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NEST-SITE SELECTION IN A HIGH-DENSITY COLONY OF BURROWING OWLS

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Abstract.—Although many Western Burrowing Owl (*Athene cunicularia hypugaea*) populations have been declining, a high-density population nests at the National Radio Transmission Facility (NRTF), Dixon, California. We compared density at NRTF to densities elsewhere, and nest-site use and reuse to available nest substrates. Breeding pairs numbered 24–44 per year, averaging 34 pairs on 83 ha, the fourth-highest on record. Occupancy of eight artificial nest sites installed in 2000 declined from six pairs in 2006 to one pair in 2007 and 2008, and none afterward. Nearest-neighbor distance among artificial nests averaged half the distance among nest sites in fossorial mammal burrows and concrete half-rounds covering aboveground power cables. Undisturbed clay soils supported pocket gophers (*Thomomys bottae*) but few ground squirrels (*Spermophilus beecheyi*), whereas disturbed soils supported both ground squirrels and Burrowing Owls. The presence of both ground squirrels and Burrowing Owls was associated with backfill soils over buried cable, cable covers, and areas where soils bordered impervious surfaces. Nest-site reuse was low, with only 12% of the sites occupied in all study years, 2006–2011. Most (78%) nest sites reused in a subsequent year involved nests in a different burrow or cable cover opening >1 m from the previous year's nest. We recommend research on whether concrete half-rounds might outperform buried utility boxes as artificial nests, especially in conjunction with efforts to conserve the fossorial mammals that naturally excavate burrows used by Burrowing Owls.

Key Words: *Western Burrowing Owl*; Athene cunicularia hypugaea; *California ground squirrel*; Spermophilus beecheyi; *artificial nest*; *breeding pair density*; *nesting*; *nest-site reuse.*

SELECCIÓN DEL SITIO DE NIDIFICACIÓN EN UNA COLONIA DE ALTA DENSIDAD DE *ATHENE CUNICULARIA*

Resumen.—Aunque muchas poblaciones de *Athene cunicularia hypugaea* han estado disminuyendo, una población de alta densidad anida en la Estación de Transmisión de Radio Nacional en Dixon, California. Comparamos la densidad en esta instalación con densidades en otros lugares, y el uso del sitio de nidificación y su reutilización con relación a los sustratos disponibles. Las parejas reproductivas llegaron a 24–44 por año, promediando 34 parejas en 83 ha, la cuarta más alta registrada. La ocupación de ocho sitios artificiales de nidificación instalados en el 2000 disminuyó de seis parejas en 2006 a una pareja en 2007 y 2008, y ninguna posteriormente. La distancia al vecino más cercano entre los nidos artificiales promedió la mitad de la distancia entre los lugares de nidificación en madrigueras de mamíferos excavadores y semicírculos de hormigón que cubren los cables de energía superficiales. Los suelos arcillosos no perturbados albergaron roedores de la especie *Thomomys bottae*, pero pocas ardillas de la especie *Spermophilus beecheyi*, mientras que los suelos alterados albergaron tanto roedores de *S. beecheyi* como individuos de *A. c. hypugaea*. La presencia de ardillas y de lechuzas se relacionó con suelos de relleno sobre cables enterrados, coberturas de cables y áreas donde los suelos limitaban con superficies impermeables. La reutilización del lugar de nidificación fue baja, con solo el 12% de los sitios ocupados en todos los años de estudio, entre 2006 y 2011. La mayoría (78%) de los lugares de nidificación reutilizados al año siguiente involucraron nidos en una madriguera o en una abertura de un cobertor de cable a >1 m del nido del año anterior. Recomendamos investigar si los semicírculos de hormigón podrían ser mejores que las cajas enterradas como nidos artificiales, especialmente en conjunción con los esfuerzos por

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conservar los mamíferos excavadores que excavan naturalmente las madrigueras utilizadas por *A. c. hypugaea*.

[Traducción del equipo editorial]

Western Burrowing Owls (*Athene cunicularia hypugaea*) are declining in abundance and distribution (James and Espie 1997, DeSante et al. 2007b, Trulio and Chromczak 2007, Shuford and Gardali 2008, Wilkerson and Siegel 2010). Principal causes of declines include degradation, loss, and fragmentation of habitat due to land conversions and abatement efforts directed at fossorial mammals to reduce nuisance complaints and secure more forage for livestock (Klute et al. 2003, Moulton et al. 2006, DeSante et al. 2007b); Burrowing Owls in western North America frequently use fossorial mammal burrows as a nesting substrate (Poulin et al. 2011). Anthropogenic sources of mortality include collisions with wind turbines (Smallwood et al. 2007, 2013), electrocutions on utility distribution poles, and collisions with automobiles and distribution lines (S. Smallwood unpubl. data, 2004–2007). To avoid "take" under the Migratory Bird Treaty Act (16 U.S.C. 703–712) or as defined under the California Department of Fish and Wildlife Code section 86 and prohibited under Code 3503.5, biologists often evict Burrowing Owls from land where habitat will be permanently lost to residential, commercial, and industrial projects (Bendix 2007) or temporarily lost to infra-structure maintenance (Catlin and Rosenberg 2006). Evicted owls are expected to relocate nearby or they are coaxed to targeted location(s) via active translocation or provisioning of artificial nest burrows (Trulio 1995, Smith and Belthoff 2001, Barclay 2007, Koshear et al. 2007). Artificial nest burrows typically consist of buried utility boxes connected to the ground surface via tubing, an elevated mound, and short perch structure (Collins and Landry 1977, Smith and Belthoff 2001, Barclay 2008). In our experience over the past decade, having prepared expert testimony in response to dozens of environmental review documents where Burrowing Owls could potentially be affected, most such documents include commitments to evict or translocate Burrowing Owls detected during preconstruction surveys, and to install nest boxes in nearby habitat. California Department of Fish and Wildlife (2012) cautioned that such measures remain unproven, could result in significant impacts, and do not qualify as mitigation. The assessment of nest-box efficacy may be informed by the investigation of nest-site selection in an undisturbed, high-density population where artificial nests were installed among natural nest alternatives absent any evictions.

Burrowing Owls nest in high density at the Naval Radio Transmitter Facility, Dixon (NRTF Dixon), Solano County, California, where Navy operations happened to protect perennial and annual grasslands while also disrupting clay soils with impervious surfaces and trenches refilled by excavated soil. Where clay soils were disturbed, California ground squirrels (*Spermophilus beecheyi*) were able to excavate burrows. Ground squirrel burrow systems thus followed distinct linear patterns of past trenching and access roads, thereby providing Burrowing Owls with nonrandom distributions of potential nest sites. In the same linear patterns as filled trenches, the Navy had installed concrete half-rounds covering power cables that Burrowing Owls also used for nesting. In 2000, the Navy also installed artificial nest boxes. The availability of these alternative nesting substrates was readily quantifiable.

