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THE ECOLOGY OF BURROWING OWLS IN THE AGROECOSYSTEM OF THE IMPERIAL VALLEY, CALIFORNIA

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Abstract. Burrowing Owls (*Athene cunicularia*) are common in some agroecosystems, yet their ecology in these environments is poorly known. To address this, we collected demographic and space-use data on the Burrowing Owl in the Imperial Valley of southeastern California during the breeding season, 1997–2000. Within our 11.7 km^2 study area, we estimated a very high density of Burrowing Owls (8.3 pairs/km^2) which remained relatively constant during the study. Owls nested predominately on the edges of constructed drains and canals that bordered agricultural fields. Clutch size ranged from 4–8 (mean = 6.7) eggs/clutch and varied little among years. Productivity averaged 2.5 young/nest and varied considerably among individuals and years. Adult annual survival rates for males (0.65) and females (0.62) were similar or higher than reported for other Burrowing Owl populations. We observed high nest-site fidelity for adults, with 85% remaining within 400 m of the previous year's nest. Females moved greater distances than males between breeding seasons; distances were greater for owls whose nests failed. Few juveniles (20 of 124, 16%) were subsequently observed as adults. This, together with a lack of a declining dispersal function, suggested juveniles frequently emigrated from the study area. Based on estimates of nocturnal movements of males, we estimated low selection for the type of crops in which they foraged. They foraged primarily (>80%) within 600 m of their nest, but long-distance movements (2–3 km) often resulted in large estimates (113.7 ± 30.4 ha) of the area traversed (minimum convex polygon method) and the area used (45.3 ± 18.2 ha; fixed kernel method). Because of the high densities of owls, home ranges overlapped considerably. Our estimates of demographic parameters and the space-use properties of Burrowing Owls contrast with those reported from non-agricultural areas. Our results suggest agricultural areas can provide high quality habitat if burrows are available, which in our study area was determined by the farmers tolerance of burrows along the canals and drains bordering their property.

Key Words: agroecosystems; *Athene cunicularia;* Burrowing Owl; California; dispersal; Imperial Valley; reproductive rates; survival rates.

LA ECOLOGÍA DE TECOLOTES LLANEROS EN LOS AGROSISTEMAS DEL VALLE IMPERIAL, CALIFORNIA

Resumen. Los Tecolotes Llaneros (*Athene cunicularia*) son comunes en algunos agroecosistemas, no obstante su ecología en estos ambientes es poco conocida. Con este propósito, durante las temporadas reproductivas de 1997–2000 se colectó información sobre la demografía y el uso espacial del Tecolote Llanero en el Valle Imperial del sureste de California. Dentro del área de estudio (11.7 km^2) se estimó una densidad muy alta de tecolotes (8.3 parejas/km^2) la cual permaneció relativamente constante durante el estudio. Los tecolotes anidaron predominantemente en los bordes de los drenajes y canales que rodean a las parcelas. El tamaño promedio de las nidadas fue de 4–8 huevos por nido (media = 6.7) y varió poco entre años. El promedio en la productividad fue de 2.5 juveniles/nido y varió considerablemente entre individuos y años. Las tasas anuales de supervivencia en machos adultos (0.65) y hembras adultas (0.62) fueron similares o más altas que las reportadas para otras poblaciones de Tecolotes Llaneros. Se observó también que los adultos muestran una alta fidelidad al sitio de anidación, con el 85% permaneciendo dentro de una distancia de 400 m del nido utilizado el año anterior. Las hembras se movieron a mayores distancias que los machos entre temporadas reproductivas, las distancias fueron mayores para aquellos tecolotes cuyos nidos fracasaron. Pocos juveniles (20 de 124, 16%) fueron observados posteriormente como adultos. Esto, junto con la ausencia de una función de dispersión disminuida, sugirió que los juveniles emigraron del área de estudio. Con base en estimaciones de movimientos nocturnos de los tecolotes machos, se estimó que hubo poca selección por el tipo de cosecha en la cual se alimentaron. Ellos forrajearon principalmente (>80%) dentro de un distancia de 600 m de su nido, aunque los movimientos a mayores distancias (2–3 km) a menudo resultaron en estimaciones mayores (113.7 ± 30.4 ha) del área atravesada (método del polígono mínimo convexo) y del área utilizada (45.3 ± 18.2 ha, método fijo kernel). Debido a la alta densidad de tecolotes, las áraes utilizadas se traslaparon considerablemente. Nuestras estimaciones de los parámetros demográficos y de las propiedades del uso del espacio de los Tecolotes Llaneros contrastan con aquellas reportadas para áreas no agrícolas. Nuestros resultados sugieren que las áreas agrícolas pueden proporcionar un hábitat de alta calidad si hay madrigueras disponibles, lo cual en nuestra área de estudio estuvo determinado por la tolerancia de los agricultores a la presencia de las madrigueras a lo largo de los canales y drenajesque rodean a sus propiedades.

Palabras claves: Agroecosistemas; *Athene cunicularia*; California; dispersión; tasa reproductiva; tasa de supervivencia; Tecolote Llanero; Valle Imperial.

The Burrowing Owl (*Athene cunicularia*) is a burrow-nesting owl characteristic of grasslands and deserts throughout western North America, Florida, and Central and South America (Haug et al. 1993). The Western Burrowing Owl (*A. c. hypugaea*) was once widespread and fairly common over western North America. Population declines led to listing of the Burrowing Owl as endangered, threatened, or a species of concern in Canada, Mexico, and in a number of U.S. states (James and Espie 1997). Declines likely reflect eradication or control of fossorial mammals, intensive pesticide use, and conversion of grasslands to agriculture and residential or commercial development (Haug et al. 1993, Trulio 1997, Desmond et al. 2000, Gervais et al. 2000).

California has one of the largest populations of both resident and wintering Burrowing Owls (James and Ethier 1989). Particularly high numbers and densities occur in the Imperial Valley, located in southeastern California (Coulombe 1971; DeSante et al. *this volume*). Historically, Burrowing Owls were present within the Imperial Valley in low densities similar to those in undisturbed habitat of the surrounding Colorado (Sonoran) desert (DeSante et al. *this volume*). Intensification of agriculture in the 1900s (Clemings 1996) enabled Burrowing Owl populations of the Valley to increase greatly. Increasing development and changing patterns of water conveyance in southern California (e.g., Clemings 1996) may have major impacts on the distribution and abundance of Burrowing Owls in the region.

Despite the large population of Burrowing Owls in the Imperial Valley, there have been few investigations of their ecology. Coulombe (1971) and DeSante et al. (*this volume*) documented the concentration of Burrowing Owls along the various watercourses. Although their research provided a framework for understanding these issues, a quantitative approach to the demography and space-use ecology of this species is needed to develop scientifically credible management strategies.

To address this need, we initiated studies of the owl's demography and space-use patterns within the agroecosystem of the Imperial Valley. In this paper, we examine (1) patterns of distribution of Burrowing Owls; (2) rates of and factors affecting survival, reproduction, and between-year movement; and (3) patterns of space-use of individuals. We explore factors that affect individuals and how this may ultimately affect the dynamics of the population.

STUDY AREA

The study area was at the southern rim of the Salton Sea, 40 km north of El Centro, California (Fig. 1). We divided the study area into several subareas. We captured and marked Burrowing Owls only in the Intensive Study Area (ISA), which totaled 1175 ha (Fig. 1). The second subarea (Area B; Fig. 1) extended 0.8 km beyond the ISA. Together, these two areas represented the Demography Study Area (DSA). The third subarea (Area C; Fig. 1) extended 0.8 km (1999) or 1.6 km (2000) beyond the DSA. Most (81%) of the ISA consisted of privately owned agricultural fields. The remainder encompassed a segment of the Sonny Bono Salton Sea National Wildlife Refuge (hereafter, Refuge; Fig. 1). The Refuge maintained a set of 35 nest boxes situated between roads and fields. Design of nest boxes were similar to those described by Trulio (1995).

The study area was characterized by agricultural fields framed by a system of concrete water-delivery ditches and canals, and earthen drains. Drains were deep (up to 8–9 m), dredged waterways maintained by the Imperial Irrigation District. Within this agricultural matrix Burrowing Owls nested almost entirely within or along drains, ditches, and canals. Fields were intensively managed for year-round production of vegetables and cattle feed. Primary crops were Sudan grass (*Sorghum bicolor*), Bermuda grass (*Cynodon dactylon*), alfalfa (*Medicago sativa*), onions (*Allium cepa*), and corn (*Zea mays*).

METHODS

Density Estimation

To estimate the density of Burrowing Owls we first estimated the probability of detecting nesting pairs of Burrowing Owls within the ISA. We divided the study area into approximately 20 800-m blocks, and surveyed each alternating block outside of the Refuge (N = 7) from 14 to 30 April 1998. We surveyed all roads and watercourses that bordered fields three times, two by vehicle and one on foot. We conducted surveys at vehicle speeds ≤10 km/hr with two observers during the morning (30 min before sunrise to 4 hrs after) and evening (3 hrs before sunset until sunset) when wind speeds were <15 km/hr. We used both behavioral and physical evidence of nesting to determine if a pair occupied a given burrow (e.g., Millsap and Bear 1997). To estimate the probability of detecting nesting owls, we applied the removal model of Zippin (1958), which estimates population size as a function of the number of new individuals, or nests as in this study, that are encountered on each survey (Otis et al. 1978:28).

Diet

We estimated the diet composition of Burrowing Owls from regurgitated pellets. We collected pellets from randomly selected nests (2000) and from nest boxes within the Refuge (1998 and 2000). All pellets from a given nest and year were treated as a single sample. We estimated the relative frequency of consumption by recording the occurrence of each taxonomic order. Because earlier observations indicated that the frequency of rodents in the diet may strongly influence productivity (D. Rosenberg et al., unpubl. data), we computed an index of rodent consumption. Skeletal remains were counted to estimate the minimum number of rodents consumed. The index was computed for each sample as the ratio of the minimum number of rodents consumed/number of pellets. We

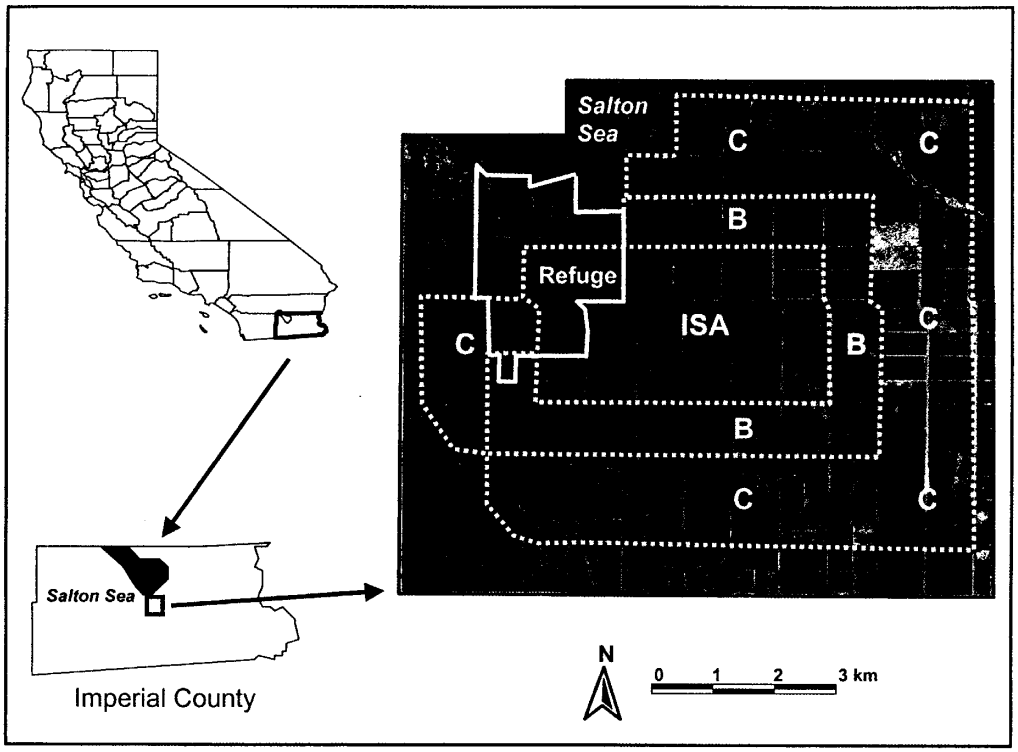

FIGURE 1. Study area in the Imperial Valley of southeastern California. Owls were banded within the Intensive Study Area (ISA) and resighted with equal effort in both the ISA and Subarea B, collectively termed the Demography Study Area. In addition, we attempted to resight owls in Subarea C, but with lower effort. All areas with owl nests within the Refuge were included in the ISA.

estimated the relative degree of variation of the index between years as the coefficient of variation (standard deviation/mean ×100).

Capture and Reobservation

We attempted to capture and mark a large segment of the population within the ISA. We captured Burrowing Owls during May 1997 and April–July 1998–2000. We captured adult owls using spring-net traps baited with a caged mouse, and two-way burrow traps (Bothelo and Arrowwood 1995). We captured young with a one-way trap, modified from that described in Banuelos (1997). We removed young from nest boxes by hand. We marked young and adult Burrowing Owls with an aluminum alpha-numeric color band (Acraft Sign and Nameplate Co., Ltd., Edmonton, Alberta, Canada) and a non-locking No. 4 U.S. Fish and Wildlife Service band. We assigned sex based on presence/absence of brood patch, plumage coloration, and behavioral observations (Haug et al. 1993).

Within the DSA (Fig. 1) we attempted to identify all marked individuals and locate their nests. Resighting efforts involved two vehicular surveys, as described above (see Density Estimation), supplemented by sightings made incidental to the surveys. We conducted a single vehicular survey for marked owls in subarea C (Fig. 1). Because of the lower effort and presumably lower resighting rates, we did not include observations of marked owls from this outer area for survival estimation but included these data for estimation of movement patterns and emigration rates.

Productivity and Breeding Phenology

To estimate productivity, we randomly selected 30 nests from privately-owned agricultural land within the ISA (1999 and 2000) and all occupied nest boxes within the Refuge not subject to experimental feeding from a concurrent study (1998, N = 13; 1999, N = 6; 2000, N = 7; Haley 2002) within the Refuge. We used the same criteria as described above (Density Estimation) to determine if a pair occupied a given burrow; only occupied nests were included for productivity estimation. Nests for which we could not estimate productivity due to limited visibility of nests or an inability to determine whether or not the nest was successful were excluded from analyses, resulting in sample sizes of 23–29 nests outside of the Refuge each year.

We defined productivity as the maximum number of 21–28-d-old young seen simultaneously at a nest during a series of five 30-min watches, each separated by at least 6 hr (Gorman et al. 2003). We aged young via visual techniques described by Haug et al (1993) and Priest (1997). Observations were made from a vehicle at a distance of 80–200 m, using either binoculars or 20–60× spotting scopes during the morning or evening as defined previously. We examined the influence

of diet (rodent index), intraspecific competition, and year on productivity from the randomly selected nests in 1999 and 2000. We used the minimum nearest-neighbor distance (log-transformed) and number of nests within 600 m (radius of foraging concentration; see RESULTS) as an index of intraspecific competition. We used a generalized linear model with a negative binomial response probability distribution and a log-link function (SAS Institute 1993). We chose this regression model because count data, such as the number of young, often conforms to a negative binomial distribution, and because this model, when the data are so distributed, provides a more powerful approach with fewer assumptions than other methods (White and Bennetts 1996).

We estimated Burrowing Owl reproductive biology by examining nest boxes within the Refuge and the Refuge headquarters, approximately 10 km east of the ISA. In 1999 and 2000, we evaluated date of first laying, clutch completion, and hatching, and measured clutch size and nest success. We monitored all nest boxes with evidence of owl use weekly until eggs were seen. During each visit, we used an infrared probe (Sandpiper Technologies, Manteca, CA) to observe nest contents. Once eggs were seen, we visited nests at 3 to 4-d intervals to estimate clutch completion dates. A clutch was defined as complete when the number of eggs did not increase by more than one egg/72 hr (Haley 2002). We estimated hatch success as the percent of eggs that hatched/nest.

Between-Year Movements

To estimate movement patterns, we used data from owls marked in 1998–1999 and resighted in 1999–2000. We estimated movements of both juveniles and adults. However, we evaluated movement functions and factors associated with movements only for adults because we likely underestimated movement rates for juveniles (see RESULTS).

We did not attempt to differentiate between adults undergoing breeding dispersal (sensu Greenwood 1980) and those moving x distance from their nest the previous year. Rather, we simply modeled distances moved between years under the notion that, based on movement data alone, there is no exact distance that can be considered fundamentally different than any other. We compared two functions, a hazard rate and a negative exponential. The hazard rate model has properties similar to those of the exponential but allows for a "shoulder" (i.e., a distance interval at which the probability to move remains constant) near zero distance. We explored the two functional forms because based on theory, a decreasing probability of movement as distance increases should exist and there were sampling and biological reasons (e.g., Olson and Van Horne 1998) to expect a shoulder near zero distance. In such cases, the hazard-rate function is often useful (e.g., Buckland et al. 1993). The hazard-rate function we used was of the form $Pr(x) = 1 - \exp(-[x/\sigma]^{-b})$ and the negative exponential function was expressed as $Pr(x) = \exp(-x/\lambda)$ (Buckland et al. 1993). To describe the probability density function, we rescaled the function by c, where c was the value of the integration of the function evaluated from zero to the furthest distance an owl was observed to move between years. We selected the most appropriate function with Akaike's Information Criterion, adjusted for small-sample size (AICc; Burnham and Anderson 1998) for adults with sexes and years pooled, and then used AICc to compare models fit as sex, year, or sex- and year-specific.

The size and geometry of the area in which movements can be detected may result in the appearance of underlying movement functions that fit models such as the exponential (Porter and Dooley 1993) or hazard-rate. We evaluated this by recreating a set of movements with a uniform probability for which distances from zero to the maximum movement distance we observed (3065 m) all had equal probabilities of occurring. We assigned each owl located in 1998 and relocated in 1999 with a new location for 1999 based on a random direction of movement and a random distance that followed a uniform distribution. Only those individuals that would have been within the DSA (and thus detected) were considered relocated. We fit these data to the same function that was selected for the observed distribution of movements. We graphically approximated the point at which the probability of moving declined from the expected uniform pattern. Similar dispersal patterns between the simulated and the observed distances would suggest that observed movement patterns were affected by the size and geometry of the study area.

We developed ten *a priori* models to explore factors that may affect the distance adults moved between years. We examined each model with multiple regression and used AICc as a basis for model selection. The response variable was the log-transformed distance an adult owl moved between years and explanatory factors included a combination of year, distance to the nearest nest, and whether or not the owl's mate was still present on the study area. The simplest model considered was a no-effects model in which only an intercept term (representing average distance moved) was estimated. For those individuals for which we estimated productivity and movement, we included as a parameter in the model whether or not their nest was successful in the previous year. We compared nine *a priori* models for this smaller data set. In both sets of analyses, we used data only from individuals that were seen in two successive years and for which both members of the pair were initially banded.

Survival

We used mark-recapture analysis to estimate apparent (i.e., we assumed no emigration from study area occurred) survival rates of Burrowing Owls first captured as adults. We excluded individuals first captured as young because we determined sex of only 17 of 242 marked young, and these were unlikely representative of the population. We fitted modified Jolly-Seber-Cormack models to the mark-recapture data using Program MARK (White and Burnham 1999). We developed ten *a priori* models to estimate survival rates. We used AICc weights (w) to compare the relative likelihood of each model. We used these weights to estimate an average survival rate from all models considered. Model averaging allows inference to be based on all models considered, thus increasing the inferential validity over that of a single model approach (Burnham

and Anderson 1998). We assessed goodness-of-fit for the global model using 1000 bootstrap simulations to evaluate the likelihood of the observed deviance (White and Burnham 1999).

Apparent survival rates reflect both mortality and emigration; however, we were interested in estimating "true" (sensu Franklin et al. 1996) survival rates. To allow estimation of survival, we estimated emigration rates of adult Burrowing Owls from observed movements of individuals between 1998–1999. We then estimated survival as

$$\hat{S} = \hat{\phi} + \hat{E}$$

where $\hat{S}$, $\hat{\phi}$, and $\hat{E}$ are the estimated probabilities of annual survival, apparent survival, and emigration of individuals from the DSA, respectively (Burnham et al. 1996). To simplify estimation, we assumed owls emigrated just before nesting and thus experienced no mortality between emigration and the time of resighting. Because the probability of emigration is a function of the location of an individual from the boundary of a study area (e.g., Barrowclough 1978), we randomized observed distances among owls and randomly selected an angle of movement to estimate a new location. We did this separately for males and females because of the differences in observed movement patterns (see RESULTS). We estimated the probability of emigration as:

$$\bar{\hat{E}} = \left(\sum_{i=1}^{R} n^*/n\right) \Big/ R,$$

where n^* was the number of adults with estimated locations outside of the study area, n was the number of marked owls in year t that survived and were relocated in year $t + 1$, and R was the number of replications of the random process of recreating movement patterns. We used $R = 1000$ replications and used the mean of $\hat{E}$ as our best estimate of emigration. This method of estimating emigration assumes that the observed distances reflect the true distribution of distances moved, such that individuals that moved outside of the study area and were not detected had movement patterns similar to those owls that were detected. This assumption was supported by the rapidly declining dispersal function (see RESULTS), similar patterns of movement for owls located in the center of the study area as for those located throughout (D. Rosenberg, unpubl. data), and a relatively uniform environment within the study area (homogeneity assumption of Zeng and Brown 1987).

Space Use

In May 1998, we radio-tracked six male owls to gain quantitative insight into the owls' space-use patterns. We used necklace-design radio transmitters (4.5 g) with a 20-cm antennae (Holohil Systems, Ltd., Carp, Ontario, Canada). We captured owls that nested within a 0.4 × 0.8 km area along the edge of the road and fields within the Refuge. We attempted to track owls each night from 2000 to 0400 hrs from 5 June–13 July. The receiving antenna assembly consisted of two H-configured antennae (Telonics, Mesa, AZ) separated by a cross boom and connected to a null combiner, mounted to a 2-m rotating tower with a fixed compass. The tower was secured in the bed of a truck, making the antennae height approximately 3 m above ground, following methods described in Gervais et al. (2003).

We established a grid system of stations at approximately 400 m intervals to obtain biangulation data. This allowed a formal search method to negate the potential bias of observers returning to known sites of occurrence, such as nests (Rosenberg and McKelvey 1999). We attempted to obtain locations of a given owl every 15 min. Only locations computed from estimates of the angle of the owl from two stations within 5 min were included in analyses. We omitted all observations that led to locations greater than 1 km from the telemetry stations because of their greater expected error (Gervais et al. 2003).

We estimated home ranges to estimate the area used (kernel methods) and the area traversed (minimum convex polygon, MCP). We used a fixed kernel estimator with least squares cross validation (LSCV) and also an adaptive kernel to estimate area used (Worton 1989). To estimate home range size we used programs KERNELHR (fixed kernel; Seaman et al. 1998), HomeRanger (adaptive kernel; Hovey 1999), and Telem (MCP; K. McKelvey, pers. comm.).

We evaluated factors that potentially affected the owls' likelihood of use. We evaluated distance of owl locations to field edge, distance to nest, and within each field the crop type, dominant crop height, and percent bare ground. The data structure consisted of a sample of cells (30-m^2 pixels) in which the individual was located by radio telemetry and a sample of randomly selected cells (Design III of Manly et al. 1993). Random cells were sampled from within a circle with a radius equal to the maximum distance an individual was located from its nest (Rosenberg and McKelvey 1999). The binary response variable was coded 1 if an individual was located in a particular cell, 0 if random. We used logistic regression to estimate selection as the odds ratio of use (Hosmer and Lemeshow 1989:40), Proc Logistic (SAS Institute 1994) to obtain parameter estimates, and AICc weights to evaluate the relative likelihood of a given model as being the best among those we considered (Burnham and Anderson 1998).

We developed seven *a priori* models to estimate habitat selection. We evaluated distance to the nest as either a 'log-function or a 3rd-order polynomial. We categorized crops using two pooling regimes based on density of vegetation: (1) crops with closed canopy structure during the study period (hay, wheat [*Triticum aestivum*], Sudan grass, Bermuda grass, alfalfa, and corn) or an open canopy structure (no crops, onions, and cotton) and (2) simply whether or not standing crops existed. Although cotton becomes dense near maturity, it was relatively open during the study. For each field, we estimated average crop height and percent of bare ground during the mid-point of the space-use study. We subjectively pooled crop types into simple classes that we expected would influence owl foraging behavior to accommodate the small number of observations/owl and the large number of different crop types. We expected a negative relationship of foraging with increasing density of vegetation, and based on central place foraging behavior of the owls, a strong decrease of use with distance from the nest. Although we were interested in investigating the selection for edge habitat, we were unable to do so because of the

TABLE 1. NEAREST NEIGHBOR DISTANCES (M) OF BURROWING OWL NESTS WITHIN THE INTENSIVE STUDY AREA, IMPERIAL VALLEY, CA, 1998–2000

Year	N	Range	Mean	SE	Median
1998	106	13–760	125.4	11.2	98.6
1999	93	8–818	149.1	15.2	101.1
2000	94	7–806	165.9	15.9	121.5

confounding effect of distance from the nest given all nests were located in edge habitat.

RESULTS

NEST DENSITY AND DISTRIBUTION

Based on the number of new nests found in the three surveys (37, 8, 0 nests), we estimated a 0.85/survey detection probability under the Zippin model. This very high detection/survey results in counting most of the Burrowing Owls within the study area from two (98%) or three (99.9%) surveys. Thus, our estimates of density based on counts should have negligible bias.

Density of nesting pairs of Burrowing Owls remained fairly constant during the three years of the survey within the ISA. In each year, we located approximately 100 nesting pairs (1998: 106; 1999: 93; 2000: 94). From these counts, we estimated an average crude (entire area) density of 8.3 pairs/km^2 and an average linear occurrence of 2.9 pairs/km of nest (edge) habitat. Nesting pairs of owls were exceptionally dense along drains and canals, resulting in an average nearest neighbor distance ranging from 125–166 m across years (Table 1). Nests, excluding those in nest boxes, were located primarily along drains (43%), delivery ditches (43%), and canals (11%), with little variation among years.

DIET

Based on frequency of occurrence in pellet samples, the diet was dominated by arthropods, particularly Orthoptera (grasshoppers and crickets), Coleoptera (beetles), and Dermaptera (earwigs; Fig. 2). Small mammals (primarily house mouse [*Mus musculus*], pocket mouse [*Perognathus* spp.], deer mouse [*Peromyscus* spp.], and Botta's pocket gopher [*Thomomys bottae*]) were the dominant vertebrate prey, though birds were frequent in 2000. The average number of rodents/pellet was similar in 1998 (0.10 ± 0.04; CV = 148%) to 2000 (0.13 ± 0.03; CV = 115%).

BREEDING PHENOLOGY AND PRODUCTIVITY

Burrowing Owls in the Refuge generally initiated breeding in April and May and extended into late summer. Egg-laying began as early as 24 April in 1999 and prior to our first observations on 7 April in 2000. Clutches were completed as early as 30 April (1999) and 9 April (2000), but average dates were 14 May (SE = 4.2 d, N = 6 nests) and 29 April (SE = 3.5 d, N = 17 nests), respectively. Pairs with early season nest failures that relaid did so as late as mid-July in 1999 and 2000. Clutch size was similar between years (1999: 6.5 ± 0.2, N = 17; 2000: 6.9 ± 0.3, N = 19), ranging from 4–8 eggs/nest attempt. Young hatched within 1–6 (3.3 ± 1.1, N = 4) days of one another in 1999 and 3–7 (4.3 ± 0.6, N = 9) days in 2000, resulting in large size variation among siblings (Haley 2002). Based on this large variation of hatch date within a clutch, females apparently began incubation prior to clutch completion. Hatching success in 1999 (70.5% ± 14.8, N = 6) was similar to 2000 (84.4% ± 6.9, N = 8) in 2000. Dates of newly hatched young ranged from 13 May–20 June in 1999 (mean 3 June ± 3.6 d, N = 10) and 30 April–June 22 in 2000 (mean 16 May ± 3.4 d, N = 16).

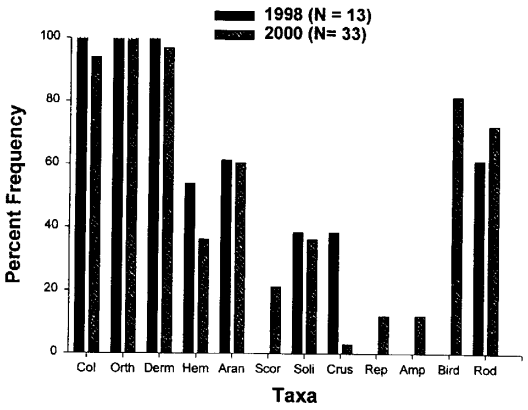

FIGURE 2. Diet of Burrowing Owls based on the % frequency of taxa within pellet samples, Imperial Valley, CA, 1997–2000. Taxa included Coleoptera (Col, beetles), Orthoptera (Orth, grasshoppers and crickets), Dermaptera (Derm, earwigs), Hemiptera (Hem, true bugs), Araneae (Aran, spiders), Scorpionida (Scor, scorpions), Solpugida (Soli, wind scorpions), Crustaceans (Crus), Reptiles (Rep), Amphibians (Amp), Birds (Bird), and Rodents (Rod). The sample size for each year is the number of nests from which pellets were collected.

Productivity varied dramatically among nests and years within the ISA. Nest failure ranged from 0 to 50% among years and location (Table 2). Productivity, as estimated for all nesting attempts and for only those that were successful, was similar between nests on private (natural nests) and Refuge (nest boxes) lands. Productivity averaged 2.5 ± 0.2 young/nest with a maximum of 7 young observed. We failed to find explanatory factors related to productivity other

TABLE 2. COMPARISON OF BURROWING OWL PRODUCTIVITY, IMPERIAL VALLEY, 1998–2000

Location[a]	Year	No. of young/nest			% failed	No. of young/successful nest		
		N	$\bar{X} \pm SE$	Range		N	$\bar{X} \pm SE$	Range
Private Lands	1999	23	1.8 ± 0.3	0–4	26.1	17	2.5 ± 0.3	1–4
	2000	29	3.0 ± 0.3	0–5	10.3	26	3.4 ± 0.3	1–5
Refuge Lands	1998	13	2.3 ± 0.6	0–7	30.8	9	3.3 ± 0.6	1–7
	1999	6	1.0 ± 0.5	0–3	50.0	3	2.0 ± 0.6	1–3
	2000	7	3.9 ± 0.6	1–6	0	7	3.6 ± 0.6	1–5

Note: Productivity was defined as the maximum number of young 14–21 d old observed during five 30-min observations (Private) or as the number observed within nest boxes (Refuge).

[a] Nests within private lands were selected randomly from all nests located within the ISA excluding the Refuge. Nests within the Refuge were from all active nest boxes, excluding those randomly selected to receive experimental manipulation.

than year. In 2000, the only year that we had estimates of both productivity and rodent consumption for an adequate sample of nests, productivity was unrelated to the rodent index (N = 28 nests, $\beta = -1.3 \pm 1.0$). Although there was high variability in nearest-neighbor distances (7–596 m) and number of neighboring nests (1–19), neither nearest-neighbor distance (N = 52, $\beta = -0.04 \pm 0.11$) nor number of nests within 600 m (N = 52, $\beta = 0.01 \pm 0.03$) were related to productivity based on the regression model with year and either the nearest-neighbor distance or number of nests as explanatory factors. So although productivity varied by year, we were unable to isolate factors associated with individual variation of productivity.

BETWEEN-YEAR MOVEMENTS

Adult Burrowing Owls exhibited strong fidelity to their nest sites and their mates. Of adult Burrowing Owls of known sex observed in two successive years (N = 91 [1998–1999] and 83 [1999–2000]), over 85% nested within 400 m of their previous year's nest (Fig. 3). Based on data from nest boxes (known nest chamber), 48% (11 of 23) and 65% (11 of 17) of nests had at least one member of the pair nesting in the same box between 1998–1999 and 1999–2000, respectively. The strong nest-site fidelity corresponded well with mate fidelity: >80% of pairs for which both members were banded and found in a successive year remained with the same mate (1998–1999: 19 of 22 pairs, 86.4%; 1999–2000: 16 of 20 pairs, 80%).

The hazard-rate function was clearly a more appropriate model than the exponential (w = 1.0) and demonstrated a rapidly declining likelihood to move long-distances (Fig. 4). There was strong evidence that the hazard-rate function was sex and year specific (w = 1.0) and fit the data ($P > 0.05$ for each sex and year). Males

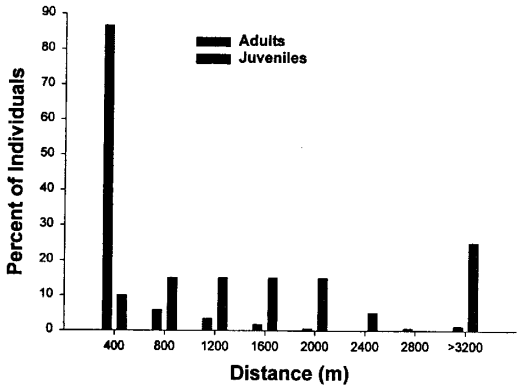

FIGURE 3. Frequency histogram of between-year movement distances of adult (N = 174) and juvenile (N = 20) Burrowing Owls from the Intensive Study Area, Imperial Valley, CA, 1998–2000. The percent of individuals located in two consecutive years is shown within 400-m distance intervals, starting at ≤400 m.

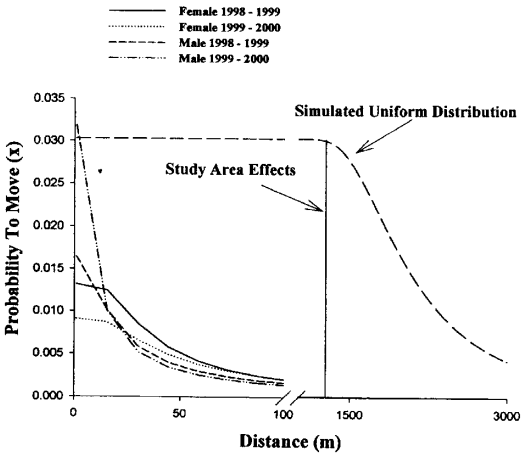

FIGURE 4. We described movement data by the hazard-rate model, $f(x) = 1 - \exp(-[x/\sigma]^{-b})$, fit to distance data of adult female and male Burrowing Owls, 1998–2000. The y-axis is the probability of an individual moving to a nest location x distance (m) from their previous year's nest site. "Study Area Effects" shows the estimated dispersal distance at which negative bias occurs given a uniform distribution of movements with a maximum of 3 km.

TABLE 3. COMPARISON OF MODELS OF FACTORS AFFECTING BETWEEN-YEAR MOVEMENT DISTANCES OF ADULT BURROWING OWLS, IMPERIAL VALLEY, CA, 1998–2000

Models[a]	r^2	ΔAICc[b]	w[c]	r^2	ΔAICc[b]	w[c]
A. 1998–2000, without nest success data	Males (N = 80)			Females (N = 60)		
Year, gone, neighbor, neighbor × year	0.03	6.2	0.02	0.03	11.8	0.01
Year, gone, log(neighbor), log(neighbor) × year	0.03	11.7	0.01	0.02	12.6	0.01
Year, gone, neighbor	0.03	8.0	0.01	0.02	9.3	0.01
Year, gone	0.02	4.4	0.06	0.01	6.1	0.03
Gone, neighbor	0.01	5.7	0.03	0.01	6.1	0.03
Year, neighbor, neighbor × year	0.03	8.0	0.01	0.03	8.5	0.01
Gone	0.01	3.5	0.09	0.01	3.0	0.12
Neighbor	0.01	3.5	0.09	0.01	3.0	0.12
Year	0.02	2.1	0.18	0.01	3.0	0.12
No effects (intercept only)	0.00	0.0	0.52	0.00	0.0	0.56
B. 1999, with nest success data	Males (N = 25)			Females (N = 14)		
Gone, neighbor, success	0.17	6.0	0.02	0.50	6.5	0.01
Gone, log(neighbor), success	0.16	6.6	0.01	0.49	6.9	0.01
Gone, success	0.16	2.4	0.12	0.48	0.7	0.22
Gone, neighbor	0.10	3.9	0.05	0.11	8.2	0.01
Neighbor, success	0.07	4.9	0.03	0.33	4.3	0.04
Gone	0.10	0.0	0.38	0.10	3.3	0.06
Neighbor	0.01	2.6	0.11	0.02	4.4	0.04
Success	0.07	1.1	0.23	0.30	0.0	0.33
No effects (intercept only)	0.0	4.4	0.04	0.0	0.2	0.29

[a] Factors in the models may include whether or not the mate was observed within study area ("gone"), distance to the nearest neighboring nest ("neighbor") or its log-transformed value, the year before the movement event ("year"), and whether or not the nest was successful ("success").
[b] The difference in AICc from the model with the lowest value (Burnham and Anderson 1998).
[c] The relative likelihood of the model, based on AICc (Burnham and Anderson 1998).

had a more rapidly declining function than females (Fig. 4) in both 1998–1999 (males: σ = 14.9 ± 7.2, b = 1.2 ± 0.1; females: σ = 30.9 ± 12.1, b = 1.5 ± 0.2) and 1999–2000 (males: σ = 6.6 ± 2.9, b = 1.1 ± 0.2; females: σ = 36.5 ± 17.6, b = 1.3 ± 0.2). We observed long distance movements of >3 km for females (N = 3) and never observed males moving >1.5 km. These results demonstrate the higher likelihood of males to remain near their previous year's nest and the small, but higher likelihood for females to move greater than several hundred m. In contrast, the estimated dispersal functions for the owls with simulated distances followed the expected uniform probability until approximately 1.2 km, at which point the declining slope resembled a negative exponential function (Fig. 4). The very different distance at which the simulated movements showed a declining probability of movement relative to the owl data provided strong evidence that the estimated movement patterns were not negatively biased due to study area constraints (Fig. 4), and thus allowed us to evaluate biological factors responsible for the observed patterns.

Individuals had a unique propensity for movement: distance individuals moved between 1998–1999 was positively correlated (r = 0.67, P < 0.001, N = 45) with distance moved between 1999–2000. However, we identified few factors associated with how far individuals moved. Based on data for which both members of a pair were banded (N = 66 [1998–1999], N = 68 [1999–2000] pairs), we found little evidence that year, whether or not the mate of the owl was presumed dead (i.e., never seen again), or distance to the nearest nest were associated with distance moved (Table 3a). Based on a subset of the data for which nest success was known, there was some evidence that both nest success and whether or not an owl's mate was presumed dead were associated with distance moved (Table 3b). Distance moved by males and females was associated weakly with nest success and the presence of their mate the following year (Table 3b). For both sexes, distance moved tended to be much greater for individuals whose nests failed, though estimates lacked precision (Table 4).

As expected, dispersal distance of juvenile owls was much greater than between-year movement of adults (Fig. 3). There was no evidence of a decline in the dispersal functions of juvenile owls as distance increased from the natal nest. That finding, in addition to only 20 of 124 (16.1%) juveniles that were banded and reobserved in a following year, suggests that a large proportion of the young emigrated from the study area (sensu Turchin 1998). Some juveniles did remain near their natal nest (Fig. 3). Of five

TABLE 4. COMPARISON OF DISTANCES MOVED (M) BETWEEN SUCCESSIVE YEARS IN RELATION TO AGE, SEX, NEST SUCCESS, AND LOSS OF MATE FOR BURROWING OWLS, IMPERIAL VALLEY, CA, 1998–2000

Summary statistic	Males				Females				Juveniles
	Mate gone	Mate present	Nest successful	Nest failed	Mate gone	Mate present	Nest successful	Nest failed	Pooled
N	38	42	20	5	18	42	10	4	20
Range	0–904	0–1363	0–346	5–643	0–3652	0–3089	0–639	194–3652	0–4300
Mean[a]	27.1	24.5	18.2	66.7	49.4	30.0	36.6	544.6	992.3
95% CI[b]	12.4–59.4	13.6–44.2	6.8–48.4	9.4–473.4	12.6–194.8	13.7–65.6	9.3–144.3	138.4–2143.1	453–2173
Median	25.0	26.0	26.5	194.0	151.0	30.0	46.5	397.0	1462.0

[a] Back-transformed from ln(distance).
[b] Computed from back-transformed SE (ln(distance)).

young banded at nest boxes that were relocated the following year, one nested in its natal nest with a non-parent mate.

SURVIVAL

The large sample of marked owls and their high recapture probabilities resulted in precise estimates of survival. From 1997–1999, a total of 239 adults were marked and released during 1997–1999; only 11 were marked during 1997. During 1998–2000, we identified over 140 marked adults each year, with similar numbers of males (N = 147) and females (N = 148). The global model, Model $\{\phi_{g*t}, P_{g*t}\}$, fit the data (P = 0.08). The models with the highest likelihoods were those that allowed recapture probabilities to vary by sex and constrained survival rates to be equivalent among years (Table 5). High estimated recapture probabilities for males (1.0 ± 0) and females (0.91 ± 0.06) suggested most marked owls were reobserved if present in the study area. There was little evidence that apparent survival rates varied appreciably among years; 95% confidence intervals overlapped for weighted annual estimates for both sexes. There was weak evidence that males had higher apparent survival rates than females. Based on estimates weighted from all models and using the interval from 1998–1999 for comparative purposes, apparent survival rates of males (0.64 ± 0.04) were marginally higher than those of females (0.58 ± 0.05; Table 5), but 95% confidence intervals overlapped.

To allow estimation of actual survival rather than apparent survival, we estimated the likelihood for an adult to disperse from the DSA. We estimated an emigration rate of 0.01 and 0.04 for males and females, respectively. Using these estimates of emigration and the apparent survival rates from the weighted average, we estimated an annual survival probability of 0.65 and 0.62 for males and females, respectively. This suggests that the difference in apparent survival rates between males and females was partially due to differential emigration, consistent with the differences in the movement patterns between sexes.

SPACE USE

Owls used areas nearest their nest most intensively, but included a relatively large area in their home ranges. On average >80% of foraging locations were within 600 m of their nest (Fig. 5). The area traversed averaged 113.7 ± 30.4 ha (Table 6), with high (33.7 ± 3.4%) overlap among owls. Estimates of the mean area used varied from 45.3 ± 18.2 ha (fixed kernel) to 184.5 ± 65.1 (adaptive kernel; Table 6). The difference between estimates from the fixed and

TABLE 5. MODEL DESCRIPTION AND RESULTS OF SURVIVAL ANALYSES OF ADULT BURROWING OWLS, IMPERIAL VALLEY, CA, 1997–2000

Model	Description	k[a]	ΔAICc[b]	AICc weight[c]	$\hat{\phi}$ (SE) females[d]	$\hat{\phi}$ (SE) males[d]
$\phi(s), P(s)$	Survival and recapture probability allowed to vary by sex	4	0.0	0.30	0.55 (0.04)	0.64 (0.04)
$\phi(\cdot), P(s)$	Common survival but recapture probability allowed to vary by sex	3	0.2	0.27	0.61 (0.03)	0.61 (0.03)
$\phi(s + t), P(s)$	Survival allowed to vary among time similarly between sexes; recapture probability allowed to vary by sex	6	0.9	0.20	0.57 (0.05)	0.61 (0.05)
$\phi(s), P(\cdot)$	Survival allowed to vary by sex but common recapture probability	3	1.9	0.12	0.53 (0.04)	0.65 (0.04)
$\phi(t), P(s)$	Survival allowed to vary by time and recapture probability by sex	5	3.5	0.05	0.63 (0.04)	0.63 (0.04)
$\phi(\cdot), P(\cdot)$	Common survival and recapture probability among all individuals	2	4.7	0.03	0.60 (0.03)	0.60 (0.03)
$\phi (s \times t), P(s)$	Survival allowed to vary by sex and time; recapture probability allowed to vary by sex	8	6.5	0.01	0.57 (0.06)	0.66 (0.05)
$\phi(t), P(s \times t)$	Survival allowed to vary by time; recapture probability allowed to vary by sex and time	8	7.3	0.01	0.63 (0.04)	0.63 (0.04)
$\phi(s \times t), P(t)$	Survival allowed to vary by sex and time; recapture probability allowed to vary by time	8	10.1	0.002	0.56 (0.06)	0.67 (0.05)
$\phi(s \times t), P(s \times t)$	Survival and recapture probability allowed to vary by sex and time	10	10.2	0.002	0.58 (0.06)	0.66 (0.05)

[a] Number of parameters in the model.
[b] Difference in small-sample size corrected AIC (AICc) from model with the lowest AICc; smaller values indicate a more desirable model.
[c] Aikaike's weights, an estimate of the likelihood of the model within the set of models considered (Burnham and Anderson 1998).
[d] Estimate for year effect models is based on survival between 1998–1999.

TABLE 6. ESTIMATED HOME RANGE SIZE FOR SIX RADIO-TAGGED MALE BURROWING OWLS NESTING WITHIN THE SONNY BONO SALTON SEA NATIONAL WILDLIFE REFUGE, IMPERIAL VALLEY, CA, MAY–JULY 1998

Owl	No. telemetry locations	Area estimate (ha)		
		100% MCP[a]	95% adaptive kernel	95% fixed kernel
A	71	158	191	13
B	17	68	187	8
C	55	247	491	122
D	77	80	73	65
E	29	63	85	53
F	52	66	80	11
Mean (SE)		113.7 (30.4)	184.5 (65.1)	45.3 (18.2)

[a] Minimum convex polygon.

adaptive kernel were often large because of the different levels of smoothing in areas farthest from the nest, where data were sparse. The fixed-kernel estimates probably underestimated the area used because of the high concentration of locations near the nest, whereas the adaptive kernel probably overestimated area because of the few distant locations.

Habitat selection patterns varied among owls. The strongest single effect was simply distance from the nest (Table 7, Fig. 5). The models with only distance had similar weights to models that also included whether or not cover existed. Although cover may have been a factor in foraging habitat selection for some owls (Table 7), estimates were imprecise (regression coefficient for cover, β, for log(distance) model: -0.31 ± 0.18; for polynomial (distance) model: -0.35 ± 0.58). Although small sample sizes made inferences from finer-scale analyses weak, several crop types were used more than others, relative to availability. Selection, however, varied with distance from the nest (Fig. 6). At locations near the nest, edge and fields without crops ("bare") had the greatest use relative to availability, whereas at distances >600 m selection was greatest for hay fields (Fig. 6). The large variation among owls (Fig. 6) was probably due to distance from the nest, maturity of the crop (i.e., accessibility), and management of a particular field, as well as individual patterns of habitat selection.

DISCUSSION

NEST DENSITY AND DISTRIBUTION

The Burrowing Owl population in the Imperial Valley of California is perhaps the largest continuous population throughout the species' range and surely one of the most dense populations over such a large area (DeSante et al. *this volume*). Coulombe (1971:Table 2) estimated 3.3 pairs/km^2 within an 8-km^2 area of the Imperial Valley during the breeding season of 1966–1967. In southern Florida, Millsap and Bear (2000) reported a density of 6.9 pairs/km^2 for the Florida subspecies (*A. c. floridana*), which they estimated from a relatively large area (35.9 km^2) relative to most other studies. Our estimate of 8.3 pairs/km^2 is one of the highest reported.

Estimates of density are sensitive to the area considered; small areas delineated by the existence of individuals may result in very high densities. For example, Desmond et al. (1995) reported ≥20 pairs/km^2 of owls in black-tailed prairie dog (*Cynomys ludovicianus*) colonies within areas of <35 ha. The spatial variability of owl densities within our study site was due

TABLE 7. COMPARISON OF HABITAT SELECTION MODELS OF MALE BURROWING OWLS (N = 6), IMPERIAL VALLEY, CA, MAY–JULY 1998

Model[a]	Log (distance)		3rd-order polynomial (distance)	
	$\hat{W}$[b]	Range (w)[c]	$\hat{W}$[b]	Range (w)[c]
Distance, crop type	0.06	0–0.20	0.07	0–0.24
Distance, crop cover	0.20	0–0.87	0.26	0–0.77
Distance	0.20	0–0.67	0.20	0–0.54
No effects (intercept only)	0.00	0	0.00	0

[a] Factors in the models may include distance from the nest as either a log effect or as a 3rd-order polynomial, and two different schemes of pooling different habitat types: (1) whether or not the field contained crops with dense cover ("crop type") or (2) whether or not the field had cover by a crop.
[b] The mean of the relative likelihood of the model, based on AICc (Burnham and Anderson 1998).
[c] The range of w among owls.

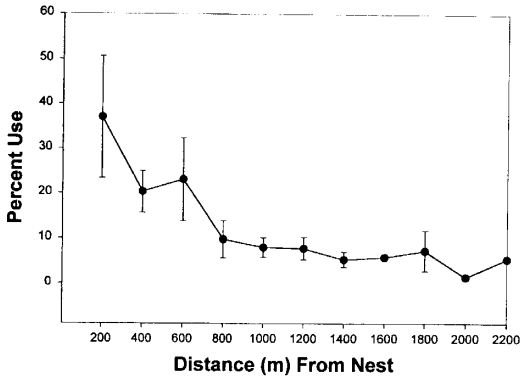

FIGURE 5. Frequency distribution of percent of locations ($\bar{X} \pm$ SE) of six male Burrowing Owls radiotracked in the Imperial Valley, CA (June–July 1998).

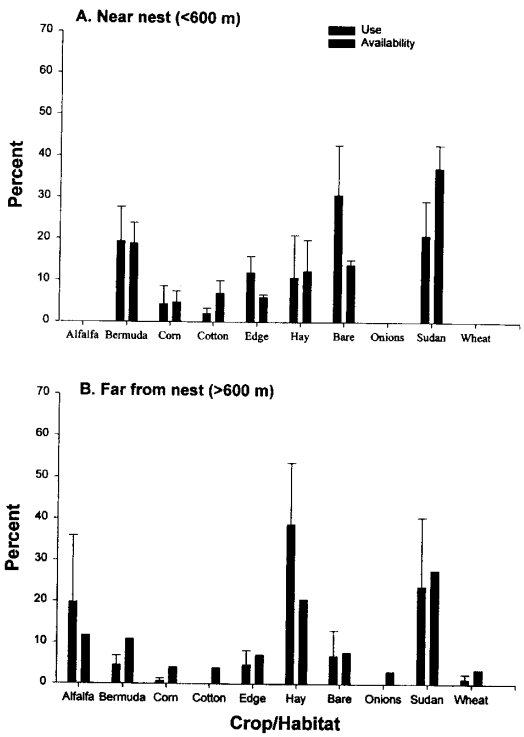

FIGURE 6. Comparison of the percent use among foraging habitats by six male Burrowing Owls, Imperial Valley, CA, June–July 1998. The error bar represents the SE among the owls. The percent use and availability of each type differed based on locations near (A) and far (B) from the nest. Estimates are based on locations gathered from nocturnal telemetry (owl use) or % composition of habitats within a circle with a radius equal to the maximum distance an owl was located from its nest (availability).

in part to the scarcity of burrows in some areas. High spatial variation in nest distribution is characteristic of Burrowing Owl populations (Desmond et al. 1995, Trulio 1997, Millsap and Bear 2000), and results in high variation of nearest-neighbor distances.

Burrowing Owls often live in close proximity to conspecifics, but defend the immediate area near their nest (Coulombe 1971; D. Rosenberg, pers. obs.). We found pairs nesting as close as 7 m to each other, with an average nearest-neighbor distance of 147 m. In a study area about twice the size of ours, Millsap and Bear (2000) reported mean nearest-neighbor distances of 176 m. There have been few studies investigating whether a benefit is gained by their clustered distribution, which often resembles a colonial nesting pattern. Green and Anthony (1989) found nest success was lower for owls that nested within 110 m of another pair, suggesting competition for resources. Although we found high variability in nest densities, we failed to find evidence, based on number of young/female, that competition drives nest distribution. Further investigation into the costs and benefits of the clustered distribution of nests will provide insight into the proximate and ultimate causes of the spatial distribution of Burrowing Owl nests.

Diet

The diet of Burrowing Owls in our study area, dominated numerically by invertebrates, is probably typical of populations within intensive agricultural ecosystems. The very broad diet we observed is characteristic of Burrowing Owls (Haug et al. 1993). During the breeding season, their diet likely represents opportunistic foraging near the nest site, consistent with central place foraging theory (e.g., Orians and Pearson 1979). In many populations, there is a seasonal shift in diet, with an increase in consumption of vertebrates during the non-breeding season (reviewed in Haug et al. 1993; Silva et al. 1995). This may not be the case in the intensive agroecosystems of the Imperial Valley, where York et al. (2002) found dominance by Orthoptera in both the breeding and non-breeding season. Given the estimate of 14 individual Orthoptera/stomach (York et al. 2002) and assuming a pellet egestion rate of 24 hr (Haug et al. 1993), an adult owl consumes about 5000 Orthoptera/yr. Based on an estimate of 13,000 adult owls in the Imperial Valley (DeSante et al. *this volume*), Burrowing Owls consume >65 million Orthoptera/yr. Although the effect of Burrowing Owl predation on crop pests remains unknown, the owls' high density and heavy predation of pest species suggest it may be important.

Analysis of pellet samples in our study area and of stomach contents (York et al. 2002) sug-

gested very low consumption of rodents in the Imperial Valley relative to other populations in California (D. Rosenberg et al., unpubl. data). The rodent index was highly variable among nests and was likely influenced by field-specific crop management. For example, after a field burn we observed greater numbers of rodent remains around owl burrows (K. Haley, pers. obs.). The flood method of irrigation may limit rodent populations. York et al. (2002) hypothesized that Burrowing Owls select small rodents over arthropods and that the low frequency of rodents in their diet in the Imperial Valley was due to low abundance and availability, consistent with findings of strong selection for rodents for a Chilean Burrowing Owl population (Silva et al. 1995).

Birds were another primary vertebrate consumed. They were much more frequent in the diet of owls in the Imperial Valley than in other areas of California (D. Rosenberg et al., unpubl. data). Prey included both small passerines, such as Wilson's Warbler (*Wilsonia pusilla*), as well as larger birds that were apparently scavenged, such as American Avocet (*Recurvirostra americana*). Birds may be an important component of the diet, especially during the breeding season when energetic demands are high.

Breeding Phenology and Productivity

The owls' nesting season is longer than elsewhere in California (D. Rosenberg et al., unpubl. data), with egg-laying extending into July, usually following nest failure. Indeed, a nest with 10–14 d old young was found during December (J. Govan, pers. comm.), giving further support to our hypothesis that year-round food availability may be greater in the Valley than elsewhere in the subspecies' range. The only other record of late-season breeding by Burrowing Owls was in Florida in an area also with high densities of owls (Millsap and Bear 1990). Despite the potential for an extended breeding season and frequent renesting following nest failure (D. Catlin and D. Rosenberg, unpubl. data), we did not observe double-brooding, which has been infrequently observed elsewhere (Millsap and Bear 1990, Gervais and Rosenberg 1999).

Clutch size within a species is believed to be a response to variation in protein and energy availability (Williams 1996, Nager et al. 1997). Burrowing Owls produce large clutches (up to 11 eggs; Haug et al. 1993), usually associated with high rodent abundance (D. Rosenberg, pers. obs.). In the Imperial Valley, we have never observed clutch size >8 during our study period; of these, few individuals typically fledge. Although an average of six eggs were laid per clutch, an average of only 2.5 young survived to 21–28 d old.

We failed to identify factors other than year associated with individual variation in productivity. We explored only two components of those often postulated to be associated with individual variation of productivity in birds: quality of diet and competition for food resources (Newton 1998). We failed to find that our index of rodent consumption or the presence of neighboring owls were related to productivity. Although it is likely that our finding of a year effect on productivity was related to food resources, our index, which estimated the abundance of only one of the many prey resources, was not indicative of individual variability in productivity. How well our estimate provided a reliable index to rodent consumption at the individual nest level is unknown. Unlike other sites in California (D. Rosenberg, unpubl. data), birds were a common component of the diet, and indeed may be more important than rodent consumption for providing sufficient energy and nutrients for a large brood. Other factors affecting individual variation in productivity that may be operative for Burrowing Owls include vulnerability to predation, parental condition, age of adults, and previous reproductive history. These factors remain to be explored with our data and future experimental studies.

That food supply limits clutch size and the number of fledglings of many bird species has been well demonstrated (Newton 1998:145). Indeed, Haley (2002) found an increase in productivity of food-supplemented Burrowing Owls in the Imperial Valley. We hypothesize that clutch size of Burrowing Owls in the Imperial Valley is limited primarily by nutrient and energy availability. We further speculate that the mechanism of reducing brood size occurs through infanticide (Wellicome 2000) and increased predation through exposure of young at the burrow (Botelho 1996), both of which are influenced by food supply. Determining the separate roles of nutrient and energy limitation in clutch size (e.g., Nager et al. 1997) and factors causing mortality of nestlings will require careful observation and experimentation.

Between-Year Movements

Burrowing Owls typically remained with their mates in successive breeding seasons. Our finding of greater than 80% mate retention is similar to the high (92%) rate Millsap and Bear (1997) reported in Florida. However, high annual mortality meant that only approximately 40% of the pairs would have both members alive by the following breeding season. Following loss of mates, through divorce, emigration, or death, new

pairs were formed; some owls moved considerable distances (e.g., >3 km) before new nest pairs were formed.

Our findings on between-year movements are in general agreement with prior studies throughout the owl's North American range. Our results are similar to the high nest-site fidelity of adults reported for the Florida subspecies by Millsap and Bear (1997) and for a migratory population nesting in Canada (Wellicome et al. 1997). Lutz and Plumpton (1999) reported lower rates for a migratory population in Colorado. Adult between- or within-year movement distances of over 40 km have been detected for both resident (J. Rosier et al., unpubl. data) and migratory (Wellicome et al. 1997) populations. The size of our study area, however, was too small to detect movements >4 km using only mark-recapture methods.

Adult Burrowing Owls, particularly females, will nest in locations distant from their previous year's nest, consistent with avian dispersal patterns (Greenwood 1980). We found such movements often followed nest failure, similar to results from Colorado (Lutz and Plumpton 1997) and grasslands in California (J. Rosier et al., unpubl. data). Millsap and Bear (1997) found that longer-distance movements were associated with loss of a mate. We found evidence for this as well, but our data provided stronger support for nest failure as the predominant factor associated with movements.

Natal dispersal patterns are poorly understood and distance distributions are typically underestimated for most bird species (Barrowclough 1978, Koenig et al. 2000). Natal dispersal patterns in Burrowing Owls are no exception. From the non-declining dispersal function (sensu Turchin 1998), it was clear that our study area was too small to properly estimate this important parameter. Natal dispersal distance of up to 300 km was reported by Wellicome et al. (1997) from a migratory population. Millsap and Bear (1997) reported a median natal dispersal distance of between 0.4–1.1 km; our median distance was similar (1.5 km), and we suspect it was severely underestimated. Careful attention to the problems of estimating dispersal, particularly natal dispersal (e.g., Koenig et al. 2000), will be required to provide a better understanding of the population ecology of this species.

Survival

It was interesting, but not surprising, that adult survival rates were similar between males and females. We suspect that causes of mortality differ between sexes, though annual mortality is similar. Costs of reproduction are likely higher for females, particularly if nutrients required for reproduction are limiting. Predation within the burrow by fossorial mammals and snakes may be an important mortality factor. If so, this should affect adult females more than males because only females incubate eggs and brood young (Haug et al. 1993). Alternatively, the male's high visibility and the greater amount of time spent foraging during the breeding season may make males more vulnerable to other predators and vehicles. Few accounts of cause-specific mortality exist. Clayton and Schmutz (1997) quantified cause-specific mortality for two Canadian populations; vehicle collisions were the predominate mortality factor for adults in fragmented environments, whereas predation by raptors and mammals predominated in the larger grassland ecosystems. Millsap (2002), in an urban environment in Florida, found vehicle collisions responsible for 70% of banded owls found dead. A deeper understanding of cause-specific mortality is needed to more fully understand factors affecting Burrowing Owl populations.

Our estimate of survival rates of Burrowing Owls is one of the few not based on return rates, which typically underestimate survival. Lutz and Plumpton (1997) reported adult survival rates that varied between 0.17 to 0.71 among years within a migratory population in Colorado. In Canada, Clayton and Schmutz (1997) estimated adult survival rates based on known fate data (radio telemetry) and generally found low rates, although they varied from 0.38–1.0 for a 4-mo period. In a study design similar to ours, Millsap and Bear (1997) found annual survival rates of females generally lower (0.52–0.69) than males (0.62–0.81), and in areas of moderate housing development they tended to be similar to our estimates (Millsap 2002).

Based on the natural history of Burrowing Owls, it is likely that population dynamics are more sensitive to juvenile than adult survival (e.g., Emlen and Pikitch 1989). Indeed, that few adults but many juveniles moved long distances and that mortality rates of adults are high, suggest that *ex-situ* recruitment of young into the breeding population is an essential feature of the dynamics of the relatively stable population we studied. Martin et al. (2000) reported similar findings for White-tailed Ptarmigan (*Lagopus leucurus*) and suggested that recruitment from external populations may be an important and common feature of avian population dynamics. In the Imperial Valley, the Burrowing Owl population is probably structured as a continuous population rather than as a set of distinct "external" populations. Indeed, genetic data suggest high mixing of individuals throughout central and southern California (Korfanta 2001).

Because of the high emigration rate of juve-

niles from our study area, as evidenced by the non-declining movement function we observed (Fig. 3), estimates of juvenile survivorship would have been severely underestimated from our data. Precise and unbiased estimates of juvenile survivorship will be important in order to model the dynamics of this population, as well as to explore how sensitive the dynamics of the population are to juvenile survivorship.

Space Use

Burrowing Owls tend to remain near their nest site during nocturnal foraging. Similar to our results, >80% of the nocturnal telemetry locations were within 600 m of the nest during the breeding season in the agricultural matrix of the Central Valley, California, and Saskatchewan, Canada (Haug and Oliphant 1990, Gervais et al. 2003). Haug and Oliphant (1990) reported male Burrowing Owls selected grass-forb areas and avoided agricultural fields during nocturnal foraging. However, their estimates of selection did not take into account distance from the nest. Because nest sites were all located within grass-forb areas (Haug and Oliphant 1990), distance alone may explain the apparent patterns of habitat selection they reported. Our results and those of Gervais et al. (2003) demonstrate that agricultural fields are often used by Burrowing Owls. Indeed, the high owl densities in the Imperial Valley, predominated by crops, suggest agricultural fields can provide quality foraging habitat. The structure of vegetation within an agricultural field is dynamic and changes throughout the growing season likely affect owl selection. Some crops, such as alfalfa, are grown without cultivation for several years, sometimes as long as six years (A. Kalin, pers. comm.). In such cases, rodent populations may increase with a parallel increase in selection by foraging Burrowing Owls.

Home range size of adult Burrowing Owls is highly variable. Estimates (MCP method) ranged from 14–480 ha ($\bar{X}$ = 240 ha) in a matrix of grazed pastures and cereal crops in Canada (Haug and Oliphant 1990) and averaged 189 ha in the Central Valley of California (Gervais et al. 2003). We found similarly high variation, regardless of the estimator used. Variation in home range size is likely due to availability of prey, reproductive success (i.e., energy demand), and characteristics of the landscape that affect the distribution of resources (Newton 1979, Kenward 1982, Haug and Oliphant 1990, Carey et al. 1992). Management practices that affect prey availability, such as field burning and harvest, were also likely responsible for the individual variation we observed in patterns of space use. Sampling variation may be responsible for much of the observed differences in estimated home range size; this deserves further attention for estimation of home ranges in general (White and Garrot 1990).

Management Concerns

In the Imperial Valley, the availability of burrows is largely dependent on the management practices of private landowners and the Imperial Irrigation District. Most of the burrows in our study site likely resulted from water seepage, muskrats (*Ondatra zibethicus*; Coulombe 1971), and gophers. When gophers reach the concrete lining, they often burrow to the surface (A. Kalin, pers. comm.), creating an initial tunnel the owls can enlarge. We also found nests within burrows initially created by the round-tailed ground squirrel (*Citellus tereticaudus*), as did Coulombe (1971). Within the agroecosystems of the Imperial Valley, the abundance of these species and their ability to provide burrows that the owls can modify as nests are determined largely by local farming practices and methods of water conveyance.

The single largest management concern for the Burrowing Owl population in the agroecosystems of the Imperial Valley is how the irrigation system is managed. Dredging of drains and grading of roads has the potential to destroy nests (Coulombe 1971; this study). Indeed, several adults and their nests were buried during road grading operations (D. Catlin and D. Rosenberg, unpubl. data). Flooding from overflow of delivery ditches also cause nest destruction and death of young (K. Haley, pers. obs.). A potential problem is the growth of tall vegetation along drains, which prevents owls from nesting; however, current management practices generally reduce or eliminate vegetation along drains. Collaboration among the Imperial Irrigation District, state and federal agencies, and landowners, such as local farmers, will be instrumental in developing strategies to allow maintenance of the irrigation system while minimizing destruction to nests. Burrowing Owls and their nests are protected under both state and federal laws but such protection in intensively managed ecosystems is difficult. Research on developing feasible methods to reduce the likelihood of destroying nests or entrapping adult owls will be essential in developing conservation strategies.

Another issue that may affect Burrowing Owl populations in the Imperial Valley is the presence of contaminant residues from current and former agricultural practices. Previous findings suggest low levels of contamination by organochlorines; *p,p'*DDE, the only organochlorine detected in eggs, was relatively low in the Imperial Valley (Gervais et al. 2000). Species that con-

sume a large proportion of their diet from aquatic environments have been reported with high levels of *p,p'*DDE and selenium within the Imperial Valley (Setmire et al. 1990, 1993). The predominance of terrestrial-based prey resources in the diet, particularly Orthoptera, may be responsible for the relatively low levels of both *p,p'*DDE and selenium reported by Gervais et al. (2000). The results of Gervais et al. (2000) were based on a small sample from within the Refuge and from only a single year; however, Gervais and Catlin (in press) found similar levels of *p,p'*DDE within and adjacent to the Refuge in 2002. Although we did not evaluate contaminate residues, the relatively high rates of adult survival and the proportion of nesting attempts that produced young do not currently indicate a problem. However, effects could occur if current patterns of pesticide use change or if natural stressors interact with pesticide exposure (Gervais and Anthony 2003).

The large numbers of Burrowing Owls in the agricultural matrix of the Imperial Valley remain vulnerable to changes in land use (e.g., urbanization) and water distribution. Although the concentration of Burrowing Owls within the Imperial Valley is clearly due to farming practices, presumably a large but sparse population existed prior to agricultural development. The few areas of native habitat that remain in the Imperial Valley may be important for the persistence of Burrowing Owls in the Imperial Valley if changes in agricultural practices prevent nesting along the irrigation system. Successful conservation strategies for Burrowing Owls in the Imperial Valley will require both a thoughtful consideration of how future changes in agricultural practices may affect populations and an evaluation of the role of native habitat for population persistence.

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