A long-standing view of what constitutes burrowing owl (*Athene cunicularia*) nest habitat is the availability of numerous burrows nearby nest burrows, often called satellite burrows (Henny and Blus 1981, Desmond and Savidge 1999). Satellite burrows have been hypothesized or demonstrated to serve as escape cover for young (Martin 1973, Plumpton and Lutz 1993, Desmond and Savidge 1999, Ronan 2002), provide locations to cache prey (Lantz et al. 2007), reduce ectoparasite infestation (Garcia 2005), and reduce crowding in the nest chamber as the young owls grow (Green and Anthony 1997), which reduces carbon dioxide levels (e.g., Reichman and Smith 1990). Studies that report correlations between the number of burrows near nests and predicted that, compared to controls, 1) nest success would be lower, 2) more young would be killed by predators, and 3) access to satellite burrows would affect movement that would minimize vulnerability to predation.

**STUDY AREA**

We conducted the study from April to July 2000 at the Carrizo Plain National Monument (Carrizo), located on the eastern edge of the Coast Range approximately 80 km southwest of Bakersfield, California (119° W, 35° N). Carrizo
METHODS

We located burrowing owl nests using call playback surveys (Haug and Didiuk 1993, Conway and Simon 2003) in which we 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 to June between 1830 and 0230 hours (PST; Ronan 2002). To locate nests, we used bi-angulations of bearings taken on owls responding to a broadcast call. We checked previously occupied nests (1996–1999) for occupancy and searched the surrounding area (~100 m) for owls and signs of activity. We also found nests in the course of related fieldwork. Our sample included only nests for which it was known that a nest attempt had been initiated, which we determined through the observation of eggs via an infrared video probe (Sandpiper Technologies, Inc., Manteca, CA; Garcia and Conway 2009).

We randomly assigned 11 nests to control and 11 nests to treatment groups. The number of satellite burrows within 20 m of the nest was similar for control (17.0 ± 3.9 [mean ± 1 SE]) and treatment nests (17.5 ± 1.9) prior to manipulation. We used 1-way door excluders, similar in design to that described in Banuelos (1997) to block access to all satellite burrows within 20 m of treatment nests. The excluders had an outward swinging door made of hardware cloth with 0.63-cm mesh and were weighted at the bottom. The door was attached to either a large (46 cm × 46 cm) or small (31 cm × 31 cm) wire frame, both with 0.63-cm mesh that was secured around the burrow entrance. The excluders allowed animals present inside the burrow to exit but prevented owls from entering the burrow. We placed excluders without the 1-way doors at burrows in the control group such that the hardware cloth mesh surrounded the burrow entrance but owls could enter and exit the burrow. We placed excluders in burrows during the egg laying and incubation stage of nesting based on underground nest observations using the infrared video probe. To estimate nest success and productivity, we conducted 10 observations at each nest in 2000 from May to July until young were of fledging age, approximately 40 days post-hatch (Ronan 2002). We terminated observations once nest failure was confirmed.

We made observations using binoculars and spotting scopes from approximately 100–500 m from the nest, and between 0445 and 1900 hours. We waited 15 minutes prior to conducting observations to allow owls to acclimate to our presence. We then observed each nest for 30 minutes on 5 separate occasions (i.e., n = 5 nest observations per nest), separated by ≥5 hours but within 5 consecutive days during which we noted the maximum number of young seen (Gorman et al. 2003). We visited nests during mornings and evenings within approximately 5 hours after sunrise and 5 hours prior to sunset when young were most active outside of burrows (N. Ronan, Oregon State University, personal observation). We defined a successful nest as having ≥1 young survive to 40 days post-hatch. To estimate the reduction in the number of young that occurred between emergence from the nest until just prior to fledging, we estimated both pre-fledging and near-fledging productivity. We defined pre-fledging productivity as the number of young alive at 14–21 days of age and near-fledging productivity as the number of young alive at 32–40 days of age. We estimated age based on observations of developmental stage (Priest 1997).

