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MODELING POST-FLEDGING SURVIVAL OF LARK BUNTINGS IN RESPONSE TO ECOLOGICAL AND BIOLOGICAL FACTORS

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Abstract. We evaluated the influences of several ecological, biological, and methodological factors on post-fledging survival of a shortgrass prairie bird, the Lark Bunting (*Calamospiza melanocorys*). We estimated daily post-fledging survival (n = 206, 82 broods) using radiotelemetry and color bands to track fledglings. Daily survival probabilities were best explained by drought intensity, time in season (quadratic trend), ages ≤3 d post-fledging, and rank given drought intensity. Drought intensity had a strong negative effect on survival. Rank was an important predictor of fledgling survival only during the severe drought of 2002 when the smallest fledglings had lower survival. Recently fledged young (ages ≤3 d post-fledging) undergoing the transition from nest to surrounding habitat experienced markedly lower survival, demonstrating the vulnerable nature of this time period. Survival was greater in mid and late season than early season, corresponding to our assumptions of food availability. Neither mark type nor sex of attending parent influenced survival. The model-averaged product of the 22-d survival calculated using mean rank and median value of time in season was 0.360 ± 0.08 in 2001 and 0.276 ± 0.08 in 2002. Survival estimates that account for age, condition of young, ecological conditions, and other factors are important for parameterization of realistic population models. Biologists using population growth models to elucidate mechanisms of population declines should attempt to estimate species-specific of post-fledging survival rather than use generalized estimates.

Key words: ovian demography; Calamospiza melanocorys; *drought; information theory; joint model; Lark Bunting; Pawnee National Grassland, Colorado, USA; post-fledging survival; progrom MARK; radiotelemetry.*

INTRODUCTION

Many ecological, biological, and physiological factors interact to influence the survival of avian species and modify their population dynamics. Predation, competition, limited food supply, adverse weather conditions, disease, and physiological stressors of breeding and migration influence survival to varying degrees throughout the life cycles of birds. Survival analysis can identify vulnerable periods in a species' life history and evaluate the relative importance of various environmental and physiological factors and their interactions. By understanding factors affecting survival, we can better identify and explain evolutionary adaptations and elucidate potential mechanisms of population declines. Robust survival estimation offers a unified approach to evaluate the myriad of factors potentially affecting survival. These methods allowed researchers to identify climate and landscape structure as major influences in adult survival of Northern Spotted Owl (*Strix occidentalis caurina*), European Dipper (*Cinclus cinclus*), and Mallard (*Anas platyrhynchos*) (Franklin et al. 2000, Marzolin 2002, Devries et al. 2003). These estimation methods also produce more reliable and realistic survival estimates than methods assuming constant daily survival.

Variation in juvenile (first-year) survival can have dramatic effects on population dynamics of passerines (Robinson et al. 2004) yet is the least-studied component of avian demographics. Post-fledging survival, defined as survival from fledging (when young leave the nest) to parental independence, has been the focus of recent passerine studies using radiotelemetry. Common to these studies is lower survival during the first week post-fledging due to predation (Sullivan 1989, Anders et al. 1997, Naef-Daenzer et al. 2001). Evidence for effects of other factors such as seasonal timing and body condition (variously defined) on post-fledging survival is equivocal. 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), but not for Wood Thrushes (*Hylocichla mustelina*; Anders et al. 1997). Body condition influenced 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)

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or Yellow-eyed Juncos (*Junco phaenotus*) (Sullivan 1989). Many factors that may affect avian post-fledging survival remain unexplored.

We estimated 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). We evaluated several ecological, biological, and methodological factors that potentially influence post-fledging survival, including time in season (related to food availability), post-fledging age, nestling condition, sex of attending parent, and mark type (radio-marked vs. band-only). Fortuitously during our study, birds experienced a broad range of climatic conditions, enabling us to examine the influence of drought on post-fledging survival. We also estimated annual density and nest survival of Lark Buntings and documented vegetation structure to provide the ecological context for our survival estimates. Because estimates of juvenile survival of passerines are largely unavailable, population modelers have assumed juvenile survival indirectly as a fraction (0.25–0.50) of adult survival (Ricklefs 1973, Donovan et al. 1995). We evaluated this assumption by comparing our empirically derived survival estimate with a popular indirect estimate used in population modeling.

