

DIET AND FOOD-NICHE BREADTH OF BURROWING OWLS (*ATHENE CUNICULARIA*) IN THE IMPERIAL VALLEY, CALIFORNIA

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ABSTRACT.—Burrowing Owls (*Athene cunicularia*) occupy intensively managed agricultural areas within the Imperial Valley of California, where they occur at high densities relative to other areas in the state, and yet reproductive rates are often low. Understanding diet and food-niche breadth may lead to insights into factors contributing to their poor reproductive performance. We tested the relative contribution of sex, year, and season on diet composition and food-niche breadth from analyses of stomach contents of adult Burrowing Owls ($n = 53$). Orthoptera dominated the diet; it accounted for 58.9% of the total number of prey items in all stomachs and was found in 98.2% of all samples. Rodents, a source of potentially limiting dietary calcium, were found in only 2 stomachs. We detected yearly and seasonal effects on estimated food-niche breadth. Mean food niche for the breeding season was broader (antilog of Shannon's index: 2.38 ± 0.15) and more even (Pielou's index: 0.67 ± 0.06) than for the nonbreeding season (1.83 ± 0.13 , 0.49 ± 0.07 , respectively) partially because of a greater frequency of Araneida, Isopoda, Lepidoptera, and Solpugida in the diet during the breeding season. Mean food-niche breadth for 1997 (2.25 ± 0.23) was broader than during 1994, 1995, and 1996 (2.07 ± 0.23 , 1.98 ± 0.20 , and 1.82 ± 0.40 , respectively) because of a greater frequency of Araneida, Dermaptera, Isopoda, Lepidoptera, and Solpugida. These results, and auxiliary diet information, suggest rodents were infrequent in the diet of Burrowing Owls in the Imperial Valley and may help explain their lower reproductive success relative to other areas of California.

Key words: diet, food-niche breadth, *Athene cunicularia*, Burrowing Owl, California, Imperial Valley.

Much published information exists on food habits of the Burrowing Owl (*Athene cunicularia*) throughout most of its range (Thomsen 1971, Marti 1974, MacCracken et al. 1985, Brown et al. 1986, Thompson and Anderson 1988, Barrows 1989, Schmutz et al. 1991, Green et al. 1993, Haug et al. 1993, Plumpton and Lutz 1993). However, all researchers identified prey from regurgitated pellets and/or remains found at the nest burrow. The unreliability of data collected from pellet analyses is well documented (Coulombe 1971, Thomsen 1971, MacCracken et al. 1985, Haug et al. 1993, Plumpton and Lutz 1993). Differential consumption of prey, decomposition rate of remains, and age- or sex-based differences in foraging may bias pellet collections. We had the unique opportunity to examine stomach contents from owls collected over both nonbreeding and breeding seasons, from 4 separate years, and from both sexes. These owls were collected from the Imperial Valley of California, where little is known about the

ecology and food habits of the Burrowing Owl (Coulombe 1971). Recent studies have suggested that the Imperial Valley is unique in that the Burrowing Owl occurs at some of the highest densities in the state, and yet it often has low reproductive success (Rosenberg and Haley in press). To provide insights into the species' reproductive biology and poor reproductive performance in the Imperial Valley, we explored variation in diet and food-niche breadth.

A broad food niche indicates high numbers of prey species nearly equally distributed in the diet. Conversely, a narrow food niche indicates relatively few prey species and unequal prey distribution. Most species have broad food niches, sacrificing efficiency in use of a narrow range of resources (specialization) for the ability to use a wide range of resources (generalization). Several researchers (Gleason and Craig 1979, Barrows 1989, Green et al. 1993, Haug et al. 1993) have suggested that Burrowing Owls are food generalists and

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opportunists. Opportunistic predators may take prey according to relative prey abundances (Murdoch and Oaten 1975, Hegazi 1981, Jaksic et al. 1981, Village 1982, Jaksic 1989, Korpimäki 1992) or may choose food items that yield the greatest net energy (MacArthur and Pianka 1966, Pulliam 1974, Stephens and Krebs 1986, McKnight and Hepp 1998). Food items also may be utilized on the basis of certain limiting nutrients (e.g., protein, calcium, sodium) necessary during times of increased energetic or nutrient requirements (Krebs et al. 1983, Edwards 1997).