We estimated burrowing owl nest success and productivity for successful and failed nests combined and successful nests only. We used logistic regression to test whether the probability of nest success differed between treatment and control nests. We used a 1-sided t-test to evaluate whether productivity and the reduction in the number of young alive between the time of emergence and near fledging was greater in the treatment group than the control group.

We visited nests twice per week until young were near fledging age to document whether nest resettlement occurred, that is, whether families moved prior to fledging from the natal nest burrow to a new central activity location and remained. To examine whether the probability of nest resettlement was greater for treatment nests than control nests we used a 1-sided Fisher’s exact test. We present mean (±1 SE) unless otherwise indicated. We received permits from the United States Fish and Wildlife Service Migratory Bird Permit Office (permit MB812316-0) and California Department of Fish and Game.

RESULTS

At all control nests, adults and young used satellite burrows regularly. Based on observations of roosting young owls at control nests, the majority (79%) of the time was spent within 20 m of their natal nest, but we observed young owls entering satellite burrows ≥50 m from the natal nest, approximately 5% of the time. We frequently observed owls enter satellite burrows soon after emergence at approximately 15 days post-hatch.

Nest success and productivity were similar between control nests and nests with their satellite burrows experimentally blocked. Six of 11 (55%) control nests and 5 of 11 (45%) treatment nests were successful (odds ratio = 0.69, 95%
CI = 0.13–3.72, \( P = 0.65 \)). Seven (63.6\%) nests in each group had young emerge but not all of these were subsequently successful; chicks died after emergence at 1 control nest and 2 treatment nests. The mean number of young/nest (control: 2.1 ± 0.7, treatment: 1.9 ± 0.7, \( P = 0.43 \)) and the mean number of young/successful nest (control: 3.8 ± 0.5, treatment: 4.2 ± 0.7, \( P = 0.35 \)) were similar between control and treatment groups. When both failed and successful nests were analyzed, we found little evidence for a difference in the mean reduction in the number of young that occurred between emergence from the nest until just prior to fledging between the groups (\( P = 0.36 \)). However, reduction tended to be greater for treatment nests when only successful nests were considered (\( P = 0.08 \); Table 1).

Although nest success and productivity were generally similar for treatment and control groups, nest resettlement differed substantially between groups. Nest resettlement involved the entire family, occurred before young had fledged, and owls did not return to the natal nest burrow. No nest resettlements were observed at control nests (\( n = 0 \) of 7 nests that had young emerge) compared to nest resettlement of 71\% at treatment nests (\( n = 5 \) of 7 nests that had young emerge; Fisher's exact test, \( P = 0.01 \)). The timing of nest resettlement among treatment nests varied, ranging from 2 to 16 days post-emergence (10.2 ± 2.8 days). Distances from the nest burrow to resettlement locations were relatively short (68 ± 18 m, range 25–120 m). Of the 2 treatment nests at which owls did not leave, young were observed roosting at blocked satellites on 2 occasions for only 1 nest; most young owls from treatment nests that did not resettle roosted at the natal burrow. All areas where burrowing owls moved their brood contained a large number of burrows, many of which we observed being used as satellite burrows.

**DISCUSSION**

At our study site, we observed young burrowing owls regularly using satellite burrows almost immediately after emergence. Most owls responded to the experimental blockage of satellite burrows by leaving the natal burrow. Prior to relocating, young owls roosted at the natal burrow and avoided blocked satellite burrows. After relocating, young owls used satellite burrows near the new primary burrow. Because almost all owls at treatment nests relocated to new areas, we were unable to test how the removal of satellite burrows affected reproductive rates. Rather, our results demonstrate that owls will often abandon the nest site when satellite burrows are not accessible.