METHODS

Study area

During 2001–2003, we estimated densities, nest survival, and post-fledging survival of Lark Buntings at three 65-ha plots on the western unit of Pawnee National Grassland, Weld County, northeast Colorado, USA (40°43′ N, 104°29′ W). The sampling frame was comprised of sections (1.6 × 1.6 km) of U.S. Forest Service land, accessible by road, in which we detected 10 or more Lark Buntings. Three sections were selected during a survey with a random starting point and random driving direction. We then randomly selected one quarter section from each of three selected sections to serve as the study plots. In 2002, severe drought and a prairie fire on one of the plots lowered breeding densities; to increase sample sizes, we expanded plots to randomly selected adjacent quarter sections for a total of 455 ha. Original and expanded study plots were all grazed shortgrass prairie dominated by buffalo grass (*Buchloe dactyloides*) and blue grama (*Bouteloua gracilis*) with a shrub component of four-winged saltbush (*Atriplex canenscens*) and broom snakeweed (*Gutierrezia sarothrae*). Potential predators include thirteen-lined ground squirrel (*Spermophilus tridecemlineatus*), coyote (*Canis latrans*), swift fox (*Vulpes velox*), long-tailed weasel (*Mustela frenata*), bull snake (*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

We 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, we estimated percent cover of grasses and sedges, forbs, and bare ground within a 20 × 50 cm frame (Daubenmire 1959). We 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 and 13 June 2001–2003, we estimated density of breeding male Lark Buntings with distance sampling (Buckland et al. 1993). We conducted 18-point transects annually (six per plot) and an additional 42 point transects in the expanded plots of 2002. We spaced points systematically at 300 m along a grid with a random first start.

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

During the nestling period, we captured adult birds on the nest using a modified walk-in Potter trap, fitted them with color and U.S. Fish and Wildlife Service (USFWS) bands, and affixed radio transmitters (BD-2G Model; Holohil Systems, Carp, Ontario, Canada) using leg harnesses (Rappole and Tipton 1991). Transmitters weighed 1.35–1.48 g (3–4% of body mass) and had a battery life of 60 d.

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

We 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. We located birds using TRX-1000S receivers (164–165 MHz band; Wildlife Materials, Carbondale, Illinois, USA) with hand-held or vehicle-mounted three- and five-element yagi antennae. Range of transmitters was approximately 600–900 m, depending upon terrain.

We 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). Individuals were identified by color bands on band-only fledglings. For unmarked fledglings we 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, cactus). We obtained resightings of live individuals and recoveries of dead fledglings. A resighting (p) consisted of either physical resighting of marked young (>90% of resightings) or, when only one young in its brood unit remained alive, by repeated food deliveries and alarm calling by a parent in a particular location. A dead recovery (r) consisted of either recovering a body or its remains, recovering a damaged transmitter, or behavioral evidence that a radio-marked parent was no longer feeding dependent 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, we watched the parent for an additional hour to establish evidence that a fledgling(s) had died. We tracked adults daily that were no longer caring for young until they left a 1.6-km (2001–2002) or 3-km (2003) search area buffer around the study plot. To confirm that missing birds had departed the study area, we used fixed-wing aircraft on 11 July 2003 to search within 10 km of each study plot.

Young of parents that were no longer located within the search area during the dependency period (20–22 d) were considered dead. We 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 fledging or by watching a marked parent unable to deliver food to a particular location. (We noted that parents would attempt to deliver food to the remains of a dead fledgling for several hours.) We continued to monitor all birds until death, battery expiration, or departure from the search area. We 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). Our field methods were approved by the Colorado State University Animal Care and Use Committee (Protocol 01-091A-01).

Data analyses

We calculated densities of male Lark Buntings for each year in Program DISTANCE version 3.5 (Thomas et al. 1998). We examined detection functions for each study plot and year and pooled detections when appropriate to obtain annual densities. We examined χ^2 values for each model to test for adequate fit ($P > 0.05$). To calculate daily nest survival probabilities (DNS) of Lark Buntings, we used generalized linear modeling based on a binomial likelihood. This approach is an extension of the model described by Bart and Robson (1982) and is available in program MARK (White and Burnham 1999). We calculated overall nest survival as DNS^{19} (Lark Buntings averaged 11 incubation days and 8 nestling days in this study).

For 2001 and 2002 post-fledging survival data, we modeled survival as a function of group and individual covariates using the Burnham Joint Model (joint live and dead recovery encounters), a combination of the Cormack-Jolly-Seber model and the band recovery models of Brownie et al. (1985), available in program MARK. 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 survival (S), resighting probability of live individuals (p), probability of recovery of dead individuals using physical and behavioral evidence (r), and probability that an individual remains in the study area and is available for resighting (F). We also used the Burnham Joint Model to estimate post-fledging survival in 2003, but because we tracked young less frequently (2-d intervals) and did not collect individual covariates in this year, we analyzed 2003 data separately from the 2001–2002 data.

