

SURVIVAL AND MOVEMENTS OF JUVENILE BURROWING OWLS DURING THE POSTFLEDGING PERIOD

J. MORGAN DAVIES AND MARCO RESTANI¹

Department of Biological Sciences, St. Cloud State University, St. Cloud, MN 56301

Abstract. Burrowing Owl (*Athene cunicularia*) populations have declined extensively throughout much of North America, and modeling demography may assist conservation. However, few studies have estimated adult survival, and fewer still have determined juvenile survival. In 2003 and 2004 we monitored survival of 40 radio-tagged juveniles during the postfledging period in the Little Missouri National Grassland, North Dakota, where owls nested in black-tailed prairie dog (*Cynomys ludovicianus*) colonies. Survival averaged 0.57 (95% CI: 0.41–0.73) prior to autumn migration. Mortality was highest during the first two weeks after nest departure when juveniles were flightless, and two to three weeks later when juveniles became independent. Predation or starvation was implicated in most deaths. Distribution and abundance of escape cover (number of prairie dog burrows within 30 m of nests and size of the natal prairie dog colony) did not affect survival. Body condition and brood size at the time of radio-tagging also did not influence survival. Juvenile owls exhibited nest-centered dispersal, and averaged 108 ± 21 (SE) m and 82 ± 17 m from nests at initiation of migration in 2003 and 2004, respectively. Mean dates of departure from the study area were 2 September (± 3 days) 2003 and 24 August (± 2 days) 2004. Mortality during the postfledging period accounted for approximately two-thirds of mortality in the first year of life.

Key words: *Athene cunicularia*, black-tailed prairie dog, Burrowing Owl, *Cynomys ludovicianus*, juvenile survival, mortality, postfledging period.

Supervivencia y Movimientos de Juveniles de *Athene cunicularia* en el Período Posterior al Abandono del Nido

Resumen. Las poblaciones de *Athene cunicularia* han declinado fuertemente a través de buena parte de Norte América. Aunque el modelado demográfico podría contribuir a su conservación, pocos estudios han estimado la supervivencia de los adultos y menos aún la de los juveniles. En 2003 y 2004 monitoreamos la supervivencia de 40 individuos juveniles marcados con transmisores de radio durante el período posterior al abandono del nido en Little Missouri National Grassland, North Dakota, un área en donde *A. cunicularia* cría en colonias de perros de la pradera (*Cynomys ludovicianus*). La supervivencia durante el período previo a la migración de otoño fue en promedio de 0.57 (IC del 95%: 0.41–0.73). La mortalidad fue máxima durante las primeras dos semanas posteriores abandono del nido, cuando los juveniles eran aún incapaces de volar, y dos a tres semanas más tarde, cuando alcanzaron la independencia. La mayoría de las muertes fueron causadas por depredación o por inanición. La distribución y abundancia de los lugares para esconderse (el número de madrigueras de *C. ludovicianus* a menos de 30 m de los nidos y el tamaño de la colonia en la que los nidos se ubicaron) no afectaron la supervivencia. La condición corporal y el tamaño de la nidada al momento del marcado con transmisores tampoco influenciaron la supervivencia. La dispersión de los juveniles se centró alrededor de los nidos, y se encontraron en promedio a 108 ± 21 (EE) m y a 82 ± 17 m de éstos al iniciar la migración en 2003 y 2004, respectivamente. Las fechas promedio de abandono del área de estudio fueron el 2 de septiembre (± 3 días) en 2003 y el 24 de agosto (± 2 días) en 2004. La mortalidad durante el período posterior al abandono del nido constituyó cerca de dos tercios de la mortalidad observada en el primer año de vida.

INTRODUCTION

The ubiquity and magnitude of Burrowing Owl (*Athene cunicularia*) population declines in

North America are of considerable concern to wildlife biologists working to conserve grassland ecosystems. Greatest population decreases are occurring along the northern and eastern periphery of the owl's range, with extirpations recorded in Manitoba, Minnesota, and eastern North Dakota (Martell et al. 2001, Murphy et al. 2001, Wellicome and Holroyd 2001). Two

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¹ Corresponding author. E-mail: restani@stcloudstate.edu

international symposia devoted to the status and management of Burrowing Owls resulted in a "conservation plan," which identifies the following research priorities: estimate demographic parameters and model population dynamics, identify mortality factors, determine habitat selection, and investigate migration and dispersal (Lincer 1997, Holroyd et al. 2001, Wellicome and Holroyd 2001).

