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DENSITY AND REPRODUCTION OF BURROWING OWLS ALONG AN URBAN DEVELOPMENT GRADIENT

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Abstract: We studied population density and reproductive success of a Florida burrowing owl (*Athene cunicularia floridana*) population on a 35.9-km^2 study area that spanned a residential development gradient ranging from <2% to >80% of lots with houses in Lee County, Florida, 1987–90. We observed 785 breeding attempts at 264 unique nest sites in an increasing population of owls. Linear regression indicated that nest site density (6.9 pairs/ km^2 in 1990) increased until 45–60% of lots were developed before decreasing. Overall nest success (69.6 ± 4.2%; $\bar{x}$ ± SE) did not vary along the development gradient, however the proportion of nests that failed from human-related causes increased with increasing development. The number of young fledged per nest site increased until development exceeded 45–60%, then stabilized. The number of young fledged per successful nest decreased as development increased above 60%. Burrowing owls that nested on lots where home construction was occurring fledged more young if a ≥10-m buffer from disturbance was provided around the nest burrow. Burrowing owls nesting in sodded yards of homes fledged fewer young than nests in vacant lots. Our results, combined with those of previous researchers, suggest that burrowing owls on our study area benefited from high prey densities around homes, but that increased human-caused nest failures and declines in the number of young fledged at successful nests in heavily developed areas offset the advantages of abundant prey.

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Key words: burrowing owl, density, development, fecundity, Florida, productivity, *Athene cunicularia*, nesting, urbanization.

The impact of urbanization is one of the greatest habitat conservation issues facing wildlife managers today. Nowhere is this issue more acute than in Florida, where over 40% of the state's wildlife taxa are thought to be declining (Millsap et al. 1990) and natural habitats are being lost to development at the rate of about 3.5% per year (Noss and Peters 1995). While it is tempting to condemn all urban development as detrimental to wildlife, the issue is complicated because not all species threatened with extinction or regional extirpation are incapable of acclimating to urban landscapes. Examples in Florida include the state-threatened least tern (*Sterna antillarum*) that increased in numbers after it shifted nesting to flat gravel rooftops (Gore 1991), and the state-threatened Big Cypress fox squirrel (*Sciurus niger avicennia*) that readily used golf courses in southwest Florida (Jodice and Humphrey 1992).

Comprehensive management of a species requires that we understand enough about life history in urban settings to take advantage of the unique conservation opportunities that exist there. If nothing else, maintaining urban populations of imperiled species increases the range

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of conservation options available to managers. The Florida burrowing owl is a non-migratory raptor in Florida that is thought to be declining, yet it is sufficiently adaptable to occur frequently in urban areas (Millsap 1997). The species' adaptability likely results from several factors. First, Florida burrowing owls feed on a wide variety of invertebrates, reptiles, amphibians, small mammals, and small birds (Hennemann 1980, Wesemann and Rowe 1987). Second, the subspecies usually excavates its own nest burrow (Millsap 1997), hence is not limited in distribution to the range of a burrow-digging host, as is the case over most of its range (Haug et al. 1993). Finally, the burrowing owl's habitat preferences are met in altered, open grassy landscapes in Florida. Historically closely associated with native prairies on the Okeechobee, Osceola, and DeSoto Plains (Rhoads 1892, Nicholson 1954), Florida burrowing owls now breed throughout peninsular Florida, and patchily in the Panhandle (Millsap 1997). This range expansion has been facilitated by the clearing of forests and filling of wetlands, and many populations occur in suburban areas, airports, and industrial parks (MacKenzie 1944, Neill 1954, Ligon 1963, Courser 1979). Observations in Florida indicate that many urban burrowing owl populations do not persist for long periods of time (Courser 1976, Consiglio and Reynolds 1987). The unexplained collapse of highly visible and popular urban populations has led to concern about the impact of human development on the burrowing owl in Florida, resulting in its listing as a species of special concern by the Florida Fish and Wildlife Conservation Commission in 1979 (Millsap 1997).

Wesemann and Rowe (1987) conducted work on burrowing owls in Cape Coral, Florida, where they documented trends in owl nesting density and prey abundance for 1 year along an urbanization gradient where homes occurred on <2% to >80% of lots. Their study suggested that burrowing owl nest density was highest where 55–65% of lots had homes (approximately 550–650 homes per km^2). We wanted to better understand this relationship, and we expanded on the work of Wesemann and Rowe (1987) by measuring trends in population size, fecundity, and survival over a 4-year period on the same study area. In this paper, we present our results on the relationship between urbanization and reproduction, and offer management recommendations that address some of the problems faced by burrowing owls in Cape Coral, Florida.

STUDY AREA

Our observations were made between 1 January 1987 and 10 July 1990 on a 35.9-km^2 study area (of which 4.1 km^2 was wetland or intensively managed golf course not suitable for nesting by burrowing owls) in Cape Coral, Lee County, Florida, latitude 81°99′N, 26°57′W longitude (Fig. 1). This was the exact study area used by Wesemann and Rowe (1987), who selected it because it was representative of the variety of development conditions in Cape Coral. The Cape Coral peninsula was historically mesic slash pine (*Pinus eliottii*) flatwoods and tidal swamp (Zeiss 1983, Wesemann 1986), and was largely unsuitable for occupation by burrowing owls. The area was drained and filled beginning in the late 1950s, and the first homes were built in 1958 in the southeastern part of our study area (Zeiss 1983).

We used existing township and range section lines to divide our study area into 14, 2.59-km^2 sections (Table 1). We used section lines to partition our study area because development statistics were available for sections from the city of Cape Coral. The area consisted mainly of single-family homes interspersed with vacant lots maintained as grassland by regular mowing by city maintenance crews. Developed lots usually contained homes surrounded by manicured lawns of fibrous mats of sod with landscaped beds of trees and shrubs. The density of homes and other buildings varied across the study area, with highest development in the eastern sections (up to 82% of lots with homes, or approximately 820 homes per km^2) and lowest in western sections (as low as 2% of lots with homes, or 20 homes per km^2; Table 1). This east–west development gradient facilitated comparison of burrowing owl demographic statistics in a similar environment but under different levels of development.

METHODS

We defined a nest site as the area within 88 m of a burrow where a breeding attempt occurred, or where a single adult burrowing owl not known to be breeding elsewhere (about 25% of adults each year were color banded) was seen on 3 or more occasions during the breeding period (1 Jan to 10 Jul). We used an 88-m radius because it was half the average distance

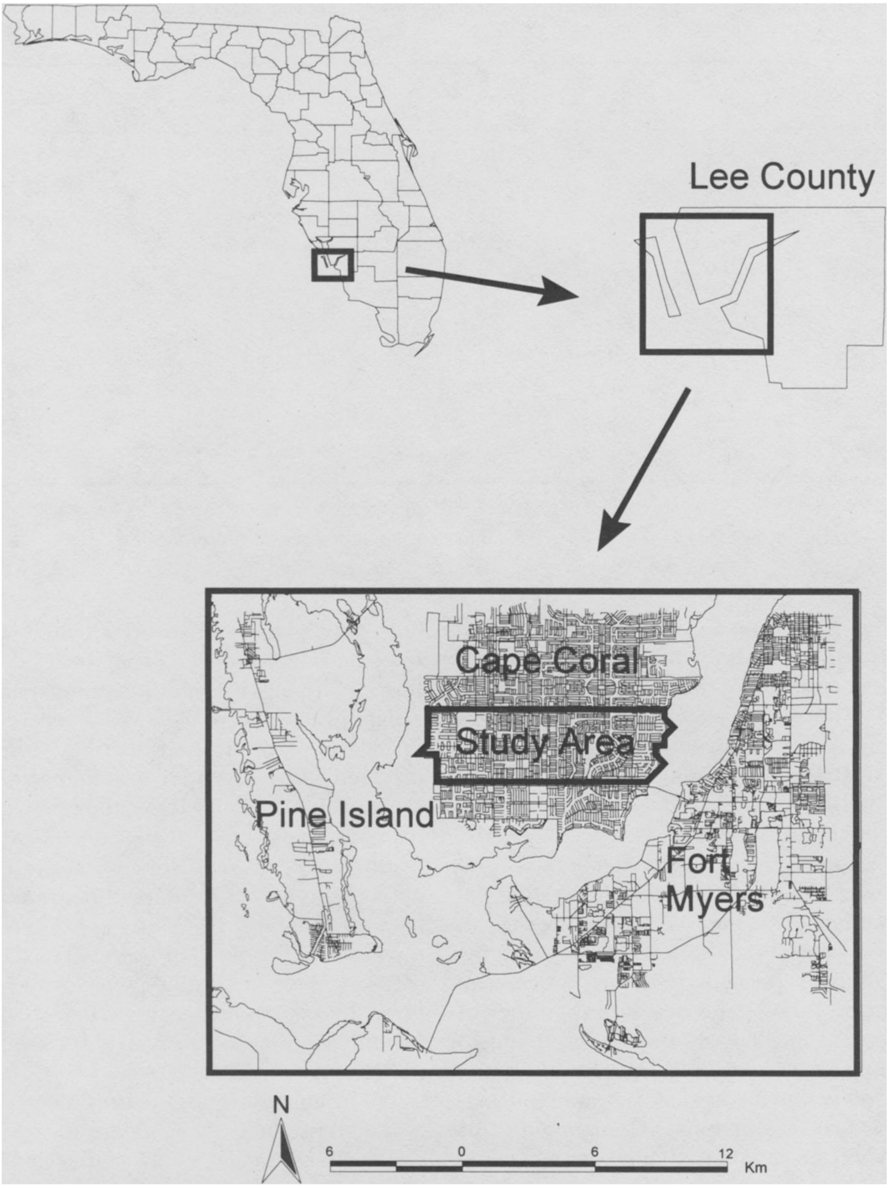

Fig. 1. **Map of the Cape Coral study area, Lee County, Florida.**

(176 ± 4.8 m, n = 264) between nearest adjacent occupied nest burrows on our study area in all years. Nest sites attended by ≥1 adult owls or decorated with shredded paper and grass (Haug et al. 1993) were considered occupied. An occupied nest site was considered successful if ≥1 young survived to fledge at 40 days of age. Productivity was the number of young raised to fledging age on an occupied nest site.

All suitable burrowing owl habitat on the study area was subdivided into building lots approximately 0.1 ha in size (City of Cape Coral, personal communication). The city maintained annual records of the percentage of lots with homes in each section on the study area. The proportion of lots with homes reflected the average density of houses in each section, and annual changes provided a measure of the rate of change in development.

We surveyed the study area by driving all roads at least twice each year between January

Table 1. Development statistics and mean number of nests by section (2.59-km² area) for our burrowing owl study area in Cape Coral, Lee County, Florida, 1987–90.

Section	Suitable burrowing owl habitat (km²)[a]	% development in section[b]	Annual change in % development	Mean number of nests 1986–90
1	2.1	77	3.3	19.8
2	2.3	67	2.8	47.6
3	2.5	65	3.8	24.0
4	2.6	43	5.3	26.2
5	2.6	3	1.8	7.6
6	2.6	2	0.8	0
7	2.3	3	0.8	2.2
8	1.7	2	0.8	4.8
9	2.6	3	0.8	3.8
10	2.6	11	2.0	7.0
11	2.6	35	5.4	23.4
12	2.2	82	1.8	3.6
13	2.6	78	5.0	11.8
14	1.1	75	5.0	2.6

[a] Excludes area within each 2.59-km² section that was either wetland or intensively managed golf course, and not suitable for nesting by burrowing owls.
[b] Average percent of 0.01-ha building lots within each section that had homes on them during the period 1987–90.

and March to locate occupied burrowing owl nest sites. Most nest sites were easily located on elevated berms along the edge of the roads. This survey approach was shown to be effective in locating all but a small percentage of occupied nest sites (Wesemann 1986, Wesemann and Rowe 1987).

We visited nest burrows at least weekly in the early morning or late afternoon when owls were active above ground throughout the nesting period to count all young visible. The length of visits varied based on the level of owl activity, but our objective at each visit was to count all young in the brood. The maximum number of young seen at any 1 time on or subsequent to the estimated fledging date was used as the number of young fledged. We found no evidence of brood switching (Henny and Blus 1981). When a nest attempt failed, we evaluated evidence at the scene (e.g., construction activity, tire tracks, condition of the burrow entrance, absence of 1 or both adults, signs of vandalism) to determine the cause of failure.

We used $\alpha = 0.10$ as our significance level in tests. We used analysis of variance (ANOVA), analysis of covariance (ANCOVA), or regression in cases where we failed to reject the null hypothesis that data were drawn from a normal distribution (Kolmogorov-Smirnov test) with equal variance (Levene Median test). In the case of ANCOVA, we screened for interaction of covariates using 2-way ANOVA, and we employed ANCOVA on ranks (Shirley 1981) when normality assumptions were violated. For parametric tests of group means, we used the Bonferroni all pairwise multiple comparison test to isolate group differences. We used arcsin transformation on proportions and rank-transformed productivity values prior to parametric analyses (Sokal and Rohlf 1981), although we present data in original units. We used a chi-square (χ^2) contingency test or Fisher's exact test to compare observed with expected distributions (Sokal and Rohlf 1981). Where we detected a significant difference in a χ^2 test with >2 categories, we determined which categories differed by constructing simultaneous 95% Bonferroni confidence intervals for observed proportions (Byers et al. 1984).

We evaluated trends in nest density, nest success, and productivity using mean values of each variable and mean levels of development for each section for the study period. We used mean values because we could not assume independence among years in data from each section. Before pooling data over years, we tested to determine if the slopes of the regression lines among years were different. To determine trends in nest density, nest success, and productivity across different development conditions, we first fitted a distance-weighted least squares (DWLS) line to the points to determine the general shape of the curve. If a linear pattern was apparent across the full range of development conditions sampled, we used linear regression to quantify the relationship. If the

DWLS line suggested the slope of the response curve changed over the range of conditions sampled, we subdivided the data at the inflection point of the curve and computed piecewise linear regression (SYSTAT 1990) on the subsamples.

To avoid biasing nest success and productivity estimates upwards by excluding nests that failed early and were overlooked (Steenhof 1987), we used only territories discovered before or during incubation for these estimates (Lehman et al. 1998). The Mayfield estimator (Steenhof 1987) could not be applied to estimate nest success because it was not readily apparent when most unsuccessful nesting attempts failed.

RESULTS

The percent of lots with homes increased throughout the study area over the study period, with the most rapid increase in sections 4 and 11 in the middle of the study area (Table 1). We observed 785 burrowing owl breeding attempts from 1987 to 1990 at 264 discrete nest sites (Table 1). The yearly trend in the number of occupied nest sites was positive ($F_{1,3} = 46.58$, $P = 0.006$, $b = 31.1 \pm 4.56$, $r^2 = 0.94$), indicating our study population increased.

The mean number of occupied nest sites per km^2 increased as the mean proportion of lots with homes increased until 45–60% of lots were developed, above which point nest site density decreased. We subdivided our sample by section at 60% development, and ran piecewise regression on the subsets. For sections where <60% of lots were developed, the slope of the line was positive and regression explained 97% of variation in burrowing owl nest site density ($F_{1,5} = 74.7$, $P < 0.001$; Fig. 2). At ≥60% development, the slope of the regression line was negative and explained about 74% of variation in nest site density ($F_{1,4} = 4.9$, $P = 0.09$).

We determined nest success and productivity at 736 occupied nest sites. On average, 69.6 ± 4.2% of occupied nest sites fledged ≥1 young. We found that nest success did not vary predictably across the range of development ($F_{1,11} = 0.8$, $P = 0.79$; Fig. 3). We were able to determine the cause of failure at 119 of the 224 (53.1%) occupied nest sites that failed. The leading causes of nest failure were nest destruction during construction of homes, harassment (largely by school-age children), and flooding (Table 2). The number of nests destroyed by

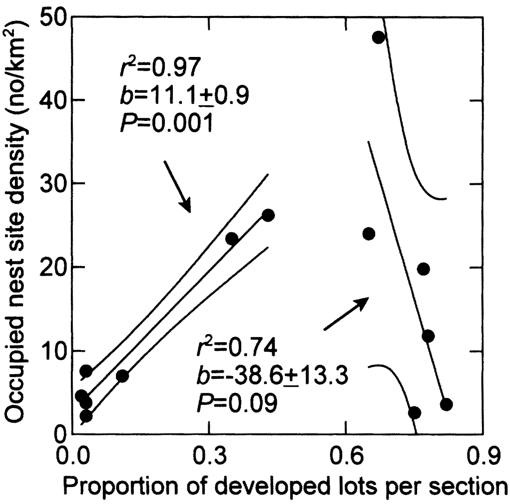

Fig. 2. Relationship between the mean proportion of lots developed within 2.59-km^2 sections and the mean density of occupied burrowing owl nest sites per section for the period 1987–90 in Cape Coral, Lee County, Florida. Regression lines are bounded by the 90% CI.

harassment was significantly greater than expected in 1987 and significantly less than expected in 1988, 1989, and 1990 ($\chi_2{}^3 = 13.0$, $P = 0.005$, Bonferroni simultaneous confidence interval $P \leq 0.10$). Other causes of failure did not differ in frequency among years ($P > 0.10$). The proportion of nests that failed due to human causes (harassment, construction, and mowing) increased with increasing development ($F_{1,11} = 9.3$, $P = 0.01$; Fig. 3). Failures not directly attributable to human causes (flooding, predation, adult mortality not attributable to humans) decreased with increasing development ($F_{1,11} = 3.8$, $P = 0.08$; Fig. 3).

Brood size ranged from 0 to 6 ($n = 736$) at nest sites, where 224 (30.4%) failed, 77 (10.4%) fledged 1, 132 (17.9%) fledged 2, 138 (18.7%) fledged 3, 107 (14.5%) fledged 4, 46 (6.3%) fledged 5, and 12 (1.6%) fledged 6 young. The mean number of young fledged per breeding attempt per occupied nest site was 2.0 ± 0.1, and 2.9 ± 0.1 per successful nest site. The proportion of developed lots per section at <60% development explained 69% of variation in the number of young fledged per occupied nest site ($F_{1,5} = 4.5$, $P = 0.09$), whereas at greater levels of development, there was no significant linear relationship ($F_{1,4} = 1.5$, $P = 0.29$; Fig. 4). When nest attempts that failed to fledge young were excluded, there was no discernable trend in the number of young fledged with the proportion of lots developed where the level of develop-

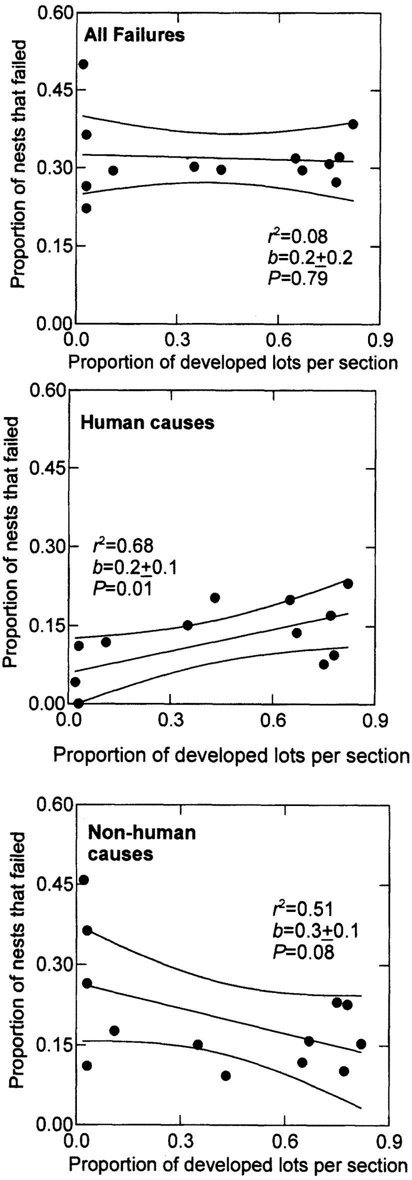

Fig. 3. Relationship between the mean proportion of lots developed and the mean proportion of successful nest attempts (i.e., nest attempts that fledged ≥1 young) per 2.59-km² section for the period 1987–90 in Cape Coral, Lee County, Florida. Regression lines are bounded by 90% CI. The top figure includes all failures, the middle figure includes only failures known to have been caused by humans, and the bottom figure includes only failures known to have been caused by natural agents.

ment was <60% ($F_{1,5}$ = 0.5, P = 0.52). Above 60% development there was a significant decrease in the mean number of young fledged per section as the mean proportion of homes increased ($F_{1,5}$ = 4.7 P = 0.09).

Table 2. Causes of failure of burrowing owl nest attempts in Cape Coral, Lee County, Florida, 1987–90. Excludes 105 failures where a cause could not be determined.

	No. of nest failures				
Cause	1987	1988	1989	1990	Total
Harassment	26	5	2	3	36
Mowing	0	1	4	0	5
Flooding	8	1	6	6	21
Predation	1	0	0	1	2
Construction	10	12	9	12	43
Adult mortality	1	7	0	4	12

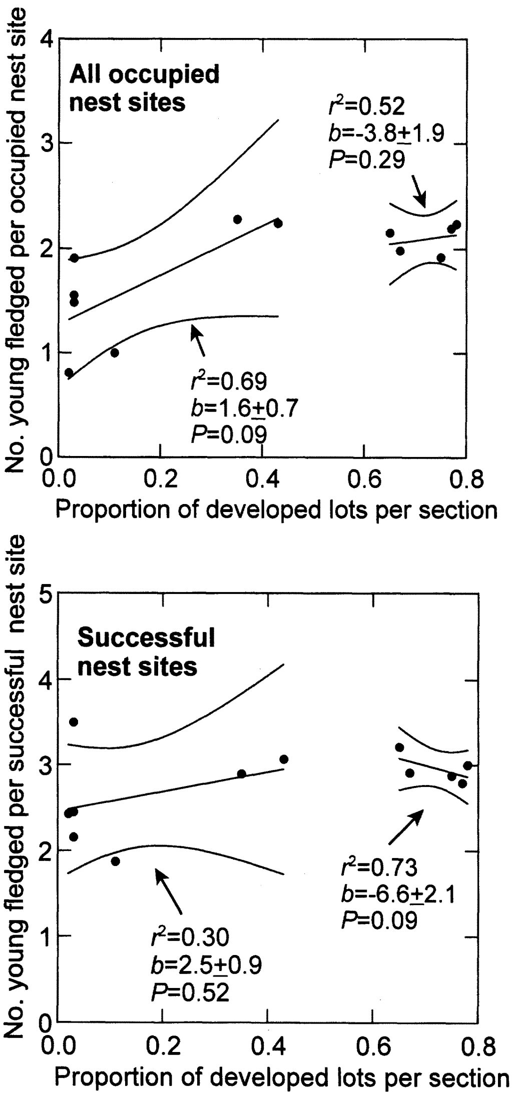

Fig. 4. Relationship between the estimated mean proportion of lots developed and the mean number of young fledged per occupied (top) and per successful (bottom) burrowing owl nest site per 2.59-km² section for the period 1987–90 in Cape Coral, Lee County, Florida. Regression lines are bounded by 90% CI.

Home construction occurred on 51 lots with burrowing owl nests during our study. Nest burrows were provided with a ≥10-m buffer zone in which no disturbance occurred on 29 lots, and mean productivity for these nest sites was 1.9 ± 0.3. On 22 lots where construction occurred without a protective buffer, productivity averaged 0.1 ± 0.6 young. Mean productivity at 685 nest sites on lots not affected by construction was 2.1 ± 0.7 young. Productivity where construction occurred without a buffer zone differed from productivity at buffered and unaffected nest sites (ANCOVA with year and section as covariates; $F_{2\ 731} = 11.08$, $P < 0.001$; Bonferroni all pairwise comparison $P < 0.10$). Productivity at burrowing owl nests in sodded yards of homes (1.8 ± 0.2, $n = 81$) was lower than productivity at nest sites on 0.1-ha (2.1 ± 0.2, $n = 112$) or >0.1-ha vacant lots (2.2 ± 0.08, $n = 543$; ANCOVA on ranks with year and section as covariates, $F_{2\ 634} = 2.36$, $P = 0.10$; Bonferroni all pairwise comparison $P < 0.10$).

DISCUSSION

The density of occupied nest sites on our study area was 6.9 pairs per km^2 at its maximum in 1990. Locally, the density of owls was much higher (up to 22.8 pairs per km^2 over a 2.59-km^2 area in section 2 in 1989), which we believe reflected that parts of the area constituted excellent burrowing owl habitat. Maximum densities reported for other burrowing owl populations are up to 9 pairs per km^2 in California (Coulombe 1971, Trulio 1997), a maximum of 17 pairs per km^2 in North Dakota (Grant 1965) and Saskatchewan (Wedgewood 1976), and up to 15 pairs per ha in small prairie dog (*Cynomys ludovicianus*) towns in western Nebraska (Desmond and Savidge 1996). Breeding nest site density of raptors is often, but not always, correlated with habitat quality (Newton 1979, 1998; Gehlbach 1994).

Spatial variation in nest site distribution of burrowing owls was similar to that reported previously by Wesemann and Rowe (1987). These authors showed that primary prey of Florida burrowing owls in Cape Coral (arthropods and anoles) was more abundant in sodded, landscaped yards than in vacant lots, hence superior foraging habitat was more abundant where houses were common. However, burrowing owl nesting density declined in the presumably food-rich heavily developed landscape, even taking into account the decrease in the amount of available nesting habitat that accompanied development (Wessemann and Rowe 1987). This suggests that other factors begin operating on owl populations at high levels of development.

Burrowing owl nest success ranges from 33% to 100% (Thomsen 1971, Martin 1973), and productivity ranges from 1.6 to 4.7 young per occupied nest site (James et al. 1997, Johnson 1997, Mealey 1997, Trulio 1997). Productivity on our study area was consistently toward the lower end of this range, yet our study population increased. Clutch sizes of burrowing owls in Florida are lower than in more temperate latitudes (Haug et al. 1993), hence the consistently smaller maximum brood sizes might simply reflect a decrease in reproductive potential at lower latitudes, a trait common to several other raptors (Newton 1977). We cannot rule out the possibility that our study area was a sink maintained by immigration, but this seems unlikely. Portions of the Cape Coral Peninsula that were within 2–3 times the maximum dispersal distance we measured in our study population (Millsap and Bear 1997) did not differ in any obvious way from the study area with regards to habitat or development. Moreover, these areas supported burrowing owl populations similar in size, distribution, and fecundity to our study population, as determined from surveys we conducted of these areas in 1988 and 1989 to locate and monitor productivity of banded emigrants from our study population.

Florida burrowing owls that occupied nest sites in moderately to heavily developed parts of our study area fledged the most young per attempt. Burrowing owls nesting in human-altered areas of Las Cruces, New Mexico and residential areas of Broward and Dade Counties, Florida, also experienced higher productivity than owls in proximate undeveloped areas (Botelho and Arrowood 1996, Mealey 1997). Gehlbach (1994) reported similar findings for the Eastern screech-owl (*Otus asio*) in northcentral Texas. Gehlbach (1994) attributed the better reproductive performance of suburban screech owls to a more moderated climate, more stable prey base, and protection from predators. Botelho and Arrowood (1996) suspected burrowing owls in Las Cruces were responding positively to higher prey availability in disturbed areas, and negatively to higher owl densities in natural areas. On our study area we suspect that the increasing abundance of prey along the development gradient (Wesemann and Rowe 1987) was primarily responsible for higher owl densities and higher burrowing owl reproductive performance at moderate levels of development. However, there was a trend toward declining numbers of young fledged at successful nests at the highest levels of development, which leads us to suspect the positive benefits of a high prey base are partly offset by other factors on nest sites where >60% of lots are developed.

MANAGEMENT IMPLICATIONS

Our results suggest some factors that may limit burrowing owl numbers at high levels of development can be ameliorated by management actions. First, the decrease in nest failures due to harassment that we observed between 1987 and 1988 coincided with the implementation of a formal, mandatory burrowing owl education program in Cape Coral public schools (C. Bear, Lee County Public Schools, unpublished data). Consequently, we believe that education is an important component of a successful management program for burrowing owls in urban settings. Second, buffer zones placed around nest sites on lots where construction occurred during the breeding season were effective in shielding owls from disturbance, and allowing nesting activity to continue to a successful conclusion. We suspect that the probability of successfully protecting a nest increases with the size of the buffer zone, but even buffers as small as 10 m were effective on our study area. Finally, we found that burrowing owls were capable of successfully nesting in the sodded yards of homes, however, the number of young fledged from nests in yards was significantly lower than from nests in vacant lots. This suggests that maintaining burrows in the yards of homes after construction has merit, but that these nest sites may not produce young at a rate sufficient to maintain the population.

Ensuring the long-term persistence of burrowing owl nest sites where ≥60% of lots are developed in the urban landscape of Cape Coral will prove challenging given the growth rates and cost of real estate. One approach that would not involve buying land would be to enter into agreements with the managers of public facilities such as schools, athletic fields, churches, parks, libraries, and office building complexes that already provide burrowing owl habitat. The primary management needs for these sites would be a long-term commitment to not plant trees and shrubs, to maintain regular mowing around burrows with devices not likely to cause burrows to collapse, to provide opportunities for owls to excavate their own burrows by strategically removing 1-m diameter plugs of sod to allow direct access to soil (Wesemann 1986), and to control excessive human disturbance while allowing for public viewing.

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