DISPERSAL PATTERNS AND POST-FLEDGING MORTALITY OF JUVENILE BURROWING OWLS IN SASKATCHEWAN

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ABSTRACT.—The dramatic decline of Burrowing Owls (*Athene cunicularia*) in Saskatchewan, Canada, during the 1980s and 1990s coincided with low return rates of 1-yr-old birds, suggesting factors affecting the survival of post-fledging juveniles may be crucial to maintaining population sizes. In 1997 and 1998, I used radiotelemetry to study survival and dispersal of juvenile Burrowing Owls between fledging and migration on the Regina Plain in southern Saskatchewan. The mortality rate of radio-tagged juveniles was significantly lower in 1997 (0%, $N = 12$ owls) than in 1998 (45.4%, $N = 33$ owls). Compared to the lack of predation on radio-tagged owls in 1997, avian predators were a major cause of mortality in 1998, accounting for 47% of the 15 deaths. Other sources of mortality included mammalian predation, collisions with vehicles, starvation, collision with barbed-wire fences, and siblicide. Juvenile owls dispersed significantly farther from their natal burrows before migration in 1997 (1297 ± 526 m, $N = 10$) than in 1998 (449 ± 98 m, $N = 18$). These differences in dispersal and mortality between years may have been related to the high abundance of voles (*Microtus* spp.) on the Canadian plains in 1997. Three general patterns of post-fledging dispersal were exhibited by radio-tagged juveniles in both years of the study. Dispersal patterns were affected by habitat continuity, with a trend toward "multiple-roost" dispersal in the most continuous habitat.

KEY WORDS: *Burrowing Owl*; Athene cunicularia; *post-fledging; mortality; dispersal; predation; habitat fragmentation; Saskatchewan.*

Patrones de dispersion y mortalidad post-emplumamiento de Búhos Cavadores juveniles en Saskatchewan

RESUMEN.—El dramático decline de los Búhos Cavadores (*Athene cunicularia*) en Saskatchewan, Canadá, durante los '80s y '90s coincidió con las bajas tasas de retorno de aves de 1 año de edad, esto sugiere que los factores que afectan la supervivencia de los juveniles post-emplumamiento puede ser crucial para mantener el tamaño de la población. En 1997 y 1998, use radio-telemetría para estudiar la supervivencia y dispersión de Búhos Cavadores juveniles entre el emplumamiento y la migración en la Llanura de Regina en el sur de Saskatchewan. La tasa de mortalidad de juveniles provistos con radios fue significativamente mas baja en 1997 (0%, $N = 12$ búhos) que en 1998 (45.4%, $N = 33$ búhos). Esta diferencia en la mortalidad entre años puede haber estado relacionada con la alta abundancia de ratones *Microtus* en la Llanuras Canadienses en 1997. En comparación a la completa ausencia de depredación de búhos marcados con radios en 1997, los depredadores aéreos fueron la mayor causa de mortalidad en 1998, dando cuenta del 47% de las 15 muertes. Otras causas de mortalidad incluyen la colisión con vehículos, inanición, colisión con cercas de alambre de púas, conflicto cain–abel/canibalismo, y causa desconocidas. La mortalidad en 1998 fue mas alta en parches aislados de pastos (<1600 m²) que en parches continuos (>1600 m²). Tres patrones generales de dispersión pos-emplumamiento fueron exhibidas por juveniles marcados con radios en los dos años del estudio. Los patrones de dispersión fueron afectados por la continuidad del hábitat, con una fuerte tendencia hacia la dispersión del tipo "múltiples-perchas" en los hábitats mas continuos.

[Traducción de Victor Vanegas y César Márquez]

Burrowing Owl (*Athene cunicularia*) populations across the Canadian prairies have undergone severe declines in the 1980s and 1990s (Wellicome and Haug 1995, James et al. 1997). Extensive research has been conducted on the ecology of Burrowing Owls on the Canadian breeding grounds (Haug 1985, Warnock 1996, Schmutz 1997, Wellicome et al. 1997, Wellicome 2000). However, the causes of the decline have yet to be determined. Most of this research was concluded by the time

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the juveniles fledge (but see King 1996 and Clayton 1997). Identifying factors that affect survival during the post-fledging, premigratory life-history stage is an important part of understanding population dynamics of the Burrowing Owl, and may provide vital information regarding the decline.

