AN ABSTRACT OF THE THESIS OF

Noelle A. Ronan for the degree of Master of Science in Wildlife Science presented on February 21, 2002. Title: Habitat Selection, Reproductive Success, and Site Fidelity of Burrowing Owls in a Grassland Ecosystem.

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Daniel K. Rosenberg

I used a comparative and experimental approach to examine nest habitat selection, reproductive success, and nest site fidelity of burrowing owls (*Athene cunicularia*) in a large, non-fragmented grassland in southwest California. In 1999, I compared habitat characteristics between nest sites ($n = 31$) and randomly selected, unoccupied burrows ($n = 31$) in the local vicinity of the nest (paired burrows). In 2000, I compared habitat characteristics between nest sites ($n = 33$) and randomly selected, unoccupied burrows ($n = 32$) within the study area (unpaired burrows). I examined reproductive success and variation in nest habitat characteristics, diet quality, and intraspecific competition using data from 1998, 1999, and 2000. I experimentally ($n = 11$ control and 11 treatment nests) assessed the effect of satellite burrow (multiple auxiliary burrows near the nest) use on productivity and behavior.

I found little variation in habitat between nest sites and unoccupied burrows. Habitat selection was not strong when nests and unoccupied burrows were spatially correlated (paired burrows). However, nest sites had a larger number of large diameter burrows, satellite burrows, and perches than the unpaired burrows.

Nest success (≥ 1 young fledged) and productivity (the number of young alive at 14 - 21 days) varied substantially among some years, though the habitat variables I tested did not explain reproductive success when both failed and successful nests were evaluated. When nests were successful, productivity was influenced by rodent consumption. Nest fidelity within the breeding season was highly correlated with nest success. Nest abandonment occurred at 83% ($n = 15$ of 18), 92% ($n = 12$ of 13), and 83% ($n = 20$ of 24) of the failed nests in 1998, 1999, and 2000, respectively.

Results of the experimental manipulation of satellite burrow access showed that productivity did not differ between groups but demonstrated that burrowing owls will adjust their behavior to use satellites. Owls in the treatment group (71%; $n = 5$ of 7) responded by moving their families to areas with access to satellite burrows but none of the control group owl families moved.

This study illustrates the importance of identifying critical factors affecting reproductive success of burrowing owls in large grasslands. Maintenance of burrowing mammal populations to provide nest and satellite burrows will be important for protecting burrowing owls. Also, temporal dynamics influenced reproductive success. Habitat characteristics that enhance foraging ability may

benefit productivity, especially in years of low rodent numbers. Furthermore,

temporal variation in nest success may lead to low nest site fidelity.

Habitat Selection, Reproductive Success, and Site Fidelity

of Burrowing Owls in a Grassland Ecosystem

by

Noelle A. Ronan

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Major Professor, representing Wildlife Science

Redacted for Privacy

Chair of Department of Fisheries and Wildlife

Redacted for Privacy

Dean of the Graduate School

I understand that my thesis will become part of the permanent collection of Oregon State University libraries. My signature below authorizes release of my thesis to any reader upon request.

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Noelle A. Ronan, Author

ACKNOWLEDGMENTS

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INTRODUCTION

Understanding wildlife habitat needs is critical to manage and conserve populations. Habitat selection theory states that individuals should select habitats that increase survival and reproductive success (Fretwell and Lucas 1970, Cody 1981, Orians and Wittenberger 1991). For birds, predation and food supply are often limiting factors that can determine habitat suitability (Fretwell and Lucas 1970, Newton 1998). Therefore, nesting sites with protective habitat features and the development of anti-predator behavioral adaptations should be selected for (Byrkjedal 1987, Martin and Roper 1988, Sieving and Willson 1998). Further, habitat can influence foraging efficiency and prey availability. For example, some raptors have been shown to benefit from perch availability and selection of foraging areas with sparse vegetation where prey is more easily captured rather than in areas with greater prey densities (Bechard 1982, Wolff et al. 1999, Sheffield et al. 2001). Nest fidelity is associated with successful breeding attempts, therefore predation (Newton 1979, Calder et al. 1983, Reed and Oring 1993) and food supply (Korpimaki 1993) can also promote breeding dispersal (movement of reproductive adults between successive breeding sites; Greenwood 1980).

The influence of predation and food supply on habitat selection, reproductive success and site fidelity are poorly understood in the burrowing owl (*Athene cunicularia*). The burrowing owl is a small, ground-dwelling raptor of arid, open grasslands and deserts which, despite an adaptability to increasing landscape change, is declining throughout some of its range in western North America (Haug et al. 1993) due to habitat loss and control of burrowing mammals (Rich 1986, Belthoff and King 1997, Johnson 1997). The burrowing owl is listed as endangered in Canada, Iowa, and Minnesota, threatened in Mexico, and is a species of management concern in the United States (Sheffield 1998).

The burrowing owl is vulnerable to many different predators such as other raptors, snakes, mustelids, and canids (Haug et al. 1993). Visibility at nest sites appears to be an important habitat selection factor and may be an anti-predator behavioral tactic. Burrowing owls have been shown to select nest sites with more bare ground, less grass coverage, less vertical density, low shrub density, and higher perches, ultimately resulting in greater visual security from predators (Rich 1986, Green and Anthony 1989, Plumpton and Lutz 1993). Furthermore, burrowing owls commonly use multiple burrows in the vicinity of the nest ("satellite burrows"; Haug et al. 1993, Desmond and Savidge 1999, pers. obs.). Because pre-fledging young are very visible and vulnerable to predation, use of satellites may be an adaptation against predation, as loss of an entire brood is less likely if young are distributed among several burrows (Desmond and Savidge 1999). Because

burrowing owls can have large broods, escape from predators may be faster when all young are not attempting to flee into one burrow entrance.

Burrowing owls forage near the nest (Haug and Oliphant 1990, Rosenberg and Haley, in press), therefore nest habitat selection may also involve decisions based on foraging efficiency as well as security from predators. Hunting methods vary depending on habitat conditions and the type of prey (Haug et al. 1993) therefore, dense vegetation may impede ground and aerial hunting and perch availability may influence aerial foraging efficiency.

I used a comparative and experimental approach to examine nest habitat selection, reproductive success, and nest site fidelity of burrowing owls in a large, non-fragmented grassland in southwest California. My objectives were to test whether 1) owls selected nesting habitat with characteristics that enhanced predator detection and avoidance and foraging efficiency, 2) owls had higher reproductive success (nest success and productivity) at nest sites that enhanced predator evasion and foraging efficiency and, 3) nest site fidelity was associated with nest success. To draw inferences about habitat selection, I compared habitat characteristics around occupied burrowing owl nest sites with characteristics around unoccupied burrows in the local vicinity of the nest (paired burrows) and with burrows within the study area (unpaired burrows). To evaluate the relative suitability of nesting habitat, I examined reproductive success and variation in nest habitat characteristics, diet quality, and intraspecific competition. Finally, ubiquitous

satellite burrow use at the study site prompted me to experimentally assess the

effect of this habitat component on productivity.

STUDY AREA

The study was conducted at the Carrizo Plain National Monument (Carrizo), located on the eastern edge of the Coast Range approximately 80 km southwest of Bakersfield, California (Fig. 1). Carrizo is jointly managed by the Bureau of Land Management (BLM), California Department of Fish and Game, and The Nature Conservancy. Within the Carrizo Plain boundaries are 100,000 ha of undeveloped, semi-desert grassland which represent the largest remnant in the San Joaquin Valley (Schiffman 2000). Carrizo includes a broad valley plain and parts of the bordering Temblor Mountains to the northeast and the Caliente Range to the southwest. The study was confined to areas less than 800 m in elevation where burrowing owls are distributed widely over the study area.

The region's climate is cool with moist winters and hot, dry summers and an average annual rainfall of 15 cm (Williams1992). Non-native grasses, such as foxtail (*Vulpia sp.*), bromes (*Bromus sp.*), filaree (*Erodium cicutarium*), and oats (*Avena sp.*) are the dominant vegetation, though some native species and communities are common, including common saltbush (*Atriplex polycarpa*), spiny saltbush (*Atriplex spinifera*), nodding needlegrass (*Nasella cernua*), blue grass (*Poa secunda sp. secunda*), lupine (*Lupinus sp.*), goldfields (*Lasthenia sp.*), red maids (*Calandrinia ciliata*) and owl's clover (*Castilleja sp.*) (Butterworth and Chadwick 1995).

Historically, Carrizo was manipulated extensively for dryland grain farming and cattle and sheep ranching which has resulted in the invasion of non-native vegetation. Though farming no longer occurs within the boundaries of Carrizo, grazing is being used as a management tool intended to enhance and support native species and communities by controlling exotic vegetation and to maintain low, open vegetative structure that some grassland species prefer and/or require (Germano et al. 2001).

