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NESTING SUCCESS AND HABITAT RELATIONSHIPS OF BURROWING OWLS IN THE COLUMBIA BASIN, OREGON¹

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Burrowing Owls (Athene cunicularia) were studied to determine their nesting Abstract. success and patterns of nest-site selection in northcentral Oregon during the breeding seasons of 1980 and 1981. Nest success was 57% for 63 nests in 1980 and 50% for 76 nests in 1981. Desertion was the major cause (32%) of nest failures and was related to the proximity of other nesting pairs. Depredation of nests by badgers (Taxidea taxus) was the next most frequent cause (14%) of nest failure. Nests lined with livestock dung were significantly less prone to predation than unlined nests. Burrowing Owls occupied three of the five habitats surveyed for pairs. Burrows with good horizontal visibility and little grass coverage were preferred. Elevated perches were used in habitats with average vegetation height >5 cm and not in habitats with vegetation <5 cm. Elevated perches presumably improved the Burrowing Owl's ability to detect both predators and prey by increasing their horizontal visibility. Low grass cover may be indicative of a high availability of prey preferred by Burrowing Owls. The nesting ecology of Columbia Basin Burrowing Owls appears to be strongly influenced by the availability of badger burrows for nesting and, in turn, on predation pressures by badgers.

Key words: Burrowing Owl; Athene cunicularia; nesting success; nesting habitat; shrubsteppe; Columbia Basin; nest predation.

INTRODUCTION

Burrowing Owls (Athene cunicularia) inhabiting the prairie grasslands of the midwestern and southwestern United States frequently use abandoned prairie dog (Cynomys spp.) and ground squirrel (Spermophilus spp.) burrows for nesting and shelter (Butts 1971, Coulombe 1971, Martin 1973, MacCracken et al. 1985). Prairie dogs and ground squirrels also modify the habitat by intense grazing and clipping of unpalatable vegetation around their burrows (Bonham and Lerwick 1976, Hansen and Gold 1977). This removal of vegetation is important to nesting Burrowing Owls as it increases their horizontal visibility (Best 1969, Coulombe 1971, MacCracken et al. 1985) which aids in early detection of potential nest predators, especially mammalian predators (Byrkjedal 1987).

Burrowing Owls in the Pacific Northwest frequently use abandoned badger (*Taxidea taxus*) burrows for nesting (Maser et al. 1971, Gleason and Craig 1979, Rich 1986) and, in the Columbia Basin, may be dependent on badgers for burrows, because the burrows of resident ground squirrels are too small. However, Burrowing Owls presumably risk lower nesting success by nesting in badger burrows (Messick and Hornocker 1981), because badgers commonly prey on Burrowing Owl eggs and nestlings (Coulombe 1971, Gleason and Craig 1979). Consequently, Columbia Basin Burrowing Owls may have adopted strategies of nest-site selection that exhibit well-developed antipredator behaviors in response to badgers.

The purpose of this paper is to describe the causes of nesting failures and characterize nest sites of Burrowing Owls in the Columbia Basin. We also discuss diet and its influence on nesting success and how nest-site selection may be influenced by prey availability and predation by badgers.

STUDY AREA

The study area was in the shrub-steppe zone of northern Gilliam, Morrow, and Umatilla counties in northcentral Oregon. The topography there ranges from flat to undulating with elevations ranging from 75 m on the loamy-sand soils near the Columbia River to 200 m on the silty-loam soils in the southern uplands. The average annual precipitation in the area is approximately 22 cm (Ruffner 1978), most of which falls during the

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winter and early spring. Summers are hot and dry with several days of maximum temperatures exceeding 40°C.

The natural vegetation of the study area is included in the Artemisia/Stipa or Artemisia/Agropyron plant associations (Poulton 1955), but vegetation climaxes are rare because of edaphic conditions, fire, or livestock grazing. Cheatgrass (Bromus tectorum), needle-and-thread (Stipa comata), blue-bunch wheatgrass (Agropyron spicatum), and Sandburg's bluegrass (Poa sandburgii) are the most abundant grasses. Important shrubs are antelope bitterbrush (Purshia tridentata), snakeweed (Gutierrezia sarothrae), gray rabbitbrush (Chrysothamnus nauseosus), and big sagebrush (Artemisia tridentata). Locally abundant forbs include hairy plantain (Plantago patogonica), filaree (Erodium cicutarium), and snowy buckwheat (Eriogonum niveum). Five distinct plant communities or habitats were selected for study: cheatgrass grassland, bunchgrass grassland, rabbitbrush shrubland, bitterbrush shrubland, and an intensively grazed habitat dominated by forbs and snakeweed (see Green 1983 for detailed descriptions).