Our objectives were to estimate and compare the food-niche breadth and diet composition of Burrowing Owls between sexes, seasons, and years.

STUDY AREA

The U.S. Fish and Wildlife Service provided specimens (none was killed for the study) recovered in 1994–1997 from an area surrounding an electric fence that borders the Calipatria State Prison, California, about 40 km north of the Mexico border (56 m below sea level). Owls were inadvertently killed from the electric fence prior to modifications. The habitat is an intensively managed agricultural matrix and includes roads, canals, ditches, and agricultural fields, similar to most of the agricultural areas of the Imperial Valley (Rosenberg and Haley in press). The temperature can reach 49°C during the summer; average annual rainfall is 6.5 cm. Principal crops during the study were alfalfa (*Medicago sativa*), Sudan grass (*Sorghum bicolor*), and row crops such as onions (*Allium cepa*) and sugar beets (*Beta vulgaris*). Burrowing Owls nested on banks of the canals and ditches.

METHODS

Diet Analyses

We assumed that our sample was representative of Burrowing Owls in the Imperial Valley. The habitat in which these birds were collected is almost entirely composed of agricultural fields and is representative of the Imperial Valley. Because Burrowing Owls in the Imperial Valley forage up to 2 km from the nest site during the breeding season and probably farther during the nonbreeding season (Rosenberg and Haley in press), the foraging

area of the owls in our sample includes an area larger than that from which they were collected.

Specimens with intact stomachs that were absent of maggots and severe desiccation or decay were included in our study. Specimens were kept frozen at –10°C until necropsied. Age of owls was determined by plumage characteristics (Haug et al. 1993); only owls ≥ 70 days of age were used in this study. We determined sex by examining gonads and classified specimens as breeding (March–August) or nonbreeding (September–February) based on collection date. Although stimuli for onset of egg laying are unknown (Haug et al. 1993), egg laying begins in March in hot, arid environments (Martin 1973, Rosenberg and Haley in press). Completion date of the breeding season varies, although August is typically the last month of nesting activity in this region (Rosenberg and Haley in press).

Prey items in stomach contents were identified to order; minimum number of prey items ingested was estimated by counting sclerotized fragments, including heads, mandibles, and elytra. Although pooling prey into order categories risks underestimating niche breadth (Greene and Jaksic 1983), finer taxonomic resolution of prey was difficult because of digestion and paucity of information available on invertebrate fauna of the area. Coleoptera was undoubtedly underestimated because the exoskeleton/elytra were generally in many small pieces, making quantification of prey items difficult. Because rodents were found infrequently (3.8% of all samples), they were excluded from analyses of sex, seasonal, and annual patterns of prey order but were included in the estimation of food-niche breadth and evenness.

Statistical Analyses

To describe the diet and to evaluate seasonal and sex changes in diet composition, we estimated mean number of items of each prey order per stomach for each sex, season and year, percent of total items for each prey order, and percent frequency of occurrence. We estimated dietary diversity by calculating food-niche breadth and dietary evenness for females ($n = 36$) and males ($n = 17$). We calculated breadth of food niches with the antilog of Shannon's index because it is readily interpretable and is linearly related to the number

of prey categories in the sample (Alatalo and Alatalo 1977). The possible breadth of the food niche for this sample was 1.00 to 8.00. We calculated dietary evenness by using Pielou's (1969) index. Evenness values ranged from 0.00 to 1.00, approaching 1.00 as prey proportions in the diet became equal.

