

SURVIVAL OF FLORIDA BURROWING OWLS ALONG AN URBAN-DEVELOPMENT GRADIENT

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ABSTRACT.—I estimated survival rates of a Florida Burrowing Owl (*Athene cunicularia floridana*) population on a 35.9-km² study area in Lee County, Florida, 1987–91 to determine if there was a relationship between annual survival and development density. The study area spanned a residential development density gradient ranging from <2% to >74% of lots with houses. Survival rates were estimated from a sample of 119 banded adult male, 152 adult female, and 310 juvenile Burrowing Owls using Cormack-Jolly-Seber capture-recapture models and Fisher's maximum likelihood method of parameter estimation. Survival rates were estimated separately for sections of the study area where <20% of 0.2-ha lots were developed (i.e., homes built), 20–39% were developed, 40–60% were developed, and >60% were developed. The most parsimonious models indicated that adult male survival was 81% (SE = 0.04) where <20% or >60% of lots were developed, and 62% (SE = 0.05) elsewhere. Adult female survival was 52% (SE = 0.06) where 40–60% of lots were developed and 69% (SE = 0.04) elsewhere. Juvenile survival was 18% (SE = 0.08) where <20% of lots were developed, 43% (SE = 0.08) where 20–39% of lots were developed, 28% (SE = 0.04) where 40–60% of lots were developed, and 11% (SE = 0.03) where >60% of lots were developed. I speculate that the inverse relationship between adult and juvenile survival across development zones reflected the greater recruitment opportunities that existed for juveniles in development zones where adult mortality was high. Patterns of adult mortality more closely tracked trends in the rate of home construction than the density of homes, suggesting factors associated with home building and the attendant landscape changes might result in high Burrowing Owl mortality.

KEY WORDS: *Burrowing Owl; demography; development; Florida; mark-recapture; Athene cunicularia floridana; survival; urban wildlife management.*

Supervivencia de *Athene cunicularia floridana* en un gradiente de desarrollo urbano

RESUMEN.—Estimé las tasas de supervivencia de una población de búhos cavadores de la florida (*Athene cunicularia floridana*) en un área de estudio de 35.9-km² en el condado Lee, Florida, 1987–91 para determinar si había una relación entre la supervivencia anual y la densidad del desarrollo. El área de estudio comprende un gradiente de densidad de desarrollo residencial que va desde <2% a >74% de lotes con casas. Las tasas de supervivencia fueron estimadas partir de una muestra de 119 machos adultos anillados, 152 hembras adultas, y 310 búhos cavadores juveniles usando los modelos de captura recaptura de Cormack-Jolly-Seber y el método de máxima probabilidad de la estimación de parámetros de Fisher. Las tasas de supervivencia fueron estimadas separadamente por secciones del área de estudio que estaban bajo desarrollo así: <20% de los lotes de 0.2 ha (V. Gr. construcciones familiares), 20–39%, 40–60%. Y >60 % en desarrollo. La mayoría de modelos de parsimonia indican que la supervivencia de los machos adultos fue 81% (SE = 0.04) en donde <20% o >60% de los lotes estaban desarrollados, y 62% (SE = 0.05) en cualquiera de los otros. La supervivencia de los juveniles fue 18% (SE = 0.08) en donde <20% de los lotes estaban desarrollados, 43% (SE = 0.08) donde 20–39% de los lotes se habían desarrollado, 28% (SE = 0.04) donde 40–60% de los lotes estaban desarrollados, y 11% (SE = 0.03) donde >60% de los lotes se habían desarrollado. Especulo que la relación inversa entre la supervivencia de adultos y juveniles a lo largo de las zonas desarrolladas reflejan las mayores oportunidades que tienen los juveniles para restablecerse en zonas desarrolladas en donde la mortalidad de los adultos fue elevada. Los patrones de mortalidad de adultos mostraron tendencias mas cercanamente asociadas a la tasa de construcción de hogares que a la densidad de los mismos, sugiriendo que los factores asociados a la construcción y a los consecuentes cambios del paisaje podrían dar como resultado una alta mortalidad de búhos cavadores.

