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The Condor 103:643–647
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MOVEMENTS AND SURVIVAL OF LARK BUNTING FLEDGLINGS

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Abstract. We quantified post-fledging pre-independence behavior and survival in Lark Buntings (*Calamospiza melanocorys*) using radio-telemetry. Brood division was recorded in six broods and was maintained throughout the observed fledgling care period. Chicks were capable of short flights (up to 25 m) by

fledgling day 6 and longer flights (to 100 m) by fledgling day 13. During the first three weeks after fledging, juveniles moved as far as 800 m from nests. Nine of 23 (39%) monitored fledglings died within 15 days of fledging, primarily due to predation by raptors. Daily survival rates were 0.953 ± 0.019 for fledgling days 0–9, 0.955 ± 0.038 for fledgling days 10–20, and 0.953 ± 0.015 for fledgling days 0–20. The probability of surviving fledgling days 0–20 was 0.367. More quantification of juvenile survival is clearly needed to understand the role of post-fledging mortality in source-sink dynamics.

Manuscript received 26 October 2000; accepted 16 April 2001.

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Key words: brood division, *Calamospiza melanocorys*, Lark Bunting, post-fledging behavior, post-fledging survival, radio-telemetry.

Los Movimientos y Supervivencia de los Volantones de *Calamospiza melanocorys*

Resumen. Cuantificamos la conducta y la supervivencia de volantones de *Calamospiza melanocorys* antes de independizarse de sus padres usando telemetría de radio. La división de la nidada se registró en seis nidadas y se mantuvo a través del período del cuidado de los volantones. Tras seis días de haber abandonado el nido, los polluelos eran capaces de realizar vuelos cortos (de hasta 25 m) y para el día trece ya realizaban vuelos más largos (a 100 m). Durante las primeras tres semanas después de salir del nido, los juveniles se movieron hasta 800 m de los nidos. Nueve de 23 (39%) volantones se murieron en los primeros 15 días fuera del nido, principalmente debido a depredación por aves rapaces. Las tasas diarias de supervivencia fueron de 0.953 ± 0.019 para los días 0 a 9, 0.955 ± 0.038 para los días 10 a 20, y 0.954 ± 0.015 para días 0 a 20. La probabilidad de sobrevivir entre los días 0 y 20 fue de 0.367. Se necesita más cuantificación de la sobrevivencia en la etapa juvenil para entender el papel de la mortalidad tras la salida del nido en la dinámica de fuente-sumideros.

Estimates of survival of juvenile birds after fledging and before parental independence are crucial in demographic studies and source-sink evaluations (Pulliam 1988, Faaborg et al. 1998), yet survival during this phase has been estimated for only a few passerine species. Although low fledgling production and low first-year survivorship may both contribute to population declines of some species (Perrins 1991), most studies of avian declines have documented nesting success only. The few weeks after fledging and before independence appear to be an especially vulnerable time for first-year birds (Sullivan 1989, Grubb et al. 1998). Difficulty in tracking fledglings is the primary reason for our limited understanding of the post-fledging pre-independence phase (Weatherhead and McRae 1990, Vega Rivera et al. 2000).

The post-fledging pre-independence phase of the life cycle of Lark Buntings (*Calamospiza melanocorys*) is largely unknown (Creighton 1971, Creighton and Baldwin 1974, Shane 2000). From July–August 2000, we studied the feasibility of using radio-telemetry to quantify post-fledging pre-independence survival of Lark Buntings in northeastern Colorado. Concurrent with our efforts to determine fledgling survival, we recorded behavior and movements of fledglings and adults.

METHODS

We conducted this study on a 130-ha site on the Pawnee National Grassland, Weld County, Colorado (40°41'N, 104°29'W). The site is grazed shortgrass prairie typified by short and mid-grasses, including buffalograss (*Buchloe dactyloides*), blue grama (*Bouteloua gracilis*), and threeawn (*Aristida* spp.), and by cacti (*Opuntia* sp.), forbs, small patches of yucca (*Yuc-*

ca glauca), and shrubs such as fourwing saltbush (*Atriplex canescens*) and broom snakeweed (*Gutierrezia sarothrae*). Surrounding land is grazed shortgrass prairie; the nearest agricultural field is 2 km away.

