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Source: Journal of Wildlife Management, 70(3):708-716. 2006.
Published By: The Wildlife Society
DOI: http://dx.doi.org/10.2193/0022-541X(2006)70[708:ABWAAU]2.0.CO;2
URL: http://www.bioone.org/doi/full/10.2193/0022-541X%282006%2970%5B708%3AABWAAU%5D2.0.CO%3B2

Research Article

Association between Wildlife and Agriculture: Underlying Mechanisms and Implications in Burrowing Owls

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Abstract

*Western burrowing owls (*Athene cunicularia hypugaea*) are endangered in Canada and several western U.S. states. Population declines have been linked with control measures aimed at burrowing mammals and loss of nesting habitat. The owls frequently associate with irrigated agriculture throughout portions of their western U.S. range. To determine potential factors driving the association of burrowing owls with agriculture, we examined availability of suitable nest burrows (burrow availability hypothesis), abundance of potential prey (prey availability hypothesis), and predation of nest burrows (predation hypothesis) for owls nesting in the Snake River Birds of Prey National Conservation Area in southwestern Idaho during 2001–2002. Nest burrow availability did not differ between agricultural and nonagricultural habitats, and occupancy rates of owls in artificial burrows were greater near agriculture. More rodent prey species were live-trapped in agricultural habitat compared with nonagricultural habitat, and there was no difference in relative abundance of prey between habitat types. Pellet remains indicated greater abundance and biomass of prey being consumed in agricultural habitat compared with nonagricultural habitat. Finally, predation rates of dummy nests in agricultural and nonagricultural habitat did not differ. These findings allow us to reject the burrow availability and predation hypotheses, while the prey availability hypothesis remains tenable. Thus, burrowing owls may nest near irrigated agriculture in southwestern Idaho because of increased diversity or availability of prey. We suggest that research is needed to determine how widespread this prey availability relationship may be and how management of burrowing owls in agricultural landscapes may take advantage of this apparent rich prey resource.* (JOURNAL OF WILDLIFE MANAGEMENT 70(3):708–716; 2006)

Key words

agriculture, Athene cunicularia, *burrow availability, burrowing owl, predation, prey availability.*

Agricultural practices historically have provided many different types of wildlife habitat, including shelterbelts, hedgerows and fencerows, cultivated fields, and fields in rotation. Although many species forage, nest, and seek cover in these habitats, wildlife and fish populations have declined significantly in areas of agricultural conversion (Carlson 1985, Murphy 2003). In fact, there is mounting evidence that converting natural landscapes into agricultural use can significantly affect a wide array of wildlife populations through erosion, exposure to herbicides and pesticides, and habitat destruction (Carlson 1985, Jahn and Schenck 1991, Gervais et al. 2000). These effects may be amplified by the shift from small-scale farming practices to large-scale monoculture farming seen throughout the United States and Canada (e.g., Peterjohn 2003).

Western burrowing owls (*Athene cunicularia hypugaea*) are listed as Endangered in Canada and several western U.S. states (Klute et al. 2003), and they too have experienced detrimental effects of agricultural conversion through destruction of nesting habitat (Haug et al. 1993), exposure to dangerous pesticides (James and Fox 1987, Gervais et al. 2000), and increasing vulnerability to predation (Haug et al. 1993). Despite this, throughout many portions of their western U.S. range, burrowing owls associate with irrigated agriculture, and they are the only raptor species that shows a significant affinity for agriculture in southern Idaho (Rich 1986, Leptich 1994). In our study areas in Idaho, burrowing owls inhabited both agricultural and nonagricultural areas (shrub steppe and disturbed grasslands), but they were most abundant and nested in greater density near irrigated agricultural fields (C. E. Moulton, Idaho Department of Fish and Game [IDFG], Boise, Id., USA, personal observation). Moreover, owls in both southeastern and southwestern Idaho can have higher productivity when nesting near irrigated agriculture (Gleason 1978, Belthoff and King 2002).

This association may be related to increased access to prey (Rich 1986) but, to our knowledge, no previous studies have tested this or alternative hypotheses. Therefore, we evaluated the following potential mechanisms for association of nesting burrowing owls with agriculture: 1) burrow availability, 2) prey availability, and 3) predation.

The burrow availability hypothesis states that burrowing owls nest more in agricultural areas because of greater burrow availability. For instance, if nonagricultural areas have fewer available burrows (i.e., nonagricultural areas are burrow-limited), then burrowing owls may nest more frequently in agricultural areas because more nest sites are available. To test the burrow availability hypothesis, we 1) established survey plots in agricultural and nonagricultural habitats, in which we determined abundance of underground burrows; and 2) placed artificial burrows of the configuration in which burrowing owls readily nest (see Smith and Belthoff 2001) in suitable agricultural and nonagricultural habitats and examined patterns of occupancy. By placing artificial burrows in both habitats, we removed potential confounding effects of burrow suitability and assessed occupancy rates in agricultural and nonagricultural areas experimentally.

The prey availability hypothesis states that burrowing owls nest in agricultural areas because of greater prey availability. Burrowing

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owls may more often nest near irrigated agricultural fields in the West because montane voles (*Microtus montanus*), which often are found in high concentrations within such fields (Gleason 1978, Rich 1986), and other important prey species may be more abundant or available than in nonagricultural plant communities. To test the prey availability hypothesis, we 1) compared relative abundance of potential prey in agricultural and nonagricultural habitats, and 2) compared abundance and composition of prey in diets of owls nesting in both habitats.

Finally, the predation hypothesis predicts that burrowing owls nest near agriculture because predation is lower. Nest predation on burrowing owls could be an important factor limiting population numbers. For example, Green and Anthony (1989) reported that up to 20% of nests failed in a given year because of nest predation, and 90% of predation was attributed to American badgers (*Taxidea taxus*). Therefore, selective forces of predation could alter nesting distributions of owls. In fact, management efforts are often directed at decreasing nest predation in declining populations of burrowing owls (e.g., Wellicome et al. 1997). Our study area (described below) reportedly supports one of the densest populations of American badgers in North America (Messick and Hornocker 1981). Although badgers and the burrows they dig provide owls with suitable nest sites, presence of badgers also increases risk of predation of owl nests and young because badgers are owl-nest predators as well. To test the predation hypothesis, we 1) compared predation rates of nests in artificial burrows within nonagricultural and agricultural habitats, and 2) compared predation rates of dummy nests placed in artificial burrows in both habitats.