[Traducción de César Márquez]

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The disjunct population of Burrowing Owls (*Athene cunicularia floridana*) in Florida was historically closely associated with native prairies in the central peninsula (Rhodes 1892, Nicholson 1954). The species began a rapid range expansion in the state in the 1950s as human settlement converted vast areas of former woodland to pasture and home development (Ligon 1963, Courser 1979, Millsap 1996). Today, many of Florida's Burrowing Owl populations occur in suburban neighborhoods, airports, and industrial parks (MacKenzie 1944, Neill 1954, Ligon 1963, Courser 1979). Several urban Florida Burrowing Owl populations have shown declines, and some urban populations have been extirpated (Courser 1976, Consiglio and Reynolds 1987). The collapse of a few highly visible urban populations prompted concern for the species' status in Florida, and it was listed as a Species of Special Concern by the Florida Fish and Wildlife Conservation Commission in 1979 (Millsap 1996).

Subsequent studies have shown that a complex relationship exists between Burrowing Owl population status and development in some urban areas. Wesemann and Rowe (1987) showed that Burrowing Owl nest density, as well as arthropod and anole (*Anolis* spp.) prey populations, were highest where houses occupied from 54–60% of the landscape in Cape Coral, Lee County, Florida. Millsap and Bear (2000) reported that productivity (number of young fledged per occupied breeding site) in this same population increased with increasing housing development until 45–60% of the landscape was developed. Productivity seemed to decline where development exceeded 70%.

The objective of this paper is to determine how Burrowing Owl survival rates varied along the development density gradient on this same Cape Coral study area. I also assess implications of variation in survival rates relative to trends in density and productivity described in the previous studies (Wesemann and Rowe 1987, Millsap and Bear 2000).

STUDY AREA AND METHODS

Study Area. I conducted this work from 1 January 1987–10 July 1991 on a 35.9-km² study area (of which 32.7 km² was suitable Burrowing Owl habitat) in Cape Coral, Lee County, Florida, latitude 81°99'N, longitude 26°57'W (Fig. 1). Climate in Cape Coral is subtropical, with an annual mean temperature of 23.1°C. Precipitation averages 125.7 cm annually, and 75% of rainfall occurs between May–September (climate data from NOAA climatological data summaries for Fort Myers, Florida, 20 km southeast of the study area). The area was historically unsuitable Burrowing Owl habitat, but it was rendered

favorable when wetland filling and land clearing for development occurred in the early 1950s (Zeiss 1983).

The study area consisted of filled upland subdivided into 0.2-ha lots suitable for homes, and dissected by access roads and saltwater canals. With the exception of a golf course (that was excluded from the study area due to access restrictions), three school campuses, and four recreation fields, the entire upland portion of the study area was subdivided for development. Groups of undeveloped lots of various configurations are interspersed with single-family homes throughout the study area. Vacant lots were maintained as grasslands by regular mowing by city maintenance crews. Developed lots usually contained manicured lawns of fibrous mats of sod with landscaped beds of trees and shrubs. The ratio of homes to vacant lots varied across the study area, with highest development in the eastern sections (where up to 74% of lots had homes built on them) and lowest in western sections (where as few as 2% of lots had homes on them).

Definitions. Burrows attended by one or more adult owls or decorated with shredded paper and grass were considered occupied nest sites. A nest site was the area within 88 m ($\frac{1}{2}$ the mean inter-nest distance [Millsap and Bear 2000]) of a burrow where a nest attempt occurred, or where a single adult Burrowing Owl not known to be breeding elsewhere was seen on three or more occasions between 1 January–10 July. The term survival (Φ) does not distinguish between individuals that survived from one year to the next and those that permanently emigrated (e) from the study area, unless it is specifically noted that adjustments to account for e were made. Recapture probability (p) is the probability of encountering a previously banded individual known to be alive in year i .

Methods. I obtained measures of the percent of lots that were developed for each of 14 legal sections (2.59 km²) on the study area in each year of the study from the city of Cape Coral. Nearly all upland throughout the study area was divided into 0.2-ha lots, so the percent of developed lots provided a reliable relative measure of the extent of home development in each section. Development was not necessarily uniform, and school campuses and clusters of undeveloped lots provided pockets of open space even in the most densely developed areas. Consequently, the percent of developed lots is best considered an index to the relative level of development around nest sites at a landscape scale.