We used an information-theoretic approach to examine post-fledging survival of Lark Bunting fledglings (2001 and 2002 only) in relation to time in season, post-fledging age, nestling condition, mark type, sex of attending parent, and drought intensity. Our a priori hypotheses addressing potential sources of variation in survival included in our model set are as follows. (1) 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, are typically highest throughout July in northeast Colorado (Capinera and Sechrist 1982, Przybyszewski and Capinera 1990). To identify a temporal trend, we included models with a quadratic trend (T^2), a linear trend (T), and no seasonal trend in survival. (2) Post-fledging age: newly fledged young (ages 0–3 d) 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 d and short flights (0.5–25 m) by ages 4–6 d. We included models that specify the first few days out of the nest (ages $\leq$ 3 d) separately, models with age as a continuous variable (not specifying the first few days out of the nest, age_{cont}), and models without age. (3) Nestling condition: post-fledging survival

would decrease as nestling condition decreases. Rank was calculated during 4–7 d post-hatching by dividing each sibling's mass by the mass of the heaviest nestling. 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). We 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. We did not expect brood size to have a strong effect because both parents provision the nest and divide the brood upon fledging (Yackel Adams et al. 2001). (4) 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 d; Yackel Adams et al. 2001). (5) Mark type: no measurable differences in survival rates would exist between radio-marked and band-only fledglings. Lightweight transmitters (<4% body mass) did not effect survival of Wood Thrush, Great Tit, or Coal Tit fledglings when compared to groups of band-only young (Powell et al. 1998, Naef-Daenzer et al. 2001). However, to evaluate the effect of mark type on survival of Lark Bunting fledglings, we included models with and without this variable.

Because drought intensity varied during 2001 and 2002, we also modeled the effects of drought (or year) on survival in these years. Drought intensity was coded as 1 for severe drought (2002) and 0 for normal precipitation (2001). Before conducting analyses, we hypothesized that post-fledging survival is lower during severe drought because of reduced food availability and that drought would have a stronger negative impact on survival of nestlings in poorer condition. 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).

We defined a set of 30 models (Appendix) based on our knowledge of the ecology of the study species relating to food habits, parental behavior, and fledgling development and on passerine breeding biology and post-fledging survival literature regarding brood size, body condition metrics, and effects of radio transmitters. In a preliminary analysis to determine which nestling condition metric to include in the model set, we considered rank, body condition, and brood size in our most general model (including all variables of interest; drought + ages ≤3 d post-fledging + parent + mark type + T^2 + nestling condition(drought)) and used Akaike's Information Criterion corrected for small sample size (AIC_c; Akaike 1973, Burnham and Anderson 2002) to select the best predictor for subsequent models. We predicted that drought intensity and age of fledglings would exhibit the strongest effects on survival and therefore included these factors each in all but three and two models, respectively. We predicted that nestling condition (e.g., rank) would be more important during severe drought, therefore we modeled fledgling rank with constant (rank) and separate effects for each drought intensity (rank(drought)). We did not consider models with single factors (except age) because we felt such models would fail to adequately explain survival. We evaluated the 30 candidate models using AIC_c.

We estimated survival during the first three weeks post-fledging; opportunistic survival information obtained beyond this period was not used in the analysis. For our 2001–2002 data, we 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 20–21 d.

Because of model selection uncertainty (models with $\Delta AIC_c < 7$ can be plausible) in the 2001 and 2002 analysis, we model-averaged daily post-fledging survival probabilities (DSP) ± SE, slope estimates, and associated confidence intervals (CI) using a logit link function. We present the model-averaged product of 22 daily survival probabilities for three scenarios, best-case (survival calculated for heaviest fledglings in mid season, 4 July), worst-case (survival calculated for lightest fledglings [rank = 0.7] in early season, 12 June), and average-case (survival calculated using mean rank [0.88] and median value of time in season, 12 July). We computed the variances of 22-d survival periods using the delta method (Seber 2002) and obtained model-averaged variance–covariance matrices based on Burnham and Anderson (2004). To compare 2003 survival estimates (with no covariates) to 2001 and 2002 estimates, we calculated a constant daily survival probability within each year.

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 young in separate locations; therefore, fates of fledglings were largely independent of one another as long as the parent survived. Further, a chi-squared goodness-of-fit test that examined brood size and number of known surviving young during a 22-d period produced an overdispersion estimate <1 ($c = \chi^2/df = 0.582$; $\chi^2 = 5.82$, df = 10, $P = 0.830$).

We modeled p (resighting probability) as a function of mark type because we 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 we used physical or

TABLE 1. Vegetation structure and annual estimates of Lark Bunting density (model averaged), nest survival, and post-fledging survival (assuming constant daily survival) on the Pawnee National Grassland, Weld County, Colorado, for 2001–2003.

