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Nest site characteristics and nesting success of the Western Burrowing Owl in the eastern Mojave Desert

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ABSTRACT

We evaluated nest site selection at two spatial scales (microsite, territory) and reproductive success of Western Burrowing Owls (*Athene cunicularia hypugaea*) at three spatial scales (microsite, territory, landscape) in the eastern Mojave Desert. We used binary logistic regression within an information-theoretic approach to assess factors influencing nest site choice and nesting success. Microsite-scale variables favored by owls included burrows excavated by desert tortoise (*Gopherus agassizii*), burrows with a large mound of excavated soil at the entrance, and a greater number of satellite burrows within 5 m of the nest burrow. At the territory scale, owls preferred patches with greater cover of creosote bush (*Larrea tridentata*) within 50 m of the nest burrow. An interaction between the presence or absence of a calcic soil horizon layer over the top of the burrow (microsite) and the number of burrows within 50 m (territory) influenced nest site choice. Nesting success was influenced by a greater number of burrows within 5 m of the nest burrow. Total cool season precipitation was a predictor of nesting success at the landscape scale. Conservation strategies can rely on management of habitat for favored and productive nesting sites for this declining species.

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1. Introduction

Nest site selection is a key component of avian habitat selection with significant consequences for survival and reproductive success (Cody, 1985). Nest site choices influence the probability of nesting success through such factors as predation, starvation, and competition (Martin, 1995). Avoidance of nest predation plays a significant role in nesting success and may be especially important for ground-nesting species (Martin, 1995). Western Burrowing Owls (*Athene cunicularia hypugaea*) nest in cavities in the ground and are the only North American raptor to do so. For this ground-nesting species, nest site selection factors that reduce predation may be pivotal for nesting success.

Burrowing Owls occur in a wide range of arid and semi-arid habitats in the western U.S. – prairie and annual grasslands, shrub-steppe, and deserts (Haug et al., 1993). They have also adapted to human landscapes including urban and agricultural areas (Haug et al., 1993). Studies examining nest site selection and reproductive success of Burrowing Owls have been conducted in prairie grassland, shrub-steppe, agricultural, and urban environments (Desmond and Savidge, 1999; Green and Anthony, 1989; Lantz et al., 2007; Lutz and Plumpton, 1999; Rich, 1986; Rosenberg and Haley, 2004; Thomsen, 1971; Wellicome et al., 1997). A few studies have been conducted on desert populations; most of these have occurred in grassland habitat in the Chihuahuan Desert of New Mexico and Mexico (Botelho and Arrowood, 1998; Martin, 1973; Rodriguez-Estrella, 1997). However, little information is available on Burrowing Owl populations in natural desert scrub habitat, such as that characteristic of the Mojave Desert. With documented population declines and range contractions occurring at northern, eastern, and western boundaries of Burrowing Owl range, estimates of nest site selection and nesting success (number of nesting attempts that produce fledged young) are essential for understanding owl population dynamics (Haug et al., 1993).

Scale is a critical component of the patterns and processes of ecological studies, including avian habitat selection (Cody, 1985; Wiens, 1989). Concentration of studies at one scale can result in the loss of information when factors influencing populations occur at multiple scales (Wiens, 1989). Studies on Burrowing Owls have identified a number of variables, at multiple scales, that influence nest site selection (Lantz et al., 2007). At the microsite, Burrowing Owls select for open ground, well-drained soils, and reduced vegetation surrounding the burrow (Green and Anthony, 1989; MacCracken et al., 1985). The presence of additional burrows

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adjacent to nest sites is important for establishment of territories (Desmond et al., 2000; Plumpton and Lutz, 1993; Poulin et al., 2005). At the landscape scale, flat or rolling terrain (Butts and Lewis, 1982) and the habitat matrix surrounding nest sites (Orth and Kennedy, 2001; Poulin et al., 2005) are important determinants. We investigated factors influencing nest site selection and nesting success at three spatial scales (i.e., microsite, territory, and landscape) in an eastern Mojave Desert population of Burrowing Owls.

2. Methods

2.1. Study area

We conducted our study at Lake Mead National Recreation Area (LMNRA; 36° 10′ N, 114° 40′ W) in the Mojave Desert of southern Nevada (2003–2005). Our study area included the Nevada portion of LMNRA west of Lake Mead and the Colorado River. LMNRA is located in the eastern Mojave Desert region of the Basin and Range physiographic province (Eaton, 1982). Local topography varies from steep mountain ranges with deep washes to rolling and gently inclined alluvial fans and valley basins. Elevations range from 160 m to 2100 m. Mean monthly temperature is 6.8 °C in January and 33.3 °C in July, with an annual bimodal precipitation cycle of <12.5 cm falling as cool season winter precipitation (74%) and mild monsoonal summer thunderstorms (26%). Precipitation patterns are highly variable both seasonally and annually. Average annual precipitation for the three years of this study (2003–2005) was 22.6 cm ± 1.93 cm, well above mean annual precipitation for the eastern Mojave Desert (National Oceanic and Atmospheric Administration, 2008). Sonora-Mojave creosote bush-white bursage desert scrub association (*Larrea tridentata-Ambrosia dumosa*; Turner, 1982) was the most widespread and dominant vegetation type. This association occurs on bajada slopes and basin floors and contains low perennial species diversity and a high diversity of annual species that germinate during years of increased precipitation.