I had insufficient data to assess survival of banded Burrowing Owls in each section, so I grouped owls into four development zones according to the percent of lots developed in the section where they were banded or last encountered. Development zones and area were: (1) zone 1, $\geq 60\%$ development, 8.0 km²; (2) zone 2, 40–60% development, 5.1 km²; (3) zone 3, 20–39% development, 7.5 km²; and (4) zone 4, $< 20\%$ development, 12.1 km². I chose the break point at 60% based on changes in owl population density and productivity that occurred at this level of development (Wesemann 1986, Wesemann and Rowe 1987, Millsap and Bear 2000).

Surveys to locate occupied nest sites were conducted from 1987–91 as described in Millsap and Bear (2000) using a team of trained volunteers. From 1987–90 this team banded 20–25% of breeding adult and juvenile Burrowing Owls in each section on the study area. Nest sites

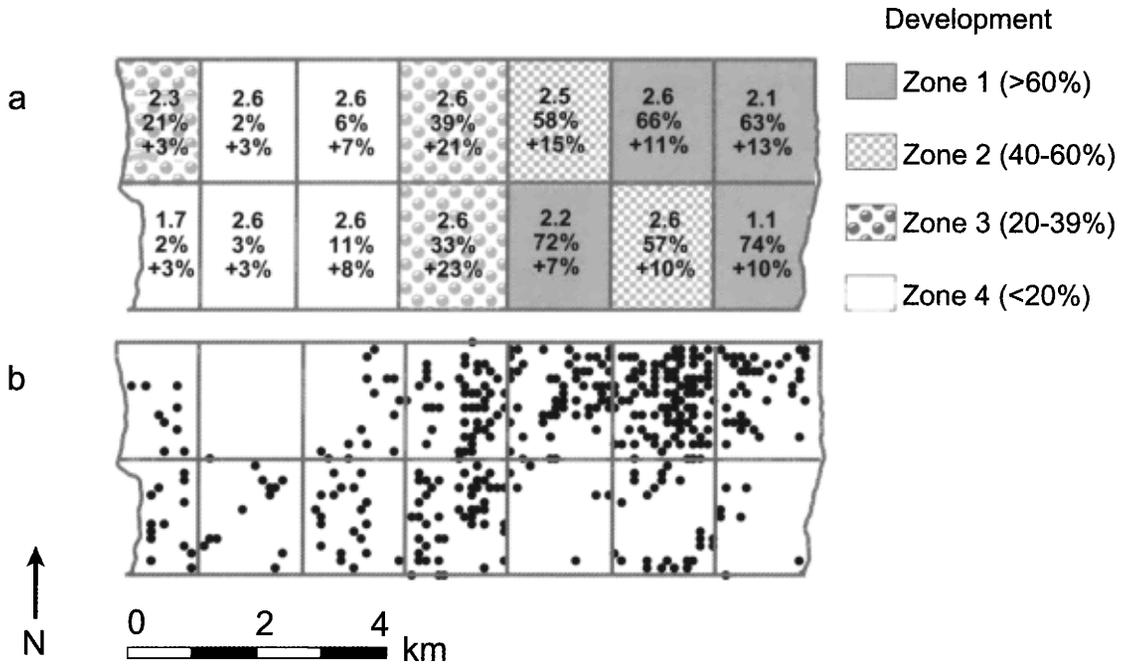


Figure 1. Map of the Burrowing Owl study area in Cape Coral, Lee County, Florida, showing (a) development zones and (b) distribution of nest sites for the period 1987–90. In a, numbers from top to bottom are: (top) number of km² of suitable Burrowing Owl habitat, (middle) mean percent of lots with homes for period 1987–90, and (bottom) percent increase in home density from 1987–90.

were randomly selected for banding from the pool of occupied sites each year, but some owls not selected *a priori* were also banded. Owls were captured with noose carpets placed at the burrow entrance and by hand at night with flashlights. Approximately 98% of adults attending known nests on the study area were checked for bands annually from 1988–91, allowing me to generate annual survival estimates for the periods 1987–88, 1988–89, 1989–90, and 1990–91. When banded owls were observed, we confirmed identification by reading band numbers with spotting scopes or binoculars or by retrapping. Members of the public who reported encounters with banded owls were queried to determine the details of the encounter. The sex of breeding adults could usually be determined at a distance by plumage (males were paler than females due to increased sun-bleaching) or behavior (Millsap and Bear 1997). Breeding females with eggs or small young could be distinguished in the hand by the presence of a large, vascularized incubation patch. We were unable to determine the sex of nestlings when they were initially banded, but sex was determined for those that were subsequently encountered as breeders.