METHODS

Nesting pairs of Burrowing Owls were located by systematically searching the study areas. All areas were searched at least twice a season to locate late-nesting pairs. When a nest was found, the immediate area was repeatedly searched for neighboring pairs.

Because young Burrowing Owls may continue to use the nest burrow for shelter into the late summer and fall, a nesting attempt was considered successful when young had reached flight stage (6 weeks of age). Occurrence of eggshells in pellets (castings) aided in determining whether nesting had occurred, as Burrowing Owls frequently ingest their own eggshell fragments (Green 1983). Behavioral activities which coincide with egg laying, incubation, and brooding (see Coulombe 1971, Martin 1973) plus the length of known occupancy were also used to determine if nesting occurred. Unsuccessful nests were those destroyed or deserted after eggs had been laid. Desertion was defined as adult abandonment of a nest occupied by eggs or young, for whatever reason, including death of the adults. Determination of desertion was made by noting a lack of tracks or fresh prey. Entrances of deserted burrows were often covered with webs of black widow spiders (*Latrodectus mactans*), common inhabitants of nest burrows in the Columbia Basin. The area within 300 m of a deserted nest burrow was intensively searched for a "new" nest burrow to determine if shifting of burrows had occurred as described by Henny and Blus (1981).

Diets of Burrowing Owls were determined by analyzing regurgitated pellets (castings). Pellets were collected in groups from around perches and burrows at each nest site approximately once monthly in 1980 and every 2 weeks in 1981. Each group was soaked overnight in a 2-M (8%) solution of NaOH, a method which dissolves hair and feathers but leaves chitin and osseus material intact (Degn 1978). After material was strained and dried, vertebrate and arthropod parts were separated from the pellet mass, identified to the lowest taxon possible, and the number of individuals per taxon counted. Head capsules, elytra, and jaws of arthropods, and lower mandibles of rodents were the main body parts used in the identification.

Abundance of badger burrows was estimated along transects by stratified random sampling; stratification was relative to the five different habitats. Burrow abundance was surveyed on 110 randomly located transects, each 500 m in length. Transect width varied between 30 and 60 m depending on vegetation density. These data were used to establish and compare burrow availability and density among the five habitats.

The importance of vegetative structure in nestsite selection was determined by comparing vegetative characteristics of occupied nest sites with the general habitat. Assuming Burrowing Owl habitat requires available burrows, vegetation measurements around unoccupied burrows ("potential" nest sites) were used in describing the general habitat. Vegetation was systematically sampled along four transects, each 50 m in length, radiating from the burrow. The transects were 90° apart with the first direction selected randomly. Percent cover of shrubs, forbs, grasses, and bare ground was estimated systematically at 40 quadrats (10×50 cm), distributed every 5 m along the transects (Daubenmire 1959). Effective height and vertical density (Wiens 1973) were also recorded at each of the 40 quadrats. Shrub cover was estimated using the line-intercept method (Piper 1973), and shrub volume was estimated by multiplying intercept distance by

Variable	Description			
Percent bare ground Percent forb Percent grass Percent shrub	Percentage estimate of coverage of bare ground, and canopy coverage of forbs, grasses, and shrubs (Daubenmire 1959).			
Shrub intercept	Meters of shrubs intercepted along a 50-m transect divided by 50 (Piper 1973).			
Shrub volume	Shrub intercept multiplied by the mean height of the intercepted shrubs.			
Effective height	Height at which 90% of a white board is obscured by vegetation when viewed 1 m from the ground at a distance of 10 m.			
Vertical density 0–10 cm Vertical density 10–20 cm Vertical density 20–30 cm Vertical density 30–40 cm Vertical density 40+ cm Vertical density total	Number of touches by plants within 10-cm height intervals along a thin vertical rod (Wiens 1973).			
Number of perches	Number of elevated perches located within 300 m of each nest site.			
Mean perch distance	Mean distance from burrow to perches at each nest site.			
Mean perch height	Mean height of perches at each nest site.			
Foliage height diversity Foliage height evenness	Indices computed from vertical density measurements according to Pielou (1975:8–15).			