Study Area

We studied burrowing owls nesting within and near the Snake River Birds of Prey National Conservation Area (NCA) in southwestern Idaho, USA, during 2001 and 2002. This area was once representative of a typical shrub–steppe community dominated by large expanses of big sagebrush (*Artemisia tridentata wyomingensis*; Hironaka et al. 1983) and perennial bunchgrasses. However, disturbances, such as range fires, military training, grazing, and off-road vehicle use, have helped convert much of the area to exotic annual grasslands dominated by cheat grass (*Bromus tectorum*) and tumble mustard (*Sisymbrium altissimum*). Surrounding areas also contained scattered residential homes, paved and dirt roads, a military training area, and public lands managed by the U.S. Bureau of Land Management. Cattle and sheep grazed many portions of the area, especially during winter. Irrigated agricultural fields (primarily alfalfa, sugar beets, and mint) comprised less than 5% of the NCA and were located primarily along its margins (USDI 1996). Otherwise, cover type was predominately disturbed shrub steppe. We considered burrowing owl nests that were within 1 km of an irrigated agricultural field to be in agricultural habitat (distance of active nests from agricultural fields ranged from 25–450 m). These nests were located in natural vegetation surrounding and between agriculture fields rather than in irrigated portions where crops grew. However, owls frequently perched on fence posts adjacent to the fields, and we often observed them hunting within fields. "Nonagricultural" habitat was the operational term we used for owl nests that were greater than 3 km from irrigated fields. Because this distance exceeded the typical foraging range of burrowing owls (Haug and Oliphant 1990), it is almost certain that owls that nested in nonagricultural habitat did not collect prey from irrigated fields. Nonagricultural areas generally were disturbed shrublands and grasslands much like that in the agricultural areas, but there were no crops or irrigation nearby.

Methods

Burrow Availability Hypothesis

Assessment of available natural burrows.—We quantified seemingly available burrows in agricultural and nonagricultural areas in 25 survey plots (50 m × 50 m) placed randomly within suitable habitats (i.e., low vegetation) in each area. These burrows presumably resulted from badger digging. We considered a burrow available if aboveground characteristics fell within the range of natural burrows that burrowing owls used previously in the study region: entrance height (8–24 cm), entrance width (12–28 cm), and entrance angle (20–41°; Belthoff and King 2002).

Artificial burrow placement and assessment of occupancy rates.—We buried clusters of 2 artificial burrows in both agricultural and nonagricultural areas in the vicinity of areas in which owls nested during the past 10 years. Habitat appeared similar in vegetation composition and topography to those areas where burrowing owls had nested. Each artificial burrow consisted of a chamber (68-L plastic tub: 50 cm × 35 cm × 40 cm, 19-L plastic bucket: 30-cm diam × 35-cm ht, or 17-L plastic container: 30 × 30 × 20 cm) and a 2-m long tunnel (10- or 15-cm diam) with a 90° turn between the entrance and the chamber. Owls in our study area have regularly nested in artificial burrows of these configurations (Belthoff and Smith 1999, Smith and Belthoff 2001, Belthoff and Smith 2003). The tunnel sloped downward toward the chamber at an angle of 20–30°, and we inserted it into the chamber on a level plane through a 10- or 15-cm diameter hole cut into the chamber. In the bottom of each chamber, we drilled 4 1-cm-diameter drain holes. The top of each chamber was at least 25 cm underground. We placed a wooden perch within each cluster (King 1996).

The clusters of 2 artificial burrows provided owls with a nest burrow and satellite burrow (Desmond and Savidge 1996, King and Belthoff 2001). We considered each cluster as 1 experimental unit in all agricultural and nonagricultural comparisons with the exception of burrow-occupancy rates. To calculate occupancy rates, each cluster was part of an occupancy group, which consisted of 4 clusters placed at increments of approximately 150 m (Fig. 1). Occupancy groups were located at least 1 km apart to help ensure that each group was independent of others. We considered a cluster to be occupied if it contained a nesting pair of owls that initiated and incubated a clutch of eggs. Because we surveyed for burrowing owl pairs and their nests beginning in mid-March of both years, we located all nests during the egg-laying stage. We calculated proportion (e.g., 0.25) of clusters occupied within each occupancy group and compared average occupancy between habitats, i.e., the occupancy group was the unit of analysis here.

Prey Availability Hypothesis

Rodent and invertebrate sampling.—To assess prey availability in agricultural and nonagricultural habitats, we conducted sampling surveys to determine occurrence and density of small mammals and invertebrates. Small mammal sampling occurred in

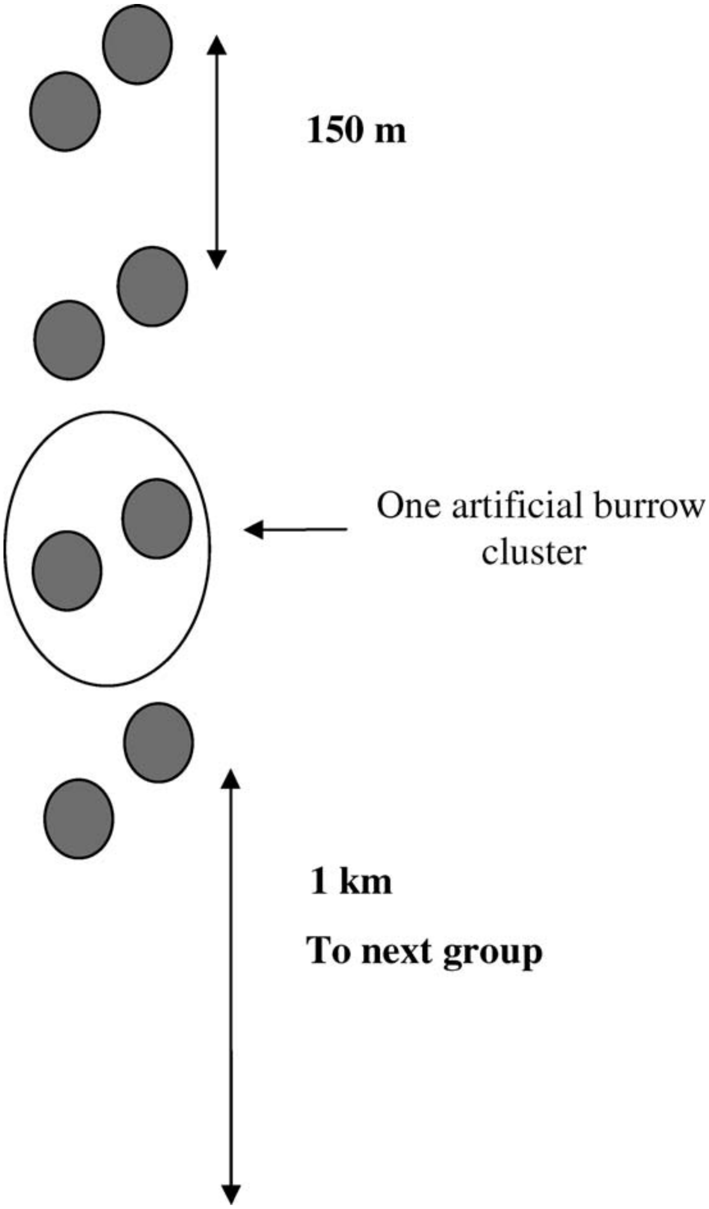

Figure 1. Schematic of one occupancy group used for assessing occupancy rates of artificial burrowing owl burrows in agricultural and nonagricultural habitats in southwestern Id., USA, 2001–2002.