2.2. Survey methods

We focused our surveys on the breeding season for Burrowing Owls in the eastern Mojave Desert; timing and other survey considerations were designed to increase detectability of the owls (Crowe and Longshore, 2010). We used Hawth's tools© extension within ArcMap software (ArcMap 9.3; Environmental Systems Research Institute, Redlands, California 2008) to create random transects throughout our study area and spatially separated transects by a minimum distance of 3.2 km. We constrained random transects to areas with slope less than 25% (Haug et al., 1993). We conducted our surveys at night because owls call primarily during nocturnal hours. We conducted surveys on-foot beginning immediately after dusk (within 30 min) for approximately 3–4 h from 20 February to 31 July, 2003–2005. We surveyed during breeding stages when owls were more apt to vocalize which included territory establishment, pair formation, egg laying, and incubation (Clark and Anderson, 1997). In addition, we conducted surveys during brood-rearing and fledgling-dependency stages thereby surveying during the entire breeding season for our study site. Each survey (sampling unit) consisted of a transect 3.2 km in length with 5 point count stations spaced 800 m apart. We played recorded Burrowing Owl primary song and alarm calls during surveys to increase detection rates (Haug and Didiuk, 1993). At each station, we conducted a point count which included a 3-min passive listening session which was followed by a 3-min owl call-broadcast session (Conway and Simon, 2003). We broadcast vocalization sequences using a cassette player which was held approximately 2 m above the ground and rotated in the four cardinal directions. Broadcast volume was adjusted between 80 and 90 db at 1 m from the cassette speaker and measured using a sound-level meter set on slow response and C weighting (Andersen, 2007). Each transect was conducted once per breeding season. We did not conduct surveys when average wind speeds were >19 km/h or when rainfall was moderate to heavy.

2.3. Nest site selection

We collected data on nest site characteristics at nest and non-nest burrows at two spatial scales: nest microsite and territory patch (Table 1). We established non-nest burrows by walking random orientations from a nest burrow searching a 50-m wide transect. Burrowing Owls in the Mojave Desert do not dig their own burrows and rely on burrows previously excavated by either the desert tortoise (*Gopherus agassizii*) or kit fox (*Vulpes macrotis*). We measured the first burrow excavated by kit fox or desert tortoise found on these random searches as a non-nest burrow. We restricted non-nest burrows to those burrows that owls might reasonably be expected to use, thereby reducing the likelihood that we would find trivial differences between nest and non-nest burrows. We did not include older burrows with blocked or collapsed entrances or simply holes without an associated tunnel dug into the ground by foraging kit foxes and coyotes (<0.5 m deep). In order to

Table 1
Nest site variables measured at multiple spatial scales used in our study of nest site selection and nesting success for Burrowing Owls at Lake Mead National Recreation Area (LMNRA), southern NV, 2003–2005. Categorical variables included burrow type, calcic layer, slope, and soil mound size. Variable description indicates which category was coded as 0 or 1.

Variable	Code	Description
Microsite		
Burrow type	type	Burrows excavated by a desert tortoise (1) versus a kit fox (0)
Height of soil mound	soil	Size of soil mound outside burrow entrance; results from the excavation process; coded 0 for no or small mound (≤7 cm); coded 1 for large mound (>7 cm)
Calcic horizon	calcic	Burrows excavated beneath a calcic soil horizon layer (1) or absence of calcic layer (0)
Slope	slope	Burrows excavated within the slope of a wash or topographic ridge (1) versus level ground (0)
Satellite burrows	b5m	Number of alternative burrows within ≤5 m of the burrow
Territory		
Satellite burrows	b50m	Number of alternative burrows >5 m and ≤50 m from the burrow
Creosote bush cover	larcov	Cover of *Larrea tridentata* measured as linear cover of this shrub along three 50 m line transects radiating from the burrow (m)
Subshrub cover	shrbcov	Cover of perennial subshrubs (e.g., *Krameria grayi*, *Ambrosia dumosa*) measured as linear cover of these shrubs along three 50 m line transects radiating from the burrow (m)
Topography	topo	Visual assessment of the topography within 250 m of the burrow, estimation based on wash height; wash height <1 m (0), wash ≥ 1 m and <2.5 m (1), wash ≥ 2.5 m and <5 m (2), wash ≥ 5 m (3).
Landscape		
Total cool season precipitation	totppt	Amount of precipitation recorded at LMNRA at three sites along the lower Colorado River during the previous winter and the following spring of each nesting season including Oct–Mar (cm).
Distance to nearest road	disroad	Distance from nesting burrow to closest road, paved or unpaved (m).

