SPACE USE AND PESTICIDE EXPOSURE RISK OF MALE BURROWING OWLS IN AN AGRICULTURAL LANDSCAPE

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Abstract: We estimated home-range size and habitat selection in a population of burrowing owls (*Athene cunicularia*) living within an agricultural landscape in the Central Valley of California, USA, in 1998 and 1999. We modeled home-range size and habitat selection of breeding male owls ($n = 33$) as a function of biological and physical factors. Biological factors included number of young fledged and diet, and physical factors included cover-type composition around the nest. We also examined patterns of space use in conjunction with agricultural pesticide application records for evidence of secondary poisoning risk to the owls. Owl home ranges varied in size within (but not between) years, and not in conjunction with any of the biological factors we measured. Foraging versus random locations were differentiated most strongly by distance from the nest, with 80% of nocturnal foraging observations falling within 600 m of the nest burrow. No single cover type was selected when distance to nest was also included in the model. Owls did use agricultural fields recently treated with pesticides, although we did not find evidence of owls selectively foraging in these fields.

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Burrowing owls were once widespread and common throughout western North America, but some populations have declined in recent years (Haug et al. 1993, Sheffield 1997). There has been much speculation regarding potential causes of these declines (James and Fox 1987, Haug et al. 1993, James and Espie 1997, Desmond and Savidge 1999), and habitat destruction and degradation are major concerns. Many burrowing owl populations persist in areas of urban development or agricultural production (DeSante et al. 1997, Rosenberg and Haley in press). Identifying components of these altered environments that are most important to the owls and those that pose the greatest threats will be useful in conservation planning.

Despite the species' frequent proximity to areas inhabited by people and relative resistance to disturbance, burrowing owl habitat selection and space-use patterns remain little-studied. Work by Haug and Oliphant (1990) in Saskatchewan indicated that male owls selected grass–forb vegetation cover for foraging during the breeding season. However, their analyses did not consider spatial configuration of cover types and distances to the nest burrow. These factors may impact patterns of habitat selection (Rosenberg and McKelvey 1999). Nearly all other studies that reported foraging observations for burrowing owls were diurnal, when the owls remained close to the nest and appeared to prey primarily on invertebrates (Coulombe 1971, Thomsen 1971, Martin 1973, Thompson and Anderson 1988, Green et al. 1993).

Agricultural environments can support very high densities of burrowing owls (Rosenberg and Haley in press). These also may pose threats to owl populations from pesticide exposure (James and Fox 1987, Gervais et al. 2000), destruction of nest burrows by farm equipment, seasonal food scarcity exacerbated by farming practices, or extermination of the fossorial mammals that dig the burrows used by the owls (Desmond et al. 2000). Given that large expanses of the burrowing owl's range are dominated by agriculture, understanding how the owls survive in these environments is necessary for conservation strategies.

We explored space use and habitat selection by a resident population of burrowing owls living in an area of intensive row-crop agriculture. We postulated that space use would be linked to diet and risk of pesticide exposure. Burrowing owls primarily consume rodents (Green and Anthony 1989, Silva et al. 1995), and owls have shown both

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functional and numerical responses to increasing vole (*Microtus* spp.) populations (Silva et al. 1995). Grass is the dominant food of the California vole (*M. californicus*; Gill 1977) and is the most stable cover type for rodents in agricultural systems.

In addition, we frequently observed burrowing owls foraging along the edges of roads and drainage ditches. We hypothesized that owls should select grass and edge cover types while foraging. Also, home ranges with greater amounts of grass and edge cover near the nest should be smaller than home ranges of owls nesting adjacent to cropland.

Because burrowing owls are central-place foragers when nesting, distance from the nest should also influence habitat selection (Rosenberg and McKelvey 1999). We postulated that owls foraging primarily in crop fields should have greater home-range sizes and lower reproductive success due to lower rodent densities and greater pesticide exposure risk. Finally, based on earlier findings of chlorpyrifos, a broad spectrum organophosphate pesticide, in footwash samples (Gervais et al. 2000), we predicted that these owls would select fields recently sprayed with pesticides in response to the availability of dead and dying prey.

We addressed these questions by radiomarking and locating adult male owls in an agricultural environment during the breeding season to create an index of minimum habitat requirements and patterns of habitat selection within the home range. We also described diet, estimated numbers of owlets surviving to fledging, and obtained documentation on pesticide spray applications within the study area.