TABLE 1. List and description of variables measured in characterizing the habitat of occupied and potential nest sites of Burrowing Owls in the Columbia Basin.

90% height of intercepted shrub. Fifteen vegetative characteristics plus three computed variables (Table 1) were used to compare occupied vs. potential nest sites and to compare nest sites among habitats.

STATISTICAL ANALYSIS

To determine whether nest desertion was related to proximity to another nest, a median test (Steel and Torrie 1980) was performed on distances between nearest-neighbor nests. Specific nearestneighbor distances were used only once in the analysis to prevent bias by pairs having reciprocal nearest neighbors. Nests known to be lost by depredation were not used in the analysis. A 2×2 contingency table was used to test for differences in nest success between nests lined and not lined with livestock dung. Direct Discriminant Function Analysis (SPSS; Klecka 1975) was used to test for differences in vegetative characteristics between occupied and potential nest sites and to determine which variables were significant (P < 0.05). One of each pair of variables that were highly correlated (r > 0.70) was removed from the variable set to eliminate interdependencies before discriminant analyses were performed. Variables were compared between habitats by t-tests.

RESULTS

NEST SUCCESS

In 1980, 33 of 63 (57%) occupied nests successfully fledged young, and 38 of 76 (50%) were successful in 1981. Desertion was the major cause of nest failure and accounted for 35% and 30% of the nesting attempts in 1980 and 1981, respectively. Predation resulting in nest failure occurred at 8% of the nests in 1980 and 20% of the nests in 1981; badgers were responsible for 18 of the 20 (90%) nests lost (as indicated by reexcavation characteristic of badgers). The other two nests were destroyed by canids; one by a coyote (Canis latrans) and the other by a domestic dog (Canis familiaris). Overall nest success (53%) of Burrowing Owls in the Columbia Basin was much lower than the 79% (n = 54) found in Oklahoma (Butts 1971) but similar to the 54% (n = 24) reported by Thomsen (1971) in California. There was a significant ($\chi^2 = 12.7$, P < 0.0001) difference in distances between nearest neighbors for successful and deserted Burrowing Owl nests. For all pairs of nests with an internest distance less than 110 m, at least one of the two nests was deserted in midnesting cycle, whereas only three of 21 (14%) pairs with internest distances greater than 110 m aban-

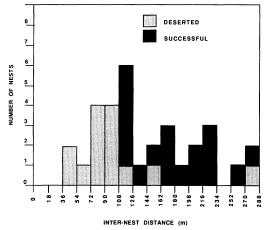


FIGURE 1. Nesting success of Burrowing Owls in relation to distance to nearest nesting pair of conspecifics. "Deserted" values are internest distances where at least one of two associated nests was deserted. If both nests fledged young, the internest distance was called "successful."

doned at least one of the nests (Fig. 1). Many of the desertions occurred after hatching, and no evidence of burrow shifting was found at badger den nest sites. In three cases, lethargic (thought to be starving) young were found at burrow entrances in which no adults were seen then or thereafter.

Martin (1973) hypothesized that Burrowing Owls line their nest and the tunnel entrance with cattle dung in order to avoid predators by masking nest odors. Many nest sites in our study were located in areas where livestock dung was not available. Thus, we had an opportunity to test this hypothesis. In 1981, 15 nests were lost by predation, of which only two (13%) were lined with dung. In contrast, of 32 nests which were successful, 23 (72%) were lined. The difference was significant ($\chi^2 = 14.1$, P < 0.0001).

DIET

Analysis of 5,559 pellets revealed that arthropods (mainly insects) comprised 92% of the total diet by number while vertebrates (mostly rodents) comprised the remaining 8%. However, because of the size difference of the two taxa, vertebrates comprised 78% of the biomass. Nearly 90% of the vertebrate prey were rodents and >99% were mammalian. Composition of the two taxa in owl diets was not constant throughout the breeding season. Burrowing Owls preyed heavily upon rodents in the spring, then shifted

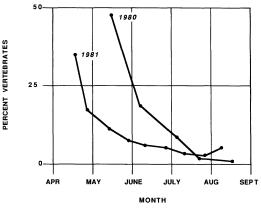


FIGURE 2. Seasonal change in vertebrate composition of the diet by frequency of occurrence (prey ≥ 3 mg) for Burrowing Owls in the Columbia Basin.

to an almost exclusively insect diet by the summer (Fig. 2). We attributed this shift in diet to an increase in concealing cover for rodents and a general seasonal increase in insects. Further analysis of diet can be found in Green (1983).