We located nests by dragging a rope between two observers 25 m apart and by observing adult behavior. We captured, affixed radio-transmitters (see below), and monitored movements and behavior of Lark Bunting fledglings and parents from 10 broods. Adults were captured using walk-in traps during incubation and nestling periods. Radio-marked individuals were banded with U.S. Fish and Wildlife Service bands and unique color-band combinations so individuals could be recognized if transmitters became detached. We attached transmitters to most nestlings 1–2 days before expected fledging. When chicks fledged earlier than expected, we used parental behavior to locate the chicks for capture and radio attachment. We radio-marked 12 adults and 21 fledglings from 10 broods. Two additional fledglings were monitored by locating banded or radio-marked parents. We radio-marked one or both parents and one or more of the heaviest chicks in nine broods (one chick in three broods, two chicks in four broods, and three chicks in two broods) and all four chicks but no adult in one brood.

Radio-transmitters (1.0 g for fledglings and 1.5 g for adults; Holohil Systems Ltd., Ottawa, Ontario, Canada, models BD-2 and BD-2G; and Wildlife Materials Inc., Carbondale, Illinois, models SOPB-2012 and SOPB-2028) were attached using epoxy resin (Eclectic Titan Corp., Lynnwood, Washington; fledglings and adults), wing harnesses (fledglings), or leg harnesses (Rappole and Tipton 1991; adults). Transmitters ranged from ca. 3% to 5% of body mass. Epoxy caused transmitter-retention problems, so subsequently we used wing and leg harnesses on fledglings and adults. We recaptured radio-marked fledglings to apply larger wing harnesses 3–7 days after initial capture. Harness material consisted of elastic ligature (fledglings) and 0.45-kg-test Cortland micron flyline backing (adults), both ca. 0.5 mm in diameter.

We tracked birds at 1–2 day intervals using a Wildlife Materials TRX-100S receiver (164–165 MHz band) with either a truck-mounted 11-element dual beam Yagi antenna (at 5 m elevation) or hand-held 3-element Yagi antennae. The range of detection for the transmitters was 600–800 m with the hand-held antennae and approximately 3 km with the truck-mounted antenna. Once we located the bird, we noted its location prior to flushing with a global positioning system (GPS), behavior (sitting, perching, hopping, flying), and dominant vegetation within 10 cm of fledgling.

We calculated estimates of survival using a modified Mayfield technique (Mayfield 1975, Hensler and Nichols 1981, Heisey and Fuller 1985). We assumed survival times of all individuals were independent and that mortality was approximately even within age-based intervals. Survival may be influenced by handling and radio-marking (White and Garrott 1990) but we did not address this possibility. All means are given \pm SE.

RESULTS

Fifteen of 29 nests were depredated, 8 during incubation and 7 during the nestling period. Mayfield esti-

mates of daily survival (and nest success) for incubation and nestling periods were 0.942 (45%) and 0.928 (55%), respectively; overall nest success was 27%.

POST-FLEDGING BEHAVIOR

Chicks left the nest 7–9 days after hatching. They spent the first few days (fledgling days 0–3) sitting motionless and alert in or under vegetation, well concealed by cryptic coloration. We observed a parent leading chicks on ten occasions, twice during onset of fledging. On these occasions, the parent generally captured an insect, flew to the fledgling, leapt in front of it several times, and then hopped away with the fledgling following closely. Distance traveled in this way ranged from 5–30 m.

By fledgling day 4, fledglings began hopping and perching on inside branches of fourwing saltbush. Many fledglings were capable of short flights (0.5–25 m) by fledgling day 6; the distance increased to 100 m during the next 7 days. From fledgling days 13–20, chicks began flying and perching with a parent. We were unable to relocate parents or fledglings after fledgling day 20 due to transmitter loss or battery expiration.

BROOD DIVISION

We observed division of the brood between male and female parents in six broods. We conducted detailed observation of two of these broods (hereafter, broods A and B) of four fledglings each. No brood-division data were collected from four broods due to adult transmitter loss or early fledgling death. Brood division appeared stable and was maintained throughout the observed fledgling care period (20 days).

In broods A and B, division occurred on the first day of fledging. In brood A, a nestling was led out of the nest by the female but was attended by the male thereafter. Body masses of the chicks (fledgling day 0) attended by the male were 21.5 and 22.5 g, and those attended by the female were 19.0 and 22.5 g (mean of all fledglings on day 0: 21.4 ± 0.5 g, $n = 17$). The female of brood A lost both her fledglings to raptor predation by fledgling day 9. She did not assist in caring for the two fledglings attended by the male and was no longer observed in the area.