prevent overlap between measured burrows, all measured burrows were spaced >100 m apart. Non-nest burrows were located <600 m from any nest burrow so they fell within a nesting territory (Gervais et al., 2003; Haug and Oliphant, 1990). We inspected non-nest burrows for signs of owl occupation which would identify present or past use; these burrows were not included as non-nest burrows. Owl sign of previous occupation included regurgitated pellets, excrement ("whitewash"), owl feathers, nest decoration and debris, and remains of disintegrated pellets (mammalian bones or insect exoskeletons). We defined microsite-scale variables as those measured ≤5 m from the nest burrow. We defined an owl nesting territory as the area containing an occupied burrow within the home range of an owl pair (Steenhof and Newton, 2007). Home range estimates from burrowing owl literature are identified as an average of 2.4 km^2 (Haug et al., 1993). Territory-scale characteristics were measured at distances of ≤600 m from the nest burrow (based on Gervais et al., 2003; Haug and Oliphant, 1990). Landscape-scale variables included those measured at distances >600 m from the burrow. We collected data after the young dispersed from nest burrows.

Nest site characteristics were selected based on both previous research and variables we predicted would be important to owls in the Mojave Desert (Haug et al., 1993). We predicted that microsite-scale characteristics would be important because Burrowing Owls nest in secondary cavities excavated by other fossorial species and available nest burrows may be limited (Holmes et al., 2003). We assigned each burrow measured to one of the two types using the distinctive burrow configuration of the desert tortoise (half moon shape entrance with gradually descending tunnel) and kit fox (circular entrance with abrupt turn or drop in tunnel). We defined potential satellite burrows as burrows located near the nesting burrowing. Satellite burrows are used for roosting throughout the nesting season by adults and young (Haug et al., 1993). We restricted the number of adjacent burrows to 5 m assuming this was a distance at which emergent young could easily escape to alternative satellite burrows (Butts and Lewis, 1982). During observation of nests, we tested this assumption by recording distances that emergent young moved away from the nest burrow during the first two weeks post-fledging. Fledging for Burrowing Owls is defined as the first time young emerge from the burrow and spend time at or near the nest above ground. We observed in previous studies that nest burrows contained at least a small mound of excavated soil in front of the burrow entrance. Therefore, we measured soil mound size to see if it influenced nest choice. A calcic layer is a well-developed soil horizon common in arid and semi-arid regions formed by the gradual precipitation of calcium carbonate, and possibly magnesium carbonate, into a hardened deposit. We investigated whether owls selected for nest burrows with a calcic layer over the top of the burrow predicting that a calcic layer would provide burrow stability and therefore burrow longevity. Long-term use of burrows may result in familiarity with a burrow site thereby increasing successful nesting (Botelho and Arrowood, 1998; Holmes et al., 2003; Lutz and Plumpton, 1999). We investigated the influence of slope on nest selection, predicting that burrows on slopes would have increased visibility to predators and therefore reduced nesting success.

For territory analysis, we confined our count of potential satellite burrows to those within a 50-m radius from the nest, which captures the distance adults and flying young could easily escape to satellite burrows and the distance at which a majority of nesting activity occurs (Haug and Oliphant, 1990). We measured distances at which adult owls consistently perched to establish vigilance locations near nest burrows. We measured perennial cover (m) of creosote bush and subshrubs as the linear intercept of these shrubs along three 50-m line transects radiating out from each burrow. Estimates of perennial cover were confined to a 50-m radius based on average distance a majority of nesting activities occur (Haug and Oliphant, 1990). We conducted a visual assessment of the topography of the territory within 250 m of the burrow. Our topography index was designed to capture differences in wash topography (number and depth) occurring near nest burrows. Desert dry washes contain a greater density and diversity of plant and animal species which would include predators of Burrowing Owls (Brown, 2004; Jorgensen et al., 1995). Based on this information, we assumed that more predators would occur within areas of increased topography in desert washes and this may influence burrow selection.

Our topographic index was determined by visual estimation of wash height along two 250-m transects radiating from the burrow and oriented perpendicular to local wash terrain (wash height <1 m = 0, wash height ≥ 1 m and <2.5 m = 1, wash height ≥ 2.5 m and <5 m = 2, wash height ≥ 5 m = 3). All wash heights were summed to produce the topographic index.

2.4. Nesting success

Since individuals should prefer nest sites that increase reproductive potential, we examined whether the nest site characteristics selected by owls influenced reproductive success, measured as apparent nest success. In addition to the microsite and territory characteristics selected by owls, we examined the influence of two landscape-scale variables on nesting success – total cool season precipitation (i.e., winter precipitation, Oct–Mar) and the distance of a nest burrow from the nearest road.