Figure 1. Map of the study area at the Carrizo Plain National Monument, California,1998, 1999, and 2000.
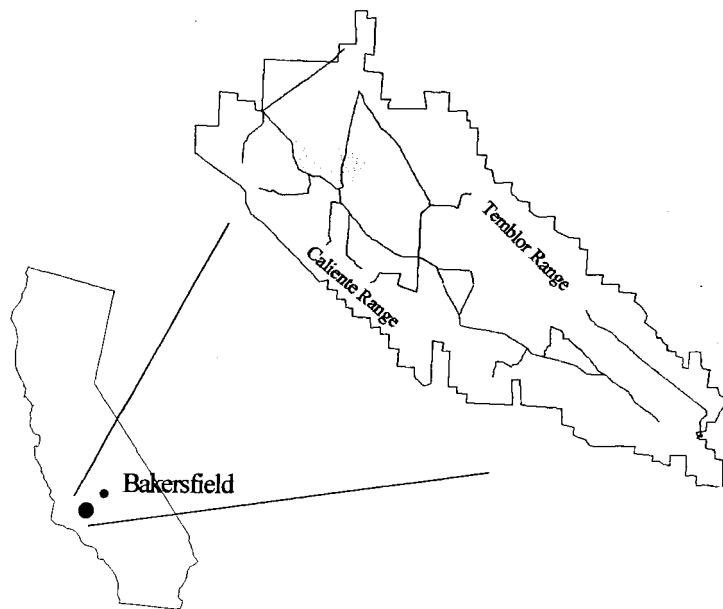
METHODS

FIELD TECHNIQUES

Locating Nests

I located burrowing owl nests from April - July 1998 to 2000 using call surveys in which I broadcast the territorial call of the burrowing owl (Cornell Laboratory of Ornithology, Ithaca, NY) at stations 0.3 km apart along vehicle-accessible roads from April - June between 1930 and 0330 hr (Haug and Didiuk 1993). To locate nests, I used bi-angulation of bearings taken on owls responding to the broadcast call (program LOCATEII; Nams 1990). Previously occupied nests (1996 to 1999) were checked for occupancy and the surrounding area (approximately 100 m) was searched for owls and signs of activity. Incidental nest discoveries occurred while driving or while working at other nest sites. A burrow was determined to be a nest based on the presence of owls, behavioral ques, and physical evidence such as pellets, prey remains, feathers, whitewash, or decoration (i.e. cow dung, coyote scat; Haug et al. 1993).

Habitat Selection

Paired Burrows

I measured habitat characteristics at nests and at unoccupied burrows between June 5 and July 6, 1999. Vegetation samples reflected conditions at the nest after the growing season was complete and after cattle were removed from pastures. Unoccupied burrows were located based on the criteria that they be the closest intact, unoccupied burrow beyond a 100 m radius of the nest burrow (the area that includes satellite burrows used by adults and young; Green and Anthony 1989, pers. obs.) and have a diameter ≥ 10 cm, the minimum size of nest burrows (Haug et al. 1993). I used the first suitable burrow that I found along a random compass bearing. In comparing habitat character between nests and unoccupied burrows nearby, I intended to examine nest habitat selection within an otherwise similar environment.

I measured habitat characteristics that may influence burrowing owl foraging efficiency and predation risk, and thus influence habitat selection. I hypothesized that 1) accumulated dead vegetation (mulch density) may obscure prey and affect an owl's ability to capture prey, 2) vegetation density and effective height may influence visibility and thus affect predator detection, 3) availability of perches may enhance foraging and predator detection ability and, 4) the use of satellite burrows around the nest may enhance predator avoidance by providing

more escape possibilities. To examine whether vegetation characteristics differed with distance from the nest burrow, I measured vegetation at 5 m and 20 m from the nest entrance.

I measured vegetation along 4 20-m transects radiating from the nest and unoccupied burrow. The compass bearing of the first transect was randomly chosen with each transect thereafter being 90 degrees apart (Green and Anthony 1989). At 5 m and 20 m along each transect, vegetation density and effective height measurements were taken (Green and Anthony 1989, Plumpton and Lutz 1993, Rich 1986). Mulch density was estimated by noting its height on a vertical rod. Vegetation density was estimated by counting the number of vegetation contacts on the vertical rod (using categories of 10 cm-gradations from 0 - 70 cm). Effective height was measured using a white board marked with centimeter gradations. The height at which 90% of the board was obscured by vegetation, as viewed from a distance of 10 m away and 1 m above the ground, was recorded (Green and Anthony 1989). I recorded the number of perches and potential satellite burrows (diameter ≥ 10 cm) within 50 m of the nest and unoccupied burrow (Green and Anthony 1989, Rich 1986). Nests located within 20 m of a road (the length of the sampling transect) were excluded.

Unpaired Burrows

I measured habitat characteristics at burrowing owl nests and unoccupied, random burrow locations within the study area between June 20 and July 21, 2000. I followed the same habitat measurement protocol as discussed above. To locate random burrows, I generated a list of random points that were within 500 m of either side of call survey transect roads (roads surveyed since 1998) using the geographic information system (GIS) and coverage data for Carrizo (California Energy Commission, 1987). Because the probability of owl detections decreased with distance from the call survey transect (D. Rosenberg and N. Ronan, unpubl. data), 500 m on either side of the transect road represented an area that most ($\bar{x}$ = 80%, 1998 - 2000) owl nests were detected in. I located random points in the field using a Global Positioning System (GPS; Garmin 12XL, Garmin International, Inc., Olathe, KS). I located the nearest intact burrow with a diameter of ≥ 10 cm within 50 m from the random point. I then measured habitat characteristics as described previously. If a burrow was not found then habitat characteristics were not measured.

Reproductive Success

I defined nest success as having ≥ 1 young survive to fledge. I defined pre-fledging productivity as the number of young alive at 14-21 days of age and fledging productivity as the number of young alive at 32-40 days of age (ageing criteria based on Haug et al.1993, Priest 1997). Fledging productivity was estimated only for nests in the experimental study to assess the reduction in young at nests (described below). I conducted observations at nests from May - July in 1998 - 2000 using binoculars and spotting scopes. I observed nests between 0545 and 2000 hr for a period of 30 min on 5 separate occasions within ≤ 5 consecutive days and separated by ≥ 5 hr, during which I noted the maximum number of young seen (Rosenberg and Haley, in press). I waited 15 min prior to conducting the observation to allow the owls to acclimate to my presence. Observations were made from approximately 100 - 500 m away from the nest.

Reproductive Success and Diet

Observations I made during 1998 - 2000 indicated that the amount of rodents consumed by burrowing owls may contribute to productivity. To evaluate the influence of diet on reproductive success, I examined the diet composition of burrowing owls from regurgitated pellets. I collected pellets from all nests during 1998-2000. All pellets from a given nest and year represented a single sample.

Pellets were dissected individually by hand (Marti 1987) and evaluated by counting

skeletal remains to estimate the minimum number of rodents consumed / number of

pellets (Rosenberg and Haley, in press).

Satellite Burrow Access Experiment

The Carrizo Plain supports a diversity of predators of the burrowing owl and

indeed, predation is the most common ($\bar{x} = 54\%$, $n = 26$ known mortalities from

1998 - 2000) cause of mortality of burrowing owl individuals. The time between

emergence (about 14 days) and fledging (about 40 days) may be one of increased

predation risk because while young are outside of the nest often they are limited to

one mode of escape from predators, which is to retreat into burrows. I was

motivated to experimentally test whether the use of satellite burrows near the nest

reduces predation of burrowing owl young because satellite burrow use was so

common at this study site and also preliminary results from 1999 suggested that

satellite burrows were important for nest habitat selection. In 2000, I randomly

assigned 11 nests to the control group and 11 nests to the treatment group. The

experimental design involved preventing access to satellites within 20 m of the

nest burrow. One-way door excluders, similar in design to that described in

Banuelos (1997), were used to block access to satellites for treatment nests. The

one-way door excluders allowed animals present inside the burrow to exit but

prevented owls from entering the burrow. The excluders were placed at treatment nests during the egg laying and incubation stage of nesting. Nesting stage was determined by behavior, nesting sign, and underground nest observations using an infrared video probe (Sandpiper Technologies, Inc., Manteca, CA). I continued the experiment until young fledged (about 40 days of age; Haug et al. 1993). The groups received similar levels of disturbance during the study period.

I predicted that more young would be predated at nests that did not have access to satellites near the nest compared to those that did have access to satellites. To evaluate this prediction, I conducted nest observations (described previously) to estimate pre-fledging and fledging productivity. This allowed me to estimate the reduction in young at nests that occurred between the time of emergence from the nest (approximately 14 days of age) until fledging (approximately 40 days of age).

I was interested in behavioral responses as well as reproductive success. I monitored family responses and behavior of young at nests. I monitored nests to document movements away from the nest burrow. Movements involved entire family moves (family movement) that were gradual yet permanent, occurred before young had fledged and were of a relatively short distance (> 25 m and < 120 m). Family movements differed from nest abandonment because abandonment involved long distance movements and occurred after loss of nest contents.

Additionally, I monitored the areas used by young for roosting around the nest and recorded the information as the number of young observed within 4

categories: at the nest, within 20 m of the nest, within 50 m, and > 50 m from the nest. Roosting locations refer to areas around the nest site and outside of burrows that young were observed. Nest monitoring was done during mornings and evenings (within approximately 5 hr after sunrise and 5 hr prior to sunset) when young are most active outside of burrows. Pin flags were placed at 20 m and 50 m from the nest to facilitate distance estimation during observations.