Year and condition	Cover grasses (%)		Cover forbs (%)		Mean grass height (cm)	
	Mean ± SE	95% CI	Mean ± SE	95% CI	Mean ± SE	95% CI
2001, normal	56.9 ± 2.2	52.7–61.2	6.6 ± 0.7	5.2–7.9	10.5 ± 0.5	9.5–11.5
2002, severe drought	42.9 ± 1.8	39.4–46.5	0.8 ± 0.1	0.5–1.0	5.7 ± 0.4	5.0–6.5
2003, mild drought	50.7 ± 3.2	44.5–56.9	7.5 ± 2.0	3.5–11.4	10.3 ± 0.9	8.5–12.1

Note: All estimates mean ± SE with 95% CI (profile likelihood confidence intervals computed for survival estimates).
† Sample sizes were n = 141 nests in 2001, n = 83 nests in 2002, and n = 153 nests in 2003.
‡ Sample sizes were n = 69 fledglings from 28 broods in 2001, n = 98 fledglings from 30 broods in 2002, and n = 39 fledglings from 24 broods in 2003.

behavioral evidence to confirm all fledgling deaths, we felt comfortable in assuming 100% dead recoveries (r = 1). Because the number of young >800 m of the natal area during the first 3 wk after fledging were so few, we felt comfortable in assuming 100% site fidelity (F = 1).

RESULTS

The shortgrass prairie region entered a drought cycle during the course of our 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, *available online*).[4] Annual precipitation in 2002 was 50–70% below the 1961–1990 mean (Pielke et al. 2004). In response, grasses diminished by 25% in cover and 46% in height during the severe drought (Table 1). Avian density estimates in 2001 and 2003 were similar and much greater than in 2002 (Table 1). In the three study plots, we detected 102 male Lark Buntings in 2001, 2 in 2002, and 92 in 2003. In 2002, we detected an additional 50 buntings from the expanded study areas.

Daily nest survival estimates were similar between years (Table 1) with overall nest survival (DNS[19]) of 0.285, 0.189, and 0.242 for the three years, respectively. We monitored 377 Lark Bunting nests across a 78-d interval (22 May–8 August). Early termination of breeding (by 2 wk) was observed during the severe drought of 2002. Number of young fledged per successful nest was 2.69 ± 0.12 (n = 51), 3.00 ± 0.17 (n = 32), and 3.00 ± 0.15 young (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 post-fledging survival estimates assuming constant daily survival (which allows comparison across years; see *Methods*) were similar among the three years of the study (Table 1), although slightly lower during the severe drought of 2002.

[4] (http://www.drought.unl.edu/dm/)

Post-fledging survival 2001–2002

From 11 June to 16 August 2001 and 2002, we tracked 206 fledglings from 82 broods for 22 d after fledging. Radio transmitters were applied to 38% (n = 69) of fledglings in 2001 and 47% (n = 98) of fledglings in 2002; fledglings were tracked for a total of 1477 bird-days, including 757 d for radio-marked fledglings and 720 d for band-only young. Mean mass at age 0 for young was similar between 2001 and 2002 (21.8 ± 0.7 g, n = 51 and 21.7 ± 0.4 g, n = 22). By age 4 d, however, young were 2.5 g heavier in 2002 (28.3 ± 0.5 g, n = 27) than in 2001 (25.8 ± 0.8 g, n = 18). Wing chords were similar across years for both age 0 (41.0 ± 1.1 mm, n = 16 and 41.2 ± 0.7 mm, n = 49) and age 4 d (58.6 ± 0.8 mm, n = 14 and 60.1 ± 0.7 mm, n = 27).

In 2001, we tracked 69 transmittered or color-marked fledglings of which 12 survived the entire 22-d observation period; we tracked 11 young during part of this period, recovered physical remains of 21 individuals, and inferred death via parental behavior for 25 fledglings (ages 0–11 d). In 2002, we tracked 98 fledglings of which 15 survived the entire 22-d period; we tracked 16 fledglings for part of the period, recovered physical remains for 29 individuals, and inferred death via parental behavior for 38 fledglings (ages 0–4 d). Primary causes of fledgling mortality were predation (39 of 50 recovered fledglings; 15 in 2001 and 24 in 2002), exposure or starvation (nine fledglings; two in 2001 and seven in 2002), and harness entanglement (two fledglings; one each year). Of predation events, we 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. Scavenging of carcasses (Bumann and Stauffer 2002) was likely minimized in our study because all but three carcasses were located within 24 h of depredation.

The model-averaged product of the 22-d post-fledging survival for the average-case scenario (survival calculated using mean rank and median value of time in season) was 0.360 ± 0.08 in 2001 and 0.276 ± 0.08 in 2002. Survival for the best-case scenario (survival calculated for heaviest fledglings in mid season) was

TABLE 1. Extended.