We calculated apparent nest success as the number of successful nests divided by the number of nesting attempts (Steenhof and Newton, 2007). We defined a nesting attempt as the observation of a pair of owls at an occupied burrow ≥2 times during the nesting season (Garcia and Conway, 2009). We monitored all occupied burrows (single owl or owl pair) at least weekly during the nesting season to determine nesting stage, timing of young above ground, and nesting outcome. We monitored burrows using both observations from a blind and inspection of the area around the burrow entrance to determine if there were nestlings. For example, at night we inspected burrows for caches of prey items left near the entrance which suggested that the male was out hunting for a brood. And from blinds, we watched for adults carrying prey items into the nest burrow. Once nestlings were detected, we watched for clues that young were above ground and 21–28 d post-hatch. To eliminate bias in estimating nesting success related to unequal observation effort and differences in sighting probabilities, we determined apparent nest success using an established nest monitoring protocol for Burrowing Owls (Gorman et al., 2003). This protocol evaluates maximum number of young counted during 30-min observation periods when young are 21–28 d post-hatch based on feather development and behavior (Priest, 1997). We monitored nests when young were most easily observed (i.e., when young are active above ground, but remain close to the nest burrow), which at our site was approximately late May to late June. We defined a successful nest as one with ≥1 young observed during the brood-rearing stage when young were 21–28 days post-hatch (Rosenberg and Haley, 2004; Steenhof and Newton, 2007). We observed nests with binoculars or spotting scopes at a distance of 80–120 m using blinds.

2.5. Statistical analysis

We used Pearson's χ^2 tests for assessing apparent nest success among years and between nest burrow types. For nest site selection, we used binary logistic regression (Hosmer and Lemeshow,

2000) to model the relationship between nest site characteristics (explanatory/independent variables) and a dichotomous dependent variable (Manly et al., 1993). The dependent variable consisted of nest burrows (used habitat) and an equal number of non-nest burrows (unused but available burrow sites). A number of burrows were reoccupied over the course of our study. Burrows that were used multiple years were only included once in the nest site analysis. For analysis of nesting success, we used binary logistic regression to assess those nest site variables preferred by Burrowing Owls (i.e., nest site choices identified in our nest selection analysis). We modeled the relationship between those explanatory variables and the dichotomous dependent variable, nesting success, using successful nest burrows ($n = 37$) and unsuccessful nest burrows ($n = 20$).

We developed alternative logistic regression models to identify the best combination of factors that would predict both nest site choice and nesting success by Burrowing Owls. We used Akaike's information criteria adjusted for small sample size (AIC_c) for model selection (Burnham and Anderson, 2002). The log-likelihood estimates from each of the alternative logistic regression models were used to determine AIC_c and ΔAIC_c values. We used the AIC_c differences to rank the set of candidate models. We present approximating models with ΔAIC_c of ≤ 2 as possible competing models. We used Akaike weights (w_i) and evidence ratios to assess the relative strength of evidence for each model. We used the β values and odds ratios from our logistic regression analysis to evaluate the strength of each nest site variable from the best approximating models. Analyses were conducted using SYSTAT statistical software version 11.0 (SYSTAT Software, Inc. Chicago Illinois 2004). We report values as mean $\pm$ 1 standard error and we considered statistical results significant at $\alpha = 0.05$.

3. Results

3.1. Nest site selection

We sampled an area of 231 km^2 over the three year period at LMNRA. We located 56 territories during 70 surveys and measured nest site characteristics at 37 unique nest sites and 37 non-nest burrows (Table 2). We evaluated 11 nest burrows in 2003, 7 nest burrows in 2004, and 19 nest burrows during 2005.

AIC analysis revealed two nest site selection models well supported by the data ($\Delta AIC_c \leq 2$, Table 3). The best approximating and most parsimonious model explaining variation in nest site selection ($w_i = 0.385$) included burrow type, soil mound size, calcic layer, burrows within 5 m, burrows within 50 m, creosote bush cover, and an interaction between calcic layer and burrows within 50 m. This model correctly classified 76% of burrows. The second most plausible model ($w_i = 0.168$) included an additional variable of slope. Based on the weight of evidence, model 1 was 2.3× more likely to be the best approximating model than model 2. Other alternative models had increasing ΔAIC_c values and ever-decreasing support. The global model included burrow type, slope, soil mound, calcic layer, burrows within 5 m, burrows within 50 m, creosote bush cover, subshrub cover, local topographic index, and several interactions (type*soil mound size, burrows within 5 m*burrows within 50 m, and calcic*burrows within 50 m).

The best supported model (Table 4) indicated that owls chose burrows with larger soil mounds and selected desert tortoise over kit fox burrows. Owls preferred nest sites with a greater number of potential satellite burrows within 5 m and a greater amount of creosote bush cover within 50 m. In addition, nest site choice was influenced by an interaction between calcic layer and the number of burrows within 50 m. In our study area, two types of habitat patches were possible within an owl's territory. One was characterized by a series of parallel dry wash drainages and the other by relatively flat, alluvial fans with few wash drainages. Generally, there were a greater number of available burrows in wash drainages. In wash drainages, burrow choice was not influenced by presence of a calcic layer. When owls selected burrows on flat alluvial fans, they strongly preferred burrows without a calcic layer.