To determine if response of young to an approaching predator would differ between groups, I conducted predator simulations. I hypothesized that young in the treatment group would remain outside longer before they retreated because lack of satellites would necessitate them all using the nest for retreat, thus extending the amount of time (therefore enabling a predator to approach closer) they would be exposed to predation risk. Simulations involved approaching the nest in a fast and direct manner (6 - 7 km/hr). I noted my distance from the young when they retreated into a burrow (approach distance) and which burrows were used for retreat. Retreat burrows were either nests or satellites. To best observe owl responses, two people worked together during simulations; one person approached the nest while the second person remained in the vehicle to observe responses through a spotting scope. Predator simulations were conducted during mornings and evenings when young are most often outside of burrows.

STATISTICAL ANALYSES

General Approach

As an alternative to conventional statistical significance testing of null hypotheses, I used an information-theoretic approach which ranks models and provides a means of assessing the strength of evidence for one model over another (Burnham and Anderson 1998). I developed a suite of *a priori* models and used Akaike's Information Criterion, corrected for small sample bias (AICc), as the basis for model selection. For model development, I included variables that were biologically relevant for each hypothesis based on the literature and field observations. For linear regression models I computed AICc with the least-squares method described by Burnham and Anderson (1998). I used AICc weights (ω_i) to evaluate the relative likelihood of the ith model given the data (Burnham and Anderson 1998). The smaller the AICc weight, the less plausible the model is relative to other candidate models.

After developing the set of *a priori* models, I examined multicollinearity among variables using the Pearson correlation coefficient (PROC CORR; SAS 1998). Because the correlation matrix may not be sufficient to detect complex correlations, I also examined the tolerance value (PROC REG with the TOL option; SAS 1998, Allison 1999). Generally, tolerance values below 0.40

correspond to high multicollinearity (Allison 1999). Of the correlated variables, I retained the most biologically relevant ones for analysis.

For generalized linear models I assessed goodness-of-fit for global models by comparing the deviance statistic of the global model of interest with a more saturated model. For simple and multiple linear regression, I used the extra-sum-of-squares F-test to assess goodness-of-fit of the global model (Ramsey and Schafer 1997).

For logistic regression analyses, I estimated the odds ratios and the 95% confidence interval for each variable for the best and competing models. Models within 2 AICc units were considered to be competing models (Burnham and Anderson 1998). Odds ratio 95% confidence intervals were estimated by

$$\exp(\beta 1 \pm (1.96)SE(\beta 1)).$$

The odds ratio is a measure of association that approximates how likely it is for the outcome of interest to be present (Hosmer and Lemeshow 1989).

For satellite burrow access experiment analyses involving models with the response variable regressed on a single explanatory variable, I used traditional null hypothesis significance testing.

Habitat Selection

I developed a suite of 15 *a priori* models to examine the influence of habitat

characteristics on nest site selection. After assessing multicollinearity, the habitat

variables included in analyses were mulch density, the number of satellites within

50 m of the nest (satellites), the number of perches within 50 m of the nest

(perches), and the diameter of the nest or the randomly selected burrow. Also, I

hypothesized that vegetation density and satellite burrow availability may interact

to affect predation rates, therefore I included this interaction term in analyses. I

used the mean values of the habitat variables for each sampling distance (5m and 20

m) and analyzed the distances separately.

I compared habitat variables between nests and unoccupied burrows in the

local vicinity of nests (paired burrows) using 1:1 matched-pairs logistic regression

because nests and unoccupied burrows were spatially correlated and therefore

lacked independence (Hosmer and Lemeshow 1989). Each nest and unoccupied

burrow pair represented 1 sample. The response variable was set equal to 1 and the

explanatory variables were the mean differences between the paired observations

for each habitat variable at each sampling distance (5 m and 20 m). I fit the logistic

regression model using PROC LOGISTIC with the NOINT (no intercept) option

(SAS 1998).

I compared habitat variables between nests and unoccupied random burrows

within the study area (unpaired burrows) using logistic regression (PROC

LOGISTIC; SAS 1998). The response variable was coded as 1 if a burrow was a nest and 0 if it was a random burrow and the explanatory variables were the mean habitat variable values for each sampling distance. The logistic regression model described the probability that a burrow was a nest as a function of the explanatory variables.

Reproductive Success

Using data from 1998 - 2000, I compared nest habitat characteristics with nest success (≥ 1 young fledged) and productivity (the number of young alive at 14-21 days). I developed 18 *a priori* models for the analyses. The habitat variables included were mulch density, effective height of vegetation, satellite burrows, perches, nearest neighbor distances, and year. I included nearest neighbor distances to examine whether competitive interactions may have influenced reproductive success. I used the mean values of the habitat variables for each sampling distance (5m and 20 m) and analyzed the distances separately. Because I conducted an experiment simultaneous with other activities in 2000, I did not include nests that were experimentally manipulated ($n = 11$) for the analyses. I used logistic regression to compare nest success with nest habitat characteristics. The response variable was the probability that a nest succeeded.

Observations I made during 1998 - 2000 indicated that nest failure was most common ($\bar{x} = 93\%$, $n = 55$) during egg laying and incubation. I hypothesized that nest habitat characteristics may affect productivity differently during the pre- and post-hatching periods. Therefore, I examined pre-fledging productivity in relation to nest habitat characteristics for 1) successful and failed nests combined and, 2) successful nests only. The response variable was the maximum number of young observed at each nest. I used a generalized linear model with a negative binomial distribution (negative binomial regression; Allison 1999) to evaluate productivity for successful and failed nests combined. The negative binomial regression model is a generalization of the Poisson model but includes a disturbance term which corrects for overdispersion and is efficiently estimated by maximum likelihood (White and Bennetts 1996, Allison 1999). Ordinary linear regression may not be adequate to analyze highly skewed count data (White and Bennetts 1996, Allison 1999). Though Poisson regression can be used to analyze such data, it often exhibits overdispersion (Allison 1999). To test for overdispersion in the data, I fit the global model to a Poisson regression model and used the deviance / deviance df to evaluate if overdispersion was present in the data. Because overdispersion was a problem for the data involving successful and failed nests (deviance / df = 3.57; Allison 1999), I used negative binomial regression.

I used Poisson regression to evaluate productivity for successful nests only. I examined the distribution of the data for successful nests and checked for overdispersion using the deviance / deviance df for the global model as discussed above. Because overdispersion was not a problem for this data set (deviance value / df = 0.88), I used the Poisson model for the analysis.

Reproductive Success and Diet

I developed 9 *a priori* models that incorporated rodent consumption into the best and competing models selected from the analyses of reproductive success. I analyzed nest success and productivity (response variables) in relation to habitat and diet using the methods described for evaluating reproductive success.

Nest Site Fidelity

I evaluated within-breeding season nest site fidelity of burrowing owls using data from 1998 - 2000. I defined within-breeding season fidelity as occupancy of a nest site for an entire, single breeding season (from egg laying to fledging). I defined a nest site as the area including the nest and satellite burrows within approximately 100 m of the nest (Green and Anthony 1989, pers. obs.). To evaluate within-breeding season nest fidelity, I compared the difference in the

percentage of nest failures associated with within-breeding season nest fidelity and nest abandonment.

Satellite Burrow Access Experiment

I evaluated nest success and productivity of nests for 1) successful and failed nests combined and, 2) successful nests only. I used logistic regression to test whether the probability of nest success differed between treatment and control nests. The response variable was nest success (y = 1) or failure (y = 0) and the explanatory variable was the treatment group (treatment = 1, control = 0). To evaluate differences in the percentage of successful nests between groups, I estimated a SE for proportions as described in Fleiss (1981) and compared 95% CI overlap. To evaluate productivity, I tested whether the reduction in young (the decrease in the number of young alive between the time of emergence and fledging) differed between groups. I used the same statistical methods previously described for productivity analyses. The response variable was the reduction of young at each nest and the explanatory variables were the treatment group and whether a family movement occurred. I included family movements because these movements resulted in satellite burrows being available for use, thus family moves may have influenced the number of young reduced at the treatment nests. Because the treatment group and family movement explanatory variables showed some

correlation (r = 0.54 for successful and failed nests, 0.67 for successful nests only),

I did not include both variables in the same model.

I was unable to perform an analysis using logistic regression to examine

whether the probability of a family movement occurring at a nest differed between

groups because the response of all nests in the control group was equal to 0 (no

movement; Allison 1999). Rather, I used Fisher's Exact Test to estimate the

randomization distribution of the difference in sample proportions. The p-value

measures the probability that the observed outcome was a result of chance

allocation of subjects to groups (Ramsey and Schafer 1997).

I used simple linear regression (PROC GLM; SAS 1998) to test whether

areas used for roosting around the nest and burrows used by young for retreat

during predator simulations differed between groups. The response variable was

the number of young observed in 4 categories (at the nest, within 20 m of the nest,

within 50 m of the nest, > 50 m). Due to a restrictively small sample size, I

analyzed these 4 categories separately rather than using a multi-variate approach.

The treatment group was the explanatory variable. I evaluated results using

traditional hypothesis testing. Also, I compared the mean (± SE) percentage of

young that were observed in the 4 area categories around the nest site between the

treatment and control nests.

I tested whether researcher approach distance (distance to young at the point

of their retreat into a burrow; response variable) during the predator-threat

simulations differed between groups with multiple linear regression (PROC GLM; SAS 1998) to fit 8 *a priori* models. The explanatory variables were treatment group, starting distance of the observer (simulated predator) from the nest, adult presence / absence, and disturbance time. I included starting distance of the observer in all models because this varied at each nest and thus was a possible confounding variable. I included the disturbance time variable because repeated research activity at the nests may have sensitized the owls to our approach and confounded the predator simulations. To estimate disturbance time, I calculated the total minutes of researcher disturbance that occurred at nests from the time I first located nests until young fledged. I included all research activities that involved approaching the nest.