Density (no. males/ha)		Daily nest survival†		Daily post-fledging survival‡	
Mean ± SE	95% CI	Mean ± SE	95% CI	Mean ± SE	95% CI
1.62 ± 0.21	1.19–2.05	0.936 ± 0.007	0.923–0.948	0.933 ± 0.010	0.913–0.950
0.17 ± 0.04	0.10–0.24	0.916 ± 0.011	0.893–0.936	0.908 ± 0.011	0.886–0.928
1.46 ± 0.19	1.08–1.84	0.928 ± 0.007	0.914–0.940	0.933 ± 0.013	0.905–0.954

0.433 ± 0.14 in 2001 and 0.511 ± 0.10 in 2002 and for the worst-case scenario (survival calculated for lightest fledglings in early season) was 0.154 ± 0.10 in 2001 and 0.018 ± 0.02 in 2002.

Post-fledging daily survival probabilities in 2001 and 2002 were best explained by models that incorporated effects of drought intensity, time in season (quadratic trend; T^2), post-fledging age (ages ≤ 3 d), and rank(drought) (Table 2). Drought intensity (drought) had a strong negative effect on fledgling survival; the model-averaged coefficient for this effect was $\hat{\bar{\beta}}_{drought} = -3.99 \pm 2.01$ (95% CI = −7.94, −0.05). Models with quadratic trends for time in season (T^2) received strong support and showed greater fledgling survival in mid and late season than early season ($\hat{\bar{\beta}}_{T^2} = -0.0017 \pm 0.0005$, 95% CI = −0.0028, −0.0007; Table 2). Models with a linear temporal trend received no support; the top model containing a linear trend on season had a $\Delta AIC_c = 15.61$ (Appendix).

Models with lower survival for recently fledged young (ages ≤ 3 d) received substantial support (Table 2). As expected, coefficient estimates were negative and large, especially for ages 0 and 1 d ($\hat{\bar{\beta}}_{age0} = -3.10 \pm 0.40$, 95% CI = −3.88, −2.32; $\hat{\bar{\beta}}_{age1} = -2.40 \pm 0.42$, 95% CI = −3.21, −1.58; $\hat{\bar{\beta}}_{age2} = -0.85 \pm 0.60$, 95% CI = −2.03, 0.32; $\hat{\bar{\beta}}_{age3} = -1.28 \pm 0.51$, 95% CI = −2.29, −0.27). The addition of post-fledging age 4 d to the general model produced a positive slope estimate ($\hat{\bar{\beta}}_{age4} = 0.57 \pm 1.04$, 95% CI = −1.05, 2.62), as illustrated by the effect of age on nestling survival for heaviest fledglings in mid season 2001 (Fig. 1). This pattern was consistent among all drought intensity, rank, and time-in-season combinations. The most general model incorporating post-fledging age as a continuous variable (age_{cont}), not specifying the first 3 d out of the nest, received no support ($\Delta AIC_c = 90.61$, $w_i = 0$; Appendix).

Rank of young within a nest (0.88 ± 0.01) varied more in 2002 (range 0.3–1.0) than in 2001 (range 0.5–1.0). Condition (−0.002 ± 0.08, range −2.4–3.5) and brood size (3.3 ± 0.09, range 1–4) also varied. In a preliminary analysis of nestling condition, rank predicted fledgling survival better than condition or brood size; the ΔAIC_c of the most general model including rank was nine 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 rank(drought). Survival increased with nestling rank (heaviest nestlings had the highest rank; Fig. 2) in 2002 ($\hat{\bar{\beta}}_{rank} = 3.80 \pm 1.59$, 95% CI = 0.68, 6.93) but not in 2001 ($\hat{\bar{\beta}}_{rank} = -0.47 \pm 1.38$, 95% CI = −3.18, 2.23).

Models incorporating mark type (radio-marked vs. 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 resighting probability. Resighting probabilities were higher for radio-marked fledglings ($\hat{\bar{p}}_{radio} = 0.980$, SE = 0.01, 95%

TABLE 2. Model selection results (models with Akaike $w_i > 0.01$) from program MARK (White and Burnham 1999) 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.

Post-fledging survival models	K	AIC_c	ΔAIC_c	w_i
Drought + ages ≤3 + T^2 + rank(drought)	13	1343.37	0.00	0.43
Drought + ages ≤3 + parent + T^2 + rank(drought)	14	1344.82	1.46	0.21
Drought + ages ≤3 + mark type + T^2 + rank(drought)	14	1345.30	1.93	0.16
Drought + ages ≤3 + parent + mark type + T^2 + rank(drought)	15	1346.77	3.40	0.08
Ages ≤3 + T^2 + rank	11	1347.59	4.22	0.05
Drought + ages ≤3 + T^2 + rank	12	1348.34	4.97	0.04

Notes: Survival is modeled as a function of the following covariates: drought intensity as normal conditions or severe drought (drought); post-fledging age (ages ≤ 3 d) modeled the first four days out of the nest separately as age 0, age 1, age 2, and age 3 d; sex of the attending parent (parent); radio-marked or band-only marked fledglings (mark type); nestling condition as measured by rank, assuming rank effects to be constant across drought intensities (rank) and to have separate effects for each drought intensity (rank(drought)); time in season as a curvilinear trend (T^2). Models with T^2 included T. Models with the lowest AIC_c are considered best based on the data, and ΔAIC_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. See the Appendix for the full set of 30 a priori models.