At NRTF Dixon, we measured nest-site selection and reuse on a study area of mostly grassland isolated within a region of intensive agriculture. Typically, each breeding pair of Burrowing Owls nests within a cavity (often a burrow) but occupies a nest site composed solely of the nest cavity or more often both the nest cavity and nearby accessory or satellite burrows (Martin 1973), all of which occur within a nesting territory (Newton 1979, Steenhof et al. 2017). Because burrows containing nests can collapse or suffer other degradation between years, Burrowing Owl selection and reuse of nest sites and nesting territories are likely more reliable than burrow (nest) selection and reuse.

In addition to measuring nest-site selection, we also estimated population size. Estimates of population size and density for Burrowing Owls require careful interpretation. A primary purpose of numerical estimation is for comparison to estimates made elsewhere or at other times (Smallwood 2002), but study-area size can explain much of the variation in density estimates that are not derived from random or systematic sampling (Smallwood 1995, 1998, 2001). For Burrowing Owls, $\log_{10}$ density declines with increasing $\log_{10}$ study-area size (Smallwood et al. 2007), but this relationship is ameliorated among very large study areas that are sampled using multiple plots (Smallwood et al. 2013). Like many other species (Taylor and Taylor 1979), Burrowing Owls are naturally aggregated, so study areas delineated around aggregations tend to yield higher densities, and study areas delineated around increasingly larger areas around aggregations will include larger areas of absence and will therefore yield increasingly lower densities. This artifact of study design can be statistically mitigated, although probably not entirely; whether a Burrowing Owl population is considered high or low density should depend on whether the estimated density is higher or lower than the density predicted by the slope of $\log_{10}$ density regressed on $\log_{10}$ study area size. Understanding the history, size, and density of the study population serves as a useful starting point for use and availability analysis in resource selection (Smallwood 2002), such as nest-site selection. It may be important to know, for example, whether nest-site selection by Burrowing Owls was quantified from an unconstrained population whose members were experienced with the social order and available nest sites, or from a small group of evicted owls sorting things out on a second-choice or no-choice property.

Our study objectives were to (1) determine distribution and abundance of Burrowing Owl nest sites at NRTF Dixon, (2) compare nest-site density at NRTF Dixon to densities estimated elsewhere, (3) compare use to availability of nesting substrates, including undisturbed soil, ground squirrel burrows, the edges of impervious surfaces, concrete half-rounds used as power cable covers, and artificial nests, and (4) compare interannual reuse of the same nest (allowing for 1-m position error) or the same nest site (allowing for 10-m variation) by type of nest substrate, density of ground squirrel burrow systems, and nearest neighbor spacing. Presence of ground squirrels was important to our study because it was the best predictor of Burrowing Owl nest-site reuse across California (DeSante et al. 2007b).

STUDY AREA

Established in 1941 for naval fleet communications, NRTF Dixon is located about 11 km southeast of Dixon, Solano County, within California's Sacramento Valley. NRTF Dixon encompasses 497 ha, including a transmitter building, associated antenna fields, support facilities, a commercial electrical power substation, diesel-powered generators, high-frequency and low-frequency transmitter antennas (two 183-m towers), and associated ancillary equipment. Most antennas were arranged in circular arrays, the interiors of which were regularly mowed. Though the US Navy retains ownership of the land, since 1979 a contractor operated and maintained all communications equipment, structures, support facilities, buildings, and grounds necessary to fulfill NRTF Dixon's military mission.

NRTF Dixon is composed of 244 ha of land leased for agriculture, a 62-ha wildlife management zone, and 191 ha of antenna fields, of which 109 ha were either disked regularly or unavailable to us due to hazardous exposure to radio-frequency radiation (RFR). We defined our study area as a contiguous 83-ha patch of grassland within the antenna fields that we intensively searched for Burrowing Owls from 2006 through 2011. Our study area was covered by grasses such as blue wildrye (*Elymus glaucus*), wild oat (*Avena fatua*), meadow barley (*Hordeum brachyantherum* ssp. *brachyantherum)*, and soft chess (*Bromus hordeaceus*). Forbs included black mustard (*Brassica nigra*), California poppy (*Eschscholzia californica*), and red dock (*Rumex aquaticus*) among many other species. Clay soils of NRTF Dixon are unsuitable for burrow construction by ground squirrels, except where soils are mechanically disturbed. Such disturbance typified buried power cables feeding power to the antenna arrays, over which ground squirrels are able to burrow into the fill soil, thereby providing candidate nest sites for Burrowing Owls.

Some reaches of power cable were laid on the ground surface and covered by abutting concrete half-rounds, each 62 cm in diameter and 1.8 m long. Occasional gaps in the cable covers afforded Burrowing Owls entry to protected nest sites within (Fig. 1). According to NRTF Dixon staff, Burrowing Owls have nested within cable covers for many years without conflict to facility operation. Other structures of NRTF Dixon potentially serving as nesting opportunities included paved road surfaces and concrete ditch liners that were sometimes underburrowed by ground squirrels. Regular mowing maintained short vegetation under antenna arrays, potentially enhancing these areas for ground squirrels and Burrowing Owls, because Burrowing Owls often select more exposed environments as nest sites (Green and Anthony 1989, 1997; Plumpton and Lutz 1993; Lantz 2005). Antenna arrays and guy-wire supports provided Burrowing Owls convenient, abundant perch sites, and enabled us to more readily detect owls guarding nest sites. Other potential perches include cyclone fencing surround-

Figure 1. Burrowing Owl perched outside nest burrow entrance into concrete half-round cable cover, National Radio Transmission Facility, Dixon, California.

ing the transmitter building and signs posting speed limits, marking buried cable, and warning of RFR exposure.

In October 2000, US Navy contractors installed 15 nest boxes beneath eight soil mounds rising 62–92 cm above grade: seven mounds with two boxes each and one mound with a single nest box. We regarded the installations as 15 artificial nests at eight artificial nest sites, because it was unlikely that two pairs of Burrowing Owls would breed in two boxes buried under the same mound. Each nest box was a single plastic irrigation valve box connected to the ground surface by two sections of 15–20-cm diameter corrugated plastic drainpipe. A wooden post was installed at each nest box for roosting and surveillance.

