

PHILOPATRY AND NEST SITE REUSE BY BURROWING OWLS: IMPLICATIONS FOR PRODUCTIVITY

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ABSTRACT.—We examined demographics of an annually migratory population of western Burrowing Owls (*Athene cunicularia hypugaea*) in Colorado from 1990–94. We banded 555 Burrowing Owls (60% of the known population on the study area) as adults or as nestlings. Five hundred thirteen banded owls (92%) were never reencountered after the year in which they were banded. Forty-two banded owls (8%) returned to the area in ≥ 1 year following banding, and used the area for 2–4 years. Males and females banded as adults returned at similar ($P = 0.45$) rates (19% and 14%, respectively); 5% of banded nestlings returned. Adult males and females nested in formerly used sites at similar rates (75% and 63%, respectively; $P = 0.71$). We found no difference in productivity between philopatric adults (those returning to any portion of the study area) and presumed new adults. However, past brood size was greater for females that returned to former nest sites ($\bar{x} = 4.9 \pm 0.69$) than for females that changed nest sites in subsequent years ($\bar{x} = 2.2 \pm 0.79$; $t_{14} = -2.52$, $P = 0.02$). Females banded as nestlings that returned as adults always did so after a 1-yr absence from the study area. Conversely, males banded as nestlings that did return, with one exception, returned first in the year following hatch. Fledge rate from 167 nests ranged from 0–9 young per nest ($\bar{x} = 3.62 \pm 0.19$). Nest density increased with the number of years sites were used by breeding owls, but density did not affect mean fledge rate.

KEY WORDS: *Burrowing Owl*; *Athene cunicularia*; *demography*; *migration*; *nest-site reuse*; *philopatry*; *reproduction*.

Filopatría y reutilización de sitios de anidación por *Athene cunicularia hypugaea*: implicaciones para su productividad

RESUMEN.—Examinamos la demografía de una población migratoria anual de *Athene cunicularia hypugaea* del oeste en Colorado entre 1990–94. Anillamos 555 lechuzas (60% de la población conocida en el área de estudio) adultos y pichones. Quinientos trece lechuzas anilladas (92%) nunca fueron encontradas después del año en que fueron anilladas. Cuarenta y dos lechuzas anilladas (8%) regresaron al área después del año en que fueron anilladas y utilizaron el área por 2–4 años. Los machos y hembras anilladas como adultos retornaron en tasas similares (19% y 14% respectivamente; $P = 0.45$); 5% de los pichones anillados regresaron. Los machos y hembras adultos anidaron en sitios previamente utilizados, con tasas similares (75% y 63% respectivamente; $P = 0.71$). No encontramos diferencias en la productividad entre adultos filopátricos (aquellos que regresaron a alguna porción del área de estudio) y los presumibles nuevos adultos. Sin embargo, los pasados tamaños de la nidada fueron mayores para las hembras que retornaron a los sitios de anidación anteriores ($\bar{x} = 4.9 \pm 0.69$) que para las hembras que cambiaron de sitio en los años subsiguientes ($\bar{x} = 2.2 \pm 0.79$; $t_{14} = -2.52$, $P = 0.02$). Las hembras anilladas como pichonas regresaron después de un año de ausencia al área de estudio. Opuestamente, los machos anillados como pichones que regresaron al área de estudio lo hicieron al año de haber eclosionado con una sola excepción. La tasa de pichones de 167 nidos osciló entre 0–9 por nido ($\bar{x} = 3.62 \pm 0.19$). La densidad de nidos se incrementó con el número de sitios/año utilizados por las lechuzas en reproducción, pero esta densidad no afectó la tasa de pichones.