To evaluate factors affecting diet composition and food-niche breadth, we sought models to approximate effects (Burnham and Anderson 1998) supported by our empirical data. We used analysis of variance (SAS 1990) and examined 10 models over 2 different response variables, examined separately, niche breadth and prey order. The most complex model allowed the response variables (niche breadth and prey order) to vary over time (by season and year), by sex, and with an interaction between season and sex effects. Intermediate models included sex, season, and year; sex, season, and sex with season interaction; sex and season; sex and year; and season and year. Our simplest models were 1-variable models consisting of sex, season, year, and a null model of only an intercept term. To evaluate all models and to select our best approximating model, we used the least-squares method of Akaike's Information Criterion with small-sample (2nd-order) bias adjustment (AIC_c) because our sample size was small with respect to the number of estimated effects (Burnham and Anderson 1998). Models were ranked and compared by use of AIC_c differences (Δ_i) and Akaike weights (w_i). AIC_c differences were calculated:

$$\Delta_i = AIC_{c,i} - \min AIC_c$$

where $AIC_{c,i}$ is the AIC_c value for the i th model in a suite of candidate models being compared and $\min AIC_c$ is the minimum value among those models. To interpret the relative likelihood of a model, we calculated Akaike weights:

$$w_i = \frac{\exp(-0.5*\Delta_i)}{\sum_{r=1}^R \exp(-0.5*\Delta_r)}$$

where Δ_i is the AIC_c difference for model i and R is the set of models. Akaike weights sum to 1 and provide a measurement for the "weight of evidence in favor of Model i as being the actual best model" (Burnham and Anderson 1998). It follows that the larger the

Δ_i , the smaller w_i will be and the less plausible is Model i as being the best model. Situations arose where several models were weighted similarly; all models within a relative likelihood of 2 of the best model were considered in making inferences. All values reported in the Results section are $\bar{x} \pm s_{\bar{x}}$.

RESULTS

Diet Composition

Araneida, Coleoptera, Dermaptera, Isopoda, Lepidoptera, Orthoptera, Rodentia, and Solpugida were identified in the diet. The average number of individual prey items per stomach was 46.8 ± 3.5 ; one breeding-season male had 113 individual prey items in its stomach. A breeding female with an egg almost fully developed in the oviduct had only mollusk shells, white pebbles, rodent bones, and Coleoptera chitin in its stomach.

Orthoptera was the dominant prey order based on prey numbers and frequency of occurrence (Table 1). Frequency of occurrence of Coleoptera, Dermaptera, and Solpugida was high, but number of individuals per stomach was low (Table 1). Rodentia and Isopoda were rare in the diet by both number and frequency of occurrence (Table 1).

The weights of several models were extremely close for both Isopoda ($w = 0.11-0.25$) and Solpugida ($w = 0.15-0.31$), indicating no best approximating model for these 2 orders. However, the null model for these 2 orders was not heavily weighted (Isopoda: $w = 0.01$, Solpugida: $w = 0.00$). The models with the greatest weight included sex and year effects for Isopoda and season and year effects for Solpugida. A greater number of Isopoda were consumed by males, and Solpugida was taken more during the breeding season; a greater number of both were consumed during a single year (Table 2). The models of sex and year, and sex, season, and year, were heavily weighted for Araneida ($w = 0.38$ and 0.24 , respectively) and Dermaptera ($w = 0.45$ and 0.20 , respectively). Males consumed a greater number of Araneida and Dermaptera than females, a greater number of both were consumed during the breeding season, and a greater number were consumed during a single year (Table 2). Consumption of Coleoptera and Lepidoptera was most affected by season and year (Coleoptera: $w = 0.38$; Lepidoptera:

TABLE 1. Composition of Burrowing Owl stomach contents ($n = 53$) collected in the Imperial Valley, California, 1994–1997.

Prey order	Number/stomach ^a		% of total ^b	Frequency of occurrence (%) ^c
	$\bar{x} \pm s_{\bar{x}}$	Range		
Araneida	1.2 ± 0.5	0–21	4.9	31.5
Coleoptera	2.0 ± 0.6	0–25	8.2	51.9
Dermaptera	2.5 ± 0.7	0–26	10.6	64.8
Isopoda	0.6 ± 0.6	0–32	2.5	3.7
Lepidoptera	1.4 ± 0.6	0–29	5.7	14.8
Orthoptera	13.9 ± 2.3	0–55	58.9	98.2
Rodentia	0.04 ± 0.03	0–1	0.2	3.7
Solipugida	2.1 ± 0.9	0–5	9.1	40.7

^aNumber of individuals of each taxa counted in Burrowing Owl stomachs.