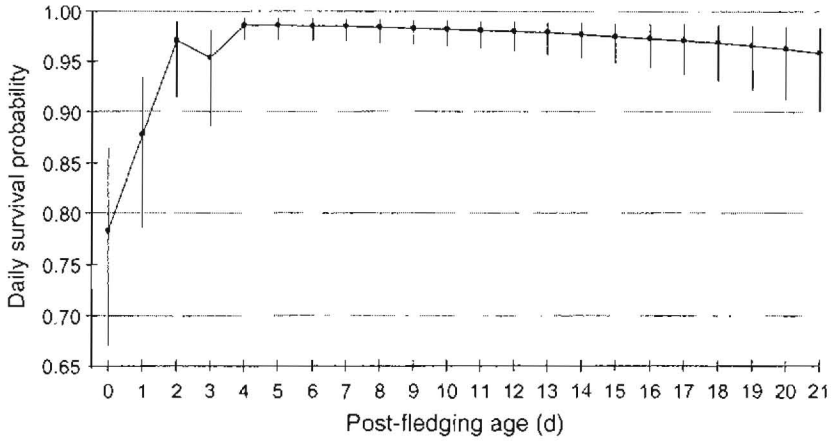

FIG. 1. Model-averaged daily survival probabilities and 95% CI for Lark Bunting fledglings of rank 1 (heaviest young within a brood) during mid to late season (4 July–25 July 2001) on the Pawnee National Grassland, Weld County, Colorado, USA. Post-fledging age represents the number of days since fledging, with age 0 as the first day out of the nest.

CI = 0.962, 0.986) than for band-only fledglings in 2001 and 2002 ($\hat{\bar{p}}_{band}$ = 0.860, SE = 0.01, 95% CI = 0.826, 0.880). Resighting probabilities for unmarked fledglings in 2003 ($\hat{\bar{p}}_{unmarked}$ = 0.875, SE = 0.02, 95% CI = 0.828, 0.913) 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 that switched from male to female care at post-fledging age 5 d. In the two years, we 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%). We 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 3 wk after fledging and stayed within 1600 m of the natal area (typically within 800 m). Independence occurred between ages 20 and 28 d. Ten of 27 fledglings tracked through the 22-d 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 d on the same day as their attending adults. In the remaining eight

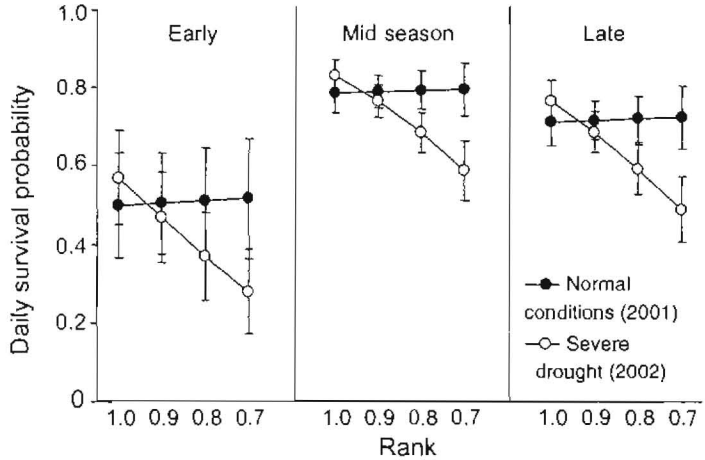

FIG. 2. Daily survival probabilities of newly fledged Lark Buntings on the Pawnee National Grassland, Colorado, vary as a function of time in season and rank, given drought intensity, illustrated for post-fledging age 0. Post-fledging age represents the number of days since fledging, with age 0 as the first day out of the nest. Rank was calculated by dividing each sibling's mass by the mass of the heaviest nestling. All estimates are model-averaged mean ± SE. Early season begins on 12 June, mid season on 4 July, and late season on 26 July.

cases, we lost the transmitter signal from the adult or fledgling between ages 21 and 30 d.

Discussion

Factors influencing post-fledging survival

Post-fledging survival of Lark Buntings was lower during the year of severe drought, increased with fledgling rank during the severe drought, increased with age >3 d, and was higher mid-to-late season than early season. Our lower Lark Bunting densities during the severe drought are consistent with George et al. (1992), who documented lower avian densities of grassland birds during drought. Although George et al. (1992) and Morrison and Bolger (2002) reported lower reproductive success of sparrows and other grassland birds during drought or abnormally dry conditions, we have no evidence of a strong drought effect on nest survival, nest productivity (number of young fledged per successful nest), or mass of young at fledgling. In the year of the severe drought, survival was reduced primarily in the post-fledging period. If lower post-fledging survival leads to reduced recruitment of young into the population and 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), elevated concern for grassland bird populations is warranted.