This paper describes results of a project recording dispersal patterns and mortality rates of juvenile Burrowing Owls in a highly-fragmented landscape. The study took place during the summers of 1997–98, and concentrated on the post-fledging/premigratory life stage. A fortuitous outbreak of voles (*Microtus* spp.) across the Canadian prairies in the spring of 1997 caused *Microtus* populations to reach levels not attained in the area since 1969 (Poulin et al. 2001). In 1998, vole populations returned to normal levels. The difference in prey abundance between the two years of this study allowed the comparison of juvenile survival and dispersal between a year of high and a year of normal prey abundance.

STUDY AREA AND METHODS

This project was conducted in southern Saskatchewan, on the Regina Plain, during 1997 and 1998. The study area encompassed approximately 12 200 km^2 in the grassland ecoregion (Harris et al. 1983), south of the cities of Moose Jaw (50°34'N, 105°17'W) and Regina (50°25'N, 104°39'W). More than 90% of the land on the Regina Plain is cultivated for production of cereal crops. The remnant grassland is highly fragmented and confined to small sections of pasture, isolated from other grassland patches by several kilometers. Because of a lack of burrows, the cropland matrix separating grassland patches is largely unavailable to Burrowing Owls for nesting, so the owls nest almost exclusively in pastures. The nesting density of Burrowing Owls in the study area is low, usually with only one or two owl pairs in each occupied pasture.

The length of the post-fledging period in raptor species ranges from a few weeks to several months (Newton 1979), but the exact timing is often difficult to determine. Therefore, in migratory species, the initiation of migration is often used to mark the end of the post-fledging period (Beske 1982, Sherrod 1983). Because Burrowing Owls nest underground and owlets can easily walk away from the nests, it is difficult to ascertain exact fledging dates. In addition, most juveniles in this study area remain on their natal territories until they migrate, making it difficult to determine the date of independence (i.e., when the post-fledging period ends). I therefore defined the post-fledging period for each juvenile owl as beginning when it made its first movement to a burrow other than its natal burrow (initiation of dispersal), and ending when it migrated from the breeding grounds.

Necklace-style radio-transmitters (Holohil Systems Ltd., Ontario, Canada), weighing 6 g (ca. 4% of adult body mass), were fitted onto one juvenile owl per nest at 45 nests (12 in 1997 and 33 in 1998). Nests included in the study were chosen randomly from available nests. Each transmitter was attached when the owlet was between 30–35 d post-hatch, immediately prior to initial dispersal. Owls were assigned ages based on the hatching day of the first hatchling in each nest. Owls were captured either inside artificial nest boxes (Wellicome et al. 1997) or using noose carpets baited with dead laboratory mice. Transmitter signals were detected using a portable receiver (Lotek SRX 400) and either a 2- or 3-element Yagi antenna, or an omni-directional, vehicle roof-mounted antenna. The location of each radio-tagged owl was determined every 2–3 d from the date its transmitter was attached until the owl died or left the study area. When signals could not be detected from the ground, aerial searches were conducted with a single-engine Cessna 172 equipped with radio-tracking gear.

At each diurnal roost (hereafter, satellite burrow) used by juvenile owls during the post-fledging period, I measured the distance and direction from the natal burrow. Distances <500 m were determined by pacing or using a 50-m measuring tape. Aerial photographs, aided by Global Positioning System (GPS) readings, were used to determine distances >500 m. To avoid influencing dispersal behavior, I tried to minimize disturbance to the owls while tracking. Therefore, whenever possible, the position of radio-tagged owls was determined using binoculars or a spotting scope, and measurements of dispersal distances were taken after the juvenile owl had moved to a different satellite burrow.