To model population dynamics, estimates of productivity and survival must be obtained, preferably from populations experiencing the full suite of environmental conditions across the owl's range. Although a large number of studies report productivity of Burrowing Owls (reviewed by Haug et al. 1993), few provide estimates of adult and juvenile survival. Analyses of band recovery and resighting data reveal that annual adult survival generally averages 55%–65% (Clayton and Schmutz 1999, Lutz and Plumpton 1999, Millsap 2002, Rosenberg and Haley 2004). Most birds experience the highest mortality during the first year of life (Newton 1989), so survival estimates from the critical juvenile and subadult periods of the life cycle are needed to complement estimates of adult survival for use in population modeling.

During the postfledging period, young birds are unskilled at flying and foraging and lack experience detecting and evading predators (Sullivan 1989, McFadzen and Marzluff 1996, Anders et al. 1997), thus mortality is often very high during this short time span. In the prairie provinces of Canada, survival of radio-tagged fledgling Burrowing Owls averages 45%–55% for the first 100 days of life (Clayton and Schmutz 1999, Todd et al. 2003). Because predation is the primary mortality agent, escape cover, in the form of nest and satellite burrows, presumably links survival to the amount and quality of habitat.

Distribution and abundance of burrows varies markedly across the geographical range of Burrowing Owls. In the Great Plains, Burrowing Owls are most strongly associated with black-tailed prairie dogs (*Cynomys ludovicianus*, Haug et al. 1993). The studies of juvenile survival in prairie Canada were conducted north of the range of black-tailed prairie dogs, in areas of fragmented habitat containing relatively limited escape cover (Clayton and Schmutz 1999, Todd 2001, Todd et al. 2003). Therefore, postfledging mortality estimates

from Canada may represent upper values, and juvenile mortality may be less severe in regions with an abundance of escape cover.

We radio-tagged juvenile Burrowing Owls in western North Dakota to test the relationship between survival and escape cover during the postfledging period. In our study area owls nested in prairie dog colonies, and we defined escape cover as the number of prairie dog burrows surrounding the nest and size of the occupied prairie dog colony. Presumably, juvenile owls fledging and dispersing from nests in large colonies would have more available escape cover, and thus higher survival, than owls raised in small colonies isolated within a matrix devoid of prairie dogs. We also examined the effects of body condition and brood size, two factors known to affect growth and survival of juvenile birds (Sullivan 1989, Naef-Daenzer et al. 2001, Todd et al. 2003). We predicted that owls in poor condition at the time of radio-tagging would have low survival. It was difficult to predict the effect of brood size on juvenile survival. Juvenile Burrowing Owls from large broods had slower growth rates and lower body mass at fledging (Bellocq 1997), which has decreased survival during the postfledging period (Todd et al. 2003). However, juveniles from large broods might have higher survival than those from small broods because of enhanced predator detection (Cresswell 1994).

METHODS

STUDY AREA

We conducted our research in the Little Missouri National Grassland (hereafter Little Missouri), an area in western North Dakota (47°15'N, 103°30'W) administered by the U.S. Forest Service. The grasslands were divided into a checkerboard of land ownership. Approximately 62% of the total land area (8620 km²) within the boundaries of the Little Missouri was managed by state and federal natural resource agencies: U.S. Forest Service (87%), State of North Dakota (8%), and National Park Service (5%; Bishop and Culbertson 1976, Murphy et al. 2001). The remainder was privately owned. Land use on public and private lands included livestock grazing, farming (mostly hay and small grains), and oil production. Black-tailed prairie dog