RESULTS

Habitat Selection

Paired Burrows

In 1999, I sampled habitat characteristics at 31 burrowing owl nests and 31 paired, unoccupied burrows. Mulch density, vegetation density at 10 cm, and effective height of the vegetation were correlated (tolerance = 0.3, 0.2, 0.3, respectively). These variables show a correlation because mulch is the accumulation of dead vegetation such that greater vegetation density and height would contribute to greater mulch density. Of these, I retained mulch density for analyses.

At 5 m from the burrow, greater burrow diameter best distinguished nest sites from unoccupied sites (Table 1), with the odds of a burrow being a nest increasing by 67% / cm (Table 2). At 20 m from the burrow, the global model was the best approximating model (Table 1), yet the best and competing models showed poor precision of estimates of odds ratios due to large SE (Table 2). For both 5 m and 20 m, model selection results were generally consistent with the mean habitat variable values which showed that nest burrows had a lower mean mulch density, a greater mean burrow diameter, more satellite burrows, and fewer perches compared with unoccupied burrows (Table 3).

Table 1. Models and model selection results of habitat characteristics to evaluate burrowing owl nest selection, Carrizo Plain National Monument, CA, 1999 and 2000. Paired burrows are nests and spatially correlated unoccupied burrows near the nests. Unpaired burrows are nests and non-spatially correlated unoccupied burrows within the study.

| | Paired Burrows | | | | Unpaired Burrows | | | |
| | 5 m | | 20 m | | 5 m | | 20 m | |
Model[a]	$\Delta AICc$[b]	w[c]	$\Delta AICc$[b]	w[c]	$\Delta AICc$[b]	w[c]	$\Delta AICc$[b]	w[c]
D, S, P, DIA, D*S	3.43	0.06	0.00	0.41	0.00	0.87	0.00	0.90
D, S, P, D*S	22.72	0.00	24.32	0.00	56.56	0.00	48.98	0.00
D, S, DIA, D*S	1.18	0.18	0.34	0.35	6.79	0.03	7.05	0.03
D, S, D*S	20.36	0.00	21.68	0.00	54.98	0.00	47.84	0.00
D, S, P	21.50	0.00	25.42	0.00	54.17	0.00	47.67	0.00
D, P	19.28	0.00	23.12	0.00	72.93	0.00	65.36	0.00
D, DIA	2.33	0.10	3.83	0.06	28.49	0.00	21.45	0.00
D, S	19.65	0.00	23.28	0.00	52.65	0.00	46.36	0.00
S	19.68	0.00	23.15	0.00	51.93	0.00	44.49	0.00
P	21.76	0.00	25.23	0.00	71.72	0.00	64.28	0.00

Table 1, Continued

D	18.95	0.00	21.82	0.00	70.74	0.00	63.24	0.00
DIA	0.00	0.33	3.47	0.07	29.98	0.00	22.53	0.00
D, S, DIA	3.14	0.07	6.23	0.02	4.37	0.10	4.96	0.08
D, P, DIA	0.53	0.25	2.99	0.09	29.47	0.00	21.50	0.00
No Effects (null)	21.02	0.00	24.49	0.00	69.63	0.00	62.18	0.00

[a] Variables may include mulch density (cm; "D"), the number of satellite burrows within 50 m ("S"), the number of perches within 50 m ("P"), and the diameter of the nest or burrow (cm; "DIA").

[b] The difference in AICc from the model with the lowest value (Burnham and Anderson 1998).

[c] The relative likelihood or weight of the model, based on AICc (Burnham and Anderson 1998). The higher the value, the more likely the model.

Table 2. Parameter estimates for the best model in the nest habitat selection analysis for comparisons of nests and spatially correlated unoccupied burrows (paired burrows) and non-spatially correlated unoccupied burrows (unpaired burrows), the Carrizo Plain National Monument, CA, 1999 and 2000. Odds ratios indicate how likely the odds of selection change relative to the explanatory variable.

| | Paired Burrows | | | | | | Unpaired Burrows | | | | | |
| | 5 m | | | 20 m | | | 5 m | | | 20 m | | |
	$\hat{\beta}$	$\hat{SE}(\beta)$	Odds Ratio	$\hat{\beta}$	$\hat{SE}(\beta)$	Odds Ratio	$\hat{\beta}$	$\hat{SE}(\beta)$	Odds Ratio	$\hat{\beta}$	$\hat{SE}(\beta)$	Odds Ratio
Model[a]												
DIA	0.52	0.21	1.67	-	-	-	-	-	-	-	-	-
Model												
D	-	-	-	-7.29	8.23	>0.001	-15.86	9.77	<0.001	0.75	1.46	2.12
S	-	-	-	-0.01	0.05	0.99	0.72	0.38	2.06	0.27	0.12	1.31
P	-	-	-	-0.16	0.34	0.85	0.13	0.07	1.13	0.07	0.03	1.07
DIA	-	-	-	1.64	0.95	5.13	3.56	1.90	35.10	1.11	0.41	3.03
D*S	-	-	-	-0.50	0.48	0.61	-0.05	0.12	0.95	-0.18	0.09	0.84

Table 2, Continued

[a] Variables include mulch density ("D"), satellite burrows within 50 m ("S"), perches within 50 m ("P"), and the diameter of the nest or unoccupied burrow ("DIA").

Table 3. Mean and SE of habitat characteristics at burrowing owl nests and unoccupied random burrows at the Carrizo Plain National Monument, CA, 1999 and 2000. Paired burrows are nests and spatially correlated unoccupied burrows near the nests. Unpaired burrows are nests and non-spatially correlated unoccupied burrows within the study.

	Paired Burrows						Unpaired Burrows					
	Nest			Random			Nest			Random		
Variable[a]	$\bar{x}$	SE	Range	$\bar{x}$	SE	Range	$\bar{x}$	SE	Range	$\bar{x}$	SE	Range
Density 5 m	0.31	0.08	0.0 - 2.0	0.62	0.15	0.0 - 2.8	0.30	0.08	0.0 - 2.5	0.53	0.22	0.0 - 7.0
Density 20 m	0.40	0.09	0.0 - 1.3	0.81	0.18	0.0 - 4.0	0.36	0.10	0.0 - 2.8	0.59	0.20	0.0 - 6.0
Diameter	18.55	1.11	12.0 - 35.0	12.77	0.51	10.0 - 21.0	20.29	0.84	12.0 - 31.0	12.31	0.56	10.0 - 22.0
Satellite	47.16	6.18	3.0 - 169.0	33.42	4.69	2.0 - 97.0	39.82	4.00	0.0 - 83.0	16.31	2.77	0.0 - 64.0
Perch	3.74	1.47	0 - 33.0	11.52	8.19	0.0 - 250.0	11.50	4.52	0.0 - 115.0	9.56	4.19	0.0 - 109.0

[a] Variables include mulch density (cm; "density"), the diameter of the nest or random burrow (cm; "diameter"), satellite burrows within 50 m ("satellite"), and perches within 50 m ("perch").

Unpaired Burrows

In 2000, I sampled habitat characteristics at 33 burrowing owl nests and 32 random burrows. I visited a total of 66 random burrow·locations but I did not obtain samples for all locations because burrows were not present at 52% ($n = 34$) of these random locations.

For both 5 m and 20 m from the burrow, the global model was selected as the best approximating model and there were no competing models (Table 1). The probability that a burrow was a nest increased as burrow diameter, satellite burrows and perches increased (Table 2), though the influence of perches on nest selection was inconclusive due to large SE for the parameter estimates. Likewise, the influence of mulch density on nest selection was inconclusive due to large SE relative to the parameter estimates; this was similar for the interaction of mulch density and satellite burrows as well. Variable means were generally consistent with the model selection results. Nests had lower mulch density, greater burrow diameter, more than 2 times the number of satellite burrows, and a similar number of perches compared with random burrows (Table 3).

Reproductive Success

I tested whether habitat variables influenced the probability of nest success at 16, 31, and 24 burrowing owl nests in 1998, 1999, and 2000, respectively. Nest

success varied substantially among some years (Table 4) and this was evident in the model selection results. Results for both sample distances were similar, with the best approximating model showing that mulch density, perches, and year influenced nest success (Table 5) but the no effects model was almost equal in its likelihood (Table 6). When I included an index of rodent consumption in the best and competing models selected from the above analysis, the no effects model was selected as the best approximating model for both sampling distances (Table 7, Table 8). That the habitat and rodent consumption models were not strongly preferred is consistent with the observation that the mean values of these characteristics differed little between successful and failed nests (Table 9).

I tested whether habitat and diet composition influenced burrowing owl productivity at 16, 28, and 24 nests in 1998, 1999, and 2000, respectively. The number of young varied considerably among years and between young / nest and young / successful nest (Table 4). When I evaluated productivity for successful and failed nests (young / nest), the no effects model was the best approximating model and there were no competing models (Table 6, 7). Therefore, none of the measured habitat variables or the rodent index adequately explained factors that may be influencing burrowing owl productivity when nest failures were included.