STUDY AREA

The population of owls we examined resided on an 80 km^2 section in the center of Naval Air Station (NAS) Lemoore, located 50 km southwest of Fresno, California, USA, latitude 36°18′N, 119°56′W longitude. Naval Air Station Lemoore is in the center of the San Joaquin Valley, an area of intense agriculture (Griggs 1992). Major crops include cotton, alfalfa, tomatoes, and corn (California Department of Pesticide Regulation 1998, 1999). The Air Operations area at NAS Lemoore is surrounded by agricultural fields in active production. Burrowing owls nested along runway easements, within the Air Operations taxiways and ramp systems, and in unmowed grassy areas surrounded by agricultural fields. These patches ranged from strips 20 m wide, extending the length of runways, to fields of 45–179 ha at the ends of runways. Owls nested in burrows excavated by California ground squirrels (*Spermophilus beecheyii*), artificial burrows, cable housings, culverts, and holes excavated under concrete slabs. The population was composed primarily of year-round residents (J. A. Gervais and D. K. Rosenberg, Oregon State University, unpublished data).

METHODS

Field Methods

We captured adult male burrowing owls during the April–June breeding season in 1998 and 1999 (Gervais 2002). Nesting males were fitted with elastic radiocollars (mass = 3.6–4.5g; Model PD-2C, Holohil Systems Ltd., Ontario, Canada) representing 2.3–2.9% of adult breeding mass. Batteries with a 14-week life expectancy were used in 1998. Heavier 24-week batteries were used in 1999. We collected location data from 15 May–1 September 1998 and 1 May–15 September 1999. Females were not radiomarked because they tend to remain near the nest burrow through the early fledgling period. During this stage in the cycle, males do most of the foraging (Haug et al. 1993).

We used a dual antenna receiving system with a null combiner (Telonics, Inc., Mesa, Arizona, USA) mounted in the back of a pickup truck. In 1998, we used H antennas for the array, and obtained a maximum reception distance of 0.8 km. In 1999, we used 4-element yagi antennas, which increased the reception range to 1.0 km. The antenna arrays were approximately 3.5 m from the ground.

Observers obtained sequential bearings at predetermined stations along a gridwork of farm roads that covered the study area. All bearings used were taken <5 min apart. Frequent owl movements while foraging made obtaining more than 2 bearings on a single owl location difficult. Because burrowing owls appear to move frequently while foraging, we recorded signal quality as well as the time, station location and bearing angle. Signals were classified as either 1, strong with obvious null; 2, strongest direction of a signal without a null (the bird was either moving, underground, or vegetation and microtopography were interfering with signal transmission); or 3, only a few good signal beats were detected. This last scenario frequently occurred if owls were foraging in ditches or farm field furrows. Even limited topographic relief was enough to cause substantial signal interference. Efforts were made to search areas >1 km from the nest site to avoid biasing observations near the nest. Location attempts on the same owl were made ≥15 min apart. Each owl was tracked at least 2 nights/week, and several locations were obtained per night. We tracked owls from dusk to 0300.

In both years, we quantified radiotelemetry error by placing radios in known locations. We then estimated those locations using observers who were not aware of radio locations. Radios were placed to mimic actual owl positions while perching or foraging, although the test radios remained in fixed locations.

All nests were visited and pellets were collected weekly or biweekly and prey remains noted. We observed all radiomarked owl nests that were accessible using a standardized protocol to estimate productivity, which we defined as the maximum number of owlets seen shortly before they were able to fly. Owlets from the same brood rarely scattered among several burrows after emergence from the natal burrow because of the paucity of available burrows. We recorded the presence of invertebrate taxa in the pellets to order or family, and we identified vertebrates to genus or species. We estimated individual rodents on the basis of dentary bone counts.

Data Analyses

Telemetry locations were estimated using program LOCATE II (version 1.5, Truro, Nova Scotia, Canada). We removed locations from the data set that fell outside the estimated maximum detection distance from stations (800 m in 1998; 1,000 m in 1999). We used program KERNELHR (Seaman et al. 1998) to compute a 95% fixed-kernel home-range estimate, and program TELEM (version 1.0, U.S. Forest Service) to compute a 100% minimum convex polygon (MCP) estimate for each owl (Jennrich and Turner 1969).