Capture-recapture data were analyzed using the Cormack-Jolly-Seber (CJS) family of models, which produce estimates and estimated standard errors (SE) of Φ and p . Goodness-of-fit tests in Program RELEASE (Burnham et al. 1987) were used to assess the adequacy and utility of the basic CJS model for my data. Parameter estimates

were calculated using Program SURGE (Pradel et al 1990). I calculated estimates of Φ and p separately for owls banded as adults (which were further separated by sex) and nestlings (which were not identified to sex upon initial banding). For both adults and young, I examined parameters over categorical time intervals (subscript t) and development zones (subscript z). For birds banded as juveniles, I also examined variation with age (subscript a).

My objective was to find the model with the simplest structure and fewest parameters that still accounted for significant variability in the data. Model notation follows Lebreton et al. (1992). I initiated model testing for adults with a global model of $\{\Phi_{t^*z^*}; p_{t^*z^*}\}$, where t denotes a time effect over the four recapture years (1988–91), z denotes an effect over the four development zones, and $*$ denotes interaction between time and development effects. Thus, my adult global model tested separate $\{\Phi_{t^*z^*}; p_{t^*z^*}\}$ for each sex over all four recapture occasions and all four development strata. The global model for owls banded as nestlings was $\{\Phi_{a^*t^*z^*}; p_{a^*t^*z^*}\}$, where a denotes an age effect over two age classes (juveniles and >1-yr-old). For the subscripts t , z , and a , I distinguished between nonspecific categorical groups with the additional subscript n , and specific categories with the subscript n' . For example, the notation $z4$ denotes a model where development zone effect is partitioned across all four zones, whereas the model subscripted $z1'$, $z2' = z3' = z4'$ de-

notes a model where development zone effect was partitioned between zone 1 and zones 2–4 pooled.

I tested reduced nested variations of these models against the global models using Akaike's Information Criterion (AIC) to distinguish the most parsimonious model from among those tested (Lebreton et al. 1992). The probability that each of the six highest-ranked nested models (based on AIC scores) was the best model was estimated by the AIC weight (ω) for each model (Burnham and Anderson 1998).

In 1988–89, my team and I searched for banded Burrowing Owls that had dispersed and settled at nest sites in a 3.2-km-wide band immediately north of study area, as well as south of study area to the southern terminus of the Cape Coral peninsula. I used these data to adjust my estimates of Φ to account for permanent emigration using the formula in Burnham et al. (1996).

I contacted persons who reported dead banded owls to determine the cause of death whenever possible. Many recoveries were reported by a local wildlife rehabilitation center (Care and Rehabilitation of Wildlife, Inc.), and center veterinarians routinely conducted necropsies on banded Burrowing Owls.

RESULTS

The percent of lots with homes ranged from <2% to 74% across the study area, as measured at the section level (Fig. 1). The extent of development changed over the course of the study in all sections, but the greatest increase in the percent of developed lots was in moderately-developed parts of the study area. In the 20–39% and 40–60% development zones, from 10–23% of lots that were undeveloped at the start of the study had homes on them when the study ended.

My team and I banded 581 Burrowing Owls involved in 785 breeding attempts on 264 discreet nest sites on the study area from 1987–90 (Table 1, Fig. 1). For the purposes of survival analyses, I assigned each banded owl to the development zone where the owl was located the preceding time it was encountered.

Recapture Probabilities and Survival. No model incorporating variation in p with year or development zone was a satisfactory fit (Table 2), so I pooled data. Overall estimates of p were relatively high: adult males = 91% (SE = 3%), adult females = 87% (SE = 4%), and juveniles = 86% (SE = 5%). No models that incorporated variation among years in Φ were a good fit, so I pooled data over years for survival analyses.

The best overall estimate of Φ was 71% (SE = 3%) for adult males, and 64% (SE = 3%) for adult females. The unadjusted overall estimate of Φ for juveniles from the 2 age-class model was 21% (SE = 3%), but this did not account for known emi-

Table 1. Capture-recapture data set used to estimate survival of Florida Burrowing Owls from Cape Coral, Lee County, Florida, 1987–91. See Fig. 1 for zone descriptions.