In brood B, the male cared for one chick (20.5 g, fledgling day 0), and the female cared for two chicks (18.5 g and 22.5 g, fledgling day 0); the fourth chick died on fledgling day 0 (attending parent was unknown). The female of brood B also lost both fledglings to raptor predation on fledgling days 14 and 15. We observed males of both broods with their fledglings for 16–20 days before we could no longer relocate them due to transmitter loss or battery expiration.

MOVEMENTS OF FLEDGLINGS

Distances that chicks and parents moved from nests gradually increased during the first week post-fledging to an average of ca. 250 m (Table 1). Distances varied widely on subsequent days because some males and females returned with their respective fledglings to the nest vicinity. Juveniles moved as far as 800 m from nests during the first 21 days after fledging (Table 1). In both broods A and B, the males and females led their respective fledglings (brood units) in different di-

TABLE 1. Distances (m) traveled by Lark Bunting fledglings from their nests, with day of fledging as day 0.

Fledg-ling day	Number of fledglings (broods)	Mean distance moved (m) \pm SE	Range (m)
0	13 (7)	27.4 \pm 9.1	0.25–90
1	17 (8)	53.9 \pm 8.7	1–127
2	12 (6)	82.8 \pm 12.8	23–145
3	11 (5)	113.8 \pm 15.3	34–182
4	10 (6)	121.6 \pm 23.5	17–262
5	10 (6)	181.1 \pm 26.6	63–300
6	10 (6)	232.4 \pm 58.8	40–700
7	7 (4)	256.0 \pm 99.2	16–800
8–9	17 (6)	248.0 \pm 33.3	59–426
10–11	11 (4)	123.5 \pm 41.1	20–394
12–13	6 (3)	213.7 \pm 63.7	60–394
14–15	5 (2)	426.8 \pm 71.0	200–580
16–20	4 (3)	238.5 \pm 56.1	137–391

rections. Individuals of a brood unit were typically 30–80 m apart during the first week; this distance diminished during subsequent days until fledglings were perching together and flying with the parent. Distances between the two brood units of a family increased during the first week after fledging (from 50–200 m) and then varied widely in subsequent days (150–600 m).

SURVIVAL OF FLEDGLINGS AND ADULTS

Nine of 23 (39%) fledglings died during monitoring, all within the first 15 days after fledging. Five chicks were assumed killed by raptors (plucked remains were located via transmitter), three within 8 days of leaving the nest and one each on fledgling days 14 and 15. Two fledglings were presumed dead (fledgling days 2 and 9) because they were incapable of sustained flight from the study area during the period when they disappeared. Two chicks died of exposure within two days of leaving the nest; their carcasses were scavenged by ants (*Pogonomyrmex occidentalis*) within 1 day. There was no adult mortality in 170 exposure days (mean = 12.1 ± 1.6 days per adult) of monitoring 14 parents (including two monitored without transmitters) after their broods fledged.

Daily survival rates of chicks after fledging were 0.953 ± 0.019 for fledgling days 0–9, 0.955 ± 0.038 for fledgling days 10–20, and 0.953 ± 0.015 across both intervals (fledgling days 0–20). The probability of surviving the first three weeks after fledging was 0.367.

DISCUSSION

POST-FLEDGING SURVIVAL

Empirical information on juvenile survival in habitats that are becoming increasingly degraded and fragmented is clearly needed to understand the role of post-fledging mortality in source-sink dynamics. Demographic models of Neotropical migrant birds often assume an indirect estimate of juvenile survival of 0.31 during the first year (Temple and Cary 1988, Howe et al. 1991, Faaborg et al. 1998). We show, how-

ever, that juvenile Lark Buntings are subject to high mortality during just the first few weeks post-fledging. Our estimate of 0.367 probability of survival during the first three weeks post-fledging is similar to the few quantified estimates for other passerines, suggesting that juvenile survival during the entire first year may be considerably lower than 0.31. Probability of survival of Wood Thrushes (*Hylocichla mustelina*) from fledging to 3 weeks (and 8 weeks) was 0.423 (Anders et al. 1997), of Yellow-eyed Juncos (*Junco phaeotus*) until 6 weeks post-fledging was 0.321 (Sullivan 1989), and of European Starlings (*Sturnus vulgaris*) to 7 weeks was 0.429 (Krementz et al. 1989). Daily survival of Lark Bunting chicks (0.953–0.955) was similar to that of Mountain Plovers (*Charadrius montanus*) (0.951–0.977) in the same region (Knopf and Rupert 1996).