Location Estimation Error.—We estimated the maximum error angle from test radios whose locations led to some topographical signal interference, which prevented the null-peak signal reception pattern. Displacement distance was calculated as the tangent of the maximum error angle multiplied by the mean distance of the radio location to the receiving stations used in that location estimate. This point-specific displacement distance was then used to offset each estimated location systematically on the cardinal directions and also NW, NE, SW, and SE. The square array of alternative points should encompass the extremes of habitat misclassification possibilities, particularly in our study landscape with its regular gridwork of agricultural fields and runways. We generated 10 data sets based on the real data in which each location estimate was drawn randomly from the 8 alternative options for that location attempt. These 10 data sets were then submitted to the same analysis as the real estimated locations.

Home-Range Size.—Fixed-kernel estimates of home range were calculated using least squares cross validation (Worton 1995, Seaman and Powell 1996, Seaman et al. 1999). We did not calculate home ranges with kernel estimators for owls with <26 locations due to instability of kernel estimators with small sample sizes (Seaman et al. 1999). Minimum convex polygons were estimated using all locations rather than 95% of observations because peripheral locations for central-place foragers are likely to be underestimated. There is more area to search at the periphery of the range, and owls are therefore more likely to be detected when near the nest. This bias will be particularly severe when a radiotagged animal cannot be detected over its entire range from a single receiving location, as was true in this study.

Habitat composition was estimated by determining the percentage of the fixed kernel home range composed of each of the major cover types. We used kernel estimates for this analysis because the kernel estimator should not include large areas of unused habitat relative to the MCP estimate.

Factors affecting estimated 95% kernel home-range size were examined using multiple regression and Akaike's Information Criterion (AIC) adjusted for small sample sizes (AIC_c; Burnham and Anderson 1998). We considered a suite of a priori models representing various potential hypotheses that might explain patterns in the data (Table 1; Franklin et al. 2001). Habitat factors included the amount of edge (road and ditch) and grass cover within 400 m of the nest, which was the mean distance owls were detected away from the nest over all owls and both years. Neighboring nests were defined as active nests within 400 m of the focal nest.

The relative importance of diet, numbers of fledglings raised, numbers of neighboring owl pairs, and cover characteristics near the nest in explaining home-range size were evaluated using AIC_c weights (Burnham and Anderson 1998).

Habitat Selection.—We examined burrowing owl habitat selection using estimated locations of radiomarked males. We defined the habitat available to each radiomarked owl as the area within the circle, centered on the nest burrow, whose radius was the maximum distance the owl was detected from the nest (Rosenberg and McKelvey

Table 1. Models exploring the relationship of 95% kernel home-range size and various explanatory variables for 33 male burrowing owls at Naval Air Station, Lemoore, California, USA, 1998–1999. Lower Akaike's Information Criterion (AIC$_c$) values indicate relatively better models and weights are the proportional likelihood of the models.

Model	r^2	AIC$_c$	Weights
grass^a + edge^b + rodents^c + chicks^d + nests^e	0.104	14.635	0.0003
grass + edge + rodents	0.054	7.622	0.0100
chicks + nests	0.074	3.548	0.0764
grass + edge	0.035	4.708	0.0428
edge	0.023	2.015	0.1644
rodents + chicks	0.031	4.801	0.0408
number of locations	0.041	1.476	0.2152
intercept only (no effects model)	0.000	0.000	0.4502

[a] Percent grass within 400 m of nest.
[b] Amount of edge habitat within 400 m of nest.
[c] Mean number of rodents/pellet.
[d] Number of chicks raised to fledging.
[e] Number of active nests within 400 m.

1999). We then selected 1,000 random locations within each circle. A cover type was assigned to each random location and owl location using ARCVIEW (Environmental Systems Research Institute, Redlands, California, USA, version 3.1). Distances to the nearest road and runway were estimated for all locations using ARCINFO (Environmental Systems Research Institute, Redlands, California, USA, version 7.2.1).

Using AIC$_c$, we evaluated a set of a priori logistic regression models comparing used versus available cover types for each owl (Table 2; Hosmer and Lemeshow 1989). Model factors included distance to nest either as a log function or a third-order polynomial function because owl use of an area declines rapidly with distance from the nest. This probably is due to the energy constraints of bringing back 1 prey item at a time to the nest. Log distance from the nest to edge cover accounted for the difficulty of locating owls directly on the roads or ditches adjacent to them, as these are very narrow cover types. Most location estimates are likely to be near, but not on, edge features if edge cover is utilized. Even small location error can result in habitat misclassification for narrow, linear cover types. However, owl use of these features would also be indicated by the model parameter of distance to edge cover. Because owls from different regions of the study area had somewhat different landscape compositions near their nests, we divided cover types into 3 general categories: GRASS, CROPLAND, and OTHER.

