mark effect (Table 2.2) and the effect of mark type was essentially zero ( $\hat{\beta} = -0.03$ , 95% CI = -0.45, 0.38).

### **Breeding-season Decisions**

Renesting occurred for 7 of the 27 (30%) females that successfully fledged young from an initial nest (Figure 2.1). Two of these 7 birds renested after successfully raising young to independence (at least 21 days); demonstrating the ability of this species to double-brood. The remaining five renested after their offspring were depredated 3-13 days post-fledging. Five of the 7 second nests failed. Four of these failures occurred 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 nest, 27 (69%) remained in the area to renest a second time (Figure 2.1). Seventeen of the 27 second nests failed, and 37% of the 27 females renested a third time. Females deciding to renest did so promptly. First eggs were laid in new nests  $6 \pm 0.52$  days (range: 4-17 days) after nest failure and  $6 \pm 1.7$  days (range: 1-14 days) after death or independence of young. Birds typically renested in close proximity to previous nests. Mean distance between initial and second nests was  $119 \text{ m} \pm 25.88$  (range: 19-672 m, only 3 nests > 490 m), initial and third nests  $96.09 \text{ m} \pm 20.87$  (range: 13-300 m, only 1 nest > 130 m), and second and third nests  $83.91 \text{ m} \pm 24.01$  (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 renest at another site. Two birds remained on site after they ceased breeding (Figure 2.1). One female cared for a fledgling until independence, which occurred on 10 July 2002. She then remained on site for an additional 14 days without evidence of renesting. 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 (Figure 2.1) between 4 June-10 July. Eleven dispersed within two days after fledgling

depredation (0-16 days post-fledging). The remaining 6 females dispersed alone or with fledglings after having cared for them 22 days post-fledging. Of the 39 females that failed on their initial nest, 11 (28%) immediately dispersed from the study area (Figure 2.1) between 1 June-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 post-fledging).

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. I was able to locate one female with her 21-day old fledgling in a small flock of lark buntings 5.27 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.

I found slight evidence of overdispersion ( $\hat{c} = 1.20$ : deviance/degrees of freedom; Burnham and Anderson 2002) in the intra-year dispersal data when evaluating the general model; therefore, I used QAIC<sub>c</sub> for model selection and  $\sqrt{\hat{c}}$  to inflate variances. In a preliminary analysis of initial body condition, clutch size predicted dispersal better than did the ratio of mass to wing chord in the most general model. The  $\Delta$ QAIC<sub>c</sub> of the general model including clutch was 4 units lower than the same model including the ratio of mass to wing chord; therefore, I built subsequent models with clutch size.

Intra-year dispersal probability was best explained by models that incorporated effects of initial nest fate (hereinafter fate), decision date, and the interaction between these variables (Table 2.3). Dispersal probabilities increased for females with successful initial nests, as indicated by a negative coefficient ( $\hat{\beta}$ ) for the explanatory variable in the top model and its model-averaged estimate (Table 2.4). Although decision date alone had no effect, the interaction between fate and decision date was an important predictor of dispersal (Table 2.4). 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 decision date did not include zero (95% CI = 0.01, 0.15) in the top model but did slightly overlap zero with its model-averaged estimate (Table 2.4). Relative importance ( $\Sigma w_i$ ) confirmed strong support for fate, decision date, and fate  $\times$  decision date, and indicated almost no support for clutch size and its interactions between fate and decision date which had substantially smaller summed weights ( $< 0.40$ ; Table 2.4).

### **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  $0.962 \pm 0.11$  female offspring female<sup>-1</sup> (range = 0-3 female young). Liberal estimates assumed that dispersed females renested at the same rate as non-dispersed 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  $1.24 \pm 0.09$  female offspring female<sup>-1</sup>.

### **Adult Survival Needed to Maintain a Stable Population**

I calculated the range of annual adult female survival necessary to maintain a stable population (Table 2.5) using point estimates for fecundity and juvenile survival (Chapter 1) along with their associated 95% confidence intervals. Using the conservative fecundity estimate of 0.96 female offspring female<sup>-1</sup> and an annual juvenile survival estimate of 0.25, I estimate that annual adult survival must be 0.76 to achieve a stable population. Using the liberal fecundity value of 1.24 female offspring female<sup>-1</sup> and an annual juvenile survival estimate of 0.25, I estimate that annual adult survival must be 0.70 to achieve a stable population.