Our study did not directly test hypotheses of how availability of satellite burrows affects nest site selection because nests were already established, but it did demonstrate that burrowing owls will relocate to nests when access to satellite burrows is blocked. This finding supports the conclusions from observational studies that burrowing owls select nest sites that have higher density of nearby burrows than non-nest sites (Plumpton and Lutz 1993, Desmond and Savidge 1999, Ronan 2002, Poulin et al. 2005, Lantz et al. 2007). The observational nature of the studies reporting a relationship of burrow density and nest-site selection and/or higher reproductive rates may not have been solely a response to the availability of satellite burrows, as has been postulated in most of these studies, because of the many factors correlated with density of burrows. Selection for a higher density of burrows could be a response to a greater number of ground-dwelling sciuroids inhabiting the area, which serve to alert owls to predators (predator avoidance), are prey to shared predators (predator dilution), and graze the area and create the sparse vegetation that is selected by nesting owls (Desmond et al. 1995, 2000). The owls' behavioral response from our experimental blockage of potential satellite burrows, however, provides evidence that burrowing owls seek nest sites with nearby satellite burrows, suggesting a causal relationship between burrow density and nest site selection.

The factors promoting use of satellite burrows have not been clearly elucidated. The primary hypothesis for satellite burrow use is to provide escape cover from predators (Martin 1973, Plumpton and Lutz 1993, Desmond and Savidge 1999, Ronan 2002), which was largely based on observations of owls using satellite burrows when alarmed (Martin 1973, Desmond and Savidge 1999, Ronan 2002). Satellite burrows are also used for caching prey (Lantz et al. 2007), reducing ectoparasite infestation by moving among burrows, and ultimately reducing crowding in the nest chamber by brood splitting (Green and Anthony 1997). In support of the ectoparasite hypothesis, burrowing owls can experience high infestation rates (Smith and Belthoff 2001a) that can affect dispersal patterns (Garcia 2005). In support of

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**Table 1.** Productivity estimates for burrowing owls at control nests and at nests where access to satellite burrows within 20 m of the nests were blocked, Carrizo Plain National Monument, California, 2000.

<table>
<thead>
<tr>
<th>Young/nest</th>
<th>Control (( n = 7 ))</th>
<th>Treatment (( n = 7 ))</th>
</tr>
</thead>
<tbody>
<tr>
<td>Pre-fledge young</td>
<td>Reduction of young</td>
<td>Pre-fledge young</td>
</tr>
<tr>
<td>Mean</td>
<td>3.1</td>
<td>1.5</td>
</tr>
<tr>
<td>SE</td>
<td>0.87</td>
<td>0.69</td>
</tr>
<tr>
<td>Range</td>
<td>0–8</td>
<td>0–5</td>
</tr>
<tr>
<td>% reduceda</td>
<td>48</td>
<td>60</td>
</tr>
</tbody>
</table>

<table>
<thead>
<tr>
<th>Young/successful nest</th>
<th>Control (( n = 6 ))</th>
<th>Treatment (( n = 5 ))</th>
</tr>
</thead>
<tbody>
<tr>
<td>Pre-fledge young</td>
<td>Reduction of young</td>
<td>Pre-fledge young</td>
</tr>
<tr>
<td>Mean</td>
<td>4.8</td>
<td>1.0</td>
</tr>
<tr>
<td>SE</td>
<td>0.87</td>
<td>0.4</td>
</tr>
<tr>
<td>Range</td>
<td>3–7</td>
<td>0–3</td>
</tr>
<tr>
<td>% reduceda</td>
<td>21</td>
<td>33</td>
</tr>
</tbody>
</table>

a The percent change from the number of pre-fledged young (the number of young at 14–21 days) to the number of young alive at near-fledging (35–40 days) at each nest.
the nest-crowding hypothesis, burrowing owl broods can be extremely large when prey is abundant. As the young grow, the nest chamber becomes crowded, which may motivate young to find additional burrows prior to fledging (Green and Anthony 1997) and may be responsible for the selection of larger nest chambers (Smith and Belthoff 2001b). Crowding would be presumably associated with higher carbon dioxide levels but the effect of these levels on burrowing owls, which have evolved a fossorial habit, is unknown. Large brood size not only affects crowding but the amount of time to enter the burrow to escape predation when numerous young are responding to parental alarm calls (D. Rosenberg, Oregon State University, personal observation). How each of these factors contributes to use of satellite burrows is unknown.