colonies occupied approximately 1800 ha in the Little Missouri; historical distribution in the grasslands was approximately 90% greater (Bishop and Culbertson 1976). Recreational shooting of prairie dogs occurred throughout the year, but was concentrated in May and June. Topography consisted of flat to rolling mixed-grass prairie interspersed with rugged badlands, at elevations of 600 to 900 m. Prairie vegetation was dominated by grasses (*Agropyron*, *Bouteloua*, and *Stipa* spp.) and shrubs (*Artemisia*, *Shepherdia*, and *Symphoricarpos* spp.). Riparian areas supported plains cottonwood (*Populus deltoides*), box elder (*Acer negundo*), and willows (*Salix* spp.), while open stands of ponderosa pine (*Pinus ponderosa*) and juniper (*Juniperus scopulorum*) dominated hill-sides in badlands. The climate was semi-arid, with mean annual precipitation about 35 cm. The Little Missouri is inhabited by a secure and stable owl population, although east to west contraction of the range of Burrowing Owls across North Dakota has encroached on the grasslands (Murphy et al. 2001, Wellicome and Holroyd 2001).

FIELD METHODS

We conducted field research from early May to mid-September 2003 and 2004. We used spotting scopes (15–45× power) and binoculars (10× power) to survey prairie dog colonies for nesting Burrowing Owls, concentrating effort in the early morning (05:00–10:00 MDT) and late afternoon (17:00–22:00), daytime periods when owls are most active and visible (Haug and Oliphant 1990). We surveyed colonies in May and June from a vehicle and on foot, and used presence of pairs, feces, shredded cow dung, and owl pellets to locate nest burrows (Restani et al. 2001). The location of nest burrows was recorded using a Global Positioning System (GPS; Garmin, Olathe, KS). We did not survey prairie dog colonies on state and private lands and did not search for owls nesting off prairie dog colonies. Nest burrows were repeatedly revisited in mid to late July to estimate brood size. We estimated brood size by observing nest burrows for at least 30 min, and recorded the maximum number of young observed outside the burrow at one time. Although our maximum counts likely underestimated brood size (Gorman et al. 2003), we believe detectability was similar among nests because of the

uniform, low height of vegetation on prairie dog colonies. Therefore, consistently underestimating brood size would not have affected our test for a relationship between brood size and juvenile survival. Successful nests fledged at least one young.

We placed push-door traps (Winchell 1999) modified with a monofilament trip line in nest and satellite burrows from early to mid July 2003 and 2004 to capture juvenile owls. Owls were fitted with U.S. Fish and Wildlife Service leg bands and measured (mass to the nearest 5 g, and flattened wing chord, exposed 8th primary, tarsus, and culmen to the nearest mm). We radio-tagged the heaviest owl from each brood captured. Radio-tagged owls averaged 136 ± 2 (SE) g (median = 135 g, range = 112–172 g, $n = 40$). We used the length of the 9th primary to estimate owl age as determined from the morphometrics of two known age young from two nests in Alberta (T. Wellicome, University of Alberta, unpubl. data). However, because we did not measure 9th primary lengths in 2003 or 2004, we estimated lengths from the equation $y = 28.62 + 0.82x$, where y is total length of the 9th primary, and x is length of the exposed 8th primary. We derived this equation from measurements of exposed 8th and total 9th primary lengths of juvenile owls captured in the study area in 2005 ($r^2 = 0.98$, $P < 0.001$, $n = 9$, SE of slope = 0.05, SE of constant = 3.19). Radio-tagged owls in 2003 and 2004 averaged 35.0 ± 1.3 days old (median = 34 days, range = 22–60 days, $n = 40$).

We attached radio-transmitters (Advanced Telemetry Systems, Isanti, MN) as a backpack (Buehler et al. 1995) with a harness sewn of 0.64 cm diameter tubular teflon tape (Bally Ribbon Mills, Bally, PA). Each transmitter and harness weighed 3.5 g (2%–3% of body mass), and batteries lasted approximately 166 days. We assumed transmitters did not adversely affect survival because: 1) the transmitter packages weighed less than those employed by Clayton and Schmutz (1999) and Todd et al. (2003), who found no negative effects of transmitters on survival of juvenile Burrowing Owls, 2) there was no correlation between mass (y) and age at radio-tagging (x) in the Little Missouri ($r^2 = 0.01$, $P = 0.67$, $n = 40$, $y = 131.32 + 0.12x$), which suggested that juvenile owls had reached adult mass, and 3) the transmitter and harness weighed less than the

maximum 3% of total body mass recommended by the U.S. Geological Survey Bird Banding Laboratory.