areas surrounding owl nests using Sherman live traps and snap traps (2002 field season only) baited with peanut butter and rolled oats. Through daily observations during dawn and dusk hours, we determined where nesting owls foraged and set traps for small mammals in and near those sites. During 2002, there were few active burrowing owl nests in nonagricultural areas. Therefore, trapping in nonagricultural habitat in that year included trap lines near 4 active burrows (1 burrow was occupied by a nonnesting owl pair) as well as 2 areas that were used the previous year by nesting owls. We trapped at each site during a 3-night period in early June (nestling period for burrowing owls in southern Idaho), and we checked each trap every 24 hours (Wellicome 2000). Each sampling area received 1 to 4 trap lines depending on the size of the field and on our estimate of the number of owl pairs potentially using the field for foraging. Because we did not have access to agriculture fields (they were privately owned), we placed trap lines along fence lines adjacent to fields. We established nonagricultural trap lines at randomly selected locations within fields and at least 250 m from other trap lines. Each trap line contained 20 paired live traps (1 appropriate for mice: 17 × 5 × 5 cm, and 1 appropriate for slightly larger rodents, such as ground squirrels, *Spermophilus mollis*: 30 × 7.5 × 9 cm), placed at 10-m intervals. During 2002, we added 5 snap traps to each trap line to help capture common prey species, such as montane voles and Ord's kangaroo rats (*Dipodomys ordii*), which we were unable to capture with live traps in 2001, although pellet and prey remains indicated their presence.

We sampled invertebrate prey using 3 pitfall traps placed near owl nest burrows. Pitfall traps were plastic paint buckets (2.3 L) placed 5 m, 20 m, and 50 m from nest burrow entrances in a single, randomly selected direction, and we buried the traps so their tops were level with the ground surface. We deployed traps 1 week after chicks hatched, and traps remained for 18 days. This approach allowed assessment of abundance of invertebrates immediately surrounding the burrow, where owls frequently captured invertebrate prey (C. E. Moulton, IDFG, Boise, Id., USA, personal observation). We checked traps during each nest visit and identified invertebrates captured on-site when possible or returned them to the laboratory for later identification.

Pellet and prey remains.—To determine the diet of owls, we analyzed regurgitated pellets and prey remains at nests in artificial burrows in agricultural and nonagricultural habitat. We collected regurgitated pellets at natural burrows in nonagricultural habitat, but we were unable to document prey remains at these nests because we could not access nest chambers as we could in artificial burrows. We quantified prey remains each time we excavated a nest in an artificial burrow to band the female, determine hatching date, and measure nestling growth (2–5 visits total). We recorded prey remains both within the artificial burrow and outside the burrow entrance. We collected regurgitated pellets from tunnel entrances, perches, and nearby mounds within 20 m of nest burrows every 3–10 days from hatching through 25 days posthatch (May–Jun). Nesting burrowing owls typically defended areas greater than this distance (Moulton et al. 2004), so there was little possibility that owls other than from focal nests deposited them. For nests at which we collected more than 20 pellets (29 of 51 nests; 22 agricultural, 7 nonagricultural), we analyzed a random sample of 20 pellets per nest. For all other nests, we analyzed all collected pellets (4–19 pellets per nest, mean = 11.2 ± 1.0 SE).

For analysis, we teased each pellet apart with forceps and grouped similar items (jaws, elytra, skulls, etc.; Marti 1987). We used skulls and dentition patterns to identify mammalian prey to species when possible. Head capsules, jaws, pronota, elytra, legs, and other distinguishing body segments helped to identify invertebrate prey to either order or family. We identified avian, reptilian, and amphibian species to class using skulls, jaws, and scales (for additional description of pellet analysis, see Moulton 2003).

Predation Hypothesis

Burrowing owl nests.—To determine predation rates of owl nests in agricultural and nonagricultural habitats, we recorded number of nests in artificial burrows that were either destroyed by predators or experienced predation attempts. Because we could not always assign predation as the cause of nest failure in natural burrows, we did not include natural burrows in our assessment of predation rates. We were interested in overall rate of predation in each habitat, so we combined predation events during all stages of nesting (egg-laying, incubation, and nestling) for analyses. We considered nests to be depredated if there were signs of digging by badgers or coyotes around tunnel entrances, over the tunnels, or directly above the nest chamber, which are characteristic signs of predation of this type.

Dummy nests.—To experimentally assess predation in agricultural and nonagricultural habitats, we used 40 dummy nests (20 in each year, 10 in each habitat) placed in artificial burrows. Dummy nests were located no closer than 150 m but frequently were more than 1 km apart. Because predators of underground nests are more likely to hunt by olfaction than by sight, we used quail (*Coturnix* sp.) eggs instead of clay eggs (Bayne and Hobson 1999) to more realistically mimic odor of an actual nest. We manually lined each dummy nest with shredded livestock dung inside the chamber and around the tunnel entrance to imitate actual burrowing owl nests, which commonly include this material (Haug et al. 1993, Rodriguez-Estrella 1997, Brady 2004).

We deployed dummy nests in early May and monitored each for up to 6 weeks. During the first 3 weeks, which corresponded with the incubation period of nesting burrowing owls, each dummy nest consisted of a clutch of quail eggs (10–12 per nest) and an air-dried quail skin to simulate scents of a female incubating eggs. During the second 3 weeks, we replaced the eggs and dried quail skin with 3 dried quail skins to simulate the scents of a brood of young owls in the nest chamber. We handled all eggs and skins with rubber gloves during deployment and subsequent monitoring to reduce residual human scent. We inspected dummy nests once each week for signs of digging by predators or the presence of rodents, such as ground squirrels, which may have affected the likelihood of a predator locating or attempting to excavate the dummy nest. We determined whether dummy nests experienced predation using the same criteria described above for actual burrowing owl nests.

Statistical Analysis

Because data were not normally distributed, we used the nonparametric Wilcoxon ranked-sums tests to compare mean number of burrows per plot in agricultural and nonagricultural habitat and to compare occupancy rates of artificial burrows in both habitats. To determine whether relative abundance of mammalian prey differed, we compared mean number of rodents captured per trap-night per trap line using a 2-factor analysis of variance, with habitat and year as factors. We included year as a factor because field observations indicated the abundance of rodents was quite different between years. We also compared mean biomass of rodents captured per trap-night per trap line in agricultural and nonagricultural habitats using a 2-factor analysis of variance, with year as a second factor.