Although many factors are likely to play a role in the use of satellite burrows, reducing predation risk may be the greatest factor responsible for shaping the behavior of young owls using satellite burrows. Owls defend their nests with aggressive displays, vocalizations, and physical attacks (Thomsen 1971, Fisher et al. 2004), demonstrate aggressive within-burrow anti-predator behaviors during incubation (Ronan 2002), and pre-fledging young use vocalizations that mimic rattlesnakes (Crotalus spp. and Sistrurus spp.; Rowe et al. 1986). At our study site, predation by raptors, mammals, and snakes on young owls has been a major cause of mortality (Ronan 2002). Behaviors that reduce the risk of nest predation are critical to an individuals’ fitness and have been found to be associated with nest selection (Martin and Roper 1988). Predation rates are a function of prey vulnerability (Bowman and Harris 1980) and nest predation can be minimized by behavior (Sonerud 1985). Therefore, vulnerability to predation has an important influence on the evolution of life-history traits (Hakkarainen et al. 2001) and habitat selection (Martin and Roper 1988).

Many mammals also use satellite burrows during pup rearing. A dominant hypothesis explaining this behavior among mammals is that splitting litters among multiple burrows minimizes predation risk (Eberhardt et al. 1983, Ryon 1986). Other factors that are believed to be responsible include minimizing disease transmission (Eberhardt et al. 1983), reducing ectoparasite loads (Butler and Roper 1996), optimizing micro-climate (Koopman et al. 1998), and reducing carbon dioxide concentrations (Reichman and Smith 1990). We are unaware of any studies that have compared the relative strength of each of these hypotheses for either burrowing owls or mammals. Neither our study nor others that have addressed use of satellite burrows can evaluate the strengths of these different (but not mutually exclusive) hypotheses. Understanding factors that are responsible for satellite burrow use could be improved through experimental approaches using nest boxes (e.g., Belthoff and Smith 2003), which provide more control regarding modifying risk factors.

MANAGEMENT IMPLICATIONS

Our experimental results confirm findings from observational studies that satellite burrows are important for burrowing owls and support the idea that burrowing owls select nest sites with satellite burrows. This study provides justification for installing multiple artificial burrows when these are used for conservation or mitigation (Trulio 1995, Belthoff and Smith 2003), including during translocation efforts (e.g., Leupin and Low 2001, Mitchell et al. 2011). Our results provide further justification for management of fossorial mammals to provide a sufficient density of burrows surrounding nest burrows. In highly managed systems, such as agricultural areas where burrowing owls occur in high densities (e.g., DeSante et al. 2004), or when mitigating loss of owl nests because of construction or other ground-disturbing events, this will require more than simply safeguarding or relocating nests.

ACKNOWLEDGMENTS

We thank the Bakersfield Field Office of the United States Bureau of Land Management (BLM) and the National Fish and Wildlife Foundation with matching funding by California Department of Fish and Game and San Luis Obispo County Fines Commission for financial support, Sandpiper Technologies, Inc. for use of the infrared video probe, S. Feige and J. Rosier for their dedication and hard work in the field, A. Kuritsubo (BLM) for her long-term support of the project, K. Sharum (BLM) for logistic support at the field site, and J. Whitney (BLM) for support during manuscript preparation. We also thank M. Desmond, J. Gervais, and D. Levey for comments on an earlier draft. Publication of this paper was supported, in part, by the Thomas G. Scott Publication Fund. This project was conducted as part of the California Burrowing Owl Research Program, a collaborative research program including The Institute for Bird Populations, Oregon State University, Oregon Wildlife Institute, the Oregon Cooperative Fish and Wildlife Research Unit, and San Jose State University.

LITERATURE CITED