Juvenile Burrowing Owls often wandered and roosted away from nest burrows before they could fly, so we defined the postfledging period as the time from radio-tagging, when owls averaged 35 days old, until dispersal and migration, described below. We used homing techniques (Samuel and Fuller 1994) to locate radio-tagged owls once every 1–3 days from the day of capture and radio-tagging until they either migrated or died. Roads existed on most section and quarter-section lines in the Little Missouri, which provided excellent access to prairie dog colonies, owl nests, and surrounding areas, thereby facilitating radio-tracking. Owls were detected using a portable receiver and either a handheld three-element yagi antenna or a vehicle-mounted omnidirectional antenna (Advanced Telemetry Systems, Isanti, MN). Visual or auditory confirmation (changes in transmitter signal strength; McFadzen and Marzluff 1996) of the status of an owl, alive or dead, was determined from a distance when possible. If we did not detect changes in transmitter signal strength throughout a 30-min period, we approached the owl on foot until it was either seen or found dead (owl carcass or intact harness and transmitter with partial remains). We visually estimated (to the nearest 5 m) short distances between the owl and its natal burrow, or in the case of long-range movements, we used a GPS to plot locations in reference to the natal burrow.

Juvenile Burrowing Owls in southern Canada and Idaho initiated autumn migration in mid-late August (Clayton and Schmutz 1999, King and Belthoff 2001, Todd et al. 2003), a time period that in the Little Missouri corresponded to approximately 35 days after radio-tagging. We assumed a radio-tagged owl had migrated from the study area if we lost its transmitter signal from mid-August to September. However, we scanned the frequencies of missing owls across the entire study area for weeks after owls disappeared from their natal prairie dog colony to ensure they did not go undetected. We did not observe any radio-tagged owls with nonfunctioning transmitters after a loss of signal was recorded.

We estimated the abundance of escape cover in two ways. First, we counted the number of

prairie dog burrows within a 30 m radius of nest burrows (Restani et al. 2001). We counted active and uncollapsed inactive burrows because both provide escape cover for juvenile owls (Desmond and Savidge 1999). Second, as an index to the landscape abundance of burrows near nests, we obtained Geographic Information System (GIS) data of the size of prairie dog colonies in the Little Missouri (U.S. Forest Service, unpubl. data). Perimeters of prairie dog colonies were mapped in 2001 on foot or by driving an all-terrain vehicle along the edge of the colony while plotting boundary locations of active prairie dog burrows (Biggins et al. 1993) with a gimble-mounted GPS unit. We used ArcGIS 9.0 (ESRI 2004) to determine the area (ha) of colonies occupied by nesting owls.

DATA ANALYSIS

We used the Kaplan-Meier (Kaplan and Meier 1958) product-limit method and Cox proportional hazard analysis (Cox and Oakes 1984) to estimate survival during the postfledging period (SPSS 2004). Reliable use of these models depends on meeting a number of assumptions (Bunck et al. 1995, Tsai et al. 1999, Winterstein et al. 2001), which we evaluated prior to data analysis. First, depending on year, our sample of radio-tagged owls was drawn from across the entire Little Missouri and included 47%–65% of colonies occupied by nesting owls and 49%–57% of pairs producing at least one young. Because we sampled a large percentage of nesting owls and did not bias capture location, we feel justified in making survival inferences to the entire owl population in the Little Missouri (Garton et al. 2001). We radio-tagged only one juvenile per brood to ensure statistical independence in analyses (Massot et al. 1994, Tsai et al. 1999, Winterstein et al. 2001). We located owls 98% ($n = 573$) of the time during radio-tracking sessions and therefore satisfied the “working radios are always located” assumption of Kaplan-Meier (Bunck et al. 1995, Tsai et al. 1999, Winterstein et al. 2001). Finally, our observations and analyses of survival extended from the time of radio-tagging (t_0 , mean owl age = 35 days) to death or migration from the study area. Although we radio-tagged owls over a two-week period each year, fledging date of juvenile Burrowing Owls in Saskatchewan during the nesting season was unrelated to

survivorship (Todd et al. 2003), so defining t_0 as the time of radio-tagging was appropriate in the Little Missouri (Winterstein et al. 2001). As described above, in general we assumed owls that disappeared prior to the initiation of autumn migration in mid-August had died, and those that disappeared after mid-August had migrated (i.e., were censored; Winterstein et al. 2001). However, our aging technique contained some uncertainty because it was based on few known-age birds; thus, we also used a combination of estimated age at disappearance, date of disappearance, and distance from the nest when last located to discriminate between dead, missing owls and owls that had migrated.