To categorize dispersal patterns, I constructed graphs for each radio-tagged juvenile, comparing distance from nest with age of the juvenile owl. Individuals were then grouped according to their dispersal profiles. The first movement made by a radio-tagged owl to a burrow other than the natal one was classified as initiation of dispersal. King (1996) and Clayton (1997) defined commencement of juvenile dispersal as a permanent movement away from the natal burrow of 300 m and 500 m, respectively. I chose to treat each movement as a dispersal event, regardless of the distance traveled, because the small patch size and lack of habitat continuity in some nesting areas may have severely limited the possibility of larger movements.

I classified nest sites as occurring in either "continuous" or "isolated" habitat, depending on the size and position of the site relative to other patches of grassland. In general, pastures ≤64 ha (one quarter-section), surrounded on all sides by cultivated fields (i.e., requiring the owl to fly over cropland to get to the next pasture) were classified as isolated. Pastures >64 ha were classified as continuous habitat.

Carcasses of dead Burrowing Owls were examined to determine cause of death. Mortality events were classified as: 1) avian predation (plucked feathers, usually in the same location as the transmitter); 2) mammalian predation (carcass, feathers, and/or transmitter chewed, with whole wings or legs bitten off and left at the site); 3) starvation (intact, emaciated carcass); 4) road kill (found dead on or near the road with evidence of a vehicle collision); 5) siblicide/cannibalism (remains of juvenile found inside nest box, usually with head partially eaten or missing; Wellicome 2000); or 6) unknown causes.

Differences in dispersal activities between years were

Table 1.   Dispersal activities (mean ± SE) of radio-tagged juvenile Burrowing Owls in Saskatchewan. P-values are from two-tailed Student's t-tests. Sample sizes are shown in square brackets.

VARIABLE	1997	1998	COMBINED YEARS		P
Age at first dispersal[a] (d)	45.8 ± 4.7 [5]	46.2 ± 1.4 [26]	46.1 ± 1.3	[31]	0.92
Closest occupied satellite burrow (m)	38.4 ± 10.1 [11]	45.6 ± 9.4 [27]	43.5 ± 7.2	[38]	0.66
Age at final sighting (d)	102.3 ± 4.6 [10]	107.8 ± 2.0 [18]	105.9 ± 2.1	[28]	0.21
Date of final sighting[b] (d)	23 Sept ± 2.6 [10]	24 Sept ± 1.8 [18]	24 Sept ± 1.5	[28]	0.84
Farthest distance from nest before migration[c] (m)	1297.8 ± 526 [10]	448.9 ± 97.9 [18]	752.1 ± 207.3 [28]		0.05

[a] Age that individual was first observed at a burrow other than its nest.
[b] An estimate of the onset of fall migration.
[c] Distances were included for all three dispersal patterns (see text).

assessed using two-tailed Student's t-tests. Following the Bonferroni procedure for multiple comparisons, the alpha level for each t-test was set at 0.01 to assure an overall significance level of 0.05 (Zar 1996). Differences in the occurrence of dispersal patterns between the two habitat types were tested using a 2 × 3 contingency table.

RESULTS

Post-fledging Activities. There were no significant differences between years in any dispersal activities, with the exception of the farthest distance traveled by a juvenile owl before migration (Table 1). Radio-tagged juveniles were found significantly farther from their natal burrows before migration in 1997 than in 1998. In both years, radio-tagged juveniles began first movements away from natal burrows at 28–57 d post-hatch, and began migration at 89–124 d. The median ages of first dispersal and final sighting were 47.0 and 109.5 d posthatch, respectively. The median date of final sighting, an estimate of the onset of fall migration, was
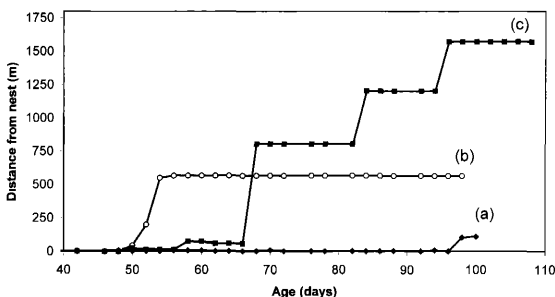

Figure 1.   Illustrations of the three patterns of juvenile dispersal exhibited by radio-tagged Burrowing Owls in Saskatchewan in 1997 and 1998: (a) nest-centered dispersal, (b) single-roost dispersal, (c) multiple-roost dispersal.