^bPercent composition of the diet for each taxa, estimated as $x_i/x \cdot 100$, where x_i is the number of individuals of the i th prey order and x is the total number of prey for all orders.

^cPercent of stomachs in which we found ≥ 1 individual of the given prey order.

TABLE 2. Mean number ($\bar{x} \pm s_{\bar{x}}$) of prey items per stomach for the Burrowing Owl, Imperial Valley, California, 1994–1997.

Effect	n	Prey order						
		Araneida	Coleoptera	Dermaptera	Isopoda	Lepidoptera	Orthoptera	Solipugida
Sex								
female	36	0.61 ± 0.21	1.72 ± 0.72	1.74 ± 0.40	0.03 ± 0.03	0.17 ± 0.06	11.33 ± 2.44	2.76 ± 1.24
male	17	2.41 ± 1.34	2.65 ± 0.93	4.09 ± 1.83	1.88 ± 1.88	0.12 ± 0.08	19.21 ± 5.03	0.82 ± 0.29
Season								
breeding	20	2.15 ± 1.06	3.10 ± 0.81	2.60 ± 1.29	1.60 ± 1.60	3.65 ± 1.60	15.10 ± 4.17	4.43 ± 2.11
nonbreeding	33	0.61 ± 0.35	1.36 ± 0.76	2.42 ± 0.72	0.03 ± 0.03	0.06 ± 0.06	13.11 ± 2.82	0.76 ± 0.35
Year								
1994	12	1.67 ± 0.96	0.50 ± 0.19	1.50 ± 0.61	0.08 ± 0.08	0	9.38 ± 3.21	1.58 ± 0.93
1995	20	0.25 ± 0.12	2.95 ± 1.31	1.95 ± 0.61	0	0.50 ± 0.41	13.30 ± 4.35	0.55 ± 0.22
1996	4	0	1.25 ± 0.48	1.50 ± 0.74	0	0	20.75 ± 7.64	1.00 ± 0.71
1997	17	2.24 ± 1.23	2.18 ± 0.84	4.06 ± 1.84	1.88 ± 1.88	3.82 ± 1.84	16.06 ± 4.41	4.68 ± 2.49

$w = 0.57$), with a greater number consumed during the breeding season, and with a single year of high consumption (Table 2). Consumption of Orthoptera was affected by sex and year ($w = 0.49$), with a greater number consumed by males and during a single year (Table 2).

Food-Niche Breadth

Food-niche breadth was narrow and uneven, demonstrating selection for a few taxa (Table 3). Although the model with season and year effects was selected as the best approximating model based on Akaike weights ($w = 0.45$), it was less than twice as likely as the next best model of sex and season effects ($w = 0.26$). Food-niche breadth tended to be broadest during the breeding season and during a single year and was slightly broader for males than for females (Table 3). Although model selection evidence did not support a sex with season interaction model ($w = 0.03$ to 0.05),

estimates of the mean were suggestive of a small effect. Males tended to have a slightly broader food niche during the breeding season (2.75 ± 0.33 , $n = 6$) than females (2.33 ± 0.24 , $n = 14$), and the sexes had similar food-niche breadths during the nonbreeding season (1.77 ± 0.24 for $n = 11$ males and 1.88 ± 0.17 for $n = 22$ females).

DISCUSSION

Diet Composition

The dominance of Orthoptera in the diet of Burrowing Owls in the Imperial Valley was maintained regardless of season or year or consumption of alternative prey types. Jaksic (1989) suggests that opportunistic predators may show a disproportionately large consumption of most abundant prey after a search image has been formed. The conditions necessary for ideal Orthoptera habitat, including warm, dry surroundings with plenty of green

TABLE 3. Food-niche breadth and evenness of the Burrowing Owl, Imperial Valley, California, 1994–1997.