Methods

We surveyed our study area for Burrowing Owls and ground squirrels in May and June 2006, and we repeated surveys for Burrowing Owls in April through June 2007–2011. Our first survey visit each year was devoted to visually scanning for pairs of Burrowing Owls and marking on maps where we detected pairs. We scanned from many stations to cover all portions of the study area, and we repeated the scans over multiple days until we detected all nesting territories. Initial detections were often of the adult male perched outside the nest, usually on one of the abundantly available antenna guy wires or on a fence or sign post. On repeat visits we detected both members of each pair, and at some nest sites we observed emerging young in late May and June. By each year's last visit, we mapped all occupied nest sites (see definition below) on printed maps of NRTF Dixon. We reserved our last visits for walking straight to the nest sites and mapping them using a Trimble Pathfinder Pro-XRS GPS in 2006 and a Trimble Geo-XT in 2007–2011, both of which were accurate to <1 m. Although most Burrowing Owls occurred within the antenna field and around support facilities, we also surveyed with reduced intensity the entire 497-ha NRTF Dixon. Outside the antenna field we walked the interior perimeter of the NRTF Dixon boundary and along systematic transects with 12–15 m spacing, covering grasslands, marshes, and agricultural fields to ensure that we detected all Burrowing Owls at NRTF Dixon. Within the perimeter of 60-m diameter antenna arrays where RFR exposure was unsafe, we used binoculars from outside the perimeter to search for Burrowing Owls and we used a GPS offset function to map occupied burrow locations based on distance and bearing from the observer. Each year we visited all artificial nests and photographed their external conditions, and recorded whether each was occupied by Burrowing Owls. We revisited all previously recorded nest sites.

We defined an occupied nest site as one where there was evidence of attempted reproduction, as indicated by the presence of a pair of adults, behaviors such as alarm-calling or repeat flights to and from or around the nest site, and fresh sign (pellets, excreta, feathers, or decorations) around one or more of the burrows or artificial structures composing the nest site, or in some cases young emerged from the burrow. Minimum evidence of an occupied nest included either emerged young or the combined occupancy of an adult male and female pair, indicative breeding behaviors, and fresh sign at one or more of the burrows or artificial structures at the site.

In 2006, we recorded positions of the approximate centers of ground squirrel and pocket gopher burrow systems along transects that we walked at 12–15 m intervals. We used a pacing method to map separate burrow systems where sign was contiguous (Smallwood and Erickson 1995), but we note that sign was not contiguous for most burrow systems. In 2009, we also mapped ground squirrel and pocket gopher burrows systems using the same methods across a 62-ha portion of the undisturbed wildlife management zone outside the antenna field.

We assessed use and availability of the landscape within the study area by comparing counts of Burrowing Owl nest sites and ground squirrel burrow systems to the availability of landscape elements. We defined landscape elements as matrix soils (meaning predominantly undisturbed soil), antenna arrays, mound and grassland within 5 m of artificial nests, grassland within 2 m of impervious surfaces such as paved roads, parking lots, and concrete ditch liners, and grassland within 5 m of fill soil overlying buried cable and linearly arranged inverted half-rounds used to cover cable laid on the ground. We calculated the number of occupied nest sites per ha within the area of each landscape element, and we used these densities as measures of effect to test whether nest sites were selected in proportion to the availability of landscape elements.

To place the counted number of occupied nests at NRTF Dixon in perspective with Burrowing Owl populations elsewhere, we compared numerical estimates of Burrowing Owls to the sizes of study areas used to make density estimates (Appendix). We regressed $\log_{10}$ mean density on $\log_{10}$ study-area size using linear regression analysis to account for the variation in density estimates due to study-area size (Smallwood et al. 2007, 2013). We saved the regression residuals (observed minus predicted $\log_{10}$ density estimates) to remove the effect of study-area size when comparing densities among study sites (Smallwood et al. 1996, Smallwood and Schonewald 1998). We did not account for study duration, so we did not account for error introduced by interannual variation in abundance. However, 46% of density estimates were based on only one breeding season, 47% were based on 2–3 yr, and only 7% were based on $\geq$4 years (Appendix). Therefore, the short duration of most Burrowing Owl studies resulted in a small source of interannual variation in abundance.

We also examined interannual nest-site reuse by first identifying occupied nest sites as interannual clusters of burrows occupied by Burrowing Owls, where a cluster consisted of occupied burrows located within 10 m of each other between years. We adopted this approach because ground squirrel burrows can be ephemeral due to collapses and backfilling, whereas burrow systems more reliably provide burrows at essentially the same site interannually. We did not track Burrowing Owl identities, so we did not know whether nest-site reuse included the same pairs between years.

RESULTS

Distribution of Fossorial Mammals. Two species of fossorial mammals constructed most of the burrow complexes across NRTF Dixon, though they used different portions of the facility. The 83-ha antenna field hosted 252 ground squirrel and three pocket gopher burrow systems in 2006, and the 62-ha Wildlife Management Zone hosted two ground squirrel and 144 pocket gopher burrow systems in 2009. Ground squirrel burrow complexes/km^2 numbered 57 times greater on the antenna field than on the Wildlife Management Zone, whereas pocket gopher burrow complexes/km^2 numbered 105 times greater on the Wildlife Management Zone than on the antenna field (Table 1). Pocket gopher burrow complexes occurred only in undisturbed,

Table 1. Density estimates of ground squirrel and pocket gopher burrow complexes in various substrates and management contexts within Dixon National Radio Transmission Facility, 2006 (2009 in Wildlife Management Zone). Numbers in parentheses are buffer distances in meters. Numbers of burrow complexes can be obtained by multiplying values under km^2 by values under burrow complexes/km^2.