26 September (mean ± SE = 24 September ± 1.5 d). Before migration, each juvenile owl used a mean of 5.7 ± 0.5 satellite burrows.

Dispersal Patterns. In each of the two years, owls exhibited three patterns of post-fledging dispersal: 1) nest-centered, 2) single-roost, and 3) multiple-roost dispersal. In nest-centered dispersal (Fig. 1a), juveniles remained close to their natal burrow for the majority of the post-fledging period (i.e., >50 d), dispersing only to satellite burrows in the immediate vicinity of their nest. These juveniles remained within a mean (±SE) of 139.4 ± 55.2 m (N = 9 owls) of their nest until abruptly leaving the area for migration. In single-roost dispersal (Fig. 1b), juveniles dispersed to a burrow, or cluster of burrows, apart from their nest and remained in that area until migration, without returning to their natal burrow. The satellite burrows for this type of dispersal averaged 859.2 ± 378.8 m (N = 10 owls) from the nest. In multiple-roost dispersal (Fig. 1c), juveniles moved farther and farther away from their nest burrow, choosing a new burrow or cluster of burrows on each step and remaining there for a few days before moving again. Owls exhibiting this latter type of dispersal behavior were farthest from their nests by the end of the postfledging period, dispersing an average (±SE) of 1534.1 ± 545.2 m (N = 9 owls) from their nests before migrating.

The three types of dispersal occurred in approximately equal proportions (χ^2 = 0.071, df = 2, P > 0.05, N = 28 owls), with slightly fewer juveniles exhibiting multiple-roost (32%, N = 9) or nest-centered (32%, N = 9) than single roost (36%, N = 10) dispersal. There was a significant difference (χ^2 = 6.720, df = 2, P < 0.05) between the dispersal

Table 2.   Distribution of dispersal patterns exhibited by radio-tagged Burrowing Owls in continuous and isolated habitat patches.

DISPERSAL PATTERN	PERCENT OCCURRENCE	HABITAT TYPE	
		CONTIN-UOUS	ISOLATED
Nest-centered	32	5	4
Single-roost	36	3	7
Multiple-roost	32	8	1

patterns exhibited in isolated and continuous habitats. Multiple roost dispersal occurred eight times more often in continuous than in isolated habitat patches (Table 2).

Mortality. Post-fledging mortality of juvenile owls was substantially lower in 1997 than in 1998. None of the 12 radio-tagged juveniles were known to have died in 1997, whereas 45.4% of the 33 radio-tagged owls died before migration in 1998 (Table 3). Most mortality occurred shortly after juveniles left the nest (mean $\pm$ SE = 11.7 $\pm$ 5.5 d, median = 4.9 d after initial dispersal), with the exception of one juvenile that failed to migrate and was found dead of unknown causes in its nest burrow early in October. Most mortality (67%, N = 15 deaths) occurred in isolated habitat patches, and half of these deaths were due to avian predators.

Avian predation accounted for 47% (N = 15 deaths) of the overall mortality in 1998. This mortality rate may be biased because, of the seven deaths caused by avian predators, three occurred at nests within a single pasture. However, even when multiple nests within a pasture are excluded from the analysis (resulting in 10 deaths, rather than 15), and only one randomly chosen nest per field is included, the trend remains the same, with most mortality (60%, N = 10) occurring in isolated habitat patches with avian predators as the predominant factor (40%, N = 10). Other sources of mortality included road kill (7%), starvation (13%), collision with barbed-wire fences (7%), siblicide/cannibalism (7%), and unknown causes (13%).

DISCUSSION

Prior to the conversion of native prairie to cropland, Burrowing Owls in Canada presumably had access to large expanses of continuous grassland. Beyond the direct negative impacts associated with extensive habitat loss, habitat fragmentation can af-

Table 3.   Cause-specific mortality for juvenile Burrowing Owls in Saskatchewan. 'Percent Dead' = 'No. of Dead'/total No. of radio-tagged juveniles. The overall mortality rate in 1997 was 0% (N = 12), and 45.4% (N = 33) in 1998.