### **DISCUSSION**

This study evaluates the stability of a breeding population of prairie birds using population-specific values for two demographic parameters. Whereas assumptions of fecundity and post-fledging survival (a component of juvenile survival) are commonly based on indirect estimates from the scientific literature, I was able to quantify these parameters for my study population. For the lark bunting in Colorado, my demographic analysis has revealed that population declines are due, at least partially, to events on the breeding grounds. Adult survival rates necessary to maintain this population of lark buntings (0.70-0.76; Table 2.5) are greater than estimates of adult survival of small passerines (0.40-0.60; Ricklefs 1973, Martin 1995) and ground-nesting species in grassland-shrub habitat (0.55; Martin 1995), indicating this population is not self-sustaining without immigration. As I 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. The field effort

necessary to derive population-specific values for important demographic parameters in population models is critical to assess causes of population declines.

To illustrate the importance of using population-specific values, I contrast my findings using population-specific values vs findings if I assumed values attained from the literature for two demographic parameters, fecundity and juvenile survival. Using my population-specific values, lark bunting adult survival of 0.70 – 0.76 is necessary to sustain the population without immigration. If I substitute only the indirect estimate of annual juvenile survival commonly used in the literature (0.31; Donovan et al. 1995, Robinson et al. 1995, Faaborg et al. 1998), adult survival of 0.62 – 0.70 is required for a stable population. If I assume prairie birds produce an average of 1.5 broods (Martin 1995) and use my population-specific value for juvenile survival (0.25), adult survival of 0.54 – 0.64 is necessary. If both indirect values for 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 unrealistic for this population because it is more likely that 1) the true rate for fecundity approaches the conservative estimate (0.96; see *conservative vs liberal fecundity estimates* below), and 2) annual juvenile survival probably does not exceed 0.25. True annual juvenile survival is probably at or below 0.25 because the liberal winter survival rate used in its calculation (0.68) excluded the migratory period (Holmes et al. 1989), and because 0.25 was the highest annual juvenile survival in this species in a four-year period (Yackel Adams et al. 2001, Chapter 1). Further, the only mark-recapture estimate available for annual juvenile survival for a migrant bird is 0.25 (Gardali et al. 2003) with a high recapture probability of 0.75; this liberal estimate fails to include mortality between fledging and independence when fledgling mortality is known to be high (Anders et al. 1997, Naef-Daenzer et al. 2001, Yackel Adams et al. 2001, Chapter 1).

My study underscores the need for robust reliable estimates of adult survival (e.g., Cilimburg et al. 2002, Dinsmore et al. 2003) for passerine populations. Because I lack a direct adult survival estimate for this species, my interpretation may be problematic. First, I 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 and the size of the search area (Cilimburg et al. 2002); if capture probability is high or the search area is large, then survival estimates may be reasonably unbiased. To adjust 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) by including information on dispersed birds located by expanding the search area; this suggests that the 0.1 adjustment is reasonable in some cases, while low in others. If I adjust adult survival estimates for ground-nesting prairie birds (0.55; Martin 1995) by 0.1, the 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 2.5).

### **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 this 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). The conservative fecundity estimate of 0.96 female offspring female<sup>-1</sup> 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). The liberal estimate of 1.24 is similar to the liberal estimate reported for meadowlarks (1.36; Kershner et al. 2004). Annual fecundity estimates of other non-prairie passerines, expressed as female offspring female<sup>-1</sup>, 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 the assumptions one makes about reneesting (Grzybowski and Pease 2005). Birds may compensate for low nest survival by persistently reneesting (Pease and Grzybowski 1995, Schmidt and Whelan 1999), but how many nests a female will initiate during a breeding season must be determined. In this study, lark buntings initiated up to three nests per season; a

maximum of three nests per season was also documented in a color-marked lark bunting population (J. B. Barna and A. S. Chaine personal communication). Renesting attempts typically occurred 6 days after failure (4-5 days is thought to be the shortest physiologically possible interval for passerines; Scott et al. 1987). Renests had similar survival probabilities as initial nests but on average contained fewer eggs. Despite reduced clutch sizes, renesting efforts increased fecundity, because 15 of 45 renests 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) estimates that prairie birds raise an average of 1.5-2 broods per year, data from this 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 day requirement 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 on both nesting attempts; they do not appear to overlap first and second broods. I documented only two females successfully raising two broods, although I was not able to follow all lark buntings that raised their 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 decision to extend parental care and forgo 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 these Nest Survival Probabilities?**

Despite the drought and use of transmitters in this study, I think my nest survival estimates are reasonable for this population in recent time. While my 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 nest survival estimates for lark buntings from 1997 to 2001 at randomly-selected plots on the Pawnee National Grassland (S. K. Skagen, unpublished data) under varying amounts of annual precipitation, represented as the percent deviation from a 29-year mean (Fig. 2.2; Western Regional Climate Data Center 2005). Annual precipitation from 1997 to 2001 varied from 40% above average in 1999 to 29% below average in 2000. While the shortgrass prairie region entered a drought of varying severity during this 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).