The occurrence of a larger soil mound increased the odds of a burrow being selected by an owl pair 72× over a burrow with a smaller soil mound. A burrow that was originally excavated by a desert tortoise had 10× greater odds of being selected over a burrow excavated by a kit fox. For each additional potential satellite burrow within 5 m of a burrow, the odds of a burrow being preferred increased by 2.5 times. For every meter increase in creosote bush cover within 50 m of a burrow, the odds of a burrow being selected increased by 22%. Nest site selection probabilities were best explained by a model that accounted for differences in burrow type, soil mound size, potential satellite burrows within 5 m, creosote bush cover, and an interaction between calcic layer and potential satellite burrows within 50 m.

3.2. Nesting success

Nesting success was monitored for 58 nesting attempts at 37 unique nest sites. Seventeen of the nest burrows (46%) were used during multiple years. Apparent nest success was 54.5% $\pm$ 15.7% ($n = 11$) for 2003, 61.1% $\pm$ 12.2% ($n = 18$) for 2004, and 69.0% $\pm$ 8.7% ($n = 29$) for 2005. We did not find a statistically significant difference among the three years (Pearson's $\chi^2 = 1.155$, df = 2, $P = 0.561$). Owls nested on average 842 m $\pm$ 71 m ($n = 58$, range 214–1475 m) from the nearest road which in most cases (95%) were unpaved. We found that average distance to a satellite burrow within 5 m of a nest burrow was 2.9 m $\pm$ 0.2 m ($n = 48$). Owls stood under a shrub nearest their nest burrow at an average distance of 0.81 m $\pm$ 0.05 m ($n = 37$). Males perched atop creosote bushes an average of 7.9 m $\pm$ 1.2 m ($n = 78$) from the nest burrow. Average distance at which fledged young stood outside the nest burrow entrance was 3.9 m $\pm$ 0.1 m ($n = 37$). When owls nested in tortoise burrows, 63% ($n = 49$) were successful; when they nested in kit fox burrows, 75% ($n = 8$) were successful. However, apparent nest success was not statistically different between the two burrow types (Pearson's $\chi^2 = 0.709$, df = 1, $P = 0.401$).

A preference for a greater number of potential satellite burrows within 5 m was the best determinant of nest burrow success. Several nest site characteristics preferred by Burrowing Owls, in

Table 2
Mean and standard error (SE) for nest site characteristic measured for the logistic regression analysis determining the probability of Burrowing Owls choosing a burrow at Lake Mead National Recreation Area, Nevada (2003–2005). Explanatory variables include: type = desert tortoise excavated burrow (1) or kit fox excavated burrow (0); slope = wash or ridge slope (1) or flat terrain (0); calcic = presence (1) or absence (0) of a calcic layer over top of burrow; soil = soil mound height ≤7 cm (0) or height >7 cm (1); number of additional burrows within 5 m (b5m), number of additional burrows within 50 m; creosote bush cover (larcov); perennial subshrub cover (shrbcov), and index of topographic relief (topo). Refer to Table 1 for detailed descriptions of burrow site characteristics.

Burrow characteristic	Nest burrow ($n = 37$)	Non-nest burrow ($n = 37$)
Type	0.78 (0.07)	0.46 (0.08)
Slope	0.87 (0.06)	0.60 (0.08)
Calcic	0.49 (0.08)	0.32 (0.08)
Soil	0.92 (0.15)	0.43 (0.07)
B5m	1.54 (0.23)	0.54 (0.18)
B50m	5.41 (1.10)	1.89 (0.42)
Larcov (m)	10.50 (0.71)	9.61 (0.66)
Shrbcov (m)	7.74 (0.73)	8.74 (0.98)
Topo	15.05 (1.50)	12.78 (1.28)

Table 3
Comparison and relative ranking of top candidate models assessing microsite- and territory-scale nest site selection (burrows) for Burrowing Owls at Lake Mead National Recreation Area, Nevada (2003–2005), with log-likelihood values, number of estimable parameters (k), AIC_c values, delta AIC_c values, and Akaike weights (w_i) provided for each model. Explanatory variables included burrow type (type), slope, soil mound size (soil), presence or absence of a calcic layer (calcic), number of additional burrows within 5 m (b5m), number of additional burrows within 50 m (b50m), creosote bush cover (larcov), perennial subshrub cover (shrbcov), and local topographic relief (topo). Relative ranking of models was determined using Akaike's Information Criteria differences (ΔAIC_c).