GRASS included all runway easements, grassland patches, and fallow fields. CROPLAND included all fields in active production, including alfalfa hay. The OTHER category incorporated ditches, industrial areas, ramps, taxiways, runways, parking lots, and wetlands. Fallow fields were categorized as GRASS cover because they typically were not disturbed by tilling or pesticide applications during the growing season. Despite its structure, permanence relative to other crops

Table 2. Comparison of mean Akaike's Information Criterion (AIC$_c$) values for habitat selection models among male burrowing owls at Naval Air Station, Lenmoore, California, USA, 1998–1999. Lower ΔAIC$_c$ values indicate better model fit to the data. Ten models were originally evaluated. An additional 2 models were evaluated after the initial analysis and the ΔAIC$_c$ values recalculated over the 12 models.

Model	ΔAIC$_c$	SE	Min	Max	$r^{2\,a}$	SE
dnest + dnest^2 + dnest^{3b} + logdedge + cover type^c	5.582	0.900	0	19.176	0.340	0.023
dnest + dnest^2 + dnest^3 + cover type	6.660	0.893	0	20.512	0.315	0.024
dnest + dnest^2 + dnest^3	7.980	1.805	0	41.448	0.308	0.025
logdnest^d + logdedge^e + cover type	13.639	2.703	0	78.303	0.302	0.024
distance + cover type + distance*cover^f	13.930	2.510	0	54.466	0.301	0.024
logdnest + cover type	15.884	2.862	0	77.179	0.287	0.025
logdnest + logdedge	16.751	3.216	0	76.566	0.279	0.025
logdnest	18.991	3.341	0	76.309	0.264	0.026
distance^g	19.309	3.251	0	63.620	0.265	0.025
cover type	88.988	10.863	5.010	272.669	0.093	0.011
logdedge	113.260	13.222	16.725	291.782	0.025	0.004
intercept only (no effects model)	118.562	13.382	21.399	293.835		

[a] Maximum rescaled generalized r^2.
[b] Polynomial distance function for distance to nest.
[c] Defined as CROPLAND, GRASS, or OTHER.
[d] Log distance to nest.
[e] Log distance to nearest habitat edge.
[f] Interaction term, a posteriori model.
[g] Linear distance to nest, a posteriori model.

(it is usually maintained for several years) and potential prey populations, alfalfa was categorized as CROPLAND due to regular cuttings, irrigation, pesticide applications, and other field operations.

Overall, we modeled owl habitat selection as a function of cover types, distance to edge, and distance to nest both separately and in combination. After examining the original set of models, we considered 2 additional models that included linear distance to nest and distance by habitat interaction.

Eight owls did not have estimated locations in either the CROPLAND or OTHER cover types. To avoid quasiseparation of the random versus actual locations in the logistic regression analysis (Allison 1999), we added a single fictional location to the unused cover type in each of those owl data sets. For these additional locations, distances to features such as nest or roads were computed as the mean distance over all locations and the cover type was classified as the missing category. This approach allowed us to use all owl data on the same set of models, rather than restricting our analyses to only a subset of the owls sampled. To estimate the precision of our models, we calculated the maximum rescaled generalized r^2 value. This statistic is based on the likelihood ratio chi-square and is scaled to account for the discrete dependent variable being <1 (Nagelkerke 1991, Allison 1999).

We examined the strength of selection for GRASS by foraging owls as a function of its availability and as a function of avoidance of CROPLAND. To do this, we estimated the regression coefficient of the parameter estimates for GRASS and CROPLAND, with the amount of grass cover within 400 m of the nest. We used AIC_c weights to obtain model-averaged parameter estimates (Burnham and Anderson 1998) for the GRASS cover type from the logistic regression analyses. The greater the selection of GRASS cover type by the owls, the larger the parameter estimate for GRASS. The larger the parameter estimate, the better the distinguishing power of GRASS between random versus actual owl foraging locations.