	NUMBER BANDED	NUMBER RECAPTURED			
		Y_{T_i}	$Y_{T_{i+1}}$	$Y_{T_{i+2}}$	$Y_{T_{i+3}}$
Σ Adult male	119	83	44	22	2
Zone 1	36	26	19	12	1
Zone 2	35	27	11	4	0
Zone 3	35	22	8	4	1
Zone 4	13	8	6	2	0
Σ Adult female	152	80	49	22	4
Zone 1	46	25	18	9	3
Zone 2	48	21	12	4	1
Zone 3	38	22	12	5	0
Zone 4	20	12	7	4	0
Σ Juvenile	310	55	26	13	4
Zone 1	83	7	1	1	0
Zone 2	113	20	11	6	3
Zone 3	91	26	12	6	1
Zone 4	23	2	2	0	0

gration. Five of 35 Burrowing Owls banded as nestlings on the study area in 1987–88 were known to have survived to breed and settled at nest sites away from the study area, yielding an estimated e of 0.14 (SE = 0.06) for juveniles. Adjusting for e , Φ for age 0–1 yr = 24%. Survival increased among owls banded as nestlings at >1 yr of age to 62% (SE = 6%). No Burrowing Owls banded as adults on the study area were found nesting off the study area, so there was no basis for adjusting Φ to account for breeding dispersal.

Patterns of Survival. The adult male survival model with the lowest AIC and fewest parameters pooled together the >60% and <20% development zones, and pooled together the 20–39% and 40–60% development zones (Table 3). The AIC weight for this model was low overall, but was over twice that of the next best model. The best adult female survival model pooled together the >60%, 20–39%, and <20% development zones, and had an AIC weight 2.5 times that of the next best model. There was little difference in AIC weights among four of the six best survival models for Burrowing Owls banded as nestlings, so there was no clear basis for pooling survival estimates for any development zones. The small sample size in the <20% development zone prevented calculation of

Table 2. Comparison of six best capture-recapture models based on Akaike's Information Criterion (AIC) for adult male, adult female, and juvenile Florida Burrowing Owls, Cape Coral, Lee County, Florida, 1987-91. Models are listed in order of decreasing fit, based on AIC weights (ω).

MODEL ^a	DEVIANCE	K ^b	AIC	ω^c
Adult males				
$\{\Phi_{z1'=z4',z2'=z3'; p}\}$	327.170	3	333.2	0.57
$\{\Phi_{z1',z2'=z3',z4'; p}\}$	326.820	4	334.8	0.26
$\{\Phi_{z4'; p}\}$	326.617	5	336.6	0.11
$\{\Phi_{z1'=z2',z3',z4'; p}\}$	331.092	4	339.1	0.03
$\{\Phi_{z1'=z2'=z3',z4'; p}\}$	334.143	3	340.1	0.02
$\{\Phi; p\}$	336.978	2	341.0	0.01
Adult females				
$\{\Phi_{z2',z1'=z3',z4'; p}\}$	410.502	3	416.5	0.54
$\{\Phi_{z1'=z4',z2'=z3'; p}\}$	412.349	3	418.3	0.22
$\{\Phi_{z4'; p}\}$	409.447	5	419.5	0.12
$\{\Phi_{z4',z1'=z2'=z3'; p}\}$	415.049	3	421.0	0.06
$\{\Phi; p\}$	417.193	2	421.2	0.05
$\{\Phi_{z4',z4'; p}\}$	404.259	17	438.3	<0.01
Juvenile				
$\{\Phi_{z2',z1'=z4',z2'=z3'; p}\}$	430.780	5	440.8	0.29
$\{\Phi_{z2',z1',z2'=z3'=z4'; p}\}$	431.317	5	441.3	0.23
$\{\Phi_{z2',z3',z1'=z2'=z4'; p}\}$	431.715	5	441.8	0.18
$\{\Phi_{z2',z1',z2'=z3',z4'; p}\}$	428.033	7	442.0	0.16
$\{\Phi_{z2',z4'; p}\}$	424.541	9	442.5	0.13
$\{\Phi_{z2'; p}\}$	441.740	3	447.7	0.001

^a Model notation is as follows: Φ = survival; p = recapture probability; a_n = categorical age, where n denotes the number of age classes (when $n = 2$ the model uses 2 age classes, one for owls ≤ 1 yr old and one for owls >1 -yr-old); t_n or $t_{n'}$ = time, where n denotes the number of nonspecific time categories modeled, and n' denotes a specific time category (i.e., $1' = 1988$, $2' = 1989$, $3' = 1990$, and $4' = 1991$); z_n or $z_{n'}$ = development zone, where n denotes the number of nonspecific development zones modeled and n' denotes a specific development zone (i.e., $1' = \geq 60\%$ development, $2' = 40-60\%$ development, $3' = 20-39\%$ development, and $4' < 20\%$ development).