NESTING HABITAT

Of the five habitats searched for Burrowing Owl nest sites, nesting pairs were found in the snakeweed, cheatgrass, and bitterbrush habitats, but not in the bunchgrass or rabbitbrush habitats. Only dispersing juveniles were occasionally observed in the latter habitats. Densities of badger burrows were estimated in all habitats to determine if burrow availability influenced the disparity in habitat selection. There was an average of 1.8 (SE = 0.42) potential burrows/ha in the three habitats used by the owls for nesting and 3.1 (SE = 1.26) potential burrows/ha in the two habitats (bunchgrass and rabbitbrush) not used. Burrow availability was obviously not the reason for the absence of nesting owls in the bunchgrass and rabbitbrush habitats.

There was a significant (P < 0.05) difference in vegetative characteristics between occupied and potential nests (burrows) in both the cheatgrass and bitterbrush habitats (Table 2). For the cheatgrass habitat, mean perch height and percent grass were important variables that discriminated between the occupied and potential sites. Burrowing Owls selected nest sites with higher perches (85.9 cm vs. 31.6 cm) and less grass coverage (28% vs. 50%) as compared to potential nest sites (Table 2). The discriminant function correctly reclassified 82% of the sites in the cheat-

Habitat	Percent correctly classified	Variables entered	Occup	ied nests ¹	Potential nests ²	
			X	(SD)	X	(SD)
Cheatgrass	82	Mean perch height (cm) Percent grass cover	85.9 28.3	(43.0) (13.1)	31.6 49.6	(37.8) (19.4)
Bitterbrush	88	Shrub volume	9.3	(4.7)	13.5	(3.7)

TABLE 2. Discriminant function analysis on vegetative characteristics of occupied and potential nest sites of Burrowing Owls in cheatgrass and bitterbrush habitats in northcentral Oregon.

n = 18 nests for each of the cheatgrass and bitterbrush habitats. n = 15 nests for each of the cheatgrass and bitterbrush habitats.

grass habitat. Shrub volume was the only variable important in discriminating the two groups in the bitterbrush habitat; Burrowing Owls selected nest sites with lower mean shrub volumes (9.3 cm vs. 13.5 cm) as compared to potential sites (Table 2). For the bitterbrush habitat, 88% of the nests were reclassified correctly by the discriminant function. Although the bitterbrush habitat provided a large number of suitable perches, high shrub cover probably obstructed vision. As a result, Burrowing Owls selected nest sites in the habitat with lower shrub volumes than surrounding areas which may indicate a trade-off between the high number of potential perches and a minimum level of horizontal visibility.

Significant correlations between the variables selected by the DFA and other variables revealed further differences between occupied and potential burrows. Percent grass cover was negatively correlated (r = -0.897) with percent bare ground and positively correlated with vertical density at the 0–10 cm (r = 0.700), 0–20 cm (r = 0.708), and total height classes (r = 0.800) for the cheatgrass habitats (Table 3). No variables were highly correlated with mean perch height (P >0.05). Shrub volume was positively correlated with shrub cover (r = 0.881) and effective height (r = 0.827) for the bitterbrush habitats. Of these correlated variables, percent bare ground, vertical density (0-10 cm), and shrub intercept were significantly different (P < 0.05) univariately between occupied and potential burrows. Therefore, Burrowing Owls selected nest sites with more bare ground and less vertical density (0–10 cm) than that available in the cheatgrass habitat, and in the bitterbrush habitat the owls selected sites with less shrub cover (Table 3).

MacCracken et al. (1985) compared canopy coverage around Burrowing Owl nest sites in South Dakota prairie dog towns with the prairie outside of towns. They too found Burrowing Owls were selecting for higher bare ground (42% vs. 39%) and less grass coverage (35% vs. 44%) and at levels closely approximating our results for the cheatgrass habitat.