		Burrow Complexes/km^2	
Burrow Substrate and Perimeter Buffer (m)	km^2	Ground Squirrels	Pocket Gophers
Antenna field (0)	0.825	305.4	3.6
Matrix soil (0)	0.545	225.8	5.5
Within antenna arrays (0)	0.117	171.0	0.0
Fill soil (5)	0.029	2343.2	0.0
Cable cover (5)	0.021	1063.8	0.0
Impervious surface (2)	0.036	503.8	0.0
Artificial mound (0)	0.079	25.5	0.0
Wildlife management zone	0.376	5.3	382.8

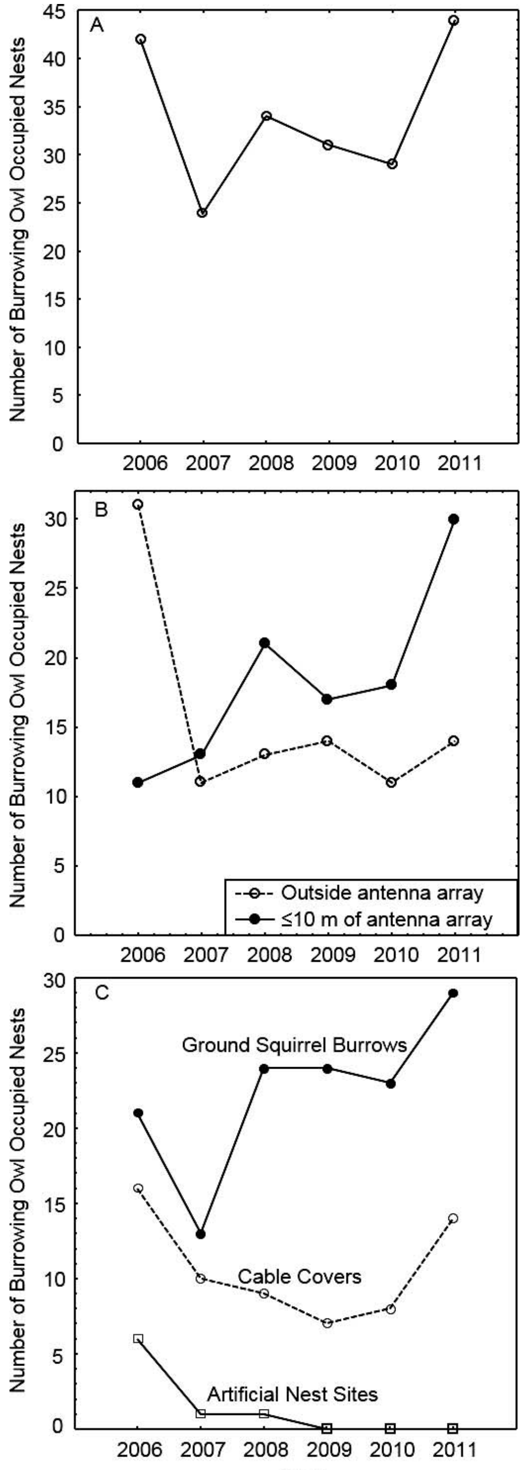
matrix soils. The number of ground squirrel burrow complexes/km^2, however, was 10 times greater in fill soils than on undisturbed matrix soils in the antenna field. Compared to the undisturbed soils in the Wildlife Management Zone, ground squirrel burrow complexes/km^2 in fill soils was 44 times greater. Ground squirrel burrow complexes were also more numerous per unit area along cable covers and impervious surfaces (Table 1).

Number and Density of Nest Sites. We counted 42 nest sites of Burrowing Owls in 2006. The number of occupied nest sites declined to a low of 24 in 2007, but increased to 44 in 2011 (Fig. 2A), and averaged 34.0 per year (90% CI: 27.7–40.4), or 41.2/km^2 per year (90% CI: 33.5–48.9/km^2). The number of occupied nest sites increased within the mowed antenna arrays during our study, and declined 50% outside the antenna arrays after 2006 (Fig. 2B).

The number of occupied artificial nests declined from six in 2006 to one in 2007 and 2008, and then to zero after that (Fig. 2C). Sixteen occupied nests were inside cable covers in 2006, but this number dropped to ten and nine in 2007 and 2008, respectively, before increasing to 14 in 2011 (Fig. 2C). Compared to the density of occupied nest sites within matrix soil (8.39 nest sites/km^2), densities averaged 56 times higher along cable covers, 43 times higher in fill soil over buried cable, 24 times higher under impervious surfaces, and 16 times higher within antenna arrays (Table 2). Compared to the number of occupied nest sites per ground squirrel burrow system within matrix soil (0.04 nest sites/ground squirrel burrow system), densities averaged 21 times higher within mowed antenna arrays, 17 times higher on artificial mounds, 11 times higher along cable covers, 10 times higher under impervious surfaces, and 4 times higher in fill soil along buried cables (Table 2).

Relative to the density of ground squirrel burrow systems across the 83-ha study area (3.03 burrow systems per ha), Burrowing Owls occupied nest sites within portions of the study area where densities of ground squirrel burrow systems averaged 3.6 times higher within 15 m of the nest site in 2006, when ground squirrels and Burrowing Owls were mapped concurrently, and 2.8 times higher in 2006–2011 combined (Fig. 3). The mean number of ground squirrel burrow systems per ha within 15 m of occupied nest sites declined only 22% when including all owl nest sites recorded 2006–2011 relative to the density in 2006 only, indicating that the ground squirrel distribution in 2006 was reasonably predictive of Burrowing Owl nest sites over the following 5 yr. Also, densities of ground squirrel burrow systems declined sharply between 15 m and 30 m from nest sites, but the 90% lower confidence limits were higher than the nest-site density of the entire study area.

Comparison to Owl Density in Other Studies. The density of occupied nests (Y) was an inverse power function of study-area size (X): $\log_{10}Y = 0.84 - 0.61 \times \log_{10} X$ ($r^2 = 0.74$, $P < 0.001$; Fig. 4). The largest positive residual of 1.025 from $\log_{10}$ occupied nest density regressed on $\log_{10}$ study-area size was derived from a study in the Imperial Valley of southern California, where owls nested in a network of concrete canals and irrigation ditches (DeSante et al. 2007a) (Fig. 4). The next-largest residual, 0.817, represented a study area in Cape Coral, Florida, which consisted of regularly mowed vacant lots



(Millsap and Bear (1997), followed by a residual value of 0.816, derived from a very small (9 ha) study area in the Dominican Republic (Wiley 1998). The fourth-largest residual of 0.724 represented the density estimate from NRTF Dixon. The fifth-largest residual of 0.709 came from Burrowing Owl pairs nesting mostly on disturbed areas and cliff faces on the New Mexico State University campus (Botelho and Arrowood 1998). These sites represented the upper 6% of occupied nest-density estimates averaged among years per study site.

Nest Spacing and Reuse. Nearest-neighbor distances among Burrowing Owl nest sites averaged 84 m (90% CI: 76.5–91.6 m). Mean nearest-neighbor distances were negatively correlated with annual nest-site densities ($r = -0.84$, $P < 0.05$), and were smallest in 2006 at 56.7 m, greatest in 2007 at 114.7 m, and smaller again after 2007 (Fig. 5A). Nearest-neighbor distances averaged 2.7 times greater in matrix soils compared to mounds installed over artificial nest boxes, the latter of which averaged only half the distance (42.1 m) of the average among all nest sites (Fig. 5B).