When I tested whether the habitat variables influenced productivity at successful nests only, the best approximating model and competing models for both sampling distances (Table 6) showed poor precision (Table 10). When I tested

Table 4. Nest success (≥ 1 young fledged) and estimated productivity (the number of young alive at 14 - 21 days) for burrowing owl nests at the Carrizo Plain National Monument, CA in 1998 ($n = 16$), 1999 ($n = 28$), and 2000 ($n = 24$).

	Nest Success	Young / Nest			Young / Successful Nest		
	%	$\bar{x}$	SE	Range	$\bar{x}$	SE	Range
1998	50	1.25	0.44	0 - 6	2.5	0.63	1 - 6
1999	57	2.96	0.57	0 - 10	5.19	0.50	2 - 10
2000	38	1.79	0.51	0 - 8	4.22	0.72	1 - 8

Table 5. Parameter estimates for the best model selected in the analysis evaluating the influence of habitat characteristics on burrowing owl nest success ($n = 71$ nests). Odds ratios indicate how likely the odds of nest success change relative to the explanatory variable.

	5 m				20 m			
	$\hat{\beta}$	$\hat{SE}$	Odds Ratio	Odds Ratio 95% CI	$\hat{\beta}$	$\hat{SE}$	Odds Ratio	Odds Ratio 95% CI
Model[a]								
Density	-0.08	0.39	0.92	0.40 - 1.99	-0.12	0.38	0.89	0.40 - 1.86
Perch	0.08	0.04	1.08	1.01 - 1.20	0.08	0.04	1.09	1.01 - 1.20
Year 1998	0.76	0.70	2.14	0.55 - 8.88	0.81	0.74	2.25	0.54 - 10.03
Year 1999	1.20	0.60	3.31	1.05 - 11.39	1.19	0.60	3.29	1.04 - 11.34

[a] Variables in the model include mulch density (cm; "density"), the number of perches within 50 m ("perch"), and year. Values for year are relative to year 2000.

Table 6. AICc weights[a] of models that include nest habitat characteristics to evaluate burrowing owl nest success (≥ 1 young fledged; $n = 71$), productivity (the number of young alive at 14 - 21 days) at successful and failed nests ("All Nests"; $n = 68$), and productivity at successful nests ($n = 33$) at the Carrizo Plain National Monument, CA, 1998, 1999, and 2000.

Model[b]	Nest Success 5 m	Nest Success 20 m	All Nests 5 m	All Nests 20 m	Successful Nests 5 m	Successful Nests 20 m
D, H, S, P, N, Y	0.03	0.04	0.00	0.00	0.00	0.00
D, S, P, N, Y	0.10	0.09	0.00	0.00	0.01	0.01
D, S, N, Y	0.01	0.01	0.00	0.00	0.01	0.02
D, H, S, N, Y	0.00	0.01	0.00	0.00	0.01	0.00
D, H, N, Y	0.01	0.01	0.00	0.00	0.02	0.01
D, N, Y	0.02	0.01	0.01	0.00	0.03	0.07
S, N, Y	0.03	0.03	0.01	0.01	0.02	0.02
N, Y	0.05	0.05	0.02	0.02	0.07	0.06
D, H, S, Y	0.01	0.01	0.00	0.00	0.03	0.01
D, S, Y	0.02	0.01	0.01	0.00	0.03	0.05
D, P, Y	0.25	0.23	0.01	0.00	0.09	0.13
D, Y	0.04	0.03	0.02	0.02	0.11	0.20
S, Y	0.05	0.05	0.02	0.02	0.07	0.06
D, H, Y	0.01	0.02	0.01	0.00	0.10	0.05
D, H, P, Y	0.07	0.15	0.00	0.00	0.08	0.03
Y	0.10	0.08	0.06	0.06	0.23	0.20
D, H	0.02	0.02	0.02	0.02	0.08	0.06
No Effects (null)	0.19	0.16	0.83	0.84	0.02	0.02

Table 6, Continued

[a] Variables in the model may include mulch density ("D"), effective height of the vegetation ("H"), the number of satellite burrows within 50 m ("S"), the number of perches within 50 m ("P"), the distance (m) to the nearest neighbor nest ("N"), and year ("Y").

[b] The relative likelihood or weight of the model, based on AICc (Burnham and Anderson 1998). The higher the value, the more likely the model.

Table 7. AICc weights[a] of models that include nest habitat characteristics and relative rodent consumption to evaluate burrowing owl nest success (≥ 1 young fledged; $n = 71$), productivity (the number of young alive at 14 - 21 days) at successful and failed nests ("All Nests"; $n = 68$), and productivity at successful nests ($n = 33$) at the Carrizo Plain National Monument, CA, 1998, 1999, and 2000.

Model[b]	Nest Success		All Nests		Successful Nests	
	5 m	20 m	5 m	20 m	5 m	20 m
D, H, S, P, N, Y, R	0.02	0.03	0.00	0.00	0.00	0.00
D, S, P, N, Y, R	0.08	0.08	0.00	0.00	0.00	0.01
D, H, P, Y, R	0.06	0.12	0.00	0.00	0.06	0.03
D, P, Y, R	0.22	0.20	0.00	0.00	0.08	0.12
D, H, Y, R	0.01	0.02	0.00	0.00	0.09	0.05
D, Y, R	0.04	0.03	0.01	0.00	0.10	0.22
Y, R	0.10	0.09	0.02	0.02	0.28	0.25
R	0.12	0.11	0.24	0.24	0.29	0.25
No Effects (null)	0.34	0.31	0.74	0.74	0.09	0.08

[a] Variables in the model may include mulch density ("D"), effective height of the vegetation ("H"), the number of satellite burrows within 50 m ("S"), the number of perches within 50 m ("P"), the distance (m) to the nearest neighbor nest ("N"), year ("Y"), and an index of rodent consumption ("R").

[b] The relative likelihood or weight of the model, based on AICc (Burnham and Anderson 1998). The higher the value, the more likely the model.

Table 8. Parameter estimates for the best and competing models selected in the analysis evaluating the influence of habitat characteristics and relative rodent consumption on burrowing owl nest success ($n = 71$ nests) at the Carrizo Plain National Monument, CA, 1998, 1999, and 2000. Odds ratios indicate how likely the odds of nest success change relative to the explanatory variable.

	5 m				20 m			
	$\hat{\beta}$	$\hat{SE}$	Odds Ratio	Odds Ratio 95% CI	$\hat{\beta}$	$\hat{SE}$	Odds Ratio	Odds Ratio 95%CI
No Effects (null)	0	0	0	0	0	0	0	0
Model								
Density	-0.08	0.39	0.92	0.42 - 1.99	- 0.13	0.38	0.88	0.41 - 1.87
Perch	0.08	0.04	1.08	0.99 - 1.18	0.08	0.04	1.08	1.00 - 1.18
Year 1998	0.54	0.74	1.71	0.40 - 7.33	0.59	0.77	1.80	0.40 - 8.15
Year 1999	1.44	0.67	4.22	1.15 - 15.54	1.43	0.67	4.20	1.14 - 15.48
Rodent	-1.29	1.37	0.27	0.02 - 3.99	- 1.30	1.36	0.27	0.02 - 3.94
Model								
Density	-	-	-	-	- 0.01	0.40	0.99	0.45 - 2.17
Height	-	-	-	-	- 0.04	0.03	0.96	0.91 - 1.03
Perch	-	-	-	-	0.08	0.05	1.09	0.99 - 1.19

Table 8,
Continued

Year 1998	-	-	-	-	1.36	1.01	3.88	0.54 - 28.16
Year 1999	-	-	-	-	1.59	0.69	4.90	1.28 - 18.81
Rodent	-	-	-	-	- 1.25	1.38	0.29	0.02 - 4.26

[a] Variables in the model may include mulch density (cm; "density"), effective height of the vegetation (cm; "height"), the number of perches within 50 m ("perch"), an index of rodent consumption in the diet ("rodent"), and year. Values for year are relative to year 2000.

Table 9. Mean and SE of habitat characteristics at successful and failed burrowing owl nests at the Carrizo Plain National Monument, CA, 1998, 1999, and 2000.

| Variable[a] | Successful Nests | | | | | | Failed Nests | | | | | |
| | 1998 | | 1999 | | 2000 | | 1998 | | 1999 | | 2000 | |
	$\bar{x}$	SE	$\bar{x}$	SE	$\bar{x}$	SE	$\bar{x}$	SE	$\bar{x}$	SE	$\bar{x}$	SE
Density 5 m	0.6	0.2	0.3	0.1	0.4	0.1	0.9	0.5	0.4	0.2	0.3	0.2
Density 20 m	1.4	0.3	0.3	0.1	0.2	0.1	0.8	0.4	0.5	0.2	0.6	0.2
Height 5 m	20.0	4.8	7.4	1.5	2.8	0.4	13.7	2.6	8.8	1.6	5.0	0.1
Height 20 m	25.2	6.2	6.8	0.8	2.9	0.5	28.8	6.5	9.9	1.5	4.7	0.9
Satellite	19.0	6.7	52.4	8.6	34.3	8.0	10.0	2.3	40.4	8.3	36.8	5.8
Perch	2.5	1.2	5.7	2.3	19.2	12.7	3.4	1.8	0.4	0.4	2.2	1.0

Table 9, Continued

Perch	2.5	1.2	5.7	2.3	19.2	12.7	3.4	1.8	0.4	0.4	2.2	1.0
Neighbor	989.2	325.9	1271.0	293.2	497.1	221.2	3033.7	1217.1	976.03	393.9	592.0	188.9
Rodent	0.1	0.02	0.5	0.1	0.1	0.02	0.1	0.03	0.5	0.1	0.3	0.1

[a] Variables include mulch density (cm; "density"), effective height (cm; "height"), satellite burrows within 50 m ("satellite"), perches within 50 m ("perch"), distance (m) to the nearest neighbor nest ("neighbor"), year, and an index of rodent consumption ("rodent").