Before testing the effects of covariates on survival, we used a log-rank test to determine if survival differed between 2003 and 2004. We used Cox regression (Cox and Oakes 1984) to test the effect of four covariates on survival: density of prairie dog burrows within 30 m of the nest burrow, area (ha) of the natal prairie dog colony, brood size, and body condition at the time of radio-tagging. We used principal components analysis to derive a single value reflecting body size of each radio-tagged owl to evaluate the effect of body condition (Griebel and Savidge 2003). The first principal component (PC1) was calculated from tarsus, wing chord, and culmen measurements. We used residuals from the regression of body mass against PC1 as the body condition index for each radio-tagged owl. Individuals in good condition had positive residuals whereas those in poor condition had negative residuals.

All statistical analyses were carried out with SPSS 13.0 (SPSS 2004), and unless indicated otherwise, results presented are mean \pm SE with significance level of $P < 0.05$. We limited the number of statistical tests to avoid reporting spurious findings, and present ranges and 95% confidence intervals (CI) as estimates of effect size (Cherry 1998, Johnson 1999, Anderson et al. 2001).

RESULTS

We searched for nesting Burrowing Owls at 71 prairie dog colonies, averaging 24.6 ± 3.2 ha, located on public land. Colonies were dispersed across the 8620 km² Little Missouri and totaled approximately 1745 ha. In 2003, we found 47 owl nests in 15 different prairie dog colonies

averaging 35.4 ± 8.9 ha (range = 2.9–121.9 ha). In 2004, we found 47 nests in 20 colonies averaging 32.3 ± 6.8 ha (range = 3.8–121.9 ha). Mean distance between nearest neighbor owl pairs was 1.4 ± 0.6 km in 2003 (range = 0.05–23.3 km), and 1.7 ± 0.6 km in 2004 (range = 0.04–23.2 km). Distribution and density of nests were similar across years, as were weather and precipitation patterns, so any potential density-dependent effects on juvenile survival should have been similar across years. In 2003, 40% of colonies occupied by owls contained only one breeding pair and in 2004, 45% of colonies contained only one breeding pair (range = 1–13 pairs per colony both years). Owls produced 2.6 ± 0.3 young per pair in 2003 (range = 0–7, $n = 47$), and 3.5 ± 0.3 young per pair in 2004 (range = 0–7, $n = 47$). Twelve pairs failed to fledge young in 2003, and six pairs failed in 2004.

From 6–19 July 2003 we trapped 32 owls, radio-tagging 20 from seven different prairie dog colonies. Age of radio-tagged owls was 31.3 ± 1.1 days (range = 22–37 days), which corresponded to an estimated hatch date of 10 June ± 1.1 day (range = 4–17 June). Mass of radio-tagged owls was 129 ± 3 g (range = 112–153 g), and brood size was 4.0 ± 0.3 (range = 2–7). From 6–25 July 2004 we trapped 34 owls, radio-tagging 20 from 13 different prairie dog colonies. Age of radio-tagged owls was 38.8 ± 2.2 days (range = 30–60 days), and hatch date was 3 June ± 2.2 days (range = 15 May–16 June). Mass of radio-tagged owls was 142 ± 3 g (range = 120–172 g), and brood size was 4.8 ± 0.2 (range = 3–7).