Of the 42 nest sites mapped in 2006, 38% were not used again through 2011, 24% were used 4–6 yr, and 12% were used all 6 yr. Over the 6 yr of nest monitoring, we identified 102 nest sites, at most of which owls nested in different burrows from year to year. Of the 47 sites where we recorded nesting in ≥2 yr, the mean distance between nest burrows was 4.3 m (90% CI: 3.3–5.4 m, SD = 0.31 m). Nine of the 47 multi-year sites (22%) averaged ≤1 m between nest burrows or cable cover entrances, 17 (36%) averaged ≤2 m, and 23 (49%) averaged ≤3 m. The maximum distance of 18.9 m was potentially erroneous because we did not determine whether the nest attempts were by the same or different pairs between years.

DISCUSSION

Adjusted for the size of the study areas used to estimate densities of Burrowing Owl-occupied nest sites, NRTF Dixon supported the fourth-highest average annual density reported to date (95^{th} percentile). Except for the small (9 ha) Dominican Republic study site, the other high-density study sites

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Figure 2. Annual counts of occupied nests of Burrowing Owls at (A) National Radio Transmission Facility (NRTF), Dixon, California, (B) within and outside mowed antenna arrays at NRTF, and (C) within ground squirrel burrows, half-round cable covers, and artificial nests at NRTF.

Table 2. Average annual density estimates of occupied nests of Burrowing Owls in various burrow substrates and management contexts within Dixon National Radio Transmission Facility, 2006–2011. Numbers in parentheses are buffer distances in meters.

Burrow Substrate and Perimeter Buffer (m)	Occupied Nests/km^2			Occupied Nests/Squirrel System in 2006		
	Mean	90% LCL	90% UCL	Mean	90% LCL	90% UCL
Antenna field (0)	41.2	33.5	48.9	0.13	0.11	0.16
Matrix soil (0)	8.4	5.9	10.9	0.04	0.03	0.05
Within antenna arrays (0)	139.7	93.5	185.9	0.82	0.55	1.09
Fill soil (5)	359.4	249.8	469.0	0.15	0.11	0.20
Cable cover (5)	467.4	281.4	653.5	0.44	0.26	0.61
Impervious surface (2)	200.6	155.9	245.3	0.40	0.31	0.49
Artificial mound (0)	17.0	0.0	41.5	0.67	0.00	1.63

were characterized as disturbed sites, including fill soils, graded berms, the interface of soil with impervious surfaces, and regular mowing. The NRTF Dixon site included all of these types of disturbances, likely contributing to its high density of occupied nests. Prior to site disturbances, the clay soils covered by tall stands of blue wildrye likely hosted few ground squirrels, as was the case in the Wildlife Management Zone where only two ground squirrel complexes were found. Since development of the antenna site for Navy operations, however, ground squirrels and Burrowing Owls have been able to use fill soils over buried cables, concrete half-rounds covering above-ground cables, concrete lining on irrigation ditches, asphalt and concrete pads used as roads and parking areas, and the mowed grasslands along cable covers and within antenna arrays. Densities of both ground squirrel burrow systems and Burrowing Owl-occu-

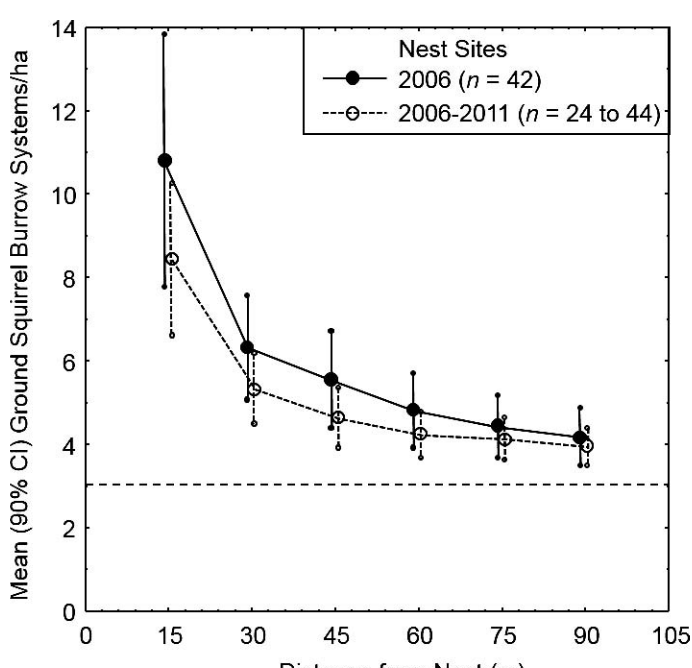

Figure 3. Mean (90% CI) number of ground squirrel burrow system centroids within increasing 15-m concentric distance intervals from occupied nests of Burrowing Owls at National Radio Transmission Facility, Dixon, California, in 2006 (solid circle, solid line) and combined 2006–2011 (open circle, dashed line). The horizontal dashed line at Y = 3.03 represents the number of ground squirrel burrow systems per ha across the entire 83-ha study area.

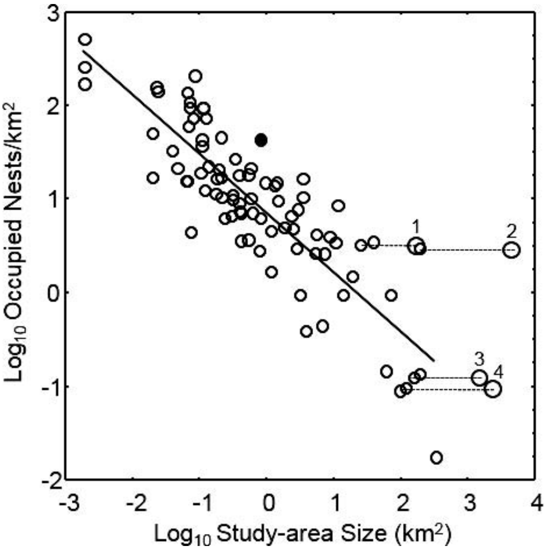

Figure 4. Log_{10} occupied nest density declines with increasing log_{10} study-area size among published estimates from throughout the geographic range of the Burrowing Owl. The solid circle denotes density at National Radio Transmission Facility, Dixon, California, and dashed lines connect density estimates derived from sampling plots that were projected to larger study areas (large circles) such as from (1) random plots in the Altamont Pass Wind Resource Area (Smallwood et al. 2013), (2) random plots in the Imperial Valley (DeSante et al. 2007), and random strip transects at (3) Lake Mead National Recreation Area, California and (4) Marine Corp Air Ground Combat Center near Twenty-nine Palms, California (Crowe and Longshore 2010). The regression slope was estimated only from sampled study areas (small circles).

pied nest sites were much higher in association with these disturbance features than on matrix soils with matrix vegetation cover.