	<i>n</i>	Food-niche breadth		Evenness	
		$\bar{x} \pm s_{\bar{x}}$	Range	$\bar{x} \pm s_{\bar{x}}$	Range
Overall	53	2.07 ± 0.19	1.00–3.93	0.56 ± 0.05	0–1.00
Females	36	2.05 ± 0.14	1.00–3.78	0.55 ± 0.05	0–1.00
Males	17	2.12 ± 0.22	1.00–3.93	0.58 ± 0.05	0–1.00
Breeding season	20	2.45 ± 0.19	1.00–3.93	0.67 ± 0.06	0–1.00
Nonbreeding season	33	1.84 ± 0.14	1.00–3.66	0.49 ± 0.07	0–1.00
1994	12	2.07 ± 0.23	1.00–3.66	0.64 ± 0.10	0–1.00
1995	20	1.98 ± 0.20	1.00–3.62	0.54 ± 0.09	0–1.00
1996	4	1.82 ± 0.40	1.00–2.62	0.38 ± 0.17	0–0.70
1997	17	2.25 ± 0.23	1.00–3.93	0.56 ± 0.08	0–0.97

food, bare ground, and water (Dempster 1963), are met in the Imperial Valley agricultural matrix. With year-round irrigation and growth of crop plants, Orthoptera could reproduce all year. We observed dense populations of Orthoptera that served as a continual prey base for the Burrowing Owl.

Rodents represented only 0.2% of the total prey found in stomachs from this study and were the only vertebrates identified in the diet. In comparison, rodents and other vertebrate prey from previous studies represented 8% (Marti 1974, Colorado), 10% (Green et al. 1993, Oregon and Washington), 14% (Brown et al. 1986, Oregon), 20% (Jaksic and Marti 1981, Chile), 30% (Jaksic and Marti 1981, California), 35% (Schmutz et al. 1991, Alberta), 41% (Thomsen 1971, California), and 52% (Plumpton and Lutz 1993, Colorado) of the total prey. The difference in the proportion of vertebrate prey apparent between this study and previous studies may be partially accounted for by sampling methods, i.e., regurgitated pellets and stomach contents. Smaller and/or more easily digestible prey items could be discovered in stomach contents and overlooked or not discovered in regurgitated pellets. Past researchers (Jaksic and Marti 1981, Green et al. 1993) have concluded that the greater proportion of vertebrate prey reflects differential prey availability. We also attribute the low frequency of rodents in the diet and the differences between the Imperial Valley diet and other diets to differential prey availability, which is affected by habitat and weather differences. The only time rodents seemed to contribute more to the diet than revealed by our stomach analyses was after a field burn when we observed a greater accumulation of rodent remains

around owl burrows (Rosenberg and Haley in press). Additionally, owls responded much quicker to our traps that use mice (*Mus musculus*) as an attractant than at any of our other study sites in California (Rosenberg personal observation). This suggests that Burrowing Owls consume this larger, calcium- and protein-rich prey item when it is available to them. The year-round cultivation and flood method of irrigation is probably inhospitable to rodents, maintaining populations to a presumably low density.

Calcium is an essential nutrient for birds and is especially limiting for egg-laying females and growing young (St. Louis and Breebaart 1991). Birds that normally consume calcium-deficient diets, such as those containing insects, often augment dietary calcium by selectively consuming items rich in this element during times of greater physiological need (St. Louis and Breebaart 1991). The presence of calcium-rich food items in the stomach of one breeding female supports the hypothesis that female Burrowing Owls seek calcium-rich items during egg laying in the Imperial Valley. These calcium-rich items, such as mollusk shells, may be difficult to locate, causing eggs with thin shells to be laid. However, eggshell thickness of Burrowing Owls in the Imperial Valley is similar to that of other California populations (Gervais et al. 2000), suggesting that calcium may not be limiting. St. Louis and Breebaart (1991) suggested that when dietary calcium is insufficient, birds produce smaller clutches. The scarcity of rodents and other calcium-rich food items in the diet and the smaller average clutch size relative to other California populations (Rosenberg and Haley in press) leads us to hypothesize that calcium

is a limiting factor for Burrowing Owls in the Imperial Valley, thus affecting clutch size and reproductive rates. A recent study by Haley (2002) lends support to this hypothesis; Burrowing Owl productivity in the Imperial Valley is greater when the diet is supplemented with rodents. These results may also support an alternative protein-limitation hypothesis. Recent literature suggests that clutch and egg size may be greater for protein-supplemented females (Williams 1996, Nager et al. 1997).