^b K = number of parameters estimated in the model.

^c ω = AIC weight, which is the estimated probability the particular model is the best of the suite of models evaluated (Burnham and Anderson 1998).

meaningful survival estimates for the >1 yr age class for this zone.

Overall, estimates of survival for adult males (from the adult model) and juveniles (from the 2 age-class model) were strongly inversely correlated across development zones (Spearman's rank $r = -0.89$). All five juvenile emigrants captured off the study area came from nest sites in the $>60\%$ (4

individuals) and 40-60% (1 individual) development zones.

Causes and Timing of Mortality. Cause of death was estimated for 27 of 41 (65.9%) banded owls. Nineteen (70.3%) were hit by cars, six (22.2%) were the victims of predation (three by domestic dogs or cats, three by other raptors), one (3.7%) was killed during home construction on the nest lot, and one (3.7%) died of an unknown illness.

The seasonal distribution of recoveries of owls >1 yr of age ($N = 30$) was not uniform ($\chi^2_3 = 17.2$, $P = 0.001$) (Fig. 2). Significantly ($P < 0.10$) more recoveries of adults were reported during the breeding season than expected, and significantly ($P < 0.10$) fewer were recovered in the fall. No marked differences were evident between males and females. The seasonal distribution of recoveries of juveniles ($N = 11$) was also not uniform ($\chi^2_3 = 10.5$, $P = 0.02$), with more recovered at and shortly after fledging in spring than expected ($P < 0.10$) and fewer recovered than expected in fall ($P < 0.10$).

DISCUSSION

Survival rates of Burrowing Owls have not been widely investigated. The only other similarly derived survival estimates in the literature are from a migratory population in central Colorado (Lutz and Plumpton 1997), where adult survival averaged 39% per yr over a 4-yr period, but varied among years (range = 18-71%), and nestling survival to 1 yr averaged 12%. Clayton and Schmutz (1997) estimated over-summer survival rates at 83% for adult female, 46% for adult male, and 48% for juvenile migratory Burrowing Owls in Alberta and Saskatchewan using radiotelemetry, but additional mortality would be expected in this population on migration and during winter. Estimates of annual survival from band resightings unadjusted for emigration range from 37-57% for adults in a migratory population in Saskatchewan (James et al. 1997), to 30% for juveniles and 81% for adults in a sedentary population in Oakland, California (Thomsen 1971). Estimates for Cape Coral fall within the upper limits of survival from these previous studies, and are most comparable to estimates for the Oakland, California population. The Cape Coral Burrowing Owl population shares several other traits with the Oakland, California population, among them relatively low productivity (Millsap and Bear 2000) and high nest site and mate fidelity (Millsap and Bear 1997). These simi-

Table 3. Estimates of annual survival of Florida Burrowing Owls in Cape Coral, Lee County, Florida, 1987–91 from best-fit models using Program SURGE (see Table 2 for models and model selection criteria).

MODEL CLASS ^a	ESTIMATED ANNUAL SURVIVAL (SE)			
	>60% DEVELOPMENT	40–60% DEVELOPMENT	20–39% DEVELOPMENT	<20% DEVELOPMENT
Adult models				
Adult male	0.81 (0.04)	0.62 (0.05)	0.62 (0.05)	0.81 (0.04)
Adult female	0.69 (0.04)	0.52 (0.06)	0.69 (0.04)	0.69 (0.04)
Age-class models				
Age 0–1 yr ^b	0.11 (0.03)	0.28 (0.04)	0.43 (0.08)	0.18 (0.08)
Age >1 yr	0.46 (0.02)	0.60 (0.09)	0.63 (0.09)	—

^a Adult models are based on birds first captured as breeding adults. Age-class models use birds first banded as nestlings at their natal burrow.

^b Age 0–1 yr survival was adjusted to account for measured emigration following the approach in Burnham et al. (1996).

larities might reflect the absence of seasonal migration and mild climate common to both study sites.