None of the artificial nest sites were occupied by Burrowing Owls after 2008, even though all were initially occupied in 2000. We note, however, that without burrow probes we were unable to verify that Burrowing Owls using artificial nest sites through 2008 actually nested in the utility boxes rather than in ground squirrel burrows excavated into the overlying constructed mounds. Declining use of artificial nest sites over the study period may have resulted from (1) insufficient spacing between artificial nest sites, (2) growth of tall dense stands of plants on the overlying mounds, (3) destruction or clogging of tubes caused by colonizing ground squirrels, or (4) naturally low nest-site reuse. Spacing of artificial nest sites was only 49 m apart on average, which was much closer to each other than the 84-m mean separation among natural nest sites. Some researchers recommend placing artificial nest boxes at least 110 m apart to avoid intraspecific competition and mid-season nest desertion (Green and Anthony 1997); thus, spacing between artificial nests at NRTF Dixon might have been intolerably close for most Burrowing Owls attempting reproduction. In addition, tall dense stands of vegetation such as black mustard grew on the mounds atop the artificial nest burrows from 2008–2011, after the Navy contractors abandoned weed control efforts post-2006 (Fig. 6). Finally, ground squirrels were attracted to the loose fill soil of the mounds, and might have burrowed directly into the tubes, some of which were visibly damaged.

Nest-site reuse was low through the study, with only 12% used all 6 yr. However, we found between-year nest-site reuse (46%) was within the range reported elsewhere: 12% (Griebel 2000), 43% (Riding and Belthoff 2015), $<$50% (Rich 1984), 55% (Rodriguez-Estrella 1997), 60% (Mealy 1997), and 87% (Holmes et al. 2003). Our low nest-site reuse over 6 yr, combined with consistently high occupied nest densities, indicates sufficient candidate nest sites were available to Burrowing Owls within our study area, and our higher between-year reuse hints at social factors such as nest-site fidelity. Other studies also reported high nest-site fidelity among Burrowing Owls. Millsap and Bear (1997) found that 83% of males and 74% of females bred on the same territories at least 2 yr at Cape Coral, Florida. Of the pairs tracked, 49% had a member of the pair that was not detected in any subsequent years of study, and there was a 9% "divorce" rate between years among the pairs whose members were both observed (Millsap and Bear 1997). In Colorado, 9% of banded owls returned to nest in the study area (Pezzolesi 1994), and in the Imperial Valley of California, 66% of 253 nesting pairs remained within 100 m of the previous year's nest location (Catlin et al. 2005). There might be some advantage to reusing nest burrows, as Mealy (1997) reported 53% of pairs reusing burrows fledged $\geq$1 young, whereas only 19% of pairs using new burrows fledged $\geq$1 young. Riding and Belthoff (2015) reported that 87% of reused artificial nest sites had fledged $\geq$1 young the year previously, whereas 59% of artificial nest sites not reused had fledged $\geq$1 young the year previously. The advantages of reusing nest sites over the short term might be offset by

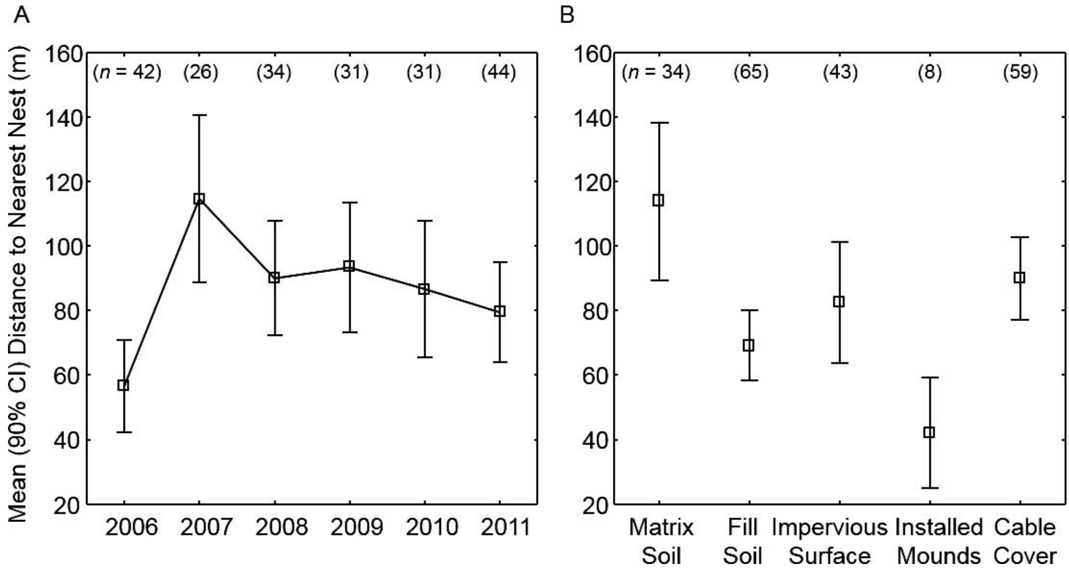

Figure 5. Mean distance (m; 90% CI) to the nearest Burrowing Owl nest by (A) year of study and (B) burrow substrate or context at National Radio Transmission Facility, Dixon, California, 2006–2011. Sample sizes are indicated above the markers, at the top of each illustration.

disadvantages over the long term, such as exhausting food supplies, attracting predators, and accumulating parasite loads (Taylor and Taylor 1979). These disadvantages might explain the hierarchy of interannual reuse we observed: lowest at occupied nests, higher at nest sites, and highest within portions of a habitat patch supporting high-density clusters of ground squirrel burrow systems.