Intrahabitat comparisons were not made in the snakeweed habitat because all badger burrows found in both years were occupied by nesting pairs. However, interhabitat comparisons showed

Discriminant function	Correlated variables	Correlation coefficients	Occupied nests ¹		Potential nests ²		
variables			<i>x</i>	(SD)	x	(SD)	Р
Cheatgrass habitat:					_		
Mean perch height	None	_	_				
Percent grass	Percent bare ground	-0.897	54.8	(15.2)	41.3	(15.5)	*
-	Vertical density 0-10 cm	0.700	1.50	(0.66)	1.64	(0.57)	*
	Vertical density 10-20 cm	0.708	0.35	(0.28)	0.61	(0.34)	ns
	Vertical density total	0.800	1.95	(0.91)	2.49	(1.07)	ns
Bitterbrush habitat:							
Shrub volume	Shrub intercept (cover)	0.881	11.4	(5.30)	19.6	(7.60)	*
	Effective height	0.827	31.1	(8.80)	38.3	(11.9)	ns

TABLE 3. Variables that are highly correlated (r > 0.700) with variables that significantly separated occupied and potential nest sites of Burrowing Owls using direct Discriminant Function Analysis.

 1 n = 18 nests for each of the cheatgrass and bitterbrush habitats. 2 n = 15 nests for each of the cheatgrass and bitterbrush habitats. * P < 0.05, ns = nonsignificant; univariate F-ratio.

that nest sites in the snakeweed habitat were not significantly different from nest sites in any of the cover classes in the cheatgrass habitat, but were significantly different (P < 0.0001) in effective height and all vertical density classes. The mean effective height for snakeweed nest sites was only 4.7 cm compared to 9.8 cm for cheatgrass nest sites. Mean bare ground for snakeweed nest sites was identical (49%) to bitterbrush nest sites. Mean percent grass coverage was 36%, again very close to the findings (35%) of MacCracken et al. (1985) in South Dakota. Furthermore, Burrowing Owls nesting in the snakeweed habitat did not use elevated perches.

The dominant plants of the bunchgrass and rabbitbrush habitats appeared to be structurally unsuitable for owl perches. Burrowing Owls that were perched on rabbitbrush (usually because of our presence near their normal perches) were unstable. Because the mean effective height of vegetation in these habitats (>20 cm) is probably great enough to restrict horizontal visibility, lack of stable perches may partially explain why Burrowing Owls avoided bunchgrass and rabbitbrush habitats for nesting.

Soil texture had a significant effect on the longevity of a burrow and hence its suitability for renesting in subsequent seasons. Of the 85 nests in loamy-sand soils, 46% were silted in by the next nesting season. Of 13 nests in silty-loam soils, none were silted in. Reuse of available (open) burrows for nesting was also different for the two soil types. Of burrows used in the previous nesting season, only 52% of those still open were reoccupied in the loamy-sand soils. However, this is higher than the 31% recorded by Rich (1984) for Burrowing Owls using badger dens in Idaho (soil type not given). In many cases, a nest in a new burrow could be found within 50 m of a previously used burrow. All nest burrows were reused in the silty-loam soils. An extensive search in 1981 also disclosed that all available burrows in silty-loam soils were reoccupied, indicating little potential for population expansion and the importance of badger burrows for nesting in this area.

DISCUSSION

Nest desertion was most frequent when two pairs nested within 110 m of each other. In contrast, Burrowing Owls in Oklahoma (Butts 1971) and California (Thomsen 1971) often nested closer than 110 m, without a high frequency of deser-

tion. Although some desertions may have been due to death of adults, the high frequency of nest desertion by nearest-neighbor Burrowing Owls in the Columbia Basin may be related to the climate of the region and its effects on the activity cycles of prey. Food habits data collected in this study showed a dramatic shift in diet from small mammals in the spring to insects in the summer (Fig. 2). Above ground activity of pocket mice (Perognathus parvus), the major small mammal prey of Columbia Basin Burrowing Owls, tends to drop dramatically in June (O'Farrell et al. 1975). At this time foraging pairs began feeding closer to the nest, consistent with Central Place Foraging theory (Orians and Pearson 1979), which predicts that foraging distances decrease as size of prey decreases. Burrowing Owls may have also foraged close to their nests because of high arthropod densities. The senior author observed captures of rodents as far as 600 m from the nest but no insect captures beyond 100 m and most within 50 m. Furthermore, activity cycles of ground-dwelling arthropods shifts from diurnal to crepuscular periods as the hot summer progresses (Rickard and Haverfield 1965). Summer foraging bouts for insects usually lasted no more than 1 hr, occurred twice daily, and were very intense. Adjacent nesting pairs may have competed for the same food source in the middle of the nest cycle and, if so, were stressed by the demands of large brood sizes (generally six to eight) at the peak of their growth. When two pairs nested closer than 60 m, both nests were abandoned, further supporting the contention that as distance between nests decreased, competition intensified.