Vehicle collisions were an important source of mortality for both juvenile and adult Burrowing Owls in Cape Coral. Most road mortality I observed was on residential streets with reduced speed limits (i.e., ≤ 56 km/hr). Highway collision was also found to be a substantial mortality factor in North Dakota (Konrad and Gilmer 1984), Saskatchewan (Haug and Oliphant 1987, Clayton and Schmutz 1997), and Alberta (Clayton and Schmutz 1997), and it is identified as a principal mortality factor in the Canadian Burrowing Owl Recovery Plan (Hjertaas 1997). In radiotelemetry studies of survival, predation has also been shown to be an important source of mortality (Clayton and Schmutz

1997), and I suspect it was more important in Cape Coral than indicated by band recoveries. This was particularly true in heavily-developed areas where cover for predators was high. During the course of the study, I observed, in order of decreasing frequency, Cooper's Hawks (*Accipiter cooperii*), Fish Crows (*Corvus ossifragus*), house cats, Merlins (*Falco columbarius*), and Peregrine Falcons (*F. peregrinus*) capture Burrowing Owls.

Although band recoveries by the public may provide a misleading picture of the timing and seasonality of Burrowing Owl mortality, my results suggest that adult Burrowing Owls are at higher risk of mortality in spring while breeding. This implies that there is a cost of reproduction to Burrowing Owls on the study area, although I have insufficient data to compare annual survival for breeders with nonbreeders. The high mortality of juveniles at about the time of fledging is not unexpected. The drop in mortality in both adults and young in fall is surprising, because it is at this time that mortality from predation by migrant raptors should probably increase. As noted earlier, however, this kind of mortality would not be detectible through band recoveries reported by the public.

The inverse relationship between survival rates for adult males, the group for which conclusions regarding survival were least apt to be confounded by emigration because of high nest site fidelity (Millsap and Bear 1997), and juveniles is curious. I suspect this occurred because high adult mortality in moderate-development zones created more opportunities for surviving banded juveniles to settle near their natal nest sites where they had a high probability of being encountered. This hypothesis

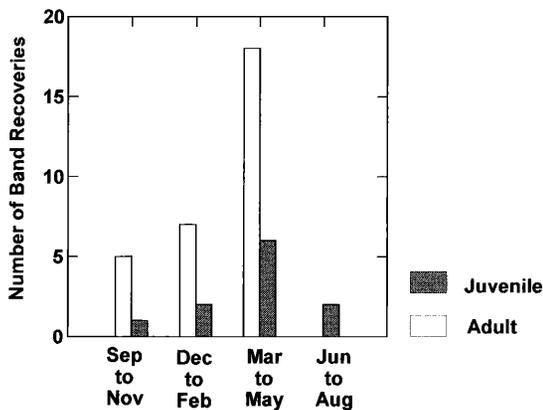


Figure 2. Histogram of recoveries of deceased banded Burrowing Owls reported by the public by season from Cape Coral, Lee County, Florida, 1987–91.

is consistent with the high natal philopatry observed in this study population (Millsap and Bear 1997), and is further supported by the limited data on juvenile emigration, which showed higher rates of movement off the study area by juveniles from heavily-developed areas than from less-developed areas. Because emigration appeared to affect apparent juvenile survival greatly, actual survival might have been much different. The only conclusion, I believe, that can be drawn safely about juvenile survival is that it was as high as 43% in some parts of the study area.

It is not immediately apparent from the available data why adult male, and, to a lesser extent, adult female survival was lowest in moderately-developed parts of the study area. Both Burrowing Owl nest site density and productivity were positively associated with home development in the <20%, 20–39%, and 40–60% development zones (Millsap and Bear 2000); hence, adult survival was lowest in areas where both density and productivity were relatively high. Although it is conceivable that low adult survival was directly related to pressures associated with high adult population density in moderate development zones, this is not consistent with the high rate of juvenile recruitment in these areas. If there was strong competition among adults for nest sites, fewer rather than more 1-yr-olds would be expected to find breeding vacancies to fill (Newton 1991). A possible explanation that better fits the available data is that the comparatively rapid rate of home construction in the 20–39% and, in particular, the 40–60% development zones (Fig. 1a) caused, either directly or indirectly, higher adult mortality. More work is needed to ascertain whether or not this is the case, and to determine the mechanism of the effect. Such work could have significant implications for future conservation of urban Florida Burrowing Owl populations.

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