Whereas mammalian predation of birds predominates during incubation and nestling periods in our study area (Knopf and Rupert 1996, Skagen et al. 1999), a shift to raptor predation appears to occur after fledging of Lark Buntings. Olendorff (1973) documented that Lark Buntings constituted 23% of the diet of Swainson's Hawks (*Buteo swainsoni*; these ate primarily fledglings) and 2% of the diet of Ferruginous Hawks (*Buteo regalis*) in northeast Colorado. We observed several raptors on the study site, including Northern Harrier (*Circus cyaneus*), Burrowing Owl (*Athene cunicularia*), Prairie Falcon (*Falco mexicanus*), Swainson's Hawk, Ferruginous Hawk, and Golden Eagle (*Aquila chrysaetos*).

BROOD DIVISION

Division of the brood after fledging is considered a parental strategy that primarily reduces predation or increases foraging efficiency (McLaughlin and Montgomerie 1985). Post-fledging brood division has been documented for a wide variety of bird species, including 15 North American passerines (McLaughlin and Montgomerie 1985, Weatherhead and McRae 1990, Kopachena and Falls 1991, Morton et al. 1991, Ogden and Stutchbury 1997), of which only the Horned Lark (*Eremophila alpestris*) is endemic to grasslands.

Several authors have documented plasticity in brood division as it varied with time of season, reproductive activities of parents (Vega Rivera et al. 2000), and ecological conditions (Harper 1985, Price and Gibbs 1987). Vega Rivera et al. (2000) documented brood division in Wood Thrushes late in the season when parents no longer were expected to reneest; brood division did not occur earlier when parents reneested. Brood division also occurred in Robins (*Erithacus rubecula*) when food was scarce more often than when food was abundant (Harper 1985).

Our observations of brood division are consistent with these studies; Lark Buntings are normally single-brooded (Shane 2000) and therefore are free to divide their brood after fledging. In our small sample, we saw no pattern of splitting the brood based on body mass, consistent with Price and Gibbs (1987). Drought conditions in northeastern Colorado during our study may have reduced food availability, and Lark Bunting parents may have divided broods to increase foraging efficiency.

We thank Jerry Godbey for providing radio-telemetry training and equipment. Jeff Barna and Alexis Chaine provided trapping expertise and equipment; Veronica Estelle and Bruce Schoerlburg assisted with radio-telemetry attachment techniques. We appreciate comments of Fritz L. Knopf, Pamela Pietz, James E. Roelle, James A. Sedgwick, Thomas Shane, and an anonymous reviewer on earlier drafts of the manuscript.

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The Condor 103:647–651
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THE FUNCTION OF DISPLAYS OF MALE RUFIOUS HUMMINGBIRDS

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Abstract. We observed 26 male Rufous Hummingbirds (*Selasphorus rufus*) on their breeding territories to quantify display behaviors and to interpret their functions. Territory holders responded to intruding conspecific males with aggressive chases until the intruder left the territory. Female intruders received dive displays and shuttle-flights, which we interpret as courtship behavior. Dive displays were J-shaped (concave upward) in both ascent and descent, contrary to other reports of oval-shaped displays. We present a representative sonogram of the sounds produced during these dive displays.

Key words: aggression, behavior, courtship, display, Rufous Hummingbird, *Selasphorus rufus*.

Función de los Despliegues de los *Selasphorus rufus* Machos

Resumen. Observamos 26 *Selasphorus rufus* machos en sus territorios de reproducción para cuantificar sus comportamientos de despliegue e interpretar las funciones de éstos. Los dueños de los territorios respondieron a intrusiones de machos coespecíficos con persecuciones agresivas hasta que los intrusos abandonaron el territorio. Por su parte, las hembras intrusas recibieron despliegues en picada y patrones de vuelo repetidos, los cuales interpretamos como comportamientos de cortejo. Los despliegues en picada tuvieron forma de J (cóncava hacia arriba) tanto en ascenso como en descenso a diferencia de reportes previos sobre despliegues en forma de óvalo. Adicionalmente presentamos un sonograma representativo de los sonidos producidos durante los despliegues en picada.

Manuscript received 2 August 2000; accepted 20 March 2001.

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