Food-Niche Breadth

A narrow food niche is expected for the Burrowing Owl; the small body size of this predator, 150 gm (Haug et al. 1993), suggests that they are not capable of consuming a large array of prey types and sizes (Barclay and Brigham 1991, Marti et al. 1993). We expected seasonal and year-to-year variation in the diet because of changing seasonal energy needs and because of differential prey availability, palatability, accessibility, and profitability (Tome 1994, Smith and Remington 1996). Because opportunistic predators may select prey relative to prey abundance, we expected food niches to broaden during the breeding season when more prey species are likely available and more abundant. We also expected food-niche to broaden during the breeding season because, as speculated by Smith and Remington (1996), individuals may decrease prey selectivity when they experience elevated requirements such as those imposed on adult birds during egg production and chick rearing. We predicted food niches would narrow during the nonbreeding season when fewer prey species are likely available and when consumers do not need to meet nutrient and energetic requirements of raising offspring. We predicted a broader food niche for males than for females during the breeding season when females remain close to the nest to care for young (Haug et al. 1993). Males forage farther from the nest (Thompson and Anderson 1988), potentially encountering a wider variety of prey species. Although the male brings food to the female, it is likely less diverse than what he encounters. We expected similar food-niche breadth between sexes of this monomorphic species during the nonbreeding season when females are not caring for eggs or young and are free to forage farther from the nest for longer periods of time.

Consistent with our expectations, we detected strong seasonal and yearly effects on food-niche breadth, and a competing model indicated a sex effect. Burrowing owls consumed a greater diversity of prey, especially Araneida, Isopoda, Lepidoptera, and Solpugida, during the breeding season and during 1997. The seasonal and yearly variations in the diet that we detected were presumably because of differential annual and seasonal prey availability, palatability, accessibility, and profitability. However, in the absence of prey abundance data, we cannot make any conclusions regarding the mechanisms that led to temporal variation.

Males are known to provide food to females and offspring during the breeding season (Haug et al. 1993), thus foraging farther from the nest and for longer periods of time than females. During the nonbreeding season, both sexes can potentially forage equal distances and for equal time periods. We expected food-niche breadth to be broader for males than females during the breeding season and to be similar for the sexes during the nonbreeding season. Our results were consistent with this prediction; however, given the sample sizes, the evidence was not strong. Regardless of season, we found evidence that males had a broader niche breadth than females. Males consumed a greater number of Araneida, Coleoptera, Dermaptera, Isopoda, and Orthoptera than females. Differences in food-niche breadth between the sexes of birds is mainly because of sexual size dimorphism (Selander 1966, Storer 1966, Earhart and Johnson 1970, Halley and Gjershaug 1998). However, Burrowing Owls are monomorphic (Earhart and Johnson 1970) or only slightly dimorphic (Plumpton and Lutz 1994) in body size, suggesting that factors other than body size are responsible for the difference in food-niche breadth observed. Although we do not know the mechanism for broader food-niche breadth in males, we speculate that males acquire a broader array of search images from the greater time spent foraging during the breeding season, allowing them to key in on a greater variety of prey types year-round than females.

CONCLUSIONS

We suggest the reason for low rodent numbers and dominance of Orthoptera in the diet,

the primary difference between the diet of Burrowing Owls in the Imperial Valley and the diet at other sites in California (Rosenberg and Haley in press) and elsewhere (Haug et al. 1993), is low availability of rodents, rather than preference for Orthoptera. Orthoptera are abundant year-round in the Imperial Valley (K. Sturm personal observation) and may explain the high density of Burrowing Owls reported by Rosenberg and Haley (in press). This prey source may be sufficient to maintain a high density of Burrowing Owls, but insufficient in quality to permit high per capita reproductive success. In particular, clutch size may be limited by the per capita availability of energy or nutrients, such as protein (Williams 1996, Nager et al. 1997). A high density of owls may influence the per capita availability of these resources through competition. We suggest that per capita prey resources may be limiting the reproductive success of Burrowing Owls in the Imperial Valley. Research on the abundance, availability, and nutrient quality of prey would allow a more thorough understanding of the foraging ecology of Burrowing Owls and of the relationship between diet and demographic characteristics.