I had no measurable effect of transmitter attachment on nest survival when comparing females with and without transmitters, consistent with Granfors et al. (1996; Eastern Meadowlarks). Radio-marked lark buntings had no observable limitations with copulations or capture and delivery of prey to young, consistent with Neudorf and Pitcher's (1997) finding that transmitter application to female Hooded Warblers (*Wilsonia citrina*) did not affect their ability to feed nestlings.

### **Conservative vs. Liberal Fecundity Estimates**

Because the reproductive output of dispersed birds is unknown, I present two estimates of fecundity based on differing assumptions of breeding decisions made by females after dispersing 5-10 km. Based on relative support for the underlying assumptions, I give greater credence to the conservative estimate. For the conservative estimate, I assumed that dispersed females did not reneest. There is very little evidence by which to evaluate this assumption, but Kershner et al. (2004) and Walk et al. (2004) reported no further breeding activity of dispersed and relocated female Eastern Meadowlarks ( $n = 7$ ) and Dickcissels ( $n = 2$ ), respectively. For my liberal estimate, I assumed that dispersed females reneest at the same rate as females that remain on site and that dispersed females experience the same productivity as those that remain on site. There is no direct evidence to support the second assumption, however, passerine studies that examine consequences for *within-site* breeding dispersal between years (Bélichon et al. 1996, Sedgwick 2004) indicate that productivity is often similar between new and old territories. Furthermore, dispersed birds risk settling into areas of high predation with depleted resources and pairing with previous unsuccessful males (e.g., female gray catbirds (*Dumetella carolinensis*) that remained with males on their territories were more successful in fledging offspring than females that dispersed to other territories within the study area; Darley et al. 1971).

### **Why do Female Lark Buntings Disperse during the Breeding Season?**

The decision to disperse during the breeding season will have a strong effect on fecundity, but whether it is advantageous is not well understood and remains "the most prominent missing piece of the songbird demographic puzzle" (Brawn and Robinson 1996). Lark bunting dispersal probabilities increased among females that (1) fledged young from initial nests, as found in other studies (Jackson et al. 1989,

Howlet 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 these hypotheses address the trade-off 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 their probability of raising an additional brood (Jackson et al. 1989, Howlett and Stutchbury 1997), is not supported by this 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 reneesting in the study area did so after raising young to independence. Nor does this 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). I found no indication that food resources were depleted in my study area. Many females chose to reneest in the area, indicating adequate resources for egg production, and females readily obtained grasshoppers prior to departing. A third hypothesis, that dispersal after fledging young allows females to cease breeding and begin premigratory maintenance (Kershner et al. 2004), may explain late-season dispersal but not early-season dispersal when at least 45 days remained for breeding.

An alternative explanation for early-season dispersal of female lark buntings after depredation of their fledglings from initial nests is that their mates are unavailable to reneest because they are providing care to their brood unit. Although lark buntings are predominantly monogamous (Shane 2000), it may be advantageous for females to find new mates, although this could probably be achieved without having to disperse >10 km. 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 reneesting nearby after failed attempts may have remained 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 (Hass 1998).

## **CONSERVATION IMPLICATIONS**

My results suggest that documented population declines in lark buntings are caused, at least in part, by breeding-ground phenomena (fecundity influenced by high rates of predation and the species' limited ability to double brood). These findings justify directing further research efforts and initial conservation actions to the breeding grounds, but they do not eliminate the need to quantify factors influencing overwinter survival. Similar to my findings, factors determining breeding success and annual productivity of four other migrant species had important effects on population growth rates (Nolan 1978, Virolainen 1984, Holmes et al. 1992, Sherry and Holmes 1992).