We also found that the distribution of badger burrows was generally clumped. Nesting pairs may have found it difficult to locate a burrow in suitable habitat not near another nesting pair. Consequently, prospective nesters may have had to choose between nesting near another pair, and the consequences that may follow, or not nesting at all.

Nest loss due to predation by badgers was much higher at nests that were not lined with livestock dung than those that were. Badgers frequently return to dens on a regular basis (Messick and Hornocker 1981) and are largely dependent on olfaction for prey detection (Knopf and Balph 1969, Lampe 1976). Presumably, Burrowing Owls line nests with dung to conceal both the odors of nest occupants and any lingering badger odors that may remain. The suggestion that birds use odiferous substances to conceal nests is not new. Kilham (1968) has described the "sweeping" of crushed insects by White-breasted Nuthatches (*Sitta carolinensis*) around the nest cavity as a defense against scent-trailing tree squirrels.

Byrkjedal (1987) described the open habitat of nesting Greater Golden-Plovers (*Pluvialis apricaria*) as an antipredator response to mammals. Early detection of predators allowed the adults to distract predators away from the nest before the predator could detect the nest scent. Presumably, Burrowing Owls nest in open habitats for the same reasons. Prairie dog towns are especially attractive to Burrowing Owls, and other open-nesters such as Mountain Plovers (*Charadrius montanus*) (Knowles et al. 1982), because open habitats required for nesting already exist and are created by prairie dogs.

Columbia Basin Burrowing Owls nested in open habitats, and habitats with tall dense vegetation were not used for nesting. The intensively grazed snakeweed habitat, although limited in availability, was particularly selected by nesting pairs as all available burrows were occupied. The cheatgrass and bitterbrush habitats were commonly used for nesting, particularly when elevated perches were available. Elevated perches increased the owl's horizontal visibility, which was probably important for both predator and prey detection in habitats with vegetation of moderate height. Coulombe (1971) has also suggested that the use of elevated perches aids in thermoregulation by Burrowing Owls, especially of males which spend much of the day watching for predators. The lightly feathered legs may act as heat dissipators, as in other species (Kahl 1963, Steen and Steen 1964, Butler 1982), if the owl is not near the soil surface where temperatures are high. Nesting in the snakeweed habitat probably does not require elevated perches, because the vegetation is so short that the males can extend their bodies partially into the shaded burrow entrance and still have good horizontal visibility.

A lack of dense grass cover was common to all occupied nest sites in all habitats. Dense grass or litter may impede movements of *Perognathus parvus* (Gano and Rickard 1982), *Peromyscus maniculatus* (Tester and Marshall 1961), and ground-dwelling arthropods (Tester and Marshall 1961, Rickard and Haverfield 1965), all important prey of Columbia Basin Burrowing Owls (Green 1983). Grasses also provide protective cover for the prey, making predation more difficult for raptors (Southern and Lowe 1968, Wakeley 1978, Bechard 1982). Also, higher populations of small mammals (Rogers and Hedlund 1980, Gano and Rickard 1982) and beetles (Rogers and Fitzner 1980) exist in shrub communities in the Columbia Basin which have relatively low grass coverage. In addition, we observed nesting Burrowing Owls invading areas which had recently burned, suggesting that fire may also play an important role in reducing vegetation around burrows.

In summary, the nesting ecology of Columbia Basin Burrowing Owls appears to be strongly linked with the denning and foraging behavior of badgers. Badgers are important to Burrowing Owls both because they are the chief provider of nest burrows and the major predator of owl nests. Selecting habitats of relatively short vegetation for nesting, utilizing elevated perches in habitats where the average vegetation height is >5 cm, and lining the nest with livestock dung appear to be strategies to prevent predation of adults or nest contents by badgers. Furthermore, the observed high rate of nest desertion by Columbia Basin Burrowing Owls may be a result of competition between closely nesting pairs, which is influenced by the clumped distribution of badger burrows.

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