We examined habitat use of juvenile burrowing owls before they dispersed from their natal nest. We summed the number of juvenile locations by cover type over all individuals to examine trends between years and among cover types. We did not estimate home ranges for juveniles nor did we define "available" habitat. These concepts are not appropriate for young owls whose movements away from their natal area increase as they begin post-fledging dispersal (King and Belthoff 2001).

Pesticide Exposure Risk.—We were interested in location-specific exposure to pesticides as we had some evidence that this occurred in the owls (Gervais et al. 2000). Field-specific agricultural chemical use data for NAS Lemoore during the study period were obtained from the California Department of Pesticide Regulation (1998, 1999). The data were examined in conjunction with owl locations to determine whether use of CROPLAND cover was exposing owls to recently applied pesticides.

We noted dates and locations of all applications of pesticides at NAS Lemoore, which had the potential to create a pulse of dead or dying prey that might attract owls. Pesticides not necessarily toxic to birds (such as pyrethroids) were included to better examine the general pattern of owl response to pesticide application events that could provide a sudden food pulse. The risk zone was defined as a sprayed field 0–3 days post-spray. Three days post-spray were used as the risk period because the pulse event of suddenly available prey is unlikely to last more than 3 days after application of a pesticide. Most currently used pesticides break down rapidly under environmental conditions (Kamrin 1997), and most prey likely were exposed to and killed by the chemicals in that time.

Each owl location was classified as either in or not in a risk zone. Available habitat was defined as fields used by the owls anywhere on the station during the days when at least 1 field was classified as a risk zone. This prevented the inclusion of fields that may have had cover characteristics precluding foraging and were not used during the risk period. We compared the use of risk-zone fields to the use of all fields on the station at that time using odds ratios.

RESULTS

Home-Range Size Relationships

We tracked 11 adult male owls in 1998 and 22 in 1999. Two individual owls were tracked in both years. The total was 31 individual birds and 33 samples. Because fledging success, rodent consumption, and habitat composition varied between years, we retained each owl in both years of the analyses. Twenty-eight of the samples had 26 locations, and 24 had ≥30 locations.

Home ranges varied substantially among individuals, but not between years (Table 3). Maximum distance traveled from the nest was similar between years ($\bar{x}$ = 1,278 m, 95% CI = 855–1,697 m, n = 11 vs. $\bar{x}$ = 1,337 m, 95% CI = 1,033–1,641 m, n =

Table 3. Mean home-range areas of burrowing owls at Naval Air Station, Lemoore, California, USA, 1998–1999, using 95% fixed-kernal and 100% minimum convex polygon (MCP) estimates. Kernel home ranges were not calculated for owls with <26 observations.

	1998				1999			
	95% kernel		100% MCP		95% kernel		100% MCP	
	$\bar{x}$	95% CI	$\bar{x}$	95% CI	$\bar{x}$	95% CI	$\bar{x}$	95% CI
Size (ha)	139	1–277	177	52–302	98	64–132	189	122–256
Locations/owl	38.8	32.6–45.0	35.6	28.7–42.5	61.9	51.6–72.2	55.9	44.7–67.1
No. owls	9		11		19		22	

Table 4. Percent habitat composition of 95% kernel home-range estimates of burrowing owls at Naval Air Station, Lemoore, California, USA, 1998–1999.

		CROPLAND[a]		GRASS[b]		OTHER[c]	
	n	$\bar{x}$	SE	$\bar{x}$	SE	$\bar{x}$	SE
1998	11	38.2	5.6	49.1	4.3	12.8	3.2
1999	22	32.4	5.1	56.6	3.9	11.0	2.9

[a] Included all regularly tilled fields, including alfalfa hay.

[b] Included fallow fields as well as runway easements and unmowed grass areas.

[c] Included runways, roads, drainage ditches, wetlands, etc.

22), as was the mean distance traveled from the nest ($\bar{x}$ = 378 m, 95% CI = 255–501 m, n = 11 vs. $\bar{x}$ = 409 m, 95% CI = 280–538 m, n = 22).

Percentages of GRASS and CROPLAND in owl home ranges were similar among owls and between years (Table 4). Individuals with high percentages of the cover type OTHER nested within the Air Operations area of the station.

Home-range size was not well explained by cover-type composition, number of owlets raised to fledging, number of neighboring nests, nor was it related to the quantity of rodents in pellets (Table 1). The null models (intercept only and number of locations/owl) were among those with the lowest ΔAIC_c value. This further suggested that the biological variables we measured are not related to home-range size. Also, none of the variables we considered had a large, overall relative likelihood as indicated by summed AIC_c weights (Table 5).