In 2003, three owls were recovered dead and seven owls disappeared prior to migration (three on 29 July, and one each on 28 July, 31 July, 6 August, and 7 August). We assumed these seven owls had died because they averaged only 52.9 ± 2.0 days old (range = 42–58 days), which was similar to ages of owls recovered dead (see below). Moreover, mean distance of juveniles from nests during the first 2–3 weeks after radio-tagging was so short that it was very unlikely we missed observing these owls if they carried nonfunctioning radio transmitters (Clayton and Schmutz 1999, King and Belthoff 2001, Todd 2001). Date of migration in 2003 was 2 September ± 3.2 days (median = 6 September, range = 16 August–13 September, $n = 10$). Owls that survived to

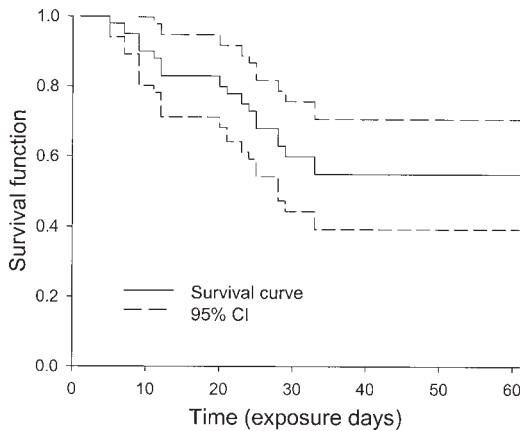


FIGURE 1. Kaplan-Meier survival curve for juvenile Burrowing Owls during the postfledging period in the Little Missouri National Grassland, North Dakota, 2003–2004.

migrate averaged 85.2 ± 4.1 days old (range = 64–98 days). In 2004, seven owls were recovered dead and one disappeared less than three weeks after radio-tagging on 30 July when 58 days old. For the reasons given above, we assumed the latter owl had died. Date of migration in 2004 was $25 \text{ August} \pm 2.0$ days (median = 24 August, range = 13 August–1 September, $n = 12$), when owls averaged 83.7 ± 3.8 days old (range = 68–108 days).

Of the 10 juveniles recovered dead, seven showed signs of predation or starvation followed by scavenging. We were unable to differentiate between these two mortality agents. One owl died deep in a burrow and was not retrieved, one drowned, and one was struck by a vehicle. Owls recovered dead averaged 52.2 ± 3.0 days old (range = 37–65 days).

Survival of radio-tagged juveniles did not differ between 2003 and 2004 ($\chi^2_1 = 1.7$, $P = 0.20$), so we pooled yearly data for subsequent analyses. Postfledging survival for both years was 0.57 ± 0.08 (Fig. 1). Mortality occurred in two distinct time periods, 0–13 days and 22–34 days postfledging (Fig. 2). Juveniles were located progressively farther from nests during the postfledging period (Fig. 3). Just prior to initiating autumn migration, juveniles were located a maximum distance of 107.5 ± 20.6 m from the nest burrow in 2003 (range = 20–300 m, $n = 16$), and 82.3 ± 16.6 m from the

nest burrow in 2004 (range = 30–250 m, $n = 13$). One juvenile was found 2 km from its nest after a day of very high winds only three weeks after radio-tagging, when 57 days old, and we removed it from distance calculations because it was a clear statistical outlier (Fig. 2, 3). There was no correlation between maximum distance moved (y) and size of the natal prairie dog colony (x ; $r^2 = 0.01$, $P = 0.71$, $n = 29$, $y = 90.75 + 0.23x$). Radio-tagged juvenile owls were located in prairie dog colonies, with the exceptions of the bird struck by a vehicle and the drowned bird.

Survival of juvenile owls during the postfledging period was not affected by the amount of escape cover either within 30 m of nests or at the colony scale (Table 1). Moreover, mean number of prairie dog burrows within a 30 m radius of successful and failed nests was similar (49.4 ± 1.4 , $n = 75$ versus 45.8 ± 4.3 , $n = 18$, respectively). There also was no difference in burrow numbers between successful and failed nests when we followed the methods of Desmond and Savidge (1999) and considered only active burrows (39.0 ± 1.2 , $n = 75$ versus 36.6 ± 3.8 , $n = 18$, respectively). Body condition (y) was not related to brood size (x ; $r^2 = 0.07$, $P = 0.11$, $n = 40$, $y = -0.96 + 0.22x$), and neither had an effect on survival (Table 1).