Regardless of the type of burrow substrate, nearness to ground squirrel burrow systems was strongly associated with Burrowing Owl nest-site use. Nest sites usually occurred within high-density clusters of ground squirrel burrow systems. Other studies reported similar relationships between nest sites and nearness to high densities of large fossorial mammals (Plumpton and Lutz 1993, Lantz 2005, Lantz et al. 2007, Poulin et al. 2005). Higher Burrowing Owl nest success in prairie dog towns may reflect benefits gained from alarm calling and the predator dilution effect of the local fossorial mammals (Desmond and Savidge 1999. Pre-fledged Burrowing Owls more often used prairie dog burrows as satellite burrows where more prairie dog burrows occurred within 75 m of the nest burrow (Desmond and Savidge 1999), and dispersing juveniles used nearby American badger (*Taxidea taxus*) burrows (King and Belthoff 2001). After access was closed to candidate satellite burrows $\leq$20 m of nest burrows, breeding Burrowing Owls relocated (Ronan and Rosenberg 2014).

Conservation Implications. Our case study of Burrowing Owls suggests that ground squirrel burrow systems are selected as nest sites, but Burrowing Owls rarely occupy specific burrows in subsequent years. To enhance habitat for Burrowing Owls in areas dominated by clay soils, trenching and backfill can loosen the soil, thereby facilitating burrow excavation by ground squirrels. For Burrowing Owls to persist long-term, our results suggest there is no suitable substitute for burrows excavated by ground squirrels in California or by other fossorial mammals elsewhere in the species' range. We posit that the conservation of Burrowing Owls is most effectively accomplished by conserving the fossorial mammals that create their burrows and benefit Burrowing Owls in other ways, such as mutual predator alarm-calling, predator dilution effect, hosting of prey species within the same burrow complexes, and provisioning of alternate and satellite burrows, food-cache sites, and refuge burrows during the nonbreeding season.

Artificial nests might help to establish Burrowing Owls in some areas. Because Burrowing Owls tend to shift nest sites within several years, we suggest that research is needed to learn whether deploying concrete half-rounds might be more effective than

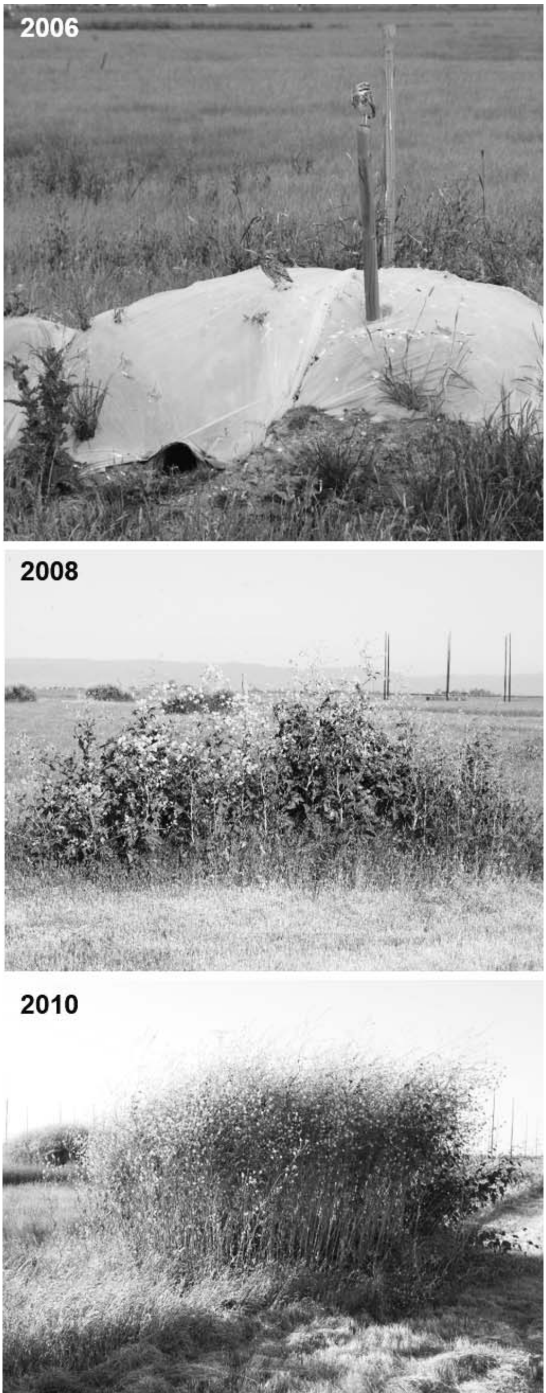

Figure 6. Vegetative cover at mounds of Burrowing Owl artificial nest burrows in 2006 (top), 2008 (middle) and 2010 (bottom), National Radio Transmission Facility, Dixon, California.

installing conventional artificial nests where environmental conditions permit. Although concrete half-rounds are too heavy for predators or fossorial mammals to move, managers can readily place or relocate them as needed. Still unknown, however, is whether environmental conditions within half-rounds are suitable for nestling production and survival. To test efficacy, we recommend placing 1.8-m long concrete half-rounds in end-to-end clusters of three or four within 15 m of occupied ground squirrel burrow systems to provide for satellite burrows, mutual predator alarm-calling, and predator diffusion. Placing them close to well-established ground squirrel burrow complexes would lessen the risk of flooding because such complexes do not persist where flooding is common. We believe that spacing clusters of concrete half-rounds at least 73 m apart should provide sufficient nearest-neighbor separation to promote long-term reoccupancy, although Green and Anthony (1997) recommended 110-m spacing.

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Appendix. Sources of density estimates available for comparison to breeding pair density of Burrowing Owls at Dixon National Radio Transmission Facility, California, 2006–2011.