Table 10. Parameter estimates for the best and competing models selected in the analysis evaluating the influence of nest habitat characteristics on burrowing owl productivity (the number of young alive at 14 - 21 days) for successful nests, Carrizo Plain National Monument, CA, 1998, 1999, and 2000.

	5 m			20 m		
	$\hat{\beta}$	SE $(\hat{\beta})$	95% CI	$\hat{\beta}$	SE $(\hat{\beta})$	95% CI
Model[a]						
Year 1998	-0.52	0.28	-1.07 - 0.02	-0.52	0.28	-1.07 - 0.02
Year 1999	0.21	0.20	-0.18 - 0.59	0.21	0.20	-0.18 - 0.59
Model						
Density	-0.22	0.20	-0.62 - 0.18	-0.32	0.19	-0.70 - 0.06
Year 1998	-0.48	0.28	-1.03 - 0.06	-0.15	0.34	-0.82 - 0.52
Year 1999	0.19	0.20	-0.19 - 0.58	0.25	0.20	-0.14 - 0.64
Model						
Density	-0.17	0.20	-0.57 - 0.23	-	-	-
Height	-0.03	0.02	-0.06 - 0.01	-	-	-
Year 1998	-0.09	0.35	-0.78 - 0.60	-	-	-
Year 1999	0.29	0.20	-0.11 - 0.69	-	-	-

Table 10, Continued

Model

Density	-0.28	0.21	-0.69 - 0.13	-0.33	0.19	-0.71 - 0.05
Perch	-0.01	0.01	-0.02 - 0.01	-0.01	0.01	-0.02 - 0.003
Year 1998	-0.59	0.28	-1.14 - -0.03	-0.24	0.34	-0.91 - 0.44
Year 1999	0.10	0.20	-0.30 - 0.49	0.17	0.20	-0.23 - 0.57

[a] Variables in the model may include mulch density (cm; "density"), effective height of the vegetation (cm; "height"), the number of perches within 50 m ("perch"), and year. Values for year are relative to year 2000.

whether the rodent index influenced productivity, the best model selected for both

sampling distances included only the rodent index and almost equal in its likelihood

was a model including a year effect as well as the rodent index (Table 7).

Productivity increased with an increasing rodent index yet results varied greatly by

year (Table 11, Fig. 2).

Nest Site Fidelity

Nest fidelity between years was generally low, as indicated by the

percentage of previously occupied nests each year (1998 = 50%, 1999 = 32.5%,

2000 = 35%). Within-breeding season nest fidelity was low when nests failed.

Nest abandonment occurred at 83% ($n = 15$ of 18) of the failed nests in 1998, 92%

($n = 12$ of 13) in 1999, and 83% ($n = 20$ of 24) in 2000. Ninety-three percent of the

failures occurred during laying and incubation.

Satellite Burrow Access Experiment

The odds of nest success was similar for the treatment and control groups

(odds ratio = 0.69, 95% CI = 0.13 - 3.72, $P = 0.67$) , with a success rate of 55%

(S$\hat{\text{E}}$ = 15; $n = 6$ of 11) for control nests and 45% (S$\hat{\text{E}}$ = 15; $n = 5$ of 11) for nests

Table 11. Parameter estimates for the best model and first competing model selected in the analysis evaluating the influence of nest habitat characteristics and rodent consumption on burrowing owl productivity (the number of young alive at 14 - 21 days) for successful nests, Carrizo Plain National Monument, CA, 1998, 1999, and 2000.

		5 m and 20 m		
		$\hat{\beta}$	$SE(\hat{\beta})$	95% CI
Model[a]				
	Rodent	0.74	0.33	0.10 - 1.38
Model				
	Rodent	0.27	0.49	-0.68 - 1.22
	Year 1998	-0.52	0.28	-1.06 - 0.02
	Year 1999	0.11	0.26	-0.40 - 0.62

[a] Variables in the model may include an index of rodent consumption in the diet ("rodent"), and year. Values for year are relative to year 2000.

Figure 2. Burrowing owl productivity and relative rodent consumption at successful nests at the Carrizo Plain National Monument, CA, 1998, 1999, and 2000.
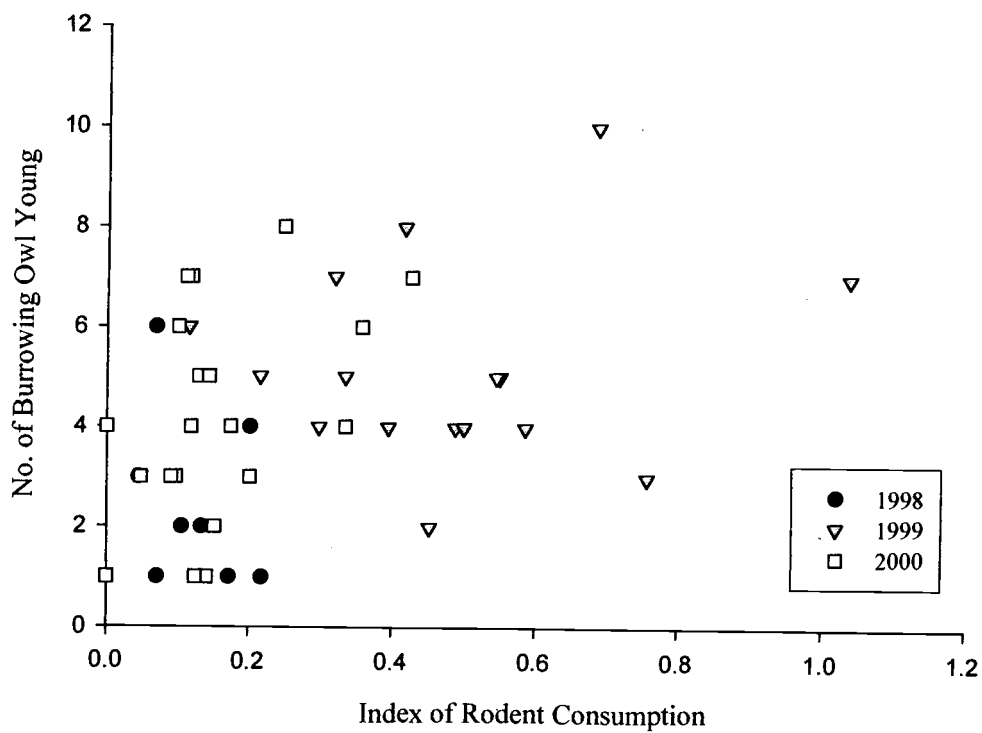
with satellite burrows experimentally blocked. For analyses evaluating the reduction of young / nest, I included all nests that had young emerge, though some (control = 14%; n = 1 of 7, treatment = 29%; n = 2 of 7) subsequently failed. There was no difference in productivity between the groups when both failed and successful nests were included but productivity varied more between treatment and control groups for nests that were successful (Table 12). Results from regression analysis (negative binomial distribution for successful and failed nests and Poisson distribution for successful nests only) though suggested that neither the treatment (blocked satellite burrows) nor family movements influenced the number of young reduced at successful and failed nests or at successful nests only, as indicated by the no effects model being selected as the best approximating model (Table 13).

The occurrence of family movements differed substantially between groups. I saw no family movements at control nests (n = 0 of 7) yet families moved at 71% of the manipulated nests (n = 5 of 7; Fisher's Exact Test 2-sided P = 0.02). These movements averaged 68 m ($\pm$ 18 m) from the nest burrow and ranged from 25 to 120 m.

The areas used by young for roosting around the nest site were generally similar between control and treatment groups. The number of young observed roosting at the original nest and observed roosting away from the original nest (within 20 m, within 50 m, > 50 m of the nest) did not differ between groups (at the nest, P = 0.37; within 20 m, P = 0.24; within 50 m, P = 0.53; > 50 m, P = 0.38). As

Table 12. Productivity estimates for experimentally manipulated burrowing owl nests, Carrizo Plain National Monument, CA, 2000.

| | Young / Nest | | | | Young / Successful Nest | | | |
| | Control (n =7) | | Treatment (n = 7) | | Control (n = 6) | | Treatment (n = 5) | |
	Pre-fledge Young	Reduction of Young	Pre-fledge Young	Reduction of Young	Pre-fledge Young	Reduction of Young	Pre-fledge Young	Reduction of Young
Mean	3.1	1.5	3.0	1.8	4.8	1.0	6.0	2.0
SE	0.87	0.69	0.91	0.34	0.87	0.4	0.55	0.4
Range	0 - 8	0 - 5	0 - 7	1 - 3	3 - 7	0 - 3	4 - 7	1 - 3
% of Young Reduced[a]	-	48	-	60	-	21	-	33

[a] The percent change from the number of pre-fledged young (the number of young at 14 - 21 days) at nests to the number of young alive at fledging (about 40 days).

Table13. Model selection results for the analysis evaluating the effect of the satellite burrow access experiment on the reduction of burrowing owl young at successful and failed nests (n = 14) and successful nests only (n = 11), Carrizo Plain National Monument, CA, 2000.