	Model[a]	−2logL	k	AIC_c	ΔAIC_c	w_i
1	Type + soil + calcic + b5m + b50m + larcov + calcic*b50m	53.322	9	74.1345	0	0.3849
2	Type + slope + soil + calcic + b5m + b50m + larcov + calcic*b50m	52.306	10	75.7981	1.66	0.1675
3	Type + soil + b5m + b50m + larcov	60.674	7	76.3710	2.24	0.1258
4	Type + soil + calcic + b5m + b50m + larcov	58.406	8	76.6214	2.49	0.1110
5	Type + soil + b5m + b50m	63.376	6	76.6298	2.50	0.1105
6	Type + soil + b5m + b50m + larcov + shrbcov	60.022	8	78.2374	4.10	0.0495
7	Type + soil + calcic + b5m + b50m + larcov + b5m*b50m	58.400	9	79.2125	5.08	0.0304
8	Type + slope + soil + b5m + b50m + larcov + shrbcov	59.920	9	80.7325	6.60	0.0142
9	Global model	51.312	14	86.4306	12.30	0.0008

[a] Top 8 models ($\Delta AIC_c < 7$; $w_i > 0.01$) and global model presented.

particular burrow type, soil mound size, and creosote bush cover, showed little difference between successful and unsuccessful nests (Table 5). AIC evaluation revealed three best approximating models with substantial support ($\Delta AIC_c \leq 2$, Table 6). The best approximating model ($w_i = 0.340$) included number of burrows within 5 m and total cool season precipitation. This model correctly classified 60% of burrows. The next best model ($w_i = 0.252$) included number of burrows within 5 m, total cool season precipitation, and distance to the nearest road. The third best model ($w_i = 0.166$) included number of burrows within 5 m and burrow type. Weight of evidence ratios showed that model 1 was 1.3× more plausible than model 2 and 2.1× more plausible than model 3. The global model included burrow type, soil mound size, calcic layer, burrows within 5 m, creosote bush cover, total cool season precipitation, distance to nearest road, and three interactions (calcic layer*burrows within 50 m, total cool season precipitation*creosote bush cover, burrow type*distance to the nearest road).

For each potential satellite burrow within 5 m of a nest burrow, there was a 1.9× greater odds of a nest burrow being successful (Table 7). For every one-cm increase in precipitation the odds of a burrow being successful increased by 9%. Number of satellite burrow within 5 m was a strong predictor of nesting success for all of the best approximating models (Table 7).

Table 4
Parameter estimates (β), standard errors (SE) of the estimates, odds ratios, and 95% confidence intervals (CI) for odds ratios for best approximating model for Burrowing Owl nest site selection at Lake Mead National Recreation Area, southern Nevada (2003–2005). Nest site characteristics included soil mound size (soil), burrow excavator species (type), presence or absence of a calcic layer over top of burrow (calcic), number of additional burrows within 5 m (b5m), number of additional burrows within 50 m (b50m), creosote bush cover (larcov), and an interaction between calcic layer and burrows within 50 m.

Effect	β	SE	Odds ratio	95% CI
Soil	4.28	1.43	72.40[a]	4.4–1191.0
Type	2.31	0.95	10.08	1.58–64.4
Calcic	−3.05	1.31	0.05	0.01–0.62
B5m	0.92	0.34	2.51	1.28–4.91
B50m	−0.14	0.21	0.87	0.58–1.32
Larcov	0.20	0.10	1.22	1.01–1.47
Calcic*b50m	0.66	0.32	1.94	1.03–3.65
Calcic (0)[b]	−3.05	1.31	0.05	0.01–0.62
Calcic (5)	0.26	0.38	1.29	0.14–11.9
Calcic (10)	3.56	4.46	35.18	0.28–4376.5

[a] Large odds ratio is the result of difference in the proportion of nest (92%) and non-nest (43%) burrows with large soil mounds and other variables in model interacting and accentuating its effect. Univariate logistic regression model for soil mound showed $\beta = 2.70$ (SE 0.69), odds ratio = 14.88 (95%CI 3.9–57.3).
[b] Calcic layer effect evaluated at three b50m values (0, 5, 10 burrows).

4. Discussion

4.1. Nest site selection

Size of the soil mound at the entrance to a burrow was the most important microsite characteristic selected by owls. All nest burrows measured were associated with at least a small mound outside the entrance. Adult owls may increase their chances of survival or survival of their young by targeting burrows with larger mounds. A large mound may be an important cue indicating a burrow with a greater amount of soil removed, thereby signaling the presence of a longer tunnel and/or larger nest chamber. Presumably, a longer tunnel would reduce access by predators (e.g., coyote) by providing an increased distance between predators and parents defending their eggs and young (Smith and Belthoff, 2001). Alternatively, owls often stand guard just outside the burrow entrance (Butts and Lewis, 1982) and they may be less conspicuous standing adjacent to a larger mound thereby increasing adult survival through predator avoidance.