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LITERATURE CITED

ALATALO, R.V., AND R. ALATALO. 1977. Components of diversity: multivariate analysis with interaction. *Ecology* 58:900-906.

- BARCLAY, R.M., AND R.M. BRIGHAM. 1991. Prey detection, dietary niche breadth, and body size in bats: why are aerial insectivorous bats so small? *American Naturalist* 137:693-703.
- BARROWS, C. 1989. Diets of five species of desert owls. *Western Birds* 20:1-10.
- BROWN, A.B., J.O. WHITAKER, T.W. FRENCH, AND C. MASER. 1986. Note on food habits of the Screech Owl and the Burrowing Owl of southeastern Oregon. *Great Basin Naturalist* 46:421-426.
- BURNHAM, K.P., AND D.R. ANDERSON. 1998. Model selection and inference: a practical information-theoretic approach. Springer-Verlag, New York. 353 pp.
- COULOMBE, N. 1971. Behavior and population ecology of the Burrowing Owl, *Speotyto cunicularia*, in the Imperial Valley of California. *Condor* 73:162-176.
- DEMPSTER, J.P. 1963. The population dynamics of grasshoppers and locusts. *Biological Review* 38:490-529.
- EARHART, C.M., AND N.K. JOHNSON. 1970. Size dimorphism and food habits of North American owls. *Condor* 72: 251-264.
- EDWARDS, G.P. 1997. Predicting seasonal diet in the yellow-bellied marmot: success and failure for the linear programming model. *Oecologia* 112:320-330.
- 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.
- GLEASON, R.L., AND T.H. CRAIG. 1979. Food habits of Burrowing Owls in southeastern Idaho. *Great Basin Naturalist* 39:275-276.
- GREEN, G.A., R.E. FITZNER, R.G. ANTHONY, AND L.E. ROGERS. 1993. Comparative diets of Burrowing Owls in Oregon and Washington. *Northwest Science* 67: 88-92.
- GREENE, H.W., AND F.M. JAKSIC. 1983. Food-niche relationships among sympatric predators: effects of level of prey identification. *Oikos* 40:151-154.
- HALEY, K.L. 2002. The role of food limitation and predation on reproductive success of Burrowing Owls in southern California. Master's thesis, Oregon State University, Corvallis.
- HALLEY, D.J., AND J.O. GJERSHAUG. 1998. Inter- and intraspecific dominance relationships and feeding behavior of Golden Eagles *Aquila chrysaetos* and Sea Eagles *Haliaeetus albicilla* at carcasses. *Ibis* 140:295-301.
- HAUG, E.A., B.A. MILLSAP AND M.S. MARTELL. 1993. Burrowing Owl (*Speotyto cunicularia*). Pages 1-20 in A. Poole and F. Gill, editors, *The Birds of North America*, No. 61. The Academy of Natural Sciences, Washington, DC.
- HEGAZI, E.M. 1981. A study of the amount of some invertebrates that are eaten by wild birds in the Egyptian western desert. *Journal of Agricultural Science* 96: 497-501.
- JAKSIC, F.M. 1989. Opportunism vs selectivity among carnivorous predators that eat mammalian prey: a statistical test of hypotheses. *Oikos* 56:427-430.
- JAKSIC, F.M., H.W. GREENE, AND J.L. YANEZ. 1981. The guild structure of a community of predatory vertebrates in central Chile. *Oecologia* 49:21-28.
- JAKSIC, F.M., AND C.D. MARTI. 1981. Trophic ecology of *Athene* owls in Mediterranean-type ecosystems: a comparative analysis. *Canadian Journal of Zoology* 59:2331-2340.

- KORPIMAKI, E. 1992. Diet composition, prey choice, and breeding success of Long-eared Owls: effects of multiannual fluctuations in food abundance. *Canadian Journal of Zoology* 70:2373–2381.
- KREBS, J.R., D.W. STEPHENS, AND W.J. SUTHERLAND. 1983. Perspectives in optimal foraging. Pages 165–216 in G.A. Clark and A.H. Brush, editors, *Perspectives in ornithology*. Cambridge University Press, New York.
- MACARTHUR, R.H., AND E.R. PIANKA. 1966. On optimal use of a patchy environment. *American Naturalist* 100:603–609.
- MACCRACKEN, J.G., D.W. URESK, AND R.M. HANSEN. 1985. Burrowing Owl foods in the Conata Basin, South Dakota. *Great Basin Naturalist* 45:287–290.
- MARTI, C.D. 1974. Feeding ecology of four sympatric owls. *Condor* 76:45–61.
- MARTI, C.D., K. STEENHOEF, M.N. KOCHERT, AND J. MARKS. 1993. Community trophic structure: the roles of diet, body size, and activity time in vertebrate predators. *Oikos* 67:6–18.
- MARTIN, D.J. 1973. Selected aspects of Burrowing Owl ecology and behavior in central New Mexico. *Condor* 75:446–456.
- MCKNIGHT, S.K., AND G.R. HEPP. 1998. Foraging-niche dynamics of gadwalls and American Coots in winter. *Auk* 115:670–683.
- MURDOCH, M.W., AND A. OATEN. 1975. Predation and population stability. *Advanced Ecological Research* 9:2–131.
- NAGER, R.G., C. RUEGGER, AND A.J. VANNOORDWIJK. 1997. Nutrient or energy limitation on egg formation: a feeding experiment in Great Tits. *Journal of Animal Ecology* 66:495–507.
- PIELOU, E.C. 1969. *An introduction to mathematical ecology*. Wiley-Interscience, New York. 286 pp.
- PLUMPTON, D.L., AND R.S. LUTZ. 1993. Prey selection and food habits of Burrowing Owls in Colorado. *Great Basin Naturalist* 53:299–304.
- _____. 1994. Sexual size dimorphism, mate choice, and productivity of Burrowing Owls. *Auk* 111:724–727.
- PULLIAM, H.R. 1974. On the theory of optimal diets. *American Naturalist* 108:59–74.
- ROSENBERG, D.K., AND K.L. HALEY. In press. The ecology of Burrowing Owls in the agroecosystem of the Imperial Valley, California. *Studies in Avian Biology*.
- SAS INSTITUTE, INC. 1990. *SAS/STAT user's guide*. Version 6, 4th edition. SAS Institute, Inc., Cary, NC.
- SCHMUTZ, J.K., G. WOOD, AND D. WOOD. 1991. Spring and summer prey of Burrowing Owls in Alberta. *Blue Jay* 49:93–97.
- SELANDER, R.K. 1966. Sexual dimorphism and differential niche utilization in birds. *Condor* 68:113–151.
- SMITH, H.R., AND C.L. REMINGTON. 1996. Food specificity in interspecies competition. *BioScience* 46:436–447.
- STEPHENS, D.W., AND J.R. KREBS. 1986. *Foraging theory*. Princeton University Press, Princeton, NJ.
- ST. LOUIS, V.L., AND L. BREEBAART. 1991. Calcium supplements in the diet of nestling Tree Swallows near acid sensitive lakes. *Condor* 93:286–294.
- STORER, R.W. 1966. Sexual dimorphism and food habits in three North American accipiters. *Auk* 83:423–436.
- THOMPSON, C.D., AND S.H. ANDERSON. 1988. Foraging behavior and food habits of Burrowing Owls in Wyoming. *Prairie Naturalist* 20:23–28.
- THOMSEN, L. 1971. Behavior and ecology of Burrowing Owls on the Oakland municipal airport. *Condor* 73:177–192.
- TOME, D. 1994. Diet composition of the Long-eared Owl in central Slovenia: seasonal variation in prey use. *Journal of Raptor Research* 28:253–258.
- VILLAGE, A. 1982. The diet of kestrels in relation to vole abundance. *Bird Study* 29:129–138.
- WILLIAMS, T.D. 1996. Variation in reproductive effort in female Zebra Finches (*Taeniopygia guttata*) in relation to nutrient-specific dietary supplements during egg laying. *Physiological Zoology* 69:1255–1275.

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