Habitat Selection

Habitat-selection patterns varied widely among individual owls with no clear "best" model evident (Table 2). Habitat selection was equally well explained by distance to the nest and cover-type composition (Table 6). However, distance-only models had greater explanatory power than the habitat-only model as indicated by the generalized r^2 value (Table 2). Distance to nest was of great importance in distinguishing foraging locations from random ones. Further, 80% of all foraging observations fell within 600 m of the nest (Fig. 1). In contrast, distance to edges of roads and irrigation ditches did not explain owl foraging locations well compared to other factors (Table 2).

Some individual owl foraging patterns were best explained by the 2 a posteriori models with linear distance and distance by habitat interaction. For most of the owls, these models were not competitive with the first 3 models we considered (Table 2). The foraging locations of most individual owls were best described by the global model containing all biological and environmental factors considered. However, owl foraging locations were frequently adequately described by only distance to nest modeled as a third-order polynomial function, and polynomial distance and cover type together, based on ΔAIC_c values. This suggests that distance to the nest was a primary factor in male owl foraging-site selection.

Selection intensity for GRASS did not seem related to its availability, nor to the proximity of CROPLAND. Parameter estimates of each cover type were highly unstable between models that included habitat only and those that also included a distance function, with the SE of estimates exceeding the parameter estimates themselves.

Juvenile Owl Habitat Use

Juveniles were most likely to be found in GRASS cover, but this pattern differed between years with greater numbers of locations occur-

Table 5. Summed Akaike's Information Criterion (AIC_c) weights over all models for each parameter in home-range size analysis of male burrowing owls, Naval Air Station, Lemoore, California, USA, 1998–1999.

	Parameters				
	Grass	Nest	Chicks	Edge	Rodents
95% kernel[a]	0.0530	0.0767	0.1175	0.2174	0.0511
MCP[b]	0.0832	0.2620	0.2863	0.3265	0.0486

[a] 95% fixed kernel home-range estimate.

[b] 100% minimum convex polygon home-range estimate.

Table 6. Mean weights for variables summed over all models in a habitat selection analysis of male burrowing owls at Naval Air Station, Lemoore, California, USA. Values are averaged over 11 adult male owls in 1998 and 22 adult males in 1999.

Variable	$\bar{x}^b$	SE	Min	Max
dnest + dnest^2 + dnest^{3a}	0.6868	0.0683	0.0058	1.0000
COVER type	0.5548	0.0603	0.0775	1.0000
log distance to edge	0.4271	0.0600	0.0221	0.9997
log distance to nest	0.3114	0.0680	0.0000	0.9942

[a] Polynomial function, distance to nest.

[b] The greater the weight, the greater the contribution of that variable to the model's fit to the data.

ring in CROPLAND in 1999 (Table 7). We frequently observed recently fledged juveniles foraging along farm roads and edges of fields.

Pesticide Exposure Risk and Habitat Selection

No adult owls were detected foraging in pesticide risk zones in 1998. In 1999, 4 different individual owls were detected in pesticide risk zones on at least 1 occasion. The odds ratio for adult male use of recently sprayed fields in 1999 was 0.467 (95% CI: 0.169–1.286, $n = 52$ observations). This suggested no tendency to use or avoid risk-zone fields. We detected 5 recently fledged juveniles in risk zones in 1998 and 3 individuals in risk zones in 1999. Juveniles in 1998 had lower odds of using a recently sprayed field than in 1999 (1998: odds ratio = 0.218, 95% CI = 0.072–0.662, n = 29 observations; 1999: odds ratio = 0.387, 95% CI = 0.106–1.409, n = 35 observations). Juvenile odds ratio values suggest that recently fledged owls are less likely to forage in CROPLAND than in other cover types.

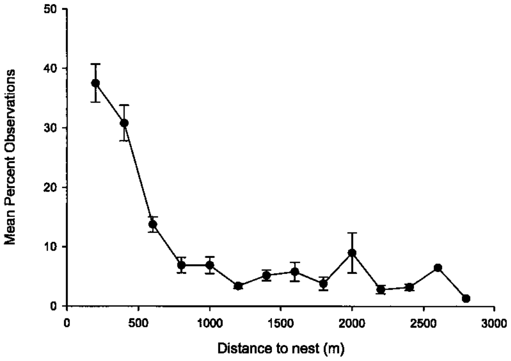

Fig. 1. Mean percentage of observations of foraging male burrowing owls at distance intervals from the nest, Naval Air Station, Lemoore, California, USA, 1998–1999. Error bars are 1 standard error of the mean.