To examine differences in amounts of prey consumed by owls nesting in agricultural and nonagricultural areas, we compared mean number of prey items per pellet per nest in each habitat using a Wilcoxon ranked-sums test. The biomass of prey items found in the pellets varied considerably from 0.23 g (Carabidae; Smith and Murphy 1973) to 200 g (*Thomomys* spp.; Steenhof 1983). To account for the potentially significant effect of biomass differences in prey items, we also compared the mean biomass of prey items per pellet per nest in agricultural and nonagricultural habitat using a Wilcoxon ranked-sums test. We determined biomass of mammalian, avian, and amphibian prey using average biomass values reported by Smith and Murphy (1973) and Steenhof (1983). We determined biomass of invertebrate prey species using biomass values estimated in our study (through direct measurement of live samples) and values reported by Smith and Murphy (1973) and Olenick (1990; see Moulton 2003 for biomass values used in this study). We based all comparisons concerning prey per pellet on the assumption that a greater number and biomass of prey per pellet indicates greater consumption of prey; numerous studies rely on this assumption (Zimmerman et al. 1996, Bellocq 1998, Smith et al. 1999), which Aparicio's (1990) study of captive kestrels (*Falco tinnunculus* and *F. naumanni*) supports.

Finally, we examined the null hypothesis that predation of dummy nests was uniform between agricultural and nonagricultural habitats using contingency analysis. Unless otherwise noted, we performed all analyses using JMPIN (SAS Institute, Inc., Cary, North Carolina) and evaluated all statistical tests at $\alpha = 0.05$. Throughout, we present means with their standard errors.

Results

Burrow Availability

Available natural burrows.—Number of available burrows per survey plot ranged from 0–20 but did not differ between agricultural (5.4 ± 1.1, $n = 25$) and nonagricultural habitat (7.0 ± 1.1, $n = 25$; Wilcoxon ranked-sums normal approximation: $Z = 1.54$, $P = 0.123$).

Occupancy rates.—We monitored 15 occupancy groups in the 2001 field season (5 agricultural; 10 nonagricultural) and 21 occupancy groups in 2002 (7 agricultural; 14 nonagricultural). Occupancy of artificial burrows was significantly greater in agricultural habitat (41.7 ± 5.9%) than nonagricultural habitat (2.1 ± 4.2%; Wilcoxon ranked-sums normal approximation: $Z = 3.90$; $P < 0.001$).

Prey Availability

Rodent prey.—We monitored 21 trap lines (3 nights each) from 3–12 June 2001 (14 agricultural, 7 nonagricultural) and 18 trap lines (also 3 nights each) from 5–14 June 2002 (12 agricultural, 6 nonagricultural). Occasionally, we found traps that were either triggered by something other than a rodent (i.e., presumably wind) or were missing bait but were not triggered, suggesting that a rodent or something else had entered the trap. We subtracted these traps on those particular nights from the total number of trap-nights for that trap line.

We captured 294 individuals during 2,027 trap-nights (1,379 agricultural; 648 nonagricultural) representing 6 rodent species (Table 1). All 6 species occurred in traps in agricultural habitat, whereas we did not capture *Mus musculus* and *Reithrodontomys megalotis* in traps in nonagricultural habitat. Even though we added snap traps in 2002 to help trap *Microtus montanus*, which occur mainly in agricultural habitat in our study area as evidenced by remains of cached prey and pellet remains (Moulton et al. 2005), this species evaded capture. We captured more *Spermophi-*

Table 1. Relative abundance of small mammals trapped per trap-night per transect in agricultural ($n = 26$) and nonagricultural ($n = 13$) habitats in southwestern Id., USA, 2001–2002.

Species	Habitat: Agricultural Mean	Agricultural SE	Nonagricultural Mean	Nonagricultural SE	*F*	*P* value
Peromyscus maniculatus	1.5	0.26	0.84	0.38	2.03	0.162
Mus musculus	0.38	0.23	0.00	—	—	—
Perognathus parvus	0.03	0.02	0.03	0.04	0.0003	0.986
Reithrodontomys megalotis	0.03	0.01	0.00	—	—	—
Dipodomys ordii	0.01	0.01	0.01	0.01	0.2	0.656
Spermophilus mollis	0.08	0.09	0.54	0.13	9.08	0.005*[a]

[a] * = Significant based on sequential Bonferroni corrections adjusted from an original α level of 0.05.

lus mollis in nonagricultural habitat in 2001 but did not capture them in either habitat in 2002. Capture of *Peromyscus maniculatus* and *Dipodomys ordii* was similar in both habitats (Table 1). Overall, we trapped significantly fewer rodents in 2002 compared with 2001 (ANOVA: $F_{1,35} = 13.53$, $P < 0.001$). Year and habitat did not interact (ANOVA: $F_{1,35} < 0.001$, $P = 0.981$), and there was no difference in small mammal abundance between agricultural ($n = 26$) and nonagricultural ($n = 13$) habitat (agricultural = 2.02 ± 0.38 prey per trap-night per trap line; nonagricultural = 1.42 ± 0.53; ANOVA: $F_{1,35} = 0.84$, $P = 0.366$).

Because the small mammals that we trapped differed markedly in biomass (range: 12–177 g; Steenhof 1983, Olenick 1990), we also calculated mean biomass per trap-night per transect in each habitat. There was a significant interaction between year and habitat (ANOVA: $F_{1,35} = 9.33$, $P = 0.004$) for prey biomass. In 2001, nonagricultural habitats had higher mean biomass (20.1 ± 2.4 g vs. 7.4 ± 1.8 g per trap-night per transect), which was driven predominately by the presence of ground squirrels. When the ground squirrel population declined in 2002 (C. E. Moulton, IDFG, Boise, Id., USA, personal observation) and concurrently we captured no ground squirrels in either habitat, biomass per transect in both habitats declined, and agricultural and nonagricultural habitats had similar mean biomass per transect (1.6 ± 1.9 g and 0.58 ± 2.6 g, respectively).

Invertebrate prey.—We monitored pitfall traps at 21 and 10 agricultural nests in 2001 and 2002, respectively. Because no owls nested in artificial burrows in nonagricultural habitat in 2001, we were unable to collect pitfall trap data in nonagricultural habitat in 2001. In 2002, we monitored pitfall traps at the 2 occupied artificial burrows in nonagricultural habitat. Because of this small sample, meaningful statistical comparisons of invertebrates between habitats were not possible. Mean number of invertebrates per nest in agricultural habitat was 10.7 ± 2.2 (positively skewed with a range of 0–59), whereas nonagricultural habitat had a mean of 3.5 ± 0.5 invertebrates per nest (Table 2).