[Traducción de César Márquez]

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The Western Burrowing Owl (*Athene cunicularia hypugaea*) is a species of concern throughout much of its range in the U.S. (Rich 1984) and Canada (Ratcliff 1986, Johnsgard 1988). Campaigns against burrowing mammals that provide nest sites for Burrowing Owls (Butts 1973, Zarn 1974) and habitat loss to development by humans (Zarn 1974, Millsap and Bear 1997) are principal factors suspected in population declines. In Colorado, Burrowing Owls depend chiefly on black-tailed prairie dogs (*Cynomys ludovicianus*) for nesting burrows, and often return to nesting areas used previously (Plumpton and Lutz 1993a). Philopatry and nest burrow reuse by Burrowing Owls have been well-documented (Martin 1973, Gleason 1978, Rich 1984). However, little is known about demographic parameters and the effects of prior reproductive success on site fidelity.

STUDY AREA

We conducted fieldwork on the Rocky Mountain Arsenal National Wildlife Refuge (RMANWR), located 16 km from Denver, CO in southwestern Adams County. This 6900 ha area is vegetated primarily by weedy forbs, cheatgrass (*Bromus tectorum*), perennial grasses and crested wheatgrass (*Agropyron cristatum*). Shrubs include yuccas (*Yucca* spp.), sand sagebrush (*Artemisia filifolia*), and rubber rabbitbrush (*Chrysothamnus nauseosus*) that occur in patches throughout the area.

METHODS

We captured and banded Burrowing Owls during the breeding seasons (1 April–31 July) from 1990–94. We used primarily Sherman and Tomahawk traps to capture nesting Burrowing Owls and their young (Plumpton and Lutz 1992, 1993b). We banded owls with color-anodized aluminum leg bands engraved with unique alpha/numeric combinations (Acraft Sign and Nameplate Co., Ltd., Edmonton, Alberta Canada) and classified owls as either young of the year or adult (≥ 1 yr). We surveyed the study site daily during the breeding season to locate nest burrows, count young and trap owls. Our surveys consisted of driving roads and using spotting scopes to identify nesting and previously banded Burrowing Owls. We also walked prairie dog towns inspecting burrows for signs of occupancy by Burrowing Owls (whitewash, castings and prey remains). We defined mated pairs as those that used a single burrow and attempted to nest. We defined successful nesting attempts as those in which ≥ 1 young fledged (Steenhof 1987). We estimated minimum brood size as the maximum number of young seen at each burrow prior to fledging.

We classified Burrowing Owls that returned to RMANWR after residency in any prior year as philopatric. We calculated the rate of philopatry by dividing the number of owls banded in any year by the number that returned in one, two, three, or four subsequent years. To explore the relationship between reproductive performance and philopatry, we tested the null hypothesis that

brood sizes of philopatric Burrowing Owls and broods from those owls nesting for only a single season were equal.

Because we did not measure individual territory sizes, we defined nest-site fidelity subjectively to include those owls that nested within the same or an adjacent $\frac{1}{16}$ section (0.162 km²) site used in any previous year. We included adjacent sites because roads surround all sections at RMANWR, often bisecting contiguous prairie dog towns, and Burrowing Owls commonly nest along roadsides (Plumpton and Lutz 1993a, 1993b). Therefore, consecutive nest attempts in adjacent sites were often in close proximity and within the same prairie dog town. The rate at which adults returned to previous nest sites was the proportion of banded Burrowing Owls that returned to previous nest sites, or those banded as nestlings that returned as adults to nest within the same or adjacent sites. To determine whether nest outcome influenced future returns to nest sites, we tested the hypothesis that brood sizes from the prior year for returning Burrowing Owls and broods from owls that changed nest sites in successive years were similar.

We banded owls as nestlings and as adults. Banded nestlings encountered in subsequent years could be aged to a specific year class. Owls banded as unknown-aged adults and encountered in subsequent years were assigned an age class by adding the number of years since initial capture to ≥ 1 . We excluded owls initially captured in the last two years of study to minimize bias in estimating returns.

We tested whether $\frac{1}{16}$ section sites that were used in more years supported more nests, and whether the density of breeding pairs influenced the average productivity of nests.