YEAR	CAUSE OF DEATH	NO. DEAD	PERCENT DEAD
1997	(Not applicable)	0	0
1998	Predation	8	24.2
	(Avian)	(7)	(21.2)
	(Mammalian)	(1)	(3.0)
	Road kill	1	3.0
	Starvation	2	6.1
	Barbed wire	1	3.0
	Siblicide/cannibalism	1	3.0
	Unknown	2	6.1
	Total	15	45.4

fect such things as the dispersal ability of Burrowing Owls. Results from this study suggest that Burrowing Owls exhibit multiple-roost dispersal behavior more often in continuous grassland than in isolated habitat patches. This pattern of dispersal may have been the most common pattern of dispersal in pre-European settlement days. Most radio-tagged juvenile owls (10 of 13) in a less-fragmented, shrub-steppe habitat in Idaho (King 1996) dispersed in a manner comparable to the multiple-roost pattern described in this study. The highly-fragmented landscape in the Regina Plain may necessitate other behaviors, such as foregoing large dispersal movements and remaining close to their natal burrow until migration. It is not clear, however, which dispersal pattern may maximize Burrowing Owl fitness.

The disparity in mortality rates between isolated and continuous habitat patches suggests that lack of habitat continuity may be associated with risk of predation. Elevated predation rates in relation to habitat fragmentation have been reported for other avian species (Whitcomb et al. 1980, Ambuel and Temple 1983, Andrén et al. 1985). Because predation events can often result from an incidental encounter between predator and prey (Angelstam 1986, Vickery et al. 1992), the probability of a predation event may be higher in smaller habitat patches (Burger et al. 1994). On the prairies, the increase in the number and density of trees that accompany farms and cities has likely compounded the habitat loss associated with the conversion

of grasslands to crops, allowing some avian predator populations to increase (Schmutz et al. 1980). Trees provide potential nesting sites for Great Horned Owls (*Bubo virginianus*), Swainson's Hawks (*Buteo swainsoni*), and Red-tailed Hawks (*B. jamaicensis*), which were not as abundant on the previously treeless prairies (Wellicome 1997). Habitat fragmentation and an elevated density of avian predators likely results in the concentration of Burrowing Owls and their predators in small patches of prairie, and probably increases predation risk to Burrowing Owls nesting in such areas.

The annual difference in juvenile mortality may have resulted directly or indirectly from the abundance of voles (*Microtus* spp.) in 1997 (Poulin et al. 2001). The high abundance of voles provided ample food for juveniles in 1997, possibly allowing them to be in better physical condition and better able to survive the post-fledging period. Similarly, Rohner and Hunter (1996) reported higher survival of juvenile Great Horned Owls during a peak in the population cycle of snowshoe hares (*Lepus americanus*). Higher survival may have occurred because juveniles were not as vulnerable to predation and disease as they were in years of low food availability, when mortality rates were significantly higher. The abundance of voles in 1997 may also have indirectly benefited juvenile Burrowing Owls. If potential predators were capable of meeting their energetic requirements by concentrating on voles, they may not have expended extra time or energy seeking other types of prey.

In 1997, the abundance of voles may also have influenced the dispersal of juvenile owls. Radio-tagged juveniles dispersed significantly farther from their nests during the post-fledging period in 1997 than in 1998, perhaps because young may have been better nourished because of the abundant food. Ferrer (1992, 1993) found that young Spanish Imperial Eagles (*Aquila adalberti*) in better physical condition tended to move farthest from their natal areas relative to those that were not as well nourished; however, Korpimäki and Lagerstrom (1988) found no relationship between food abundance and dispersal distance in juvenile Boreal Owls (*Aegolius funereus*, Tengmalm's Owl).

In 1998, an average year in terms of prey abundance (Poulin et al. 2001), almost half of the juvenile Burrowing Owls that fledged died before migration. Considering the high energetic costs and risks usually associated with migration, such a high premigratory mortality rate could have a consid-

erable impact on population dynamics, suggesting that post-fledging mortality may be an important factor in the decline of this species in Saskatchewan.

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