Pellet remains.—We analyzed 602 regurgitated pellets from 34 nests in agricultural habitat and 257 pellets from 19 nests in nonagricultural habitat (total: 859 pellets; 395 in 2001; 464 in 2002). All pellets collected in agricultural habitats were from nests in artificial burrows, whereas 17 of 19 nonagricultural nests from which we collected pellets were in natural burrows. We identified 7,402 prey items representing at least 23 different species (Table 3). To determine whether the number of prey differed in agricultural and nonagricultural habitat, we compared mean number of prey items per pellet per nest in each habitat. Pellets collected from agricultural habitat contained a greater total number of prey items per pellet (Wilcoxon ranked-sums normal approximation: $Z = 4.42$, $P < 0.001$, Fig. 2). Interestingly, the number of vertebrate prey per pellet (predominately rodents) did not differ between habitats ($Z = 1.26$, $P = 0.209$), but the number of invertebrate prey per pellet was significantly higher in the agricultural habitat ($Z = 4.43$, $P < 0.001$, Fig. 2).

In addressing questions of prey availability and its effect on reproduction and growth, overall biomass consumed is often more important than actual number of prey consumed. Therefore, we calculated mean biomass of prey per pellet per nest from nests in

Table 2. Relative abundance of invertebrates trapped per nest in pitfall traps in agricultural ($n = 31$) and nonagricultural ($n = 2$) habitats in southwestern Id., USA. Means for agricultural habitat include nests from both 2001 and 2002. Means for nonagricultural habitat include only nests from 2002 because burrowing owls did not nest in artificial burrows in nonagricultural habitat in 2001.

Order	Habitat: Agricultural Mean	Agricultural SE	Agricultural Min.	Agricultural Max.	Nonagricultural Mean	Nonagricultural SE	Nonagricultural Min.	Nonagricultural Max.
Orthoptera	0.3	0.1	0	2	0.0	0.0	—	—
Coleoptera								
Carabidae	2.3	0.6	0	12	0.5	0.5	0	1
Tenebrionidae	6.0	2.2	0	58	1.0	1.0	0	2
Scorpionida	0.4	0.2	0	3	2.0	2.0	0	4
Solpugida	1.4	0.3	0	5	0.0	0.0	—	—
Total	10.7	2.2	0	59	3.5	0.5	3	4

Table 3. Minimum number of prey items detected in 859 pellets collected at burrowing owl nests in agricultural ($n = 34$) and nonagricultural ($n = 19$) habitat in southwestern Id., USA, 2001–2002.

Prey category	Common name	Agricultural	Nonagricultural
Mammals			
Spermophilus mollis	Piute ground squirrel	5	6
Thomomys townsendii	Townsend pocket gopher	16	0
Perognathus parvus	Great basin pocket mouse	42	64
Dipodomys ordii	Ord's kangaroo rat	14	14
Reithrodontomys megalotis	Harvest mouse	5	0
Peromyscus maniculatus	Deer mouse	68	16
Mus musculus	House mouse	13	0
Microtus montanus	Montane vole	65	0
Rodent, unidentified		24	4
Birds, unidentified		6	4
Reptiles and amphibians			
Bufo woodhouseii	Woodhouse's toad	0	1
Phrynosoma platyrhinos	Horned lizard	1	0
Snake, unidentified		2	0
Scolopendromorphs	Centipede	2	0
Arachnids			
Scorpiones	Scorpion	155	154
Solpugida	Windscorpion	204	196
Orthopterans			
Acrididae	Grasshopper	99	54
Gryllidae	Cricket	2,572	51
Unknown Orthoptera		170	143
Dermapterans (Forficulidae)	Earwig	47	0
Homopterans (Cicadidae)	Cicada	0	8
Coleopterans			
Carabidae	Ground beetle	1,192	61
Scarabaeidae	Scarab beetle	352	166
Silphidae	Carrion beetle	304	135
Tenebrionidae	Darkling beetle	529	140
Coleoptera, unidentified		236	62
Total vertebrates		261	109
Total invertebrates		5,862	1,170
Total prey		6,123	1,279

agricultural and nonagricultural habitat. Pellets from agricultural habitat contained greater total biomass of prey per pellet ($Z = 2.11$, $P = 0.035$) and biomass of invertebrates per pellet ($Z = 3.03$, $P = 0.002$; Fig. 3). Biomass of rodents per pellet did not differ between habitats ($Z = 0.83$, $P = 0.404$).

Cached prey items.—We recorded cached prey remains at 43 nests in artificial burrows (41 agricultural, 2 nonagricultural). Because the 2 nonagricultural nests were both in the 2002 field season and the number of cached prey per visit was significantly lower during this second field season (Wilcoxon ranked-sums normal approximation; $Z = 3.16$, $P = 0.002$), we report only 2002 data. To address differences in biomass of cached prey items, we calculated biomass of all cached prey items per nest per visit in agricultural and nonagricultural habitat. Mean total biomass of cached prey per nest per visit was 108.3 ± 43.3 g ($n = 107$) in agricultural habitat and 23.2 ± 12.2 g ($n = 10$) in nonagricultural habitat. We made no statistical comparisons of cached prey items between agricultural and nonagricultural habitat because of the small sample size for nonagricultural nests.

Predation

Burrowing owl nests.—We monitored 96 artificial burrow clusters in nonagricultural habitat (40 in 2001, 56 in 2002). Of these, nesting owls occupied only 2 artificial burrows (both in 2002). Neither of these nests in nonagricultural habitat was depredated. In agricultural habitat, coyotes (*Canis latrans*), weasels (*Mustela* spp.), or American badgers depredated 19 of 69 actual nests (28%). Weasels depredated 12 (63%) of these nests during egg-laying or incubation in 2002. Because sample sizes for nonagricultural habitat were too small, we made no statistical comparisons of predation rates of actual burrowing owl nests between agricultural and nonagricultural habitats.

Dummy nests.—We monitored 40 dummy nests (20 in both years) in agricultural and nonagricultural habitat. Several weeks into the experiment, burrowing owls occupied 2 burrows in which we deployed dummy nests in agricultural habitat (1 each year), so we removed these from analyses. Signs of ground squirrels or other rodent species were present in 11 dummy nests during the course of the study (agricultural = 6, nonagricultural = 5). Because presence of rodents could potentially affect predation, we excluded these 11 nests as well. Of the remaining 27 nests (agricultural = 12, nonagricultural = 15), predators depredated 12 (44.4)%. There was no significant difference in predation rate of dummy nests in agricultural (41.6% depredated) and nonagricultural habitat (46.6% depredated; Contingency analysis: $\chi^2 = 0.07$, $P = 0.795$).