For all paired analyses, we used *t*-tests when data were normally distributed and Wilcoxon 2-sample tests (*z*) to make comparisons when data were nonnormally distributed. For comparisons involving > 2 samples, we used Kruskal-Wallis *H* tests (SAS Inst. Inc. 1988). For small sample size tests for differences in proportion (e.g., return rates between sexes), we used pooled *t*-tests. All statistical tests were conducted at a significance level of $\alpha = 0.05$. Means are expressed \pm SE.

RESULTS

We banded 555 Burrowing Owls from 1990–94, providing 4 consecutive years of potential return to RMANWR involving 514 individuals (those banded before 1994). During all nesting years, 201 of 334 nesting adults (60%) were known individuals (banded or band-resighted; Table 1). We estimated that this population fledged 533 owlets prior to 1994, of which we banded 369 (69%).

Of the 514 Burrowing Owls banded prior to 1994, 42 (8%) returned in ≥ 1 year after the year of banding. The return rate of banded owls was highest in the year immediately following banding for both sexes and age classes (Table 2). Males and females banded as adults returned at similar rates (19% and 14%, respectively; $P = 0.45$).

Table 1. Burrowing Owls banded or band-resighted (percentage of breeding population^a) at Rocky Mountain Arsenal Wildlife National Wildlife Refuge, Colorado, 1990–94.

AGE/SEX	YEAR					TOTAL
	1990	1991	1992	1993	1994	
Adult/F	15 (56)	26 (68)	22 (56)	32 (76)	14 (67)	109
Adult/M	19 (70)	21 (55)	21 (54)	22 (52)	9 (43)	92
Nesting/Unk.	61 (56)	114 (69)	57 (37)	137 (85)	36 (51)	405
Total	95	161	100	191	59	606

^a # banded or identified from banding in a previous year/# breeding.

Of the 369 Burrowing Owls banded as nestlings prior to 1994, 18 (5%) returned in one or more years after hatch. Of these, 13 (72%) were male and 5 (28%) were female. None of the females returned in the year following their hatch; all returned after a 1-yr absence from RMANWR. Conversely, all but one of the males banded as nestlings that returned in any year, returned first in the year following hatch. Brood sizes of philopatric owls were not different from those of single-season nesters for males (philopatric males: $N = 16$, $\bar{x} = 4.2 \pm 0.66$; single season males: $N = 43$, $\bar{x} = 3.7 \pm 0.43$; $z = 0.47$, $P = 0.64$) or females (philopatric females: $N = 15$, $\bar{x} = 3.7 \pm 0.63$; single season females: $N = 69$, $\bar{x} = 3.8 \pm 0.28$; $z = -0.22$, $P = 0.83$).

Of the owls that returned to RMANWR, 75% of the males banded as adults returned to previously used nest sites, while 63% of females returned to former nest sites ($P = 0.71$). Adult males that returned to nest sites supported broods in the previous year ($\bar{x} = 3.9 \pm 0.81$) no different in size from returning males that changed nest sites ($\bar{x} = 5.0 \pm 1.08$, $t_{14} = 0.69$, $P = 0.49$). However, productivity in the preceding year was greater for fe-

males that returned to former nest sites ($\bar{x} = 4.9 \pm 0.69$) than for females that changed nest sites in subsequent years ($\bar{x} = 2.2 \pm 0.79$; $t_{14} = -2.52$, $P = 0.02$).

Five hundred thirteen owls (92%) banded at the RMANWR were encountered in only the year of banding. Excluding the last two years of study, of those encountered during at least one year after banding, males ($N = 17$) occupied RMANWR for 2 or 3 yr, and females ($N = 13$) for 2–4 yr. The longest-lived owls we encountered were females; one was banded as a nestling and encountered during its fourth year, and one was at least one year old when banded, and encountered three years thereafter, in at least its fourth year (Fig. 1). The

Table 2. Philopatry rate (%) of Burrowing Owls banded at Rocky Mountain Arsenal National Wildlife Refuge, Colorado, 1991–94.