Model[a]	Successful & Failed Nests		Successful Nests Only	
	ΔAICc[b]	w[c]	ΔAICc[b]	w[c]
Treatment	3.30	0.14	2.06	0.23
Family Movement	3.31	0.14	3.14	0.13
No Effects (null)	0.00	0.72	0.00	0.64

[a] Variables include the treatment group ("treatment") and whether an owl family made a short-distance movement away from the nest burrow ("family movement").

[b] The difference in AICc from the model with the lowest value (Burnham and Anderson 1998).

[c] The relative likelihood or weight of the model, based on AICc (Burnham and Anderson 1998). The higher the value, the more likely the model.

indicated by the mean percentage of young observed around the nest site, young in the treatment group were rarely observed within 20 m of the nest (where the excluders were present) yet 13% (± 9.5) of control group young occupied this area (Fig. 3).

Results of the predator-threat simulations were consistent with the areas young occupied for roosting. The number of young using burrows around the nest site for retreat did not differ between the groups (at the nest, $P = 0.24$; within 20 m, $P = 0.19$; within 50 m, $P = 0.21$; > 50 m, $P = 0.35$). Although young from the experimentally manipulated nests could not retreat into satellite burrows within 20 m of the nest (because of the excluders), 12% (± 9.5) of control group young used this area for retreat (Fig. 4).

During the predator-threat simulations, the approach distance was similar between control (122 ± 32 m, $n = 7$) and treatment nests (153 ± 24 m, $n = 6$) and the treatment (manipulation of satellite burrow access) did not influence the approach distance to young. The distance the observer began the predator simulation (start distance) was the only variable in the best approximating model and there were no competing models (Table 14). As starting distance from the nest decreased, the observer was able to approach closer before young retreated into a burrow (Fig. 5).

Figure 3. Mean percentage of burrowing owl young occupying areas around the original nest site for roosting in the control (*n* = 7) and treatment (*n* = 6) groups, Carrizo Plain National Monument, CA, 2000. Categories describing the areas occupied include at the nest, within 20 m of the nest, within 50 m of the nest, and > 50 m from the nest.
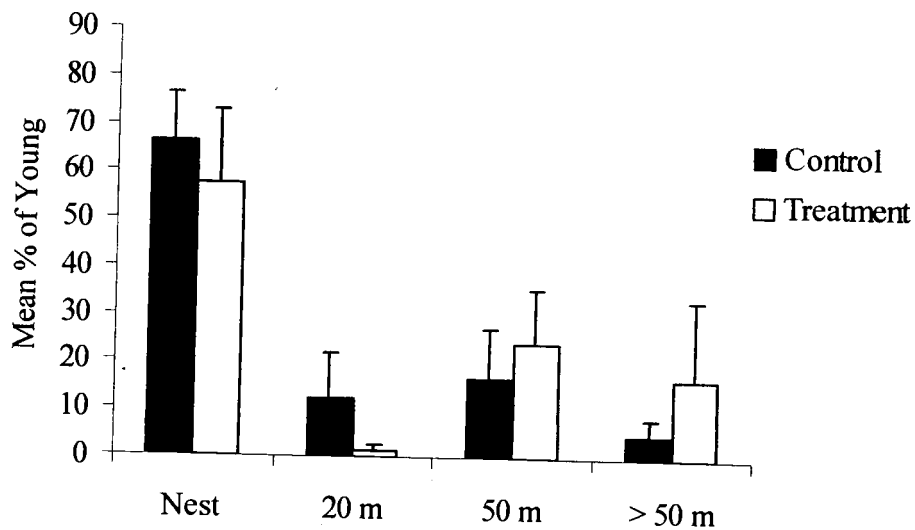
Figure 4. Burrows used for retreat during predator-threat simulations by burrowing owl young in the control ($n = 7$) and treatment ($n = 6$) groups, Carrizo Plain National Monument, CA, 2000. Categories describing the location of burrows used include at the nest, within 20 m of the nest, within 50 m of the nest, and > 50 m from the nest.
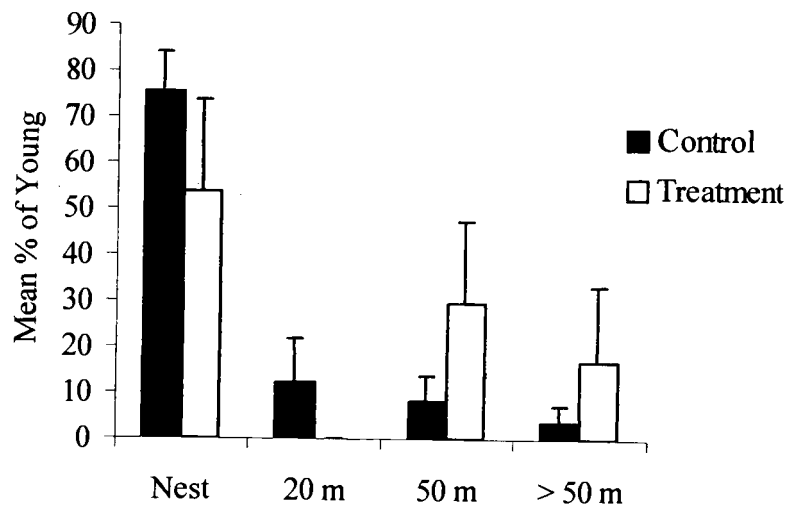
Table 14. Models and model selection results for the analysis evaluating whether satellite burrow access influenced the approach distance (the observer's distance from young when young retreated into a burrow) to burrowing owl young ($n = 7$ control nests, $n = 6$ treatment nests) during the predator-threat simulations, Carrizo Plain National Monument, CA, 2000.

Model[a]	R^2	$\Delta AICc$[b]	w[c]
Treatment, start, disturbance, adults, treatment*disturbance	0.52	25.18	0.00
Treatment, start, disturbance, treatment*disturbance	0.44	16.84	0.00
Treatment, start, adults	0.46	8.90	0.01
Start, disturbance, adults	0.47	8.51	0.01
Start	0.41	0.00	0.68
Start, disturbance	0.44	3.85	0.10
Treatment, start	0.42	4.30	0.08
Null (no effects)	0.00	3.48	0.12

[a] Variables in the model may include the treatment group ("treatment"), the starting distance of the observer approaching the nest for the predator-threat ("start"), the total number of minutes of disturbance each nest received ("disturbance"), and whether adults were present or absent at the time of the predator-threat simulation ("adults").

[b] The difference in AICc from the model with the lowest value (Burnham and Anderson 1998).

[c] The relative likelihood or weight of the model, based on AICc (Burnham and Anderson 1998). The higher the value, the more likely the model.

Figure 5. The approach distance (the observer's distance from young when young retreated into a burrow) to burrowing owl young and the starting distance of the observer (the distance from the nest the observer began the simulation) during the predator-threat simulations ($n = 7$ control nests, $n = 6$ treatment nests), Carrizo Plain National Monument, CA, 2000.
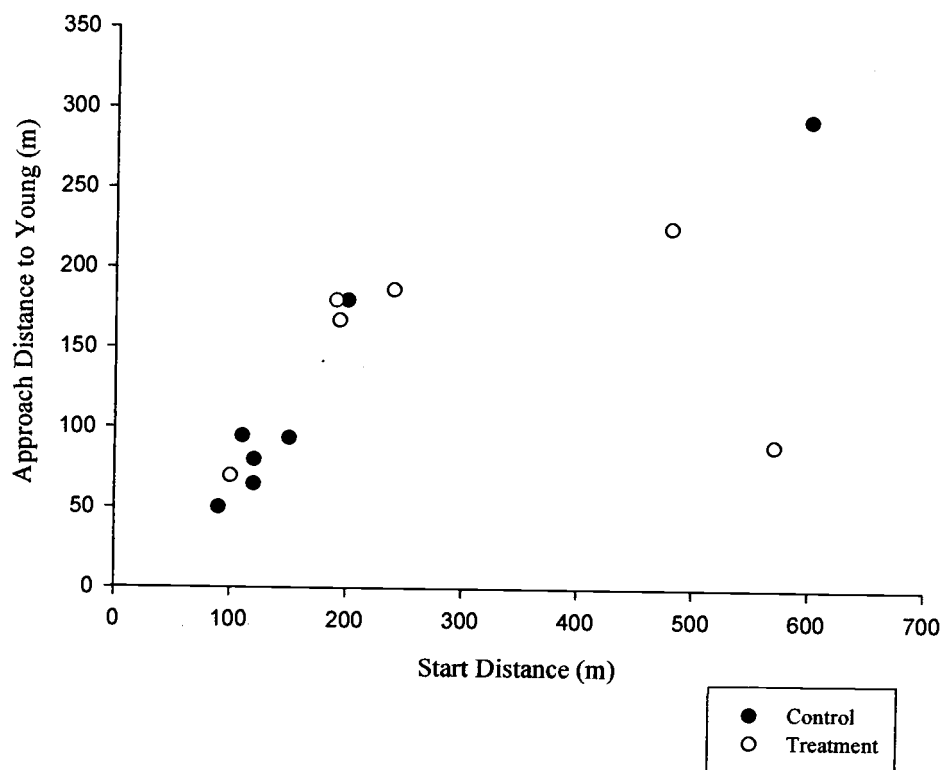
DISCUSSION

Habitat Selection

Identifying factors used by individuals in habitat selection depends on variability among the characteristics present in the habitat (Orians and Wittenberger 1991). Habitat varied little between spatially correlated nests and unoccupied burrows (paired burrows), probably due to their close proximity, thus selection between nests and unoccupied burrows was not strong. Similar factors (i.e. grazing, presence of ground squirrels) were likely affecting the habitat character within the relatively small area of the paired burrows. Furthermore, the relatively small sample size made detection of potentially small effect sizes difficult (Steidl et al. 1997).