Table 7. Mean percentage of observations of juvenile burrowing owls in different habitat types, Naval Air Station, Lemoore, California, USA.

		No. locations		Crop^a		Grass^b		Other^c	
Year	n	$\bar{x}$	SE	$\bar{x}$	SE	$\bar{x}$	SE	$\bar{x}$	SE
1998	30	11.5	1.5	11.8	2.3	78.5	3.0	9.8	2.6
1999	31	14.2	1.9	35.8	8.1	57.5	5.3	13.3	4.1

[a] Crops include all regularly tilled fields, including alfalfa hay.

[b] Grass included fallow fields as well as runway easements and unmowed grass areas.

[c] Other included runways, roads, drainage ditches, wetlands, etc.

Location Estimation Error

Just over half of all location estimates were made with at least 1 bearing whose signal quality was <1, meaning that there was no null-peak signal pattern. Based on test transmitter location estimates with less than perfect signal reception, we estimated 15 degrees as the maximum error angle still leading to estimated locations within receiver detection range. All 10 data sets resulting from the randomly drawn maximum error displacement supported the conclusions reached regarding habitat selection with the actual estimated locations (Table 8; Gervais 2002). Therefore, we concluded that neither location error nor habitat misclassification had influenced analysis results.

DISCUSSION

Home-range sizes of breeding male burrowing owls during the nesting season were highly variable among individuals and were not accounted for by reproductive output as defined by number of fledgling owlets, numbers of nearby nests, cover-type composition near the nest, nor the numbers of rodents in the diet as indexed by pellet analysis. The poor explanatory power of these factors is surprising, given that intuitively they would seem to be important in determining the amount of space required to obtain adequate food. Relationships among factors may be more complex than we assumed, and we may have failed to measure important components. Home-range size estimates may be a poor indicator of the types and quantities of resources an organism needs for a given life-history stage.

Burrowing owls in this study area used the agricultural fields extensively. However, habitat selection patterns were not nearly as clear as those found in earlier work in other landscapes (Haug and Oliphant 1990). Breeding burrowing owls

Table 8. Radiotelemetry error test results for the space use study of male burrowing owls at Naval Air Station (NAS) Lemoore, California, USA, 1998–1999. Ten tests incorporating maximum estimated location error were performed, and each was summarized over the 33 owls. The results of the 10 tests are averaged below and the Akaike Information Criterion weights (AIC_c) calculated for the mean result.

Model	AIC_c	95% CI	ΔAIC_c	AIC_c weights
dnest + $dnest^2$ + $dnest^3$	414.7032	414.1834–415.2230	0	0.7639
dnest + $dnest^2$ + $dnest^3$ + cover type	418.0771	417.5796–418.5747	3.3739	0.1414
dnest + $dnest^2$ + $dnest^3$ + log dist to edge + cover type	420.2999	419.6848–420.9150	5.5767	0.0465
linear distance to nest + grass cover + dist*grass cover	422.4255	421.7597–423.0913	7.7223	0.0161
linear distance to nest	422.7802	421.9656–423.5949	8.0770	0.0135
log distance to nest	423.6412	422.8044–424.4780	8.9380	0.0087
log distance to nest + log distance to edge	424.7089	423.8376–425.5802	10.0057	0.0051
log distance to nest + cover type	425.4778	424.7060–426.2497	10.7746	0.0035
log distance to nest + log distance to edge + cover type	427.5112	425.6286–429.3937	12.8080	0.0013
cover type	490.8776	489.9950–491.7602	76.1744	0.0000
log distance to edge	509.6501	509.0140–510.2862	94.9469	0.0000
intercept only	511.1309	510.8591–511.4027	96.4277	0.0000

carry single prey items back to the nest burrow and consequently fit the classic-central-place, single-prey-loader foraging models (Stephens and Krebs 1986). It is therefore not surprising that distance was consistently an important component of models distinguishing random from actual foraging locations during the breeding season. Although energetic demands, on male owls in particular fluctuate greatly depending on nesting stage, we were unable to explore finer-grained home-range sizes or habitat selection by individual owls. Too few locations during each individual owl's nesting cycle existed to make such a comparison meaningful.