Although other burrow types were available at our study site, e.g., antelope ground squirrel (*Ammospermophilus leucurus*), Merriam's kangaroo rat (*Dipodomys merriami*) and desert kangaroo rat (*Dipodomys deserti*), Burrowing Owls only choose nest burrows constructed by either desert tortoise or kit fox. When choosing between these two excavators, owls preferred desert tortoise over kit fox burrows. Selection of desert tortoise burrows may be associated with burrow quality. Studies have shown that tortoises move between breeding season and winter burrows thereby providing a number of alternative burrows with long-term use and maintenance by tortoises (Woodbury and Hardy, 1948). Nesting burrows

Table 5
Means and standard errors (SE) for explanatory variables measured at successful and unsuccessful Burrowing Owls nests at Lake Mead National Recreation Area, Nevada (2003–2005). Nest site characteristics selected included four microsite-scale variables: number of burrows within 5 m (b5m); type = desert tortoise (1) or kit fox (0) excavated burrow; soil mound height ≤7 cm (0) or height >7 cm (1); and calcic = presence (1) or absence (0) of calcic layer. A territory-scale variable selected by the owls included creosote bush cover (larcov). Landscape-scale variables were total cool season precipitation (totppt) and distance to nearest road (disroad).

Variable	Successful burrow ($n = 37$)	Unsuccessful burrow ($n = 20$)
B5m	1.97 (0.22)	1.43 (0.31)
Type	0.84 (0.06)	0.86 (0.08)
Soil	0.89 (0.05)	0.91 (0.07)
Calcic	0.57 (0.08)	0.43 (0.11)
Larcov (m)	9.86 (0.58)	10.05 (0.90)
Totppt (cm)	22.66 (1.93)	20.29 (2.64)
Disroad (m)	842.4 (71.1)	677.2 (81.4)

Table 6
Comparison and relative ranking of candidate models for Burrowing Owl successful and unsuccessful nest burrows at Lake Mead National Recreation Area, NV (2003–2005) with log-likelihood values, number of estimable parameters (k), AIC_c values, delta AIC_c values, and Akaike weights (w_i) provided for each model. Nest site characteristics included burrow excavator type (type), soil mound size (soil), presence of a calcic layer (calcic), number of additional burrows within 5 m (b5m), creosote bush cover (larcov), total cool season precipitation (totppt), and distance to nearest road (disroad). Relative ranking of models was determined using Akaike's Information Criteria differences (ΔAIC_c).

	Model[a]	−2logL	k	AIC_c	ΔAIC_c	w_i
1	B5m + totppt	66.630	4	75.2097	0	0.3395
2	B5m + totppt + disroad	64.920	5	75.8024	0.593	0.2524
3	Type + b5m	68.064	4	76.6437	1.434	0.1657
4	Type + b5m + totppt	66.502	5	77.3844	2.145	0.1144
5	Type + soil + b5m + totppt	66.346	6	79.5997	4.390	0.0378
6	Totppt + calcic + disroad	69.588	5	80.4704	5.261	0.0245
7	Type + b5m + larcov + totppt + totppt*larcov	65.366	7	81.0630	5.853	0.0182
8	Totppt	72.992	3	81.5717	6.362	0.0141
9	Type + soil + b5m + larcov + totppt	66.334	7	82.0310	6.821	0.0112
10	Global model	59.642	12	88.7568	13.547	0.0004

[a] Top 9 models ($\Delta AIC_c < 7$; $w_i > 0.010$) and global model presented.

that require less modification would reduce energy costs associated with less suitably configured burrows (Butts and Lewis, 1982; Poulin et al., 2005).

Contrary to other studies, which have shown a consistent association between nest site selection and reduced cover and height of vegetation surrounding nest sites (Green and Anthony, 1989; MacCracken et al., 1985; Plumpton and Lutz, 1993), we found that greater cover of creosote bush surrounding the nest site was a predictor of nest site choice. This preference probably reflects differences in vegetation structure between other owl habitats (e.g., prairie dog towns in grasslands) and desert scrub habitat. Mojave Desert scrub habitat is generally characterized by less than 30% vegetation cover and consists of sparsely occurring shrubs with large intervening open areas. Because intervening areas at our study site are so open, owls may not need to select for reduced cover around the burrow as they do in grasslands or sagebrush habitats. Green and Anthony (1989) identified perches as a limiting resource for Burrowing Owls in grassland habitat. At our study site, male owls spent a majority of the breeding season either standing guard within the nest entrance, under a shrub located <1 m from the burrow entrance, or perched substantially higher on a creosote bush at an average distance of <10 m from the nest burrow. A greater number of creosote bushes adjacent to the nest may provide a greater number of perches from which to scan the area immediately surrounding the nest burrow, aiding in both defending nest sites and optimizing prey acquisition (Green and Anthony, 1989; Schmutz, 1997).

Our study identified nest site choices made by Burrowing Owls at multiple spatial scales, thereby demonstrating the hierarchical nature of nest site selection (Wiens, 1989). Although owls selected nest features at two different spatial scales; selection was also influenced by an interaction between spatial scales (i.e., microsite and a territory scale). Differences in the number of potential satellite burrows within 50 m of a burrow, a territory-scale variable, modified the choice of a microsite variable, presence of a calcic layer over the top of a burrow. When owls settled in a territory patch of flat terrain without dry wash drainages, they clearly avoided burrows with a calcic layer. Conversely, when owls settled in a territory patch consisting of several drainages, they chose burrows without respect to calcic layer. Burrows with a calcic layer in relatively flat alluvial fans may not have the necessary nesting site characteristics (e.g. burrow construction) favored by owls.