Although large prairie patches are generally associated with higher avian productivity than fragments (Johnson and Temple 1990, Winter and Faaborg 1999, Davis and Sealy 2000, Herkert et al. 2003, Winter et al. 2004), my data indicate that an extensive shortgrass prairie (62% native prairie remaining within a 21,600 km<sup>2</sup> area; Howard et al. 2001) is unable to sustain lark buntings in the absence of immigration. These findings highlight the need to extend conservation actions beyond the acquisition and protection of large habitat patches, but to also evaluate breeding areas in the context of the predator communities they support and to seek understanding of the myriad of factors affecting predation rates. Predator-prey communities can be altered by changing land use practices, habitat loss and fragmentation, and such changes can, in turn, modify nest encounter rates, nest vigilance and defense, and predator search effort and strategy (Chalfoun et al. 2002). For instance, the degree of matrix fragmentation surrounding a plot (quarter section; 65 ha) in my study area appears to affect thirteen-lined ground squirrel populations (this species has been observed and filmed depredating lark bunting nests [J. B. Barna and A. S. Chaine, personal communication; AYA, personal observation]). Ground squirrels account for 83% and 64% of the small mammal species trapped on fragmented (< 40% native grassland in a 2,266 ha area surrounding plots) and intact sites (100% native grassland in a 2,266 ha area surrounding plots), respectively (T. R. Stanley, unpublished data). In these same fragmented sites, artificial and lark bunting nests had lower survival, (S. K. Skagen, unpublished data); suggesting that further fragmentation of this landscape would likely increase rates of nest predation through increased thirteen-lined ground squirrel numbers (assuming this species is a dominant nest predator).

Increasing evidence through use of video cameras has documented thirteen-lined ground squirrels (Pietz and Granfors 2000, Renfrew and Ribic 2003) and snakes (Thompson et al. 1999) as important nest

predators in other grassland systems. While identification of dominant predators is important for targeting conservation efforts, available management tools may be limited. Implementing predator control to improve reproductive success of songbirds is typically not advocated (Bradley and Marzluff 2003) because removal of one subset of predators is often compensated by numerical increases or changes in foraging habits of another subset (Dion et al. 2000, Heske et al. 2001). Manipulating habitat features to alter predator communities at a local scale, although potentially costly and labor-intensive, has shown success in improving avian reproductive output (Morse and Robinson 1999, Heske et al. 2001).

The use of population-specific values for the breeding demographic parameters, rather than generalized estimates from the scientific literature, allowed more rigorous evaluation of the stability of my study population. Investment in the field effort necessary to attain species- and population-specific estimates of breeding demographic parameters should be standard for future endeavors determining whether breeding ground phenomena contribute to population declines.

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Table 2.1. Reproductive parameters (mean  $\pm$  SE) for initial and subsequent nests (second and third attempts combined) of lark buntings on the Pawnee National Grassland, Weld County, Colorado, 2001-2003.

Parameter	Initial nests	Subsequent nests
Daily nest survival	0.940 $\pm$ 0.009 (0.920, 0.956) <i>n</i> = 66	0.941 $\pm$ 0.010 (0.919, 0.959) <i>n</i> = 45
Clutch size	4.62 $\pm$ 0.10 (4.42, 4.82) <i>n</i> = 66	4.02 $\pm$ 0.14 (3.75, 4.30) <i>n</i> = 45
Hatch rate <sup>a</sup>	0.86 $\pm$ 0.03 (0.81, 0.92) <i>n</i> = 39	0.85 $\pm$ 0.05 (0.76, 0.94) <i>n</i> = 25
Hatchlings per nest attempt	3.77 $\pm$ 0.14 (3.50, 4.04) <i>n</i> = 39	3.40 $\pm$ 0.21 (2.99, 3.81) <i>n</i> = 25
Nestling survival per successful nest <sup>b</sup>	0.86 $\pm$ 0.04 (0.78, 0.95) <i>n</i> = 27	0.79 $\pm$ 0.07 (0.65, 0.93) <i>n</i> = 15
Fledglings per nest	1.33 $\pm$ 0.21 (0.93, 1.74) <i>n</i> = 66	0.87 $\pm$ 0.21 (0.46, 1.27) <i>n</i> = 45
Fledglings per successful nest	3.26 $\pm$ 0.15 (2.97, 3.55) <i>n</i> = 27	2.60 $\pm$ 0.29 (2.03, 3.17) <i>n</i> = 15

<sup>a</sup>Proportion of fully incubated eggs that hatched, a function of infertility and embryo mortality.