Reference	Location	Year	No. Years	Study Area (km^2)	Pairs	Pairs/km^2
Coulombe (1971)	Dahlia Drain, Imperial County, CA	1966	2	1.925	9.25	4.806
	Greeson Slough, Imperial County, CA	1966	2	7.680	19.50	2.539
Thomsen (1971)	Oakland Airport, CA	1966	2	0.607	12.75	21.005
Desmond and Savidge (1976)	Western NE prairie dog town	1990	1	0.002	1.00	500.0000
		1990	1	0.002	0.50	250.0000
		1990	1	0.002	0.33	165.0000
		1990	1	0.021	1.00	48.8759
		1990	1	0.021	0.34	16.6178
		1990	1	0.025	3.38	136.0709
		1990	1	0.041	1.30	31.9332
		1990	1	0.067	9.00	134.8719
		1990	1	0.078	0.34	4.3512
		1990	1	0.111	4.65	41.8053
		1990	1	0.111	3.95	35.5120
		1990	1	0.218	9.85	45.2707
		1990	1	0.218	3.62	16.6376
		1990	1	0.225	2.27	10.0840
		1990	1	0.326	3.15	9.6567
		1990	1	0.397	6.87	17.3284
		1990	1	0.554	9.85	17.7901
		1990	1	0.815	2.24	2.7501
		1990	1	1.203	1.99	1.6542
		1990	1	1.568	14.70	9.3750
		1990	1	2.400	15.44	6.4333
Gleason and Johnson (1985)	Idaho National Engineering Lab, ID	1976	1	348.000	6.00	0.017
Wesemann and Rowe (1987)	Cape Coral, Lee County, FL	1986	1	35.900	133.00	3.705
Haug and Oliphant (1990)	Ardath, Saskatchewan, Canada	1983	2	0.320	3.50	10.938
	Bounty, Saskatchewan, Canada	1983	2	0.650	4.50	6.923
Rodriguez-Estrella and Ortega-Rubio (1993)	Mapimi Biosphere Reserve, Durango, Mexico	1986	2	200.000	26.00	0.130
Pezzolesi (1994)	Rocky Mountain Arsenal, CO	1992	3	5.590	36.33	6.500
Silva et al. (1995)	Fray Jorge National Park, Chile	1991	3	0.150	1.67	11.110
Johnson (1997)	University of California, Davis campus, CA	1981	11	1.500	22.00	14.667
Martell et al. (1997)	Tyree II, Badlands National Park, SD	1992	2	0.390	1.50	3.846
	Tyree I	1992	2	1.180	5.00	4.237
	Roberts	1992	2	1.300	0.50	0.385
	Burns	1992	2	2.040	2.50	1.226
	Sage	1992	2	3.080	0.00	0.000
	Kocher I	1992	2	3.270	6.50	1.989
	Other	1992	2	3.800	5.50	1.447
	Total, Badlands National Park, SD	1992	2	15.060	21.50	1.428
Mealey (1997)	Imagination Farms, Inc., Dade & Broward Counties, FL	1989	3	2.400	9.00	3.750
	Miami International Airport, FL	1989	3	3.879	27.67	7.132
Millsap and Bear (1997)	Cape Coral, Lee County, FL	1988	4	35.900	183.60	5.114

Appendix. Continued.

Reference	Location	Year	No. Years	Study Area (km^2)	Pairs	Pairs/km^2
Trulio (1997)	Shoreline Park, San Jose, CA	1992	3	1.120	8.33	7.441
	Moffett Field, San Jose, CA	1992	3	1.520	20.33	13.377
Botelho and Arrowood (1998)	New Mexico State University	1994	1	3.640	59.00	16.209
Wiley (1998)	Southwestern Dominican Republic	1976	1	0.090	18.00	200.000
Griebel (2000)	Wall District, Buffalo Gap National Grassland, SD	1999	1	0.048	1.00	20.833
		1999	1	0.066	1.00	15.152
		1999	1	0.067	1.00	14.925
		1999	1	0.069	4.00	57.971
		1999	1	0.084	6.00	71.429
		1999	1	0.607	6.00	9.885
		2000	1	0.108	2.00	18.519
		2000	2	0.124	1.50	12.097
		2000	1	0.139	3.00	21.583
		2000	1	0.180	2.00	11.111
		2000	2	0.188	3.00	15.957
		2000	1	0.200	4.00	20.000
		2000	2	0.247	1.50	6.073
		2000	2	0.315	2.00	6.349
		2000	2	0.346	9.00	26.012
		2000	2	0.396	3.50	8.838
		2000	2	0.414	3.00	7.246
		2000	2	0.427	1.50	3.513
		2000	2	0.431	3.00	6.961
		2000	2	0.555	2.00	3.604
		2000	1	0.829	5.00	6.031
		2000	2	1.233	5.50	4.461
		2000	2	2.596	12.00	4.623
		2000	2	2.813	8.00	2.844
		2000	2	40.000	136.00	3.400
Arrowood et al. (2001)	Kirkland Air Force Base, Albuquerque, NM	1999	3	4.410	45.67	10.355
Restani et al. (2001)	Custer and Prairie Counties, MT	1998	1	14.250	13.00	0.912
Shyry et al. (2001)	Hanna, AB	1997	6	63.996	9.00	0.141
	Brooks, AB	1997	7	102.449	9.00	0.088
Holmes et al. (2003)	Naval Weapons Systems Training Facility, Boardman, WA	1995	1	20.000	29.00	1.450
		1997	2	9.150	35.00	3.825
Rosenberg and Haley (2004)	South rim of Salton Sea, Imperial County, CA	1999	3	11.750	97.67	8.312
Lantz (2005)	Thunder Basin National Grassland, WY	2004	2	73.810	68.00	0.921
Teaschner (2005)	Zone 4, Carson County, TX	2004	3	0.023	3.50	150.538
	Pantex Lake, Carson County, TX	2004	3	0.075	8.00	106.670
	School, Lubbock County, TX	2004	3	0.076	7.00	92.715
	L103, Lubbock County, TX	2004	3	0.117	10.50	89.670
	12-36 Carson County, TX	2004	3	0.119	11.00	92.750
	X-Fab, Lubbock County, TX	2004	3	0.128	9.00	70.313
DeSante et al. (2004, 2007)	Imperial County, CA	1993	2	200.0	71.97	2.879
		1993	2	4575.0	71.97	2.879
Barclay (2007)	Mineta International Airport, CA	1997	18	1.340	18.07	13.485

Appendix. Continued.

Reference	Location	Year	No. Years	Study Area (km^2)	Pairs	Pairs/km^2
Koshear et al. (2007)	Colonel Allensworth State Park, CA	2002	4	1.00	14.50	14.500
Trulio and Chromczack (2007)	Parkland sites, south San Francisco Bay, CA	2001	1	5.40		2.600
	Urban sites, south San Francisco Bay, CA	2001	1	11.10		3.300
Crowe and Longshore (2007)	Lake Mead National Recreation Area, CA	2004	2	162.0	19.65	0.121
		2004	2	1470.0	19.65	0.121
	Marine Corps Air Ground Combat Center, CA	2005	2	123.5	11.50	0.093
		2005	2	2415.0	11.50	0.093
Smallwood et al. (2009)	Vasco Caves Regional Preserve, CA	2007	2	5.630	23.00	4.085
Smallwood et al. (2013)	46 sampling plots, Altamont Pass Wind Resource Area, CA	2011	1	25.625	78.00	3.201
	Extended to sampled area	2011	1	167.6	537.00	3.201
Smallwood and Morrison, this study	Dixon National Radio Transmission Facility, CA	2009	6	0.826	34.00	41.160