DISCUSSION

Survival of radio-tagged juvenile Burrowing Owls during the postfledging period was 57% in the Little Missouri. Taking into account some uncertainty in the aging technique, mortality occurred 0–13 days and 22–34 days after radio-tagging. Predation and starvation were the primary causes of mortality. The most likely predators included Swainson's Hawks (*Buteo swainsoni*), badgers (*Taxidea taxus*), and other small carnivores. Contrary to our predictions, abundance of escape cover, body condition, and brood size did not affect survival. Although the Little Missouri contained a greater abundance of escape burrows and larger contiguous grasslands than southern Canada, our results generally corroborated juvenile survival and mortality patterns reported from radio-telemetry studies conducted in Saskatchewan and Alberta (Clayton and Schmutz 1999, Todd 2001, Todd et al. 2003).

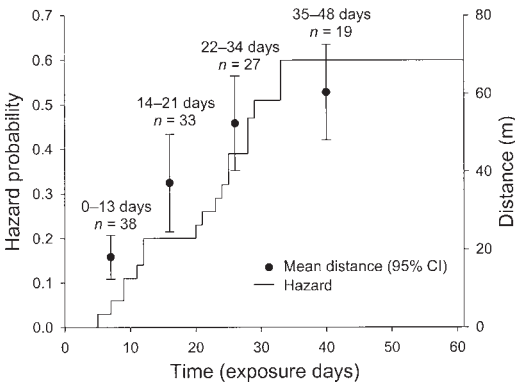


FIGURE 2. Relationship between the hazard function (i.e., conditional mortality rate) and distance from nests in relation to age of juvenile Burrowing Owls during the postfledging period in the Little Missouri National Grassland, North Dakota, 2003–2004.

High mortality during the first two weeks postfledging was probably due to failure of juveniles to detect and avoid predators, exacerbated by poor flying skills. It is unlikely that starvation was a major mortality factor during this time period because juveniles were still being fed by adults. No mortality occurred during the subsequent 10 days, even though the average distance of juveniles from nest burrows had doubled, from 18 to 37 m. At this time, the majority of juveniles were still quite close to familiar nest and satellite burrows, and mortality was probably absent because juveniles were now capable fliers, likely had some experience avoiding predators, and continued to associate with adults. The risk of mortality increased during the third and fourth weeks postfledging as juveniles became independent foragers and

moved farther from nest burrows. The relationship between mortality rates and ontogeny of behavior in juvenile Burrowing Owls mirrored findings reported by Sullivan (1989) and Anders et al. (1997) for fledgling small passerines.

Juvenile survival was unaffected by the number of burrows within 30 m of nests or the area of the natal prairie dog colony. High burrow density near nests also did not improve nest success, in contrast to results from Nebraska (Desmond and Savidge 1999). Density of active prairie dog burrows in the Little Missouri was more than double that found in Nebraska (138 burrows per ha versus 54 burrows per ha, respectively) and probably offered ample protection to nesting adults (dilution effect) and fledging juveniles (escape cover), accounting for differences between study areas. Wildlife managers working to conserve Burrowing Owls within the prairie dog ecosystem should strive to maintain high burrow density, but achieving this goal this will be difficult because unpredictable yet recurring epizootics of sylvatic plague (*Yersinia pestis*) throughout the Great Plains reduce prairie dog populations and thus burrow density.

The configuration and patch size of habitats surrounding nests appeared to affect the postfledging movements of juvenile Burrowing Owls. With the exception of one individual, juveniles followed the sequence of “nest-centered dispersal” described by Todd (2001): short movements (mean maximum 140 m) to and from the nest during postfledging, terminating with abrupt departure from the study area when individuals initiated autumn migration. Although most prairie

TABLE 1. Relationship between escape cover, body condition, and brood size and survival of juvenile Burrowing Owls during the postfledging period in the Little Missouri National Grassland, North Dakota, 2003–2004.

Covariate	Owl fate	Mean ± SE	n
Number of prairie dog burrows within 30 m of nest	Died	50 ± 3	18
	Survived	52 ± 3	22
Size (ha) of natal prairie dog colony	Died	22 ± 4	18
	Survived	23 ± 4	22
Body condition index ^a	Died	0.016 ± 0.246	17
	Survived	-0.013 ± 0.211	22
Brood size	Died	4.1 ± 0.3	18
	Survived	4.5 ± 0.3	22

^a See text for calculation based on body size and mass. One owl was not measured.