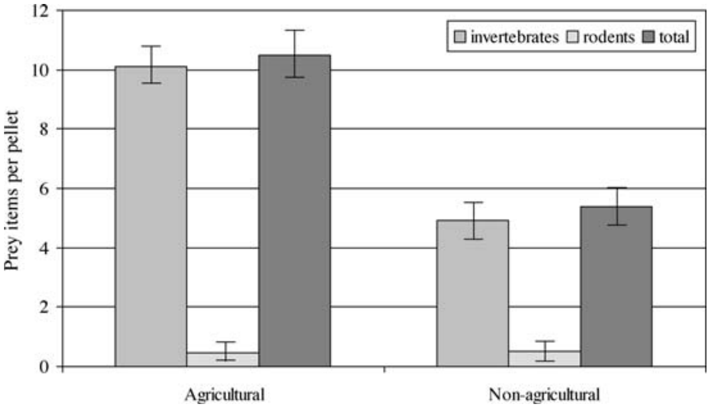

Figure 2. Mean (± SE) number of invertebrates, rodents, and total prey per pellet per nest of active burrowing owl nests in agricultural ($n = 34$) and nonagricultural ($n = 19$) habitats in southwestern Id., USA, 2001–2002.

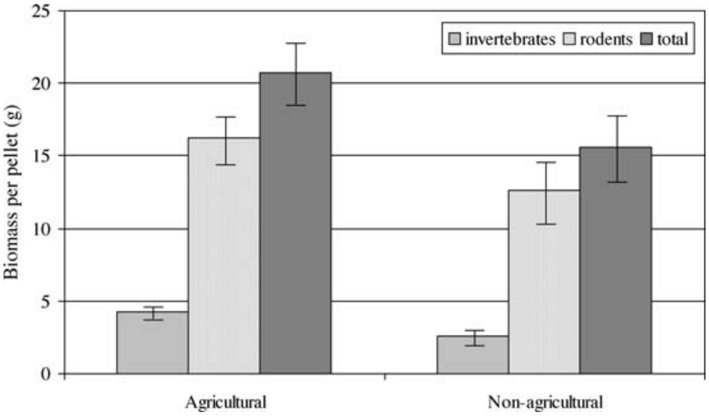

Figure 3. Mean (± SE) biomass of invertebrates, rodents, and total prey per pellet per active burrowing owl nest in agricultural ($n = 34$) and nonagricultural ($n = 19$) habitats in southwestern Id., USA, 2001–2002.

Discussion

Although previous studies have examined importance of burrow availability immediately surrounding nest burrows (i.e., satellite burrows; Schmutz 1997, Desmond and Savidge 1999, Uhmann et al. 2001, Ronan 2002), fewer studies (Gleason and Johnson 1985, Bellocq 1997) have addressed whether landscape scale burrow availability might drive burrowing owl nesting distributions. Differences in burrow availability between agricultural and nonagricultural habitats also were poorly documented for most areas. We found that number of burrows in each habitat was not significantly different and, when we provided additional artificial burrows of the type owls readily use (Smith and Belthoff 2001, Belthoff and Smith 2003), occupancy rates in nonagricultural areas were significantly lower than agricultural areas. Therefore, collective results of survey plots and occupancy rates of artificial burrows suggest that a lack of suitable burrows in nonagricultural habitat is not driving the association of burrowing owls with agriculture.

There also was no evidence that predation rates of dummy nests differed between agricultural and nonagricultural habitats. In contrast, Desmond (1991) found a tendency for greater predation of aboveground dummy nests near agricultural areas in Nebraska. However, Desmond's (1991) results were inconclusive because of low replication. For actual burrowing owl nests, Haley (2002) documented relatively low predation (9%) in agricultural habitats but was unable to compare those results with nearby nonagricultural (natural grasslands) habitat. Although we were unable to compare predation rates of actual nests, the fact that so many nests in agricultural habitat were depredated indicates that agricultural nests were not immune to predation. If anything, our results suggest that predation rates of actual burrowing owl nests may be higher near agriculture, as predators depredated neither of the nests in nonagricultural habitat. Thus, the combined results of predation on dummy and actual nests allow us to reject the hypothesis that burrowing owls associate with agriculture because of decreased predation.

In contrast, we were unable to reject the prey availability hypothesis because pellet analysis revealed significantly higher prey consumption in agricultural habitat. Although agricultural and nonagricultural habitats had similar numbers and biomass of vertebrates (mostly rodents) in their diet, and there was no interaction between habitat and year, number and biomass of invertebrate prey in pellets were significantly higher in agricultural habitat. This resulted in owls in agricultural habitat having significantly higher numbers and biomass of overall prey in their diets.

We found a significant interaction between biomass of rodents trapped and year of study such that biomass was greater in nonagricultural habitat in 2001 and no different in 2002. This pattern was predominately driven by presence of ground squirrels in 2001 and their absence from both habitats in 2002. This result highlights the potential importance of fluctuating ground squirrel populations, particularly in nonagricultural habitats, on predatory species, including burrowing owls. It is important to note that the presence of montane voles in agricultural habitat may actually offset this difference in biomass seen between agricultural and nonagricultural habitats during trapping in 2001. This is supported by pellet analysis, as discussed below, where there was no difference in biomass of rodents in owl diets between habitats and no interaction between habitat and year.

As opportunistic predators, burrowing owls can take advantage of a variety of prey resources, and they respond both numerically and functionally to fluctuations in prey populations (Gleason and Johnson 1985, Silva et al. 1995, Bellocq 1997, Gervais and Anthony 2003). Rosenberg and Haley (2004) suggest that high densities of burrowing owls near irrigated agricultural fields in the Imperial Valley of California are a result of quality foraging habitat. It is possible that agricultural habitat in our study area provides a more stable environment of prey availability relative to nonagricultural habitat. Pellet analysis revealed significantly greater number and biomass of prey in the diet of owls nesting near agricultural fields. Interestingly, this difference was primarily a result of greater invertebrate prey in agricultural habitats. Although some have suggested that burrowing owls associate with irrigated agriculture because of the high abundance of montane voles (Gleason 1978, Rich 1986), presence of high numbers of invertebrate prey in owl diets in agricultural habitat may indicate an overlooked importance of invertebrate prey. For example, York et al. (2002) found that burrowing owls nesting near agricultural areas in the Imperial Valley of California, where rodent prey are presumably infrequently available, feed almost exclusively on invertebrates. Although this population of burrowing owls experiences relatively low productivity, it is likely the largest concentration of burrowing owls in its range (DeSante et al. 2004).