Severe drought can reduce fledgling survival via two mechanisms. Greater starvation may occur during periods of reduced food availability, as suggested by the greater incidence of fledglings that died of exposure or starvation in 2002. Predation may also increase if young are in poor condition or are more exposed in suppressed vegetation structure, as in 2002. Several lines of evidence suggest a substantial reduction of the bunting's main prey (grasshoppers) during the severe drought. Grasshoppers are known to depart deteriorating habitats caused by drought and decreasing forage (Pfadt 1994). During the severe drought of our study, anecdotally we noted a decline in numbers of grasshoppers, evidenced by reduced flushing from the drought-stressed vegetation. Depressed grasshopper densities were documented during severe droughts in North Dakota (Fowler et al. 1991) and Montana (Hawkins and Holyoak 1998). George et al. (1992) associated the reduction in grassland bird densities during severe drought with a reduction of grasshopper abundance. Early termination of Lark Bunting breeding in 2002 was also likely due to low food availability (DeSante and Baptisa 1989, George et al. 1992). Two plausible mechanisms inversely relate food availability to predation risk. When food is scarce, (1) well-fed young would beg more vigorously, thereby attracting more predators; and (2) parents would devote less time to fledgling defense (e.g., we occasionally witnessed adults chasing away thirteen-lined ground squirrels and mobbing foxes in the vicinity of fledglings).

Nestling condition (rank) was important as a predictor of survival only during the severe drought, illustrating the need to use caution when interpreting survival estimates obtained under "normal" environmental conditions (Anders et al. 1997, Maxted 2001) or when only largest young are radio-marked (e.g., Cohen and Lindell 2004). Our findings suggest that the effects of differential feeding in the nest during the severe drought year of 2002 extended into the post-fledging period. Asynchronous hatching in altricial birds results in a size-related dominance hierarchy within the nest; when food is scarce, the last-hatched nestling often receives disproportionately less food and grows more slowly than its siblings (Skagen 1987). The greater disparity in size of nestlings during the severe drought, evidenced by the broader range in nestling ranks, suggests that differential feeding occurred during the nestling phase; however, the mortality consequences did not manifest until the post-fledging stage. Whereas the mean rank of all fledglings in 2002 was 0.87, the mean rank of young that succumbed to starvation or exposure was 0.90, suggesting that predation also played an important role in reducing the survival of lightest young.

In this study, survival of Lark Bunting fledglings was lowest the first 3–4 d out of the nest and higher thereafter, consistent with other avian studies that found higher mortality during the first week post-fledging (Sullivan 1989, Anders et al. 1997, Naef-Daenzer et al. 2001, Cohen and Lindell 2004, Kershner et al. 2004; Wiens, *in press*). Predation, the primary cause of fledgling Lark Bunting mortality (78%), was likely correlated with developmental behaviors associated with different chick 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.

The time periods when young birds undergo major transitions, from egg to nest at hatching and from nest to surrounding habitat at fledging, are filled with many physiological stressors, such as exposure to environmental conditions and the need for thermoregulation, greater energy demands and the development of digestive organs, and increased vulnerability to predation, among others. Collectively, these stressors can result in high mortality, especially during the first week post-fledging in birds. Birth of mammals is an analogous transitional period, and interestingly, high neonatal mortality is widespread across many mammalian taxa, including brown bat (*Myotis austroriparius*; Foster et al. 1978, Hermanson and Wilkins 1986), cheetah (*Acinonyx jubatus*; Caro 1994), pronghorn (*Antilocapra americana*; Gregg et al. 2001), Steller sea lion (*Eumetopias jubatus*; Kaplan 2005), and human (*Homo sapiens*; Machado and Hill 2005). Across diverse avian and mammalian taxa, a myriad of factors and their

interactions contribute to early mortality of young, including poor body condition, congenital anomalies, undeveloped locomotory skills, infection and disease, low food availability, adverse weather, and age of parents.

Specific adaptive responses to high mortality in birds during the first few days post-fledging have received little attention because the universality of this survival trend is only now emerging. Discussions of evolutionary traits in breeding birds most often focus on the nesting phase rather than the post-fledging period, although one mechanism, brood division, is thought to reduce predation after fledging (McLaughlin and Montgomerie 1985). Whether adaptive mechanisms have evolved that operate specifically to counteract high mortality during the first days of the avian post-fledging period remains a fruitful area for research.