Table 7
Parameter estimates (β), standard errors (SE) of the estimates, odds ratios, and 95% confidence intervals (CI) for the odds ratios for the best approximating model and two closely competing models ($\Delta AIC_c < 2$) for Burrowing Owl nesting success at Lake Mead National Recreation Area, NV (2003–2005). Explanatory variables include number of burrows within 5 m (b5m), total cool season precipitation (totppt), distance to nearest road (disroad) and burrow excavator type (type).

	ΔAIC_c	Effect	β	SE	Odds ratio	95% CI
Model 1	0.000	B5m	0.633	0.28	1.88	1.09–3.27
		Totppt	0.084	0.07	1.09	0.95–1.24
Model 2	0.593	B5m	0.572	0.28	1.77	1.02–3.08
		Totppt	0.111	0.07	1.12	0.97–1.29
		Disroad	0.001	0.001	1.00	0.99–1.003
Model 3	1.434	B5m	0.567	0.27	1.76	1.04–2.98
		Type	−0.404	0.94	0.67	0.11–4.18

4.2. Nesting success

Our estimate of nesting success for owls using desert tortoise and kit fox burrows is similar to those found in larger burrows excavated by badgers (*Taxidea taxus*) in sagebrush habitat (50%–67%; Green and Anthony, 1989; Holmes et al., 2003) and by badgers (73%), desert tortoise (67%) and fox (73%) in the southern Chihuahua Desert grasslands of central Mexico (Rodriguez-Estrella, 1997). Although these studies provide information on desert grassland and sagebrush our results are the first reported for Burrowing Owls in desert scrub habitat of the Mojave Desert.

At the landscape-level scale, nesting success was influenced by total cool seasonal precipitation. The amount of precipitation during the three years of this study ranged from average to above average (National Oceanic and Atmospheric Administration, 2008). Weather variability can affect avian reproductive success especially in arid environments where breeding success is linked to precipitation (Curry and Grant, 1989; Preston and Rotenberry, 2006). Cool season precipitation is particularly important for the germination of winter annuals which are important food resources for prey species. An increase in precipitation has been associated with an increase in the numbers of both desert vertebrates and arthropods (Kenagy and Bartholomew, 1985; Wrege and Emlen, 1991), all of which are known prey items of Burrowing Owls during the nesting season (Hall et al., 2009).

Burrowing Owls at our study site selected for a greater number of alternative burrows adjacent to the nest burrow; this nest site choice best explained apparent nest success. Multiple studies on Burrowing Owl have found an association between nest site choice and a greater number of burrows surrounding nests at various distances but few have linked this selection with increased nesting success (Desmond and Savidge, 1999; MacCracken et al., 1985; Plumpton and Lutz, 1993; Poulin et al., 2005). Burrowing Owls are susceptible to many ground and aerial predators. Both coyotes (*Canis latrans*) and kit foxes are capable of digging up nest burrows (Wellicome et al., 1997). Avian species associated with predation on

Burrowing Owls include Red-tailed Hawks (*Buteo jamaicensis*), Prairie Falcons (*Falco mexicanus*), Peregrine Falcons (*Falco peregrinus*), and Great Horned Owls (*Bubo virginianus*) (Haug et al., 1993). All of these species were documented at our study site. Additional burrows close to a nest may be an important benefit for escaping predators, thereby increasing owl survival and reproduction (Desmond and Savidge, 1999; Holmes et al., 2003; Martin, 1973). In the closely related Little Owl (*Athene noctua*), Tomé et al. (2004) found that a large number of alternative cavities surrounding a nest site and lower predator presence emerged as important preferences in nest site selection. Alternative burrows relatively close to nest burrows may be particularly important when mortality is highest during the first two weeks after young fledge (Todd et al., 2003). Other factors that we were not able to address during this study, but that may affect reproductive success at individual burrows, include variation in quality of adult owls (e.g., differences in food provisioning rates), intraspecific and interspecific competition, and aspects of nest site quality (e.g., availability of food resources).

5. Conclusions

Our results show that nest site selection of Burrowing Owls in the Mojave Desert was influenced by environmental variables at several spatial scales. At the microsite scale, owls selected desert tortoise over kit fox burrows, large soil mounds outside the burrow entrance, and a greater number of satellite burrows. At the territory scale, owls selected for increased shrub cover. Nesting success was influenced by the number of satellite burrows at the microsite and amount of cool season precipitation across the landscape. Large soil mounds and a greater number of satellite burrows are common nest burrow features for most Burrowing Owl habitat. Selection for greater shrub cover at the nest burrow appears to be unique for the Mojave Desert.

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