YEARS POST-BANDING	AGE AT BANDING			
	NESTLING <i>N</i> (%)	ADULT		BOTH <i>N</i> (%)
		MALE <i>N</i> (%)	FEMALE <i>N</i> (%)	
1	12 (3)	11 (19)	12 (14)	23 (16)
2	7 (3)	2 (5)	2 (4)	4 (4)
3	3 (1)	0 (0)	1 (3)	1 (2)
4	1 (1)	0 (0)	0 (0)	0 (0)

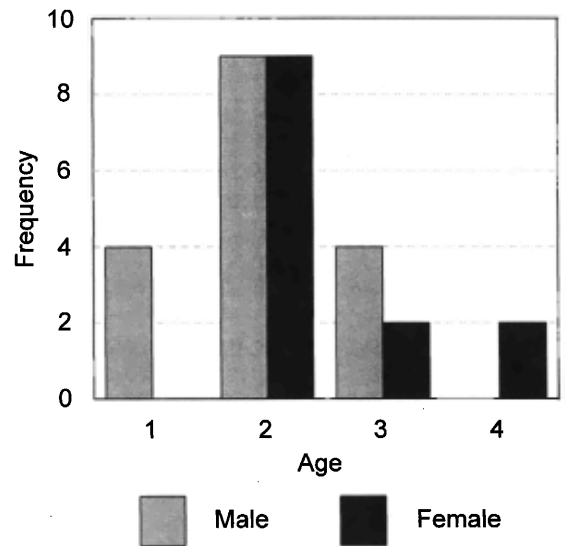


Figure 1. Age classes of banded Burrowing Owls reencountered (including multiple reencounters for some individuals) at Rocky Mountain Arsenal National Wildlife Refuge.

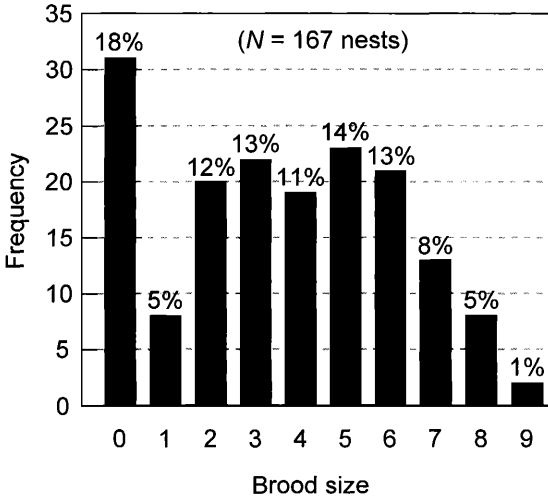


Figure 2. Productivity of 167 Burrowing Owl nests at the Rocky Mountain Arsenal National Wildlife Refuge.

median number of years that owls of both sexes were reencountered at the RMANWR was two.

From 1990–94, 167 nests were observed. At least 31 nests (18%) failed to produce a single chick. Nest success ranged from 0–9 young fledged ($\bar{x} = 3.62 \pm 0.19$; Fig. 2).

The $\frac{1}{16}$ section sites were occupied from 0 to all 5 yr of this study (0/5: $N = 361$, 1/5: $N = 19$, 2/5: $N = 18$, 3/5: $N = 4$, 4/5: $N = 6$, 5/5: $N = 4$). The study area was not homogeneous, and not all sites were suited for occupancy by owls. The mean number of nests/site increased with the number of years of five that the site was occupied (1/5: $\bar{x} = 1.2 \pm 0.12$, 2/5: $\bar{x} = 2.5 \pm 0.12$, 3/5: $\bar{x} = 4.25 \pm 0.75$, 4/5: $\bar{x} = 7.33 \pm 0.61$, 5/5: $\bar{x} = 8.5 \pm 0.87$; $h_4 = 42.48$, $P < 0.0001$; Fig. 3). However, the mean fledging rate did not differ among the 5 levels of annual reuse (1/5: $\bar{x} = 3.8 \pm 0.61$, 2/5: $\bar{x} = 4.1 \pm 0.37$, 3/5: $\bar{x} = 3.4 \pm 0.69$, 4/5: $\bar{x} = 3.4 \pm 0.28$, 5/5: $\bar{x} = 3.7 \pm 0.24$; $h_4 = 1.58$, $P = 0.8$; Fig. 3).