The higher mid-to-late-season survival may be due to the temporal pattern of grasshopper abundance; grasshopper densities in northeast Colorado are typically highest throughout July (Capinera and Sechrist 1982, Przybyszewski and Capinera 1990). Higher survival mid-to-late season may also be due to predator swamping resulting from the increased production of Lark Bunting fledglings and abundant young from alternate prey species (Sundell et al. 2003), e.g., recently weaned thirteen-lined ground squirrels. The observed temporal trend of post-fledging survival in this population of Lark Buntings suggests that breeding later in the season would be more adaptive than early breeding. Birds in seasonal environments can exhibit flexibility in reproductive traits and may adjust the timing of breeding to local conditions (Hahn et al. 1997). We recognize, however, that many factors exert selective pressures on the timing of breeding, including food availability, weather, and predation during the breeding season, and trade-offs with post-breeding energetic investments in molt and migration (Norris et al. 2004). The advantages of mid-to-late-season breeding in this population are counteracted by higher nest survival early in the season (Jehle et al. 2004), the onset of molting in early August, and early departure for southward migration from late July to mid August.

Our observation of no measurable effect of transmitter attachment on survival of fledglings is consistent with the only two available studies (Powell et al. 1998, 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 and that body mass upon return was 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. Passerines are thought to be better suited for telemetry studies than larger birds because of their ability to carry proportionally heavier loads (Caccamise and Hedin 1985). Also, our field methodology was designed to reduce the possible effects of transmitter attachment. We tried to minimize handling stress and premature fledging of young by banding young as nestlings and by placing transmitters on young after leaving the nest. Even though mark type did not affect post-fledging survival during the 22-d period, five older birds (older than age 21 d) caught their lower mandibles in the wing harness ligature, possibly while preening. To avoid such entanglement issues, we encourage use of the leg harness method (Rappole and Tipton 1991) on fledglings when possible (e.g., Anders et al. 1997, Cohen and Lindell 2004, Kershner et al. 2004). We were unable to use this method, however, because Lark Bunting young equipped with transmitters on leg harnesses had difficulty walking and tended to fall backwards.

Direct and indirect survival estimates

Average-case 22-d survival scenarios for Lark Bunting fledglings of 0.360 in 2001, 0.276 in 2002, and a previously reported estimate of 0.350 in 2000 (Yaekel Adams et al. 2001) are lower than reported three-week survival estimates for other passerines studied using radio-telemetry, such as Wood Thrush (0.423, Anders et al. 1997), Eastern Meadowlark (*Sturnella magna*; 0.680, Kershner et al. 2004), and White-throated Robin (*Turdus assimilis*; 0.670, Cohen and Lindell 2004). Survival rates for 15 additional passerine species, determined across varying time frames and using various methods, average 0.677 ± 0.044 during a 22-d period; only one species, Skylark (*Alauda arvensis*; Delius 1965), had a lower 22-d survival rate (0.263) than fledgling Lark Buntings.

Low survival rates are probably realistic for Lark Buntings because drought conditions are frequent in the shortgrass ecosystem (N. Doesken, R. A. Pielke, Sr., and O. A. P. Bliss, *data available online*).[5] The pattern we observed is likely not due to methodological problems. Radios on adults did not hamper 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) also found that short-term transmitter application to female Hooded Warblers (*Wilsonia citrina*) did not affect their ability to feed and care for nestlings. Further, low survival estimates are consistent with Ricklefs' (1973) observation that species with short nestling periods (e.g., Lark Bunting) generally have lower post-fledging survival than species with longer nestling periods and whose young fledge in a more developed state (e.g., Wood Thrush and Eastern Meadowlark).

Sensitivity analyses from several population growth models for migratory passerines demonstrate that models are sensitive to the estimate of juvenile survival (Thompson 1993, Powell et al. 1999, 2000). 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.

[5] ⟨http://ulysses.colostate.edu/climateofcolorado.php⟩

1998); however, our 22-d survival estimates suggest that juvenile survival during the first year may be considerably lower than 0.31 for some species. We estimated annual juvenile survival in 2001 and 2002 as the product of our post-fledging survival estimates (0.360 and 0.276) and a mean winter survival rate of 0.680, a liberal estimate based on juvenile warbler species (Holmes et al. 1989), yielding annual juvenile survival rates of 0.245 and 0.188. Both of these values are well below 0.31. The choice of which juvenile survival estimate to apply to demographic models is important because their performances vary dependiug on other parameters, such as fecundity and adult survival, used in the model. For example, when assuming annual fecundity of 1.25 female offspring/female and adult survival of 0.62, the application of 0.31 vs. our direct estimate for post-fledging survival leads to differing conclusions about the stability of this population of Lark Buntings. Until species-specific juvenile survival estimates are available, we advocate the use of a range of values (Gardali et al. 2003) for modeling population dynamics of declining species. Ultimately, empirically derived estimates of juvenile survival and other demographic parameters would enhance efforts to evaluate population stability and identify causes of population declines.

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