Invertebrate prey may supplement the diet of breeding owls in agricultural habitat during years of low rodent abundance, allowing them to successfully breed, whereas owls in nonagricultural habitat may have lower productivity or forego breeding during low rodent years. We observed potential evidence of this in 2002, after burrowing owls arrived in both habitats at the beginning of the season. In both 2001 and 2002, the majority (approx 95%) of owls that we located in agricultural habitat early in the season, nested at the burrows where we first located them. Similarly, all 13 pairs of owls that we located in nonagricultural habitat early in 2001, nested and were confirmed with owlets later in the season. This contrasts with the 13 pairs that we located early in 2002, where only 3 pairs nested, 4 pairs stayed in the area but did not breed successfully, and the remaining 6 pairs disappeared. This suggests that the decrease in rodent prey in 2002 in both habitats, as shown in the small mammal trapping, potentially had more effect on owls in nonagricultural habitat than those in agricultural habitat. It is possible that this difference results from significantly higher availability of invertebrate prey in agricultural habitat that may have compensated for a season of decreased rodent abundance. Greater availability of invertebrates in agricultural areas may be related to presence of suitable habitat for prolific Orthopteran species (particularly Gryllidae), which make up the majority of the biomass of the invertebrate diet of owls in agricultural areas within our study area (Moulton et al. 2005).

Management Implications

As western burrowing owls continue to decline in abundance, knowledge of how this species responds to changes in habitat and available resources will be crucial to conservation and management. Our results suggest that irrigated agricultural areas scattered among more natural habitat provide burrowing owls with a stable and abundant prey source of rodents and invertebrates. Thus, as Rich (1986) noted earlier and given our documentation of high artificial burrow use near agricultural fields, there is potential to install artificial burrows in habitat near agriculture to augment burrowing owl nesting habitat. This would give burrowing owls increased access to a significant prey resource. Management of agricultural fields themselves may also be adapted to further increase prey availability and help control rodent and invertebrate populations as a benefit to farmers. For example, the potential exists for adjusting crop harvest timing to correspond with peak burrowing owl prey needs (i.e., midnestling stage), as the resulting short vegetation gives burrowing owls increased access to rodents, especially montane voles. Finally, management of burrowing owls within nonagricultural lands could focus on restoring healthy rodent and invertebrate populations, likely through restoration of native vegetation.

Acknowledgments

We thank T. Booms, K. Donohue, C. Eaton, J. Egbert, G. Fairhurst, K. Hasselblad, S. Lysne, R. Medeck, J. Rausch, J. Soules, M. Troxler, and J. Urbanic for assistance with fieldwork. Financial and logistical support for this study was provided through an EPA STAR Fellowship awarded to C. Moulton, the Bureau of Land Management, Idaho Department of Fish and Game, and by the Department of Biology and Raptor Research Center at Boise State University. J. Clark, J. Doremus, and J. Sullivan facilitated our work in the Snake River Birds of Prey National Conservation Area, and M. Fuller, Director of the Raptor Research Center, was helpful in numerous ways. Finally, we thank J. Gervais, J. Munger, I. Robertson, and J. Schmutz for helpful comments on previous versions of our manuscript.

Literature Cited

Aparicio, J. M. 1990. Use of pellets of kestrels (*Falco tinnunculus* and *Falco naumanni*) as a sign of daily biomass intake. Ardeola 37:85–89.

Bayne, E. M., and K. A. Hobson. 1999. Do clay eggs attract predators to artificial nests? Journal of Field Ornithology 70:1–7.

Bellocq, M. I. 1997. Ecology of the burrowing owl in agrosystems of central Argentina. Journal of Raptor Research Report 9:52–57.

Bellocq, M. I. 1998. Prey selection of breeding and nonbreeding barn owls in Argentina. Auk 115:224–229.

Belthoff, J. R., and R. A. King. 2002. Nest-site characteristics of burrowing owls (*Athene cunicularia*) in the Snake River Birds of Prey National Conservation Area, Idaho, and applications to artificial burrow installation. Western North American Naturalist 62:112–119.

Belthoff, J. R., and B. W. Smith. 1999. Monitoring burrowing owls and assessment of artificial burrow features useful in conservation and management. Final Report. Unpublished Technical Report to Idaho Bureau of Land Management, Boise, USA.

Belthoff, J. R., and B. W. Smith. 2003. Patterns of artificial burrow occupancy and reuse by burrowing owls in Idaho. Wildlife Society Bulletin 31:138–144.

Brady, R. S. 2004. Nest-lining behavior, nest microclimate, and nest defense behavior of burrowing owls. Thesis, Boise State University, Boise, USA.

Carlson, C. A. 1985. Wildlife and agriculture: can they coexist? Journal of Soil and Water Conservation 40:263–266.

DeSante, D. F., E. D. Ruhlen, and D. K. Rosenberg. 2004. Density and abundance of burrowing owls in the agricultural matrix of the Imperial Valley, California. Studies in Avian Biology 27:116–119.

Desmond, M. J. 1991. Ecological aspects of burrowing owl nesting strategies in the Nebraska panhandle. Thesis, University of Nebraska, Lincoln, USA.

Desmond, M. J., and J. A. Savidge. 1996. Factors influencing burrowing owl (*Speotyto cunicularia*) nest densities and numbers in western Nebraska. American Midland Naturalist 136:143–148.

Desmond, M. J., and J. A. Savidge. 1999. Satellite burrow use by burrowing owl chicks and its influence on nest fate. Studies in Avian Biology 19:128–130.

Gervais, J. A., D. K. Rosenberg, D. M. Fry, L. Trulio, and K. K. Sturm. 2000. Burrowing owls and agricultural pesticides: evaluation of residues and risks for three populations in California, USA. Environmental Toxicology and Chemistry 19:337–343.

Gervais, J. A., and R. G. Anthony. 2003. Chronic organochlorine contaminants, environmental variability, and the demographics of a burrowing owl population. Ecological Applications 13:1250–1262.

Gleason, R. L. 1978. Aspects of the breeding biology of burrowing owls in southeastern Idaho. Thesis, University of Idaho, Moscow, USA.

Gleason, R. L., and D. R. Johnson. 1985. Factors influencing nesting success of burrowing owls in southeastern Idaho. Great Basin Naturalist 45:81–84.

Green, G. A., and R. G. Anthony. 1989. Nesting success and habitat relationships of burrowing owls in the Columbia Basin, Oregon. Condor 91: 347–354.

Haley, K. L. 2002. The role of food limitation and predation on reproductive success of burrowing owls in southern California. Thesis, Oregon State University, Corvallis, USA.

Haug, E. A., B. A. Millsap, and M. S. Martell. 1993. Burrowing owl (*Speotyto cunicularia*). No. 611 *in* A. Poole and F. Gill, editors. The Birds of North America. The Academy of Natural Sciences, Philadelphia, Pennsylvania, USA, and The American Ornithologists' Union, Washington, D.C., USA.