<sup>b</sup>Proportion of hatchlings that survived to fledging, a function of starvation, inclement weather, and partial predation.

Table 2.2. Model selection results for nest survival of lark buntings, Pawnee National Grassland, Weld County, Colorado, 2001-2003. Models are listed beginning with the best-fitting model and sorted by  $\Delta AIC_c$ , the difference between the  $\Delta AIC_c$  value for the current model and the model with the lowest  $\Delta AIC_c$  (Burnham and Anderson 2002).  $K$  is the number of parameters in each model and  $w_i$  represents Akaike's model weight.

Nest survival models	$K$	$AIC_c$	$\Delta AIC_c$	$w_i$
1. Temporal variation ( $n = 111$ nests in 2001-2003)				
Constant	1	440.90	0.00	0.58
Nest attempt (initial and subsequent)	2	442.90	2.00	0.21
Time in season	2	442.90	2.00	0.21
2. Radio-marking ( $n = 154$ nests in 2003)				
Constant	1	581.81	0.00	0.73
Mark type (radio-marked vs. unmarked)	2	553.79	1.98	0.27

Table 2.3. Model selection results (balanced model set) from logistic regression analysis of three predictor variables (body condition = Clutch size; initial nest fate = Fate; decision date = Date) and their interactions on intra-year dispersal probabilities ( $P_{\text{dispersal}}$ ) for female lark buntings in Weld County, Colorado, 2001-2003 ( $n = 62$ ). Models are sorted by  $\Delta\text{QAIC}_c$ .  $K$  is the number of parameters in each model and  $w_i$  represents Akaike's model weight. Top and general model maximum-rescaled  $R^2 = 0.31$  and  $0.40$ , respectively.

$P_{\text{dispersal}}$ models	$K$	$\text{QAIC}_c$	$\Delta\text{QAIC}_c$	$w_i$
Fate + Date + (Fate $\times$ Date)	5	57.78	0.00	0.27
Fate	3	58.15	0.37	0.22
Clutch size + Fate + Date + (Fate $\times$ Date)	6	60.08	2.30	0.08
Fate + Date	4	60.39	2.61	0.07
Clutch size + Fate	4	60.43	2.65	0.07
Date	3	60.96	3.18	0.05
Clutch size + Fate + Date + (Clutch size $\times$ Fate) + (Fate $\times$ Date)	7	61.21	3.43	0.05
Clutch size + Fate + (Clutch size $\times$ Fate)	5	61.67	3.89	0.04
Clutch size + Fate + Date + (Clutch size $\times$ Fate) + (Clutch size $\times$ Date) + (Fate $\times$ Date)	8	61.93	4.15	0.03
Clutch size + Fate + Date + (Clutch size $\times$ Date) + (Fate $\times$ Date)	7	62.60	4.82	0.02
Clutch size + Fate + Date	5	62.75	4.97	0.02
Clutch size + Date	4	63.17	5.40	0.02
Constant	2	63.34	5.56	0.02
Clutch size + Fate + Date + (Clutch size $\times$ Fate)	6	64.11	6.33	0.01
Clutch size	3	65.09	7.31	0.01
Clutch size + Fate + Date + (Clutch size $\times$ Date)	6	65.19	7.41	0.01
Clutch size + Date + (Clutch size $\times$ Date)	5	65.53	7.75	0.01
Clutch size + Fate + Date + (Clutch size $\times$ Fate) + (Clutch size $\times$ Date)	7	65.76	7.98	0.00

Table 2.4. Estimated relative importance values (summed QAIC<sub>c</sub> weights;  $\Sigma w_i$ ), top-model and model-averaged effect sizes  $\pm$  SE, and 95% confidence intervals (CI) from logistic regression analysis of body condition (Clutch size), initial nest fate (Fate), decision date (Date) and their interactions on intra-year dispersal of lark buntings in Weld County, Colorado, 2001-2003 ( $n = 62$ ). Estimates presented for fate effect represent the failure of the initial nest.