The western burrowing owl does not dig its own burrow and hence is dependent on other burrowing mammals. Selection for burrow diameter may simply be a function of a minimum biological requirement. MacCracken and Uresk (1985) found a significant difference between nest and non-nest burrow diameter and suggested that this may be due to modification of burrows by the owls. The mean burrow diameter (18.5 cm) I observed is consistent with other reported dimensions (Haug et al. 1993, Belthoff and King 1997) but contrasts with a study of

nest selection at artificial burrows which found that selection for smaller diameter tunnels may provide for protection from predators (Smith and Belthoff 2001).

Comparisons between non-spatially correlated nests and random burrows (unpaired burrows) provided a greater ability to detect differences in nest selection. The importance of burrow diameter, satellites, and perches at nest sites was more clearly demonstrated for the unpaired burrow comparison than for the paired burrow comparison. The affect of mulch density varied with distance from the burrow but owl activity may account for some of this difference because the vegetation closer to the nest entrance had been trampled due to owl activity.

Random locations at Carrizo had a lower density of potential satellite burrows or perches compared to nest sites. Owls nested in areas that provided them with a greater probability of finding more burrows and ones with a larger diameter. Selecting for availability of many potential satellite burrows and the ubiquitous use of satellites (see discussion on experimental results) may be beneficial for predator evasion.

I observed only a small effect of having more perches present but having at least one perch may be enough to provide an advantage in detecting predators and aiding foraging ability. Green and Anthony (1989) found that perches were important for burrowing owls nesting in areas where average vegetation height was > 5 cm. At Carrizo, the density of vegetation was generally low during 1999 and

2000, therefore the need for perches may not have been as important and thus selection for perches would not be as detectable or prominent.

Habitat selection by animals existing in low densities may be influenced by allee effects (Fretwell and Lucas 1970, Greene and Stamps 2001). At low to moderate population densities, individual fitness may increase as a function of density (Allee effect) and clumped distributions can result (Greene and Stamps 2001). Animals facing high predation risk may benefit by settling near conspecifics. This has been suggested for burrowing owls and may explain their sometimes clumped distribution (Desmond et al.1995). The distribution of nests at Carrizo exhibit a somewhat clumped distribution yet the nests are at low density (1.0 pairs / km2; Rosenberg et al., unpubl. data). The importance of the rodent index on productivity and the large mean nearest neighbor distances suggests that the distribution is based on competitive costs and distribution of burrows.

Reproductive Success

When burrowing owl nests were successful, productivity appeared to be influenced by the higher proportion of rodents in the diet. Raptors show a marked variation in the production of young and the weight and survival of fledglings in response to food supply (Newton 1998). Korpimaki (1992a, 1992) found that abundant rodent prey was related to the positive reproductive success of long-eared

owls (*Asio otus*) and determined the lifetime reproductive success of male

Tengmalm's owls (*Aegolius funereus L.*). In grasslands, burrowing owls forage on a

diversity of vertebrate and invertebrate taxa (Thomsen 1971, Haug et al. 1993).

Rodents are an important diet component because they often provide a greater

biomass than smaller invertebrates (Gleason and Johnson 1985, Silva et al. 1995)

and may be an important protein source, especially during the breeding season

(Williams 1996, Wellicome 1997). Also, healthier young have a greater chance of

avoiding predators because nutritional state can influence predation risk; when food

is scarce individuals become less vigilant, allowing predators to approach closer

(Newton 1998).

Because vegetation can affect prey movements and an owl's ability to detect

prey (Bechard 1982, Rich 1986, Green and Anthony 1989), sparse vegetation

potentially influenced burrowing owl productivity. At Carrizo, annual plants

respond to winter moisture with thick growth. Rainfall varied greatly during the

study period (1998 = ~ 76 cm, 1999 = ~ 13 cm, 2000 = ~ 21 cm; BLM, Bakersfield,

California, unpubl. data) which influenced the vegetative character of the area.

Also, during 1999 - 2000, the number of cattle in pastures was increased. The

combination of low rainfall and the increased grazing pressure after 1998 likely

contributed to the low variability in vegetative characteristics across Carrizo and the

generally low vegetation density and height during 1999 and 2000, which

potentially positively influenced foraging ability for the owls.

The habitat variables I tested did not explain nest success or productivity when both failed and successful nests were evaluated. Differing predation risks may be acting upon two nesting stages such that variation between the stages may be too complex to describe using the variables I measured. Predation appears to be a cause of low nest success at Carrizo, with mammalian, avian, and reptilian predation being the most common cause of mortality. Most nest failures at Carrizo occur during the egg laying and incubation period and it is likely that predation risks differ between pre- and post-hatching. Eggs are more vulnerable to burrow-entering predators than young prior to fledging. For example, owls defend nests during the pre-hatching period against ground squirrels but tolerate ground squirrel presence after young emerge (pers. obs.). Perches may be important for the male because he functions as a nest sentry (Green and Anthony 1989) whereby he can detect and distract predators from the nest, a role that may be particularly important during the pre-hatching period. Similarly, greater golden-plovers (*Pluvialis apricaria*) were able to distract predators from nest sites when predators were detected early (Byrkjedal 1987). Finally, the death of a mate during the pre-hatching period results in nest failure yet if this occurs during the post-hatching period it is possible for a single adult to fledge young, especially if prey numbers are favorable. For example, during 1999, a year that represented the highest index of rodent consumption at Carrizo, I observed a "widowed" male fledge 7 young.

Nest Site Fidelity

Nest success has been documented to affect nest site fidelity for bird species (Calder et al. 1983, Dow and Fredga 1983, Reed and Oring 1993). Similarly, nest predation has been documented to elicit changes in re-nesting locations in birds, presumably to avoid subsequent predation (Shields 1984, Sieving and Willson 1998). Hakkarainen et al. (2001) found that male Tengmalm's owl exposed to an experimental predation risk displayed an increased shifting in nest holes and greater dispersal distances. Nest fidelity within the breeding season was highly correlated with nest success, therefore by re-nesting at different locations burrowing owls may be attempting to avoid further predation. Large dispersal distances following nest failure may also result in the lack of nest site fidelity. Dispersal distances for owls at Carrizo were documented to be between 0.2 - 53.0 km (median = 3.1 km; Rosier et al., in review). Because of the variation in nesting success between years and large dispersal distances occurring after nest failure, low site fidelity may be common in some years.

Satellite Burrow Access Experiment

Predation risk may be highest from the time of emergence of young from the nest and fledging because young are outside the burrow often but have a limited

ability to escape predation. At Carrizo, burrowing owls regularly use satellite burrows almost immediately after emergence, consistent with Desmond and Savidge (1999). This behavior may reduce the chance that all young are lost to predation (Desmond and Savidge 1999, 2000). For example, I observed that young moved to a satellite burrow approximately 75 m from the nest immediately following a predation event.

Detecting an effect of predation on the number of young that survive to fledging was difficult because the daily probability of predation occurring at nests was small. Owls in the treatment group responded by moving their families to areas with similar access to satellite burrows as the control group. This should result in a decrease in predation rates and demonstrates the importance of satellite burrows for predator evasion. The experimental manipulation of satellite burrow access demonstrated that burrowing owls will adjust their behavior to use sites with satellite burrows.

CONCLUSION

Identification of critical factors affecting reproductive success of burrowing owls in large grassland ecosystems is central to developing management strategies to protect these populations. This information contributes to the few studies conducted on the demography of the burrowing owl in undisturbed grassland environments (Green and Anthony 1989, Lutz and Plumpton 1997, Desmond et al. 2000).

This study suggests that burrowing owls select for habitat that provides large-diameter burrows, satellite burrow access, and perches, which may be important for predator detection and avoidance, and foraging efficiency in this grassland. Furthermore, results from the experimental manipulation of satellite burrow access shows that burrowing owls will adjust their behavior to use satellites and suggests that such behavioral tactics may be important for predator avoidance. Maintenance of burrowing mammal populations to provide nest and satellite burrows will be important for protecting burrowing owls in extensive grasslands. Also, in areas with limited burrow availability, these results may provide some guidance for artificial nest box installation (King and Belthoff 2001).

When both failed and successful nests were evaluated, the habitat variables I tested did not explain reproductive success, possibly due to complex processes influencing reproductive success at different nesting stages. The habitat

characteristics studied represent only a subset of potential breeding requirements for burrowing owls in a large grassland. Other criteria to consider include interior nest dimensions and micro-climate and individual differences among owls, such as breeding experience and hunting proficiency. Temporal dynamics of the Carrizo Plain ecosystem influenced burrowing owl reproductive success. When nests were successful, relative rodent consumption influenced productivity, though both the amount of rodents in the diet and productivity varied yearly. Habitat conditions that enhance foraging ability may benefit productivity, especially in years of low rodent numbers. Furthermore, temporal variation in nest success may lead to low nest site fidelity.

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