Haug, E. A., and L. W. Oliphant. 1990. Movements, activity patterns, and habitat use of burrowing owls in Saskatchewan. Journal of Wildlife Management 54:27–35.

Hironaka, M., M. A. Fosberg, and A. H. Winward. 1983. Sagebrush–grass habitat types of southern Idaho. Forest, Wildlife and Range Experiment Station, University of Idaho, Bulletin 35, Moscow, USA.

Jahn, L. R., and E. W. Schenck. 1991. What sustainable agriculture means for fish and wildlife. Journal of Soil and Water Conservation 46:251–254.

James, P. C., and G. A. Fox. 1987. Effects of some insecticides on productivity of burrowing owls. Blue Jay 45:65–71.

King, R. A. 1996. Post-fledging dispersal and behavioral ecology of burrowing owls in southwestern Idaho. Thesis, Boise State University, Boise, Idaho, USA.

King, R. A., and J. R. Belthoff. 2001. Post-fledging dispersal of burrowing owls in southwestern Idaho: characterization of movements and use of satellite burrows. Condor 103:118–126.

Klute, D. S., L. W. Ayers, M. T. Green, W. H. Howe, S. L. Jones, J. A. Shaffer, S. R. Sheffield, and T. S. Zimmerman. 2003. Status assessment and conservation plan for the western burrowing owl in the United States. U.S. Department of Interior, Fish and Wildlife Service, Biol. Tech. Publ. FWS/BTP–R6001–2003, Washington, D.C., USA.

Leptich, D. 1994. Agricultural development and its influence on raptors in southern Idaho. Northwest Science 68:167–171.

Marti, C. D. 1987. Raptor food habits studies. Pages 67–80 *in* B. G. Pendleton, B. A. Millsap, K. W. Kline, and D. A. Bird, editors. Raptor management techniques manual. National Wildlife Federation, Washington, D.C., USA.

Messick, J. P., and M. G. Hornocker. 1981. Ecology of the badger in southwestern Idaho. Wildlife Monographs 76:1–53.

Moulton, C. E. 2003. Ecology of burrowing owls in southwestern Idaho: association with agriculture, food habits, and territorial behavior. Thesis, Boise State University, Boise, Idaho, USA.

Moulton, C. E., R. S. Brady, and J. R. Belthoff. 2004. Territory defense of nesting burrowing owls: responses to simulated conspecific intrusion. Journal of Field Ornithology 75:288–295.

Moulton, C. E., R. S. Brady, and J. R. Belthoff. 2005. A comparison of breeding season food habits of burrowing owls nesting in agricultural and nonagricultural habitat in Idaho. Journal of Raptor Research 39:421–430.

Murphy, M. T. 2003. Avian population trends within the evolving agricultural landscape of eastern and central United States. Auk 120:20–34.

Olenick, B. E. 1990. Breeding biology of burrowing owls using artificial nest burrows in southeastern Idaho. Thesis, Idaho State University, Pocatello, USA.

Peterjohn, B. G. 2003. Agricultural landscapes: can they support healthy bird populations as well as farm products? Auk 120:14–19.

Rich, T. 1986. Habitat and nest-site selection of burrowing owls in the sagebrush steppe of Idaho. Journal of Wildlife Management 50:548–555.

Rodriguez-Estrella, R. 1997. Nesting sites and feeding habits of the burrowing owl in the biosphere reserve of Mapimi, Mexico. Journal of Raptor Research Report 9:99–106.

Ronan, N. A. 2002. Habitat selection, reproductive success, and site fidelity of burrowing owls in a grassland ecosystem. Thesis, Oregon State University, Corvallis, USA.

Rosenberg, D. K., and K. L. Haley. 2004. The ecology of burrowing owls in the agroecosystem of the Imperial Valley, California. Studies in Avian Biology 27: 120–135.

Schmutz, J. K. 1997. Selected microhabitat variables near nests of burrowing owls compared to unoccupied sites in Alberta. Journal of Raptor Research Report 9:80–83.

Silva, S. I., I. Lazo, E. Silva-Aranguiz, F. M. Jaksic, P. L. Meserve, and J. R. Gutierrez. 1995. Numerical and functional response of burrowing owls to long-term mammal fluctuations in Chile. Journal of Raptor Research 29:250–255.

Smith, B. W., and J. R. Belthoff. 2001. Effects of nest dimensions on use of artificial burrow systems by burrowing owls. Journal of Wildlife Management 65:318–326.

Smith, D. G., and J. R. Murphy. 1973. Breeding ecology of raptors in the eastern Great Basin of Utah. Brigham Young University Scientific Bulletin, Biology Series 18:69–76.

Smith, R. B., M. Z. Peery, R. J. Gutierrez, and W. S. Lahaye. 1999. The relationship between spotted owl diet and reproductive success in the San Bernardino Mountains, California. Wilson Bulletin 11:22–29.

Steenhof, K. 1983. Prey weights for computing percent biomass in raptor diets. Journal of Raptor Research 17:15–27.

Uhmann, T. V., N. C. Kenkel, and R. K. Baydack. 2001. Development of a habitat suitability index model for burrowing owls in the eastern Canadian prairies. Journal of Raptor Research 35:378–384.

U.S. Department of the Interior. 1996. Effects of military training and fire in the Snake River Birds of Prey National Conservation Area. BLM/IDARNG Research Project Final Report. U.S. Geological Survey, Biological Research Division, Snake River Field Station, Boise, Idaho, USA.

Wellicome, T. I. 2000. Effects of food on reproduction in burrowing owls (*Athene cunicularia*) during three stages of the breeding season. Dissertation. University of Alberta, Edmonton, Canada.

Wellicome, T. I., G. L. Holroyd, E. R. Wiltse, and K. Scalise. 1997. The effects of predator exclusion and food supplementation on burrowing owl (*Speotyto cunicularia*) population change in Saskatchewan. Pages 478–496 *in* J. R. Duncan, D. H. Johnson, and T. H. Nicholls, editors. Biology and conservation of owls of the northern hemisphere: second international symposium. MB. Gen. Tech. Rep. NC–190. USDA Forest Service, North Central Forest Experiment Station, St. Paul, Minnesota, USA.

York, M. M., D. K. Rosenberg, and K. K. Sturm. 2002. Diet and food-niche breadth of burrowing owls (*Athene cunicularia*) in the Imperial Valley, California. Western North American Naturalist 62:280–287.

Zimmerman, G., P. Stapp, and B. Van Horne. 1996. Seasonal variation in the diet of great horned owls (*Bubo virginianus*) on shortgrass prairie. American Midland Naturalist 136:149–156.

Associate Editor: Schmutz.