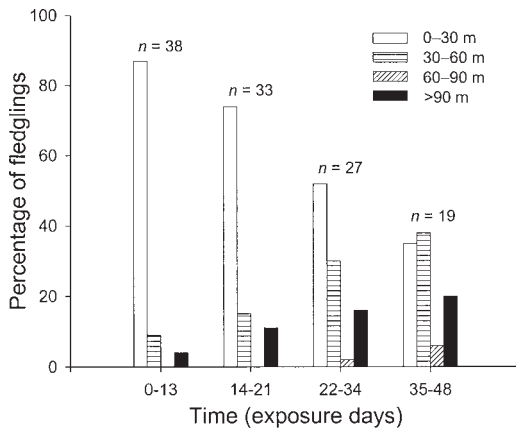


FIGURE 3. Percentages of juvenile Burrowing Owls found at varying distances from nests during the postfledging period in the Little Missouri National Grassland, North Dakota, 2003–2004.

dog colonies occupied by breeding owls were surrounded by a mixture of native and planted grasses rather than agriculture, colonies nonetheless formed a habitat type distinct from the surrounding grassland matrix. Juvenile owls appeared to respond to this contrast and treat prairie dog colonies as isolated habitat, because during dispersal they were located only in prairie dog colonies containing their natal nest. The average size of prairie dog colonies occupied by nesting owls was only 35 ha, which provided limited habitat to support the wide-ranging movements typical of owls that use multiple-roost dispersal. In Canada and Idaho, juveniles exhibited nest-centered and single-roost dispersal patterns when natal territories were located in small grassland patches (<64 ha), and multiple-roost dispersal when nests were surrounded by more continuous grassland (Clayton and Schmutz 1999, King and Belthoff 2001, Todd 2001).

Body condition and brood size of juvenile owls did not affect survival during the post-fledging period. Although these results are consistent with many studies of juvenile survival (Newton and Moss 1986, McFadzen and Marzluff 1996, Anders et al. 1997), our failure to find an effect of body condition may also have been an artifact of sampling. When multiple owls from a single brood were captured, we radio-tagged the heaviest individual to reduce the possibility of the transmitter

lowering survival. Consequently, the youngest and smallest owls, those that were most likely to suffer from competition with older and larger siblings, were not radio-tagged. Moreover, almost all juvenile owls had reached adult mass by the time of radio-tagging, which further limited variation in body size. A single estimate of body condition obtained at the time of capture and radio-tagging may also have been too crude to detect subtle yet important differences in survival over the 100-day post-fledging period. For example, in some passerines the relationship between body condition and survival was complex, and varied depending on whether juveniles were being fed by adults (no effect), foraged independently (effect), fledged early in the season (less effect) or fledged later (more effect; Sullivan 1989, Naef-Daenzer et al. 2001).

On average, juveniles migrated from the study area in early September 2003 or late August 2004, with the difference between years reflecting a one-week shift in hatching dates. By the time of migration juveniles were 12 weeks old, had been radio-tagged for seven weeks, and were about 100 m from natal nests. Mean ages at migration were similar, and departure dates fell within the range of average dates reported from Idaho, Alberta, and Saskatchewan (Clayton and Schmutz 1999, King and Belthoff 2001, Todd et al. 2003).

In summary, although published data are limited, the sum of evidence from several independent banding studies across the range of Burrowing Owls suggests that annual survival of juvenile owls is approximately 20%–30% (James et al. 1997, Johnson 1997, Millsap 2002, Rosenberg and Haley 2004). Augmenting these annual survival estimates from banding with survival estimates from the postfledging period illustrates that two-thirds of mortality during the first year of life takes place near the natal area prior to autumn migration. Strong selection exerted by predation and starvation during the relatively short 90–100 day post-fledging period may be a major force shaping local population dynamics, because annual recruitment correlates with juvenile survival the previous year (Todd et al. 2003) and adults typically have high annual survival (Rosenberg and Haley 2004). The postfledging period is also important to lifetime reproductive success of other short-lived hole-nesters (Newton 1989).

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