Variable	$\Sigma w_i$	Top-model		Model-averaged	
		$\beta \pm$ SE	95% CI	$\beta \pm$ SE	95% CI
Intercept	1.00	-0.17 $\pm$ 2.00	-1.35, 3.81	-0.88 $\pm$ 5.22	-11.12, 9.36
Fate	0.90	-3.24 $\pm$ 1.26	-6.18, -1.05	-1.78 $\pm$ 2.22	-6.14, 2.58
Date	0.64	0.00 $\pm$ 0.03	-0.07, 0.07	0.03 $\pm$ 0.07	-0.11, 0.17
Fate $\times$ Date	0.45	0.08 $\pm$ 0.03	0.01, 0.15	0.06 $\pm$ 0.05	-0.03, 0.15
Clutch size	0.37	-	-	0.37 $\pm$ 0.69	-0.98, 1.72
Clutch size $\times$ Fate	0.13	-	-	-0.24 $\pm$ 0.42	-1.07, 0.59
Clutch size $\times$ Date	0.07	-	-	-0.01 $\pm$ 0.01	-0.03, 0.02

Table 2.5. Adult survival estimates of female lark buntings necessary to maintain a stable population (Pulliam 1988) given specific estimates for fecundity and juvenile survival with 95% confidence intervals (CI). A conservative fecundity estimate assumes that dispersed females did not reneest and a liberal estimate assumes that females that dispersed reneested at the same rate, experienced the same nest survival probabilities and productivity as females that remained on study plots. Annual juvenile survival was calculated as the product of lark bunting post-fledging survival in 2001 and a mean winter survival rate of 0.680 (Holmes et al. 1989). Estimates in boldface represent adult survival values necessary given reasonable values for fecundity and annual juvenile survival.

		Fecundity					
		Conservative Estimate			Liberal Estimate		
		Lower CI	Estimate	Upper CI	Lower CI	Estimate	Upper CI
Annual Juvenile Survival		0.75	0.96	1.18	1.06	1.24	1.42
Lower CI	0.14	0.89	0.86	0.83	0.85	0.82	0.80
Estimate	0.25	0.82	<b>0.76</b>	<b>0.71</b>	<b>0.74</b>	<b>0.70</b>	0.65
Upper CI	0.35	0.74	0.67	0.59	0.63	0.57	0.51

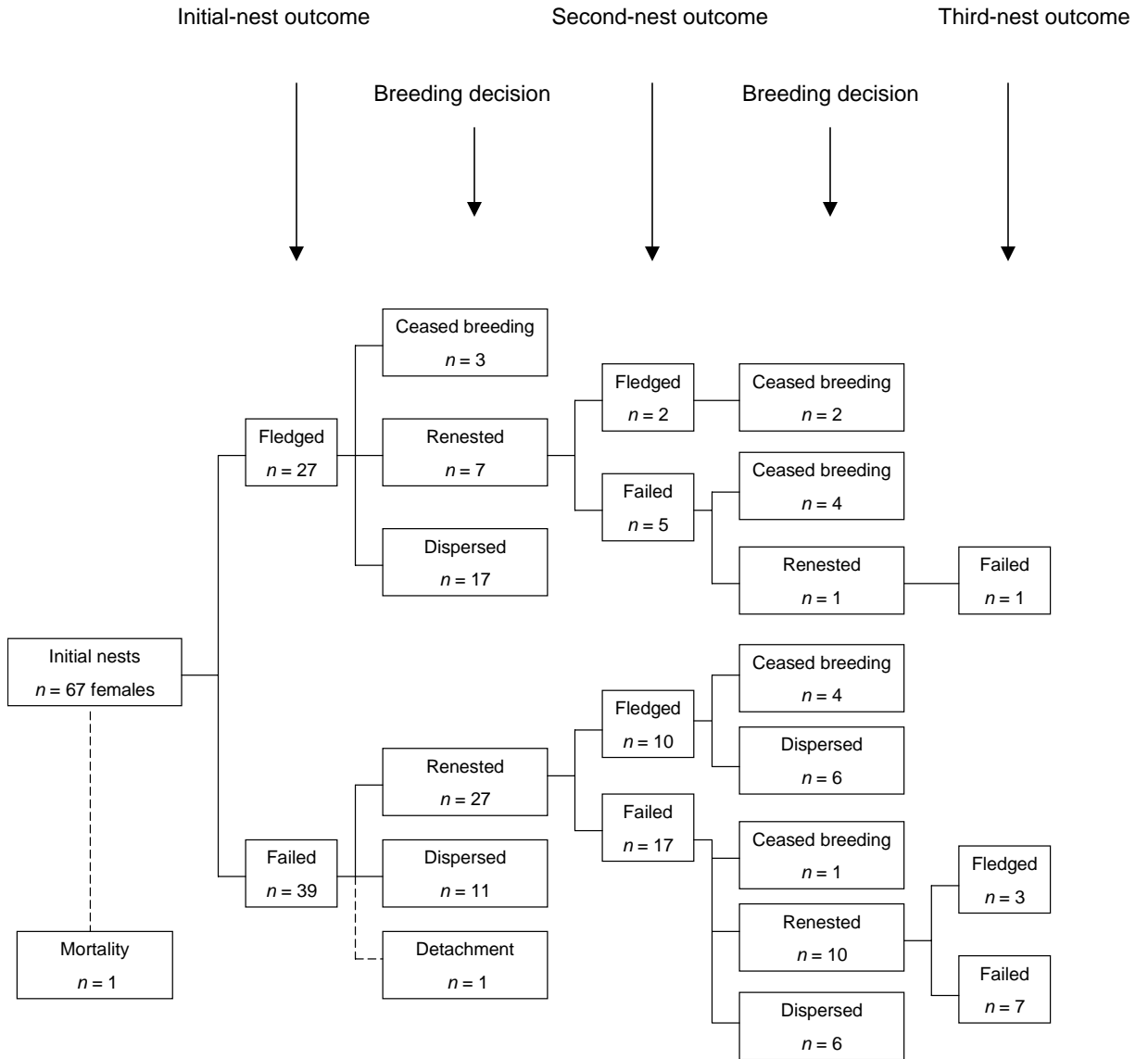


Figure 2.1. Decision tree depicting nest outcome and breeding decisions of 67 female lark buntings during the 2001-2003 breeding seasons on the Pawnee National Grassland, Weld County, Colorado.

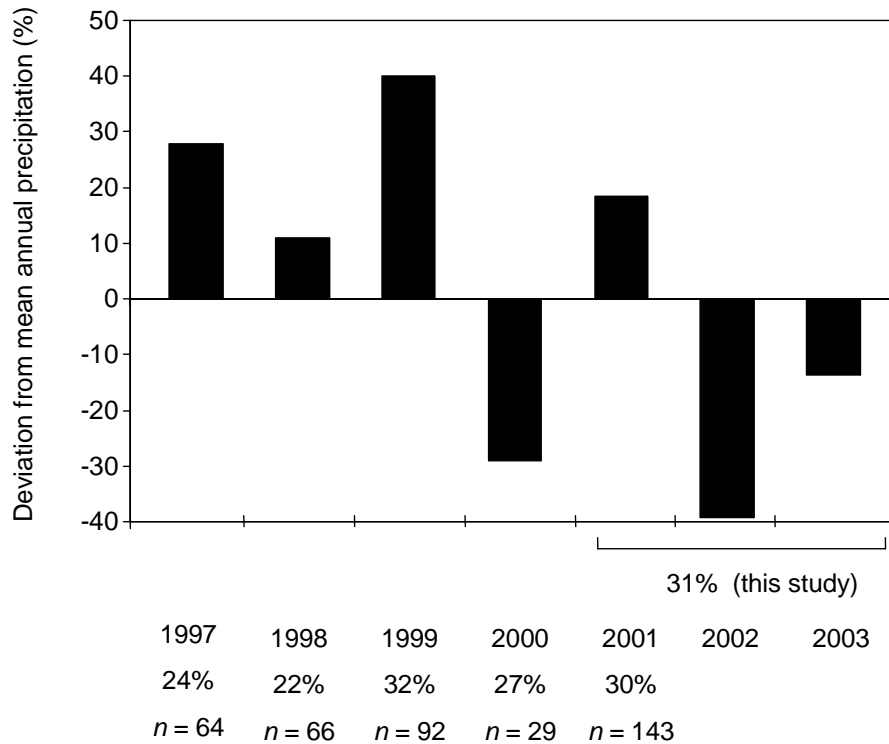


Figure 2.2. The overall nest survival of lark buntings documented during this study (31%) was similar to the overall nest survival measured for this species on the Pawnee National Grassland, Weld County, Colorado under varying amounts of precipitation (1997-1999, and 2001: S. K. Skagen, unpublished data; 2000: Yackel Adams et al. 2001). Figure depicts deviation from mean annual precipitation based on a 29-year (1976-2004) climate record obtained from the Western Regional Climate Data Center for the Pawnee National Grassland. Long-term mean precipitation is  $32.9 \pm 8.2$  (SD) cm.