Contrary to our initial predictions, male owls selected neither GRASS cover nor edges of roads or irrigation ditches for foraging. Owls also did not appear to avoid CROPLAND, which suggested that the resources needed by the owls may have been distributed across owl home ranges independent of cover types. Therefore, no selection for any particular cover type was needed for successful foraging. In our study, it was difficult to determine whether male owls selected particular cover types once distance was accounted for. All nest burrows were either in GRASS cover or located under structures immediately adjacent to GRASS.

Haug and Oliphant (1990) found that burrowing owls were more likely to use grass–forb areas than croplands or grazed pasture. The landscape in their study had much greater interspersion of cover types than that of NAS Lemoore. But it would be interesting to reexamine those data including distance to nest as a potential explanatory variable. After distance has been accounted for, interpretation of apparent habitat selection may change dramatically (Rosenberg and McKelvey 1999).

Burrowing owls are opportunistic foragers that eat a wide variety of vertebrate and invertebrate prey (Green et al. 1993, Haug et al. 1993, Gervais et al. 2000, York et al. 2002). The birds consistently choosing one cover type over another seems unlikely when faced with spatially and temporally varying prey populations, provided that cover characteristics did not preclude successful foraging altogether. Agricultural lands composed of row crops can be adequate habitat in and of themselves, as demonstrated by the high densities of burrowing owls in the Imperial Valley where few fallowed or uncropped fields exist (Rosenberg and Haley in press).

Owls in all parts of the study site were detected foraging in CROPLAND recently treated with agricultural pesticides, although we found no evidence of selection for the CROPLAND cover type. Ingestion of pesticide-contaminated prey is a demonstrated threat to nontarget species (Henny et al. 1985, White and Kolbe 1985, Hunt et al. 1991). Whether animals may be attracted to pesticide application events is less clear. Burrowing owls certainly are capable of tracking shifting resource availability. We witnessed a shift in their diets in 1999 in response to a major increase in rodent densities (Gervais 2002). In any case, owls used agricultural fields in our study landscape. Depending on chemical persistence and toxicity, they may be at risk from either direct exposure of pesticides or ingestion of contaminated prey. Owls foraged in fields recently treated with compounds that are highly toxic to birds, including the organophosphate compound chlorpyrifos and the carbamate compound aldicarb (Gervais 2002). No radiomarked owls died after foraging in these fields during the study, however. Use of agricultural fields alone cannot be a basis for formal risk assessment, although it indicates that some estimation of exposure risk may be necessary.

We estimated a much greater radiotelemetry error than is typical of null-peak receiving systems (e.g., Haug and Oliphant 1990). Burrowing owls generally are poor candidates for fine-scale radiotelemetry work because they move frequently and rapidly while foraging. Sampling error biases location estimates toward cover types with the greatest detection probability. These issues have not been well explored in radiotelemetry data collection and analysis, although a tremendous potential exists for spurious results (McKelvey and Noon 2001). However, our study landscape was composed of large, contiguous blocks of cover type as individual farm fields are typically approximately 65 ha, and GRASS areas ranged between 45 and 179 ha, decreasing the impact of relatively poor system performance.

MANAGEMENT IMPLICATIONS

In view of the tremendous variability in the home-range estimates among individual birds, we caution against using any single number as an indication of how much space a breeding owl pair may need. However, habitat selection was heavily influenced by distance to the nest. Habitat improvements for breeding owls should focus efforts within 600 m of nest burrows to maximize foraging efficiency. In addition, because owls are central-place foragers, pesticide risks may be mitigated by avoiding pesticide applications near nest burrows (James and Fox 1987). Our data suggested that adults concentrate foraging efforts within 600 m of the nest burrow, as was observed in Canada (Haug and Oliphant 1990) and southern California (Rosenberg and Haley in press). Maintaining a buffer zone of 500–600 m would prevent most primary and secondary poisonings, although this might pose a substantial negative impact on the farmer in the case of cropland under active production.

Dispersing juvenile burrowing owls used a number of burrows as they moved away from their natal territories (Desmond and Savidge 1999, King and Belthoff 2001). We recommend that disturbance or pesticide exposure of non-nest burrows in areas of nesting populations be minimized in late summer, when young owls are most likely to be using them. Nonbreeding owls can be cryptic and determining their presence should not be based only on casual observations.

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