DISCUSSION

Traditionally, differences in philopatry between sexes have been explained as mechanisms to enhance reproductive success (Greenwood 1980). In our study, males and females were equally philopatric and returned to nest sites at an equal rate, but females obtained a reproductive advantage in this behavior by increasing their productivity. However, the relationships we observed between philopatry and reproductive success suggested that, for

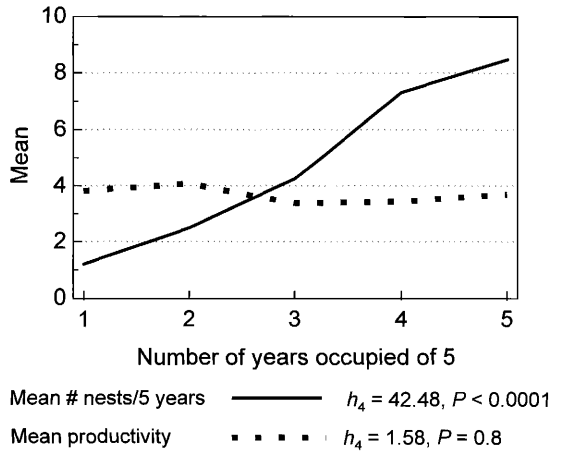


Figure 3. The effects of increasing annual site reuse on mean Burrowing Owl nest-site density and productivity at the Rocky Mountain Arsenal National Wildlife Refuge, 1990–94.

females, a former mate is not as important to reproductive success as is the former nest site. The actual criteria used by females to choose mates are not known for most species (Wittenberger 1983). In our earlier work, we found only weak relationships between morphological characteristics in mated owl pairs (Plumpton and Lutz 1994) and only moderate differences between nesting burrows used and those available, but unused by nesting Burrowing Owls (Plumpton and Lutz 1993a). Assuming female selection, male Burrowing Owls may be chosen for the nesting territories they hold preferentially over other criteria.

For Florida Burrowing Owls (*A. c. floridana*), Millsap and Bear (1997) observed much higher reencounter rates for both sexes of adults, and for owls banded as nestlings. They also observed that male adults reused former nest territories most frequently. As Millsap and Bear (1997) observed for the Florida subspecies, we observed two pairings between a female and her offspring from the previous year. We concur that migration would tend to separate breeding pairs, and that returns to natal sites by yearling males, combined with nest-site fidelity by their mothers, could contribute to such mother-son pairings. Millsap and Bear (1997) also reported adult male Burrowing Owls excavated burrows for themselves on their prior territories, while allowing their sons to occupy their own natal burrow for nesting. They attributed this behavior to reproductive advantages gained by the male in instances where female

selection favors a mate with previous site familiarity, in this instance her son. We offer as an alternative (though not mutually exclusive), hypothesis that the father of the yearling male may increase his inclusive fitness by guaranteeing his son a nest territory and mate, while assuring a territory for himself, and presumably not reducing his own direct fitness. Density of breeding pairs appeared to be unrelated to brood size in our study, so a male sharing a territory with his son may not suffer decreased direct fitness as a result.

Millsap and Bear (1997) also indicated the possibility that there may be little advantage, in terms of retained site familiarity, conferred upon migratory owls. Our population consisted of complete annual migrants, and yet we did observe nest-site reuse in successive years. Therefore, migration may lessen the advantages gained by previous experience on a nest site, but may not eliminate them entirely. Because we lack band returns from elsewhere in the migratory cycle, we do not know whether owls that failed to return to the study area were killed or migrated elsewhere.

Unlike results from Millsap and Bear (1997) our study found that nest-site reuse by females was more often preceded by above-average brood sizes. In our work, broods from previous years were significantly larger for females that reused a site than